frontiers | Research Topics

Bioinoculants with nano-compounds to improve soil health: A step toward sustainable agriculture

Edited by
Parul Chaudhary, Shaohua Chen and Vishnu D. Rajput

Coordinated by
Durgesh K. Jaiswal

Published in
Frontiers in Environmental Science
Frontiers in Microbiology
Frontiers in Agronomy
Frontiers in Plant Science

ISSN 1664-8714
ISBN 978-2-8325-3287-4
DOI 10.3389/978-2-8325-3287-4

About Frontiers

Frontiers is more than just an open access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers journal series

The Frontiers journal series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the *Frontiers journal series* operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews. Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view. By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the *Frontiers journals series*: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area.

Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers editorial office: frontiersin.org/about/contact

Bioinoculants with nano-compounds to improve soil health: A step toward sustainable agriculture

Topic editors
Parul Chaudhary — Graphic Era Hill University, India
Shaohua Chen — South China Agricultural University, China
Vishnu D. Rajput — Southern Federal University, Russia

Topic Coordinator
Durgesh K. Jaiswal — Savitribai Phule Pune University, India

Citation
Chaudhary, P., Chen, S., Rajput, V. D., Jaiswal, D. K., eds. (2023). *Bioinoculants with nano-compounds to improve soil health: A step toward sustainable agriculture*. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-8325-3287-4

Table of contents

frontiers | Frontiers in Environmental Science

TYPE Editorial
PUBLISHED 07 August 2023
DOI 10.3389/fenvs.2023.1270002

OPEN ACCESS

EDITED AND REVIEWED BY
Yuncong Li,
University of Florida, United States

*CORRESPONDENCE
Parul Chaudhary,
parulchaudhary1423@gmail.com,
parulchaudhary@gehu.ac.in

RECEIVED 31 July 2023
ACCEPTED 02 August 2023
PUBLISHED 07 August 2023

CITATION
Chaudhary P, Chen S, Rajput VD and Jaiswal DK (2023), Editorial: Bioinoculants with nano-compounds to improve soil health: a step toward sustainable agriculture.
Front. Environ. Sci. 11:1270002.
doi: 10.3389/fenvs.2023.1270002

Editorial: Bioinoculants with nano-compounds to improve soil health: a step toward sustainable agriculture

Parul Chaudhary[1]*, Shaohua Chen[2], Vishnu D. Rajput[3] and Durgesh Kumar Jaiswal[4]

[1]School of Agriculture, Graphic Era Hill University, Dehradun, Uttarakhand, India, [2]National Key Laboratory of Green Pesticide, Integrative Microbiology Research Centre, South China Agricultural University, Guangzhou, China, [3]Academy of Biology and Biotechnology, Southern Federal University, Rostov-on-Don, Russia, [4]Department of Botany, Savitribai Phule Pune University, Pune, Maharashtra, India

KEYWORDS

agriculture, bioinoculants, crop production, nano-compounds, soil health, nano-bioinoculants

Editorial on the Research Topic
Bioinoculants with nano-compounds to improve soil health: a step toward sustainable agriculture

Introduction

Modern agriculture is largely concerned with the sustainable cultivation of cereals and other food-based crops to meet the food difficulties of a growing worldwide population. However, intensive agricultural methods and widespread use of agrochemicals cause soil fertility deterioration, pollution, disturbance of soil diversity, pest resistance and declines in crop yield (Singh and Singh, 2017; Chaudhary et al., 2022). As a result, researchers are changing their focus to more environmentally friendly fertilizing technologies in order to preserve agriculture sustainability (Parveen et al., 2023; Srivastava et al., 2023). The usefulness of beneficial microbes and nanoparticles have been well recognised in reducing the negative impacts of agrochemicals (Mushtaq et al., 2020; Chaudhary et al., 2021; Shah et al., 2021). Applying different nanoparticles/nano-based fertilizers to boost crop production has also resulted in a revolution in agriculture. Given their mutually advantageous qualities, bioinoculants and NPs can be utilized in conjugation to maximize benefits (Kukreti et al., 2020; Agri et al., 2021). However, combination of both or their synergistic use has improved crop-modulating effects in terms of crop production and soil fertility restoration (Kumari et al., 2020; Agri et al., 2022). Bioinoculants and Si-NPs use significantly affects sugar beet growth and yield under soil salinity stress (Alharbi et al., 2022a). Combined application of *Azotobacter, Pseudomonas* spp. along with silica NPs (Si NPs: 500 mg/L), reduce the negative effects of irrigation with saline water on the growth and productivity of barley (Alharbi et al., 2022b). Silver NPs and *Bacillus cereus* promoted maize plant development, reducing harmful fungal pathogens growth (Kumar et al., 2020). Silicon dioxide NPs (100 ppm) and *B. cereus-Amazcala* were applied together, and improved the

chilli pepper growth (Ferrusquía-Jiménez et al., 2022). We accepted 11 papers on this Research Topic. The main points of the Research Topic are discussed below.

Bioinoculants and nanoparticles

According to Adeleke et al. nanomaterials derived from endophytic microorganisms can minimize the abiotic stresses on plants, increase photosynthesis, nutrient absorption and microbial diversity and improved plant and soil health parameters. Applying nano-growth enhancers derived from beneficial bacteria like nano-fertilizers, nano-herbicides and nano-pesticides is considered safe and environmentally benign in assuring sustainable agriculture.

Ayilara et al. provide a wide-ranging summary of the growing use of biopesticide, phyto-pesticides, nano-pesticides and nano-biopesticides to combat plant diseases, enhance plant nutrition and provides crop protection. These are good substitutes for chemical pesticides because they are affordable, have a specific mode of action, are environmentally beneficial and do not create greenhouse gases. As a result, their addition to the currently used synthetic pesticides will be a more effective way to protect crops from pests and ensure sustainable agriculture.

Upadhayay et al. emphasize on the combined effect of different microbes and nanomaterials to maximize the crop production for the growing people, amelioration of biotic and abiotic stress, maintain soil health and lessen the massive dependence on chemical-based fertilizers.

Mishra et al. developed and utilized the urea nanoparticles as nano-biofertilizers. The foliar spray of calcium phosphate urea NPs (CaP-U NPs) on finger millet seeds showed improvement in plant growth parameters such as shoot length, chlorophyll content and enzymatic activities like guaiacol peroxidase and superoxide dismutase under drought circumstances. They reported that CaP-U NPs (0.5%–1%) were effective for growth indices and defence activation.

Kashyap et al. concentrated on the benefits of microbial inoculants and their potential and mechanism of action for increasing agricultural productivity. They also highlighted the screening, characteristics, and importance of bioinoculants as biocontrol agent for controlling plant disease against different pests and insects.

Ayilara et al. examined the role of microorganisms and nanotechnology in cleanup process of harmful pollutants. They discussed about the natural attenuation method of remediation, which encourage and improved the ability of microbes in degradation of pollutants. They also studied nano bioremediation's role in deleting harmful contaminants from the environment.

Ayilara and Babalola talked about several remediation techniques. They discussed the use of microbial enzymes for cleanup and function of various microorganisms, including bacteria, fungi and algae. They also discussed how various microbial consortiums might be a more effective approach to bioremediation.

Ahamad et al. evaluated the efficacy of beneficial microorganism such as arbuscular mycorrhizal fungi (AMF) and vermicompost, both separately and together in reducing the detrimental effects of *Meloidogyne incognita* on carrot growth. Applying AMF in carrot plants repressed root galls and nematode inhabitants and improved plant growth, carotenoid, chlorophyll and phenol content, respectively. AFM and vermicompost may be useful alternatives to plant development under biotic stress conditions.

Zhang et al. reported that application of different microbial inoculants, such as *Bacillus velezensis* and *Brevundimonas faecalis*, inhibit the growth of pathogenic fungus. These microbial inoculants also improved the plant length and seedling biomass while controlling oat root rot.

Naitam et al. demonstrated the capacity of the halophilic archaea *Halolamina pelagica* CDK2 to promote wheat growth and to diminish the negative effects of salinity. This strain possesses the potential to produce indole acetic acid and solubilize the essential nutrient such a potassium, phosphorus and zinc, which involved in promoting plant growth. The inoculated treatments showed significantly higher amounts of total protein, chlorophyll and sugar content in presence of haloarchaea. Additionally, the inoculation caused a significant decrease in the antioxidant activity.

Bhandari et al. offers a thorough understanding on nano-biochar applications in different fields. Nano-biochar modulates the transport and absorption of essential micro and macronutrients and harmful pollutants. Nano-biochar is a detoxicant for managing waste, reducing soil erosion and preserving soil nutrients. Additionally, nano-biochar serves as a biosensor for the detection and monitoring of harmful pollutants.

Author contributions

PC: Conceptualization, Visualization, Writing–original draft, Writing–review and editing. SC: Writing–review and editing. VR: Writing–review and editing. DJ: Writing–review and editing. All authors contributed to the article and approved the submitted version.

Acknowledgments

The authors would like to express their gratitude to the Senior Editor of Frontier in Environmental Science Journals for their valuable input during the Research Topic creation. The authors would like to thank the School of Agriculture, Graphic Era Hill University, Dehradun, Uttarakhand, India.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Agri, U., Chaudhary, P., and Sharma, A. (2021). *In vitro* compatibility evaluation of agriusable nanochitosan on beneficial plant growth-promoting rhizobacteria and maize plant. *Natl. Acad. Sci. Lett.* 44, 555–559. doi:10.1007/s40009-021-01047-w

Agri, U., Chaudhary, P., Sharma, A., and Kukreti, B. (2022). Physiological response of maize plants and its rhizospheric microbiome under the influence of potential bioinoculants and nanochitosan. *Plant Soil* 474, 451–468. doi:10.1007/s11104-022-05351-2

Alharbi, K., Hafez, E., Omara, A. E. D., Awadalla, A., and Nehela, Y. (2022a). Plant growth promoting rhizobacteria and silica nanoparticles stimulate sugar beet resilience to irrigation with saline water in salt-affected soils. *Plants* 11, 3117. doi:10.3390/plants11223117

Alharbi, K., Rashwan, E., Mohamed, H. H., Awadalla, A., Omara, A. E., Hafez, E. M., et al. (2022b). Application of silica nanoparticles in combination with two bacterial strains improves the growth, antioxidant capacity and production of barley irrigated with saline water in salt-affected soil. *Plants (Basel).* 11 (15), 2026. doi:10.3390/plants11152026

Chaudhary, P., Khati, P., Chaudhary, A., Gangola, S., Kumar, R., and Sharma, A. (2021). Bioinoculation using indigenous *Bacillus* spp. improves growth and yield of *Zea mays* under the influence of nanozeolite. *3 Biotech.* 11, 11. doi:10.1007/s13205-020-02561-2

Chaudhary, P., Singh, S., Chaudhary, A., Agri, U., and Bhandari, G. (2022). "Chapter 3 Agrochemicals and their effects on soil microbial population," in *Plant protection: From chemicals to biologicals*. Editors R. Soni, D. Suyal, and R. Goel (Berlin, Boston: De Gruyter), 45–58. doi:10.1515/9783110771558-003

Ferrusquía-Jiménez, N. I., González-Arias, B., Rosales, A., Esquivel, K., Escamilla-Silva, E. M., Ortega-Torres, A. E., et al. (2022). Elicitation of *Bacillus cereus-Amazcala* (B.c-A) with SiO2 nanoparticles improves its role as a plant growth-promoting bacteria (pgpb) in chili pepper plants. *Plants* 11, 3445. doi:10.3390/plants11243445

Khan, N., and Bano, A. (2015). Role of plant growth promoting Rhizobacteria and Ag-nano particle in the bioremediation of heavy metals and maize growth under municipal wastewater irrigation. *Int. J. Phytoremediation* 6514, 211–221. doi:10.1080/15226514.2015.1064352

Kukreti, B., Sharma, A., Chaudhary, P., Agri, U., and Maithani, D. (2020). Influence of nanosilicon dioxide along with bioinoculants on *Zea mays* and its rhizospheric soil. *3Biotech* 10, 345. doi:10.1007/s13205-020-02329-8

Kumar, P., Pahal, V., Gupta, A., Vadhan, R., Chandra, H., and Dubey, R. C. (2020). Effect of silver nanoparticles and *Bacillus cereus* LPR2 on the growth of *Zea mays*. *Sci. Rep.* 10, 20409. doi:10.1038/s41598-020-77460-w

Kumari, S., Sharma, A., Chaudhary, P., and Khati, P. (2020). Management of plant vigor and soil health using two agriusable nanocompounds and plant growth promotory rhizobacteria in Fenugreek. *3 Biotech.* 10, 461. doi:10.1007/s13205-020-02448-2

Mushtaq, T., Shah, A. A., Akram, W., and Yasin, N. A. (2020). Synergistic ameliorative effect of iron oxide nanoparticles and *Bacillus subtilis* S4 against arsenic toxicity in *Cucurbita moschata*: Polyamines, antioxidants, and physiochemical studies. *Inter J Phytoremediation* 22 (13), 1408–1419. doi:10.1080/15226514.2020.1781052

Parveen, H., Chaudhary, P., Srivastava, P., Priya, S., Bhandari, G., and Chaudhary, A. (2023). "Role of nanoparticles in agriculture," in *Advances in nanotechnology for smart agriculture: Techniques and applications*. Editors P. Chaudhary, A. Chaudhary, A. K. Nadda, and P. Khati 1st ed (Boca Raton, Florida: CRC Press). doi:10.1201/9781003345565-1

Shah, A., Nazari, M., Antar, M., Msimbira, L. A., Naamala, J., Lyu, D., et al. (2021). PGPR in agriculture: A sustainable approach to increasing climate change resilience. *Front. Sustain. Food Syst.* 5, 667546. doi:10.3389/fsufs.2021.667546

Singh, R., and Singh, G. S ((2017). Traditional agriculture: A climate-smart approach for sustainable food production. *Energy Ecol. Environ.* 2, 296–316. doi:10.1007/s40974-017-0074-7

Srivastava, P., Chaudhary, P., and Parveen, P. (2023). "Nanoparticles and their effect on plant health and productivity," in *Advances in nanotechnology for smart agriculture: Techniques and applications*. Editors P. Chaudhary, A. Chaudhary, A. K. Nadda, and P. Khati 1st ed (Boca Raton, Florida: CRC Press), 33487–2742. doi:10.1201/9781003345565-6

frontiers | Frontiers in Environmental Science

TYPE Review
PUBLISHED 24 November 2022
DOI 10.3389/fenvs.2022.1015897

OPEN ACCESS

EDITED BY
Parul Chaudhary,
G. B. Pant University of Agriculture and Technology, India

REVIEWED BY
Priyanka Khati,
Indian Council of Agricultural Research (ICAR), India
Govind Kumar,
Central Institute for Subtropical Horticulture (ICAR), India

*CORRESPONDENCE
Olubukola Oluranti Babalola,
olubukola.babalola@nwu.ac.za

SPECIALTY SECTION
This article was submitted to Soil Processes, a section of the journal Frontiers in Environmental Science

RECEIVED 10 August 2022
ACCEPTED 14 November 2022
PUBLISHED 24 November 2022

CITATION
Adeleke BS, Akinola SA, Adedayo AA, Glick BR and Babalola OO (2022), Synergistic relationship of endophyte-nanomaterials to alleviate abiotic stress in plants.
Front. Environ. Sci. 10:1015897.
doi: 10.3389/fenvs.2022.1015897

Synergistic relationship of endophyte-nanomaterials to alleviate abiotic stress in plants

Bartholomew Saanu Adeleke[1,2], Saheed Adekunle Akinola[2,3], Afeez Adesina Adedayo[2], Bernard R. Glick[4] and Olubukola Oluranti Babalola[2]*

[1]Department of Biological Sciences, Microbiology Unit, Faculty of Science, Olusegun Agagu University of Science and Technology, Okitipupa, Nigeria, [2]Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mahikeng, South Africa, [3]Department of Clinical Biology, School of Medicine and Pharmacy, College of Medicine and Health Sciences, University of Rwanda, Kigali, Rwanda, [4]Department of Biology, University of Waterloo, Waterloo, ON, Canada

Plant responses to abiotic stresses through diverse mechanisms and strategic measures in utilizing nanomaterials have positively impacted crop productivity. Stress can cause membrane depletion, reactive oxygen species formation, cell toxicity and death, and reduction in plant growth. However, nanomaterials can mitigate some of the negative impacts of abiotic stresses and enhance crop yield. Some endophytic microbes can synthesize nanomaterials, which can maintain and enhance plant health and growth *via* nitrogen fixation, siderophore production, phytohormones synthesis, and enzyme production without any pathological effects. Nanoparticle-synthesizing endophytes also help boost plant biochemical and physiological functions by ameliorating the impact of abiotic stresses. The increase in the use and implementation of nano-growth enhancers from beneficial microbes, such as nano-biofertilizers, nano-pesticides, nano-herbicides, and nano-fungicides are considered safe and eco-friendly in ensuring sustainable agriculture and reduction of agrochemical usage. Promisingly, nanotechnology concepts in agriculture aim to sustain plant health and protect plants from oxidative stresses through the activation of anti-oxidative enzymes. The mechanisms and the use of nanomaterials to relieve abiotic plant stress still require further discussion in the literature. Therefore, this review is focused on endophytic microbes, the induction of abiotic stress tolerance in plants, and the use of nanomaterials to relieve abiotic plant stresses.

KEYWORDS

environmental stressors, food security, plant health management, soil-plant microbe interactions, sustainable development goal 2, zero hunger

Introduction

The environmental problems linked to climate abiotic-induced stresses pose serious threats and ecological pressures on soils and plant health, limiting crop productivity (Varshney et al., 2011). Thus, the need to devise a problem-solving approach to enhance crop yield under stress becomes imperative. The biotic factors, such as bacterial and fungal pathogens, insect and nematode pests as well as abiotic factors such as temperature, salinity, drought, flooding, heavy metals, and pH cause a large number of modifications in plant biochemical and physiological processes (Kumar et al., 2019). The approaches to mitigate these stresses in crops should be targeted to maximally address the food supply and demand of the world population. Over time, the use of chemical fertilizers to improve crop productivity has been employed, but with profound detrimental effects on the ecosystems (Adeleke and Babalola, 2022). Hence, developing modern technology remains important to ensure Sustainable Development Goals (SDGs) without any significant negative impact on the ecosystem.

Nanotechnological approaches have been employed in agriculture, industry, and medicine (Audah, 2019; Elemike et al., 2019; Zulfiqar et al., 2019). Nanoparticles (NPs), are characterized by sizes ranging from 1 to 100 nm in diameter, various physical, chemical features, biochemical activity, and increased reactivity (Dutta and Sugumaran, 2021). Different methods have been employed in the synthesis of NPs, which include inert gas condensation, physical ball milling, biological and chemical processes (Aboyewa et al., 2021). The biological means of synthesizing NPs can be achieved by harnessing some endophytic microbes, such as bacteria and fungi (Ahmad F. et al., 2012; Eid et al., 2021). Some examples of NPs produced by endophytic microbes include titanium, platinum, cadmium, gold, zirconium, selenium, magnetite, usnic acid, gold-silver alloy, uraninite, tellurium, and palladium (Aboyewa et al., 2021). NPs from endophytic fungi have been reported to play an important role in plant disease management due to the presence of NP-assisted genes (Sonawane et al., 2022).

Endophytic microbes are microbes inhabiting the internal tissues of plants, which can be beneficial or pathogenic (Adeleke and Babalola, 2022). The beneficial types help ensure sustainable plant and soil health under a variety of stresses including drought stress (Premachandra et al., 2020). Some of these microbes also possess the ability to synthesize nanomaterials, which can be exploited in maintaining plant health without any pathological effects (Sonawane et al., 2022). Promisingly, NP-synthesizing endophytic microbes can help boost plant physiological functions and can be used as bioinoculants in developing eco-friendly agriculture. Nevertheless, information on the actual mechanisms and the use of nanomaterials to relieve abiotic plant stresses have not been fully discussed in the literature. Depending on the type, application and use, various NPs of carbon-based, metallic and non-metallic and organic polymers have been developed (Kumar et al., 2021; Fadiji et al., 2022b). The use and implementation of known nano-growth enhancers, nano-biofertilizers, nano-pesticides, nano-herbicides, and nano-fungicides are on the increase in modern agricultural systems (Imade et al., 2022; Sonawane et al., 2022). Based on experience to date, this approach is considered safe, eco-friendly for improved soil nutrition and crop yield.

Plants are prone to different environmental stressors, such as ultraviolent light, drought, flooding, salinity, temperature extremes (low or high), and the presence of heavy metals (Chaudhary et al., 2021c). All of these factors can induce oxidative stress causing membrane depletion, reactive oxygen species formation, cell toxicity and death, which cause a reduction in plant growth (Thomas and Puthur, 2017; Hasanuzzaman et al., 2019). Regardless of the nature of the abiotic stress, NPs may be involved in plant cellular metabolism, growth, and stress protection (Ajilogba et al., 2021). Also, some NPs exhibit the ability to modify the expression of genes involved in electron transport, energy transport, cell biosynthesis, and cell organization under stress conditions (Pandey, 2018; Sonawane et al., 2022). Thus, many studies have validated the multifunctional attributes of NPs in crop improvement (Abd-Alla et al., 2019; Chavan and Nadanathangam, 2019; Kibbey and Strevett, 2019).

Notwithstanding the positive attributes of NPs, information on the mechanisms of how NPs alleviate stresses and how endophytic microbes induce plant stress tolerance are still required. Consequently, this review addresses the role of endophytic microbes in inducing abiotic stress tolerance in plants, and the use of nanomaterials to relive abiotic plant stresses.

Microbe-nanomaterial interactions

Biological activities through alterations in the function and structure of bacteria can be unveiled using modern and advanced nano-technological processes (Chaudhary et al., 2021b). Recent methods are been used to assess the surface chemistry, structural form of NPs and their effects on biocidal activities (Noukelag et al., 2022; Rehman et al., 2022). Examples of ecofriendly nano-sized agents include a variety of phyto/zooplankton, fungal spores, bacteria, and other microorganisms. NPs react differently with microbes, which shows that the microbial cell surfaces can differ substantially in their reactivity and attraction (Gangadoo et al., 2022). Silica NPs react effectively with microorganisms of different groups (Wang et al., 2020). For instance, bacteria and microalgae are smaller with less reactive attributes compared to fungal spores. A comprehensive mechanism showing the harmful effect of metallic nano-sized particles on bacteria cells is still required. In addition, there is a need for special attention to the structural alteration of bacterial cells using *in vitro* studies.

The continuous upsurge in the cases of fungal infections in immunocompromised patients, which require urgent medical treatment has caught the attention of most researchers. Meanwhile, the need for an ecofriendly measure for treating mycoses and identification of the source of infection has prompted researchers toward the use of metallic NPs (Singh et al., 2019; Soliman et al., 2021). Several studies have assessed the antifungal effects of NPs (Khatoon et al., 2018; Ahmadpour et al., 2021; Sadek et al., 2022). A study by Masoumizadeh et al. (2022) reported the effect of AgNPs on fungal pathogens, *Candida spp*. Also, the findings of Santhoshkumar et al. (2019) on the toxicological ad antidermatophytic activity of AgNPs synthesized using leaf extract of *Passiflora caerulea* revealed the maximum antifungal activities against dermatophyte, *Trichophyton rubrum*.

Nanomaterial-microbial compatibility

Bacteria and NPs

Plasmolysis of bacteria is a slaying event that involves the breakdown of cytoplasmic components and morphological reduction of cytoplasm due to the loss of intracellular components and plasma membrane contraction from the cell wall. It has been reported that metallic NPs induce pleiotrophic effect on bacteria cells. Nanomaterials bind with bacteria proteins (thiol moieties) hindering their activities, forming an attachment with the cell membrane and causing cell death. Consequently, altering cell permeability by obstructing the activities of electrons in cells and obstructing respiration (Radzig et al., 2013; Mohanty et al., 2014). ROS generated as a result also inhibits respiratory enzymes. Oxidized DNA precursors result in DNA lesions (Park et al., 2009).

Advances in the cell to the non-cell formation, the reaction against resistant, persistent strains and swarming motility have encouraged researchers about bacterial genes encoding guanine nucleotide exchange factors. NPs enhance the activities and response of genes encoding guanine nucleotide exchange factors, which gives scientists better insights into improved NPs applications as antibacterial agents. Because of these highlighted responses, several studies have been conducted to verify the expression of bacterial genes to nano-sized particles (Khati et al., 2018). Exposure to metallic NPs revealed consistent gene patterns using transcriptional analytical methods such as RT qPCR or microarray. For instance, when *E. coli* was subjected to AgNPs, it exhibited a distinctive expression in gene functions, such as homeostasis of iron, silver and copper, which regulate the oxidative balance *via* the use of microarray experiment and its features to metabolize sulfur (Nagy et al., 2011; McQuillan and Shaw, 2014). In other studies, researchers assessed alterations in gene expression of bacteria subjected to the treatment with carbon NPs. A study by Kang et al. (2008) showed the leakage of cellular material, disrupted membrane, reduced viability and metabolism of *E. coli* when subjected to single-walled nanotubes. In another study by Pelletier et al. (2010) using microarray, *E. coli* was exposed to cerium oxide NPs, the NPs upregulated several oxidoreductases sowing depletion in iron deficiency, oxidation stress and cellular respiration. Yang et al. (2012b) exposed *Pseudomonas aeruginosa* to quantum dots and genes controlling metal efflux transporters and oxidative stress were upregulated.

To check the compatibility of nanomaterials and bacterial cells, Dimkpa et al. (2012) showed that NPs could also affect microorganisms and plants by causing modifications in cellular levels of siderophores (pyoverdine) of plant growth-promoting bacterium (Dimkpa et al., 2012).

Fungi and NPs

Almost all NPs are capable of creating holes in the membrane of most fungal cells. The alteration in physiological traits of fungi releases biomolecules resulting in cell death. In a study by Kim et al. (2009), Kim and co. observed the reaction between AgNPS and *Candida albicans* and discovered membrane depolarization in *C. albicans*. Pits and pores were formed on the cell wall of the organism. This leads to the release of trehalose and glucose into the prepared suspension. The antifungal activity of AgNPs was also performed on other fungal species such as *Saccharomyces cerevisiae*, *Candida tropicalis*, *Phomopsis spp*., *Penicillium expansum*, *Botrytis cinerea* and *Trichophyton rubrum* (He et al., 2011; Nasrollahi et al., 2011; Mallmann et al., 2015). The effect of Fe_3O_4NPs was tested against *Candida* spp and perforation of cell membranes was observed (Prucek et al., 2011). The cell wall and the membrane of *Cryptoccocus neoformans* were also depleted when *C. neoformans* was exposed to AgNPs in a study by Ishida et al. (2013).

The use of *In silico* and mathematical modelling could help provide a better understanding of microbe-nanomaterial compatibility and interactions. Studies to experiment with the interaction between microbes and NPs are extremely important to unveil the details of these interactions. Meanwhile, bioinformatics tools are also needed to ensure statistical analysis and data curation about the future occurrences of microbial interaction with NPs (Singh et al., 2019; Adeleke et al., 2022).

Synergistic relationship: Endophyte-induced NPs

Recent developments required to ensure an ecofriendly interface for nanoscience studies have delivered exciting results by revealing multifaceted metal-based NPs with

numerous applications and functions (Baker et al., 2015a; Kumari et al., 2020). Ecofriendly biological resources viz. algae, fungi, bacteria and plants have been adopted to synthesize NPs, with each bio-factory having its pros and cons (Iravani et al., 2014; Rahman et al., 2019). Microorganisms are said to be an attractive option because of their dependable and unlimited metabolite production which are useful as reducing agents. In the case of plants, the disturbing plant diversity/species most times complicate the usage (because of selection problem) (Baker et al., 2015b). Even though microorganisms have been identified as the best option for the ecofriendly synthesis of NPs, the potential of endophytes remains under-explored. Adopting endophytes as reducing agents for the biosynthesis of nanomaterials opens new opportunities for the discovery of novel NPs with various applications (Rahman et al., 2019). Microorganisms (e.g., endophytes) remain the biological agents with harmless, clean and the most commercially available approach for NPs synthesis. That said, limitations faced by often synthesized endophyte NPs affect the stability of NPs because microbes are retarded overtime. With the variation in parameters such as substrate condition, synthesis condition, growth on media, pH, temperature and physicochemical parameters (stability, shape, and size) of NPs, which might change easily (Ovais et al., 2018).

The diverse endophytic microbes from different sources have been used in the synthesis of NPs. These include; the biosynthesis of AgNPs using *Bacillus cereus* isolated from *Adhatoda beddomei* and *Garcinia xanthocymus* as recapping agents to produce AgNPs with antibacterial properties (Sunkar and Nachiyar, 2012a; b). A study by Devi and Joshi (2015) also reported the use of *Cryptosporiopsis ericae* isolated from *Poteotilla fulgens* L. in the synthesis of NPs. The synthesized nanomaterial had an absorbance peek of ≈430 nm, spherical, and a diameter ranging between 2 nm and 16 nm. Rahi and Parmar (2014) and Singh et al. (2013) also synthesized AgNPs using *Penicillium* spp. isolated from the tissue of *Curcuma longa* and *Aloe vera* root. The synthesized NPs had a size range between 15 nm and 45 nm with immense antibacterial activity against antibiotic-resistant pathogens. Several studies have used endophytes as an ecofriendly route for the biosynthesis of multifunctional metal-based NPs. These include; Hulikere and Joshi (2019)—*Cladosporium cladosporoides*, Ramalingmam et al. (2015)—*Cochliobolus lunatus*, Qian et al. (2013)—*Epicoccum nigrum*, Yashavantha Rao et al. (2016)—Endophytic bacterium EH419, Neethu et al. (2018)—*Penicillium polonicum* and Abdel-Aziz et al. (2018)—*Aspergillus* spp.

Impact of nanomaterials on microbial diversity and soil health

In natural ecosystems, microorganisms drive ecological processes (Chaudhary et al., 2022). These processes include; anaerobic digestion, removal of nutrients in wastewater treatment, and biogeochemical cycling (Ahmed et al., 2012). On a single cell or population of microbes, antimicrobial activities and the potency of nanomaterials have been studied extensively elucidating their effects on the microbial community. As a result, there is an extensive understanding of the pros and cons associated with the ecotoxicity of NPs. Recently, scientists have studied the effect of nanomaterials on the community structure and functions of microorganisms in natural environments, such as water treatment facilities, marine, rivers and soils (Mohanty et al., 2014).

Effect of nanomaterials on microbial diversity

Microbial diversity in the soil plays a crucial role in nutrient cycling, plant diversity and agricultural output (Mohanty et al., 2014). Scientists have shown that important nanomaterials properties viz., aggregation, size, shape and charge, could be influenced by the environment (Lowry et al., 2012; Liu et al., 2014). NPs migrate at different levels in the soil matrix, and as such altering the microbial community structure in the soil. Also, the type of soil affects the impact of NPs. In a study by Frenk et al. (2013), the microbial community in clay and sandy soils were shown to respond differently to magnetite and copper oxide NPs. In a related study by Pawlett et al. (2013), a similar result was obtained from the reaction of microorganisms in the sandy soil to zero-valent iron nanomaterials. Herein, the microbial groups obtained from the combination of sandy soil and FeNPs were more susceptible than microbial communities in clay soil. Also, AgNPs were suspected to affect the community profile of freshwater microbial habitat in a study by Das et al. (2012). Both microbial biofilms and planktonic communities were influenced by nanomaterials as related in the study by Flemming and Wingender (2010) and Ding et al. (2014). Although, planktonic communities most times exhibit low tolerance to antimicrobial agents and toxic environments compared to their biofilm counterparts (Cao et al., 2012). For instance, the exposure of marine biofilm to AgNPs does not affect the community structure, succession and biofilm development of the community (Fabrega et al., 2011). However, apart from the reduction in microbial communities associated with a biofilm, the integrity of cells in a biofilm could be compromised because of its exposure to NPs (Battin et al., 2009).

In an engineered ecosystem using nanomaterials, most researchers adopt microbial communities associated with waste plants as model systems. Often, the impact of microbial communities and their community composition is of utmost interest to researchers. Meanwhile, most studies concentrate on the impact of NPs on commonly studied bioprocesses with the inclusion of methanogenesis, phosphorus and nitrogen removal. Even though most studies have reported the negative of

nanomaterials on microbial community structure (Liang et al., 2010; Ahmed and Rodrigues, 2013), some other studies showed that the microbial communities associated with sludge digester were not affected by nanomaterials (Nyberg et al., 2008; Yang et al., 2012a). This discrepancy could be associated with variations in the physical and chemical properties of nanomaterials and their complex reaction with several other materials from either organic or inorganic sources (Mohanty et al., 2014).

Impact of nanomaterials on microbial community functions

The effect of nanomaterials on microbial community functions is another important aspect of NPs-induced community variation yet to be explored. Some studies have further highlighted possible alterations in microbial functions induced by the exposure of the environment to nanomaterials. These include functions associated with nutrient removal and methanogenesis in wastewater treatment plants. In a study by Alvarez and Cervantes (2012), the process of methane production was significantly inhibited by nanomaterials such as Al_2O_3 and its toxicity was reduced when coated with humic acids. In a similar study, Yang et al. (2012a) reported the effect of AgNPs on methane production in landfill bioreactors at different concentrations.

Several studies viz., Masrahi et al. (2014), Liang et al. (2010), and Li et al. (2014) also reported nitrogen removal processes using nanomaterials such as TiO_2 and AgNPs. The negative impact of graphene oxide was also reported on wastewater treatment by removing nitrogen and phosphorus from waste materials (Ahmed and Rodrigues, 2013). To discuss the effect of nanomaterials on microbial diversity, structure and functions, organism-determined toxicity of nanomaterials is required i.e., each microorganism with susceptible nanomaterials because bacteria tolerate nanomaterials differently. For instance, Gram-positive bacteria react positively to single-walled carbon nanotubes by changing their membrane lipid composition. The mechanism of nanomaterials-microbe specificity is widely unknown and there is a need to further investigate the process (Jin et al., 2014; Mohanty et al., 2014).

Mechanisms of mitigating abiotic stress in plants

Abiotic stresses remain one of the most significant factors limiting the growth and yield of plant crops (Yadav, 2017). There is a need for plants to resist stressful edaphic and environmental conditions using either innate or induced biological mechanisms. For induced biological mechanisms to relieve the plant of unwanted stressors, an environmentally friendly method is needed to avoid complications associated with the use of synthetic chemicals. In this regard, the use of endophytic microbes remains one of the more reliable methods to mitigate the effects of abiotic stresses. Microbes are ubiquitous in diverse natural environments and exhibit diverse metabolic responses to manage soil stressors (Meena et al., 2017; Akinola and Babalola, 2020; Akinola et al., 2021b). Due to the proximity between plants and microbes in the soil, the plant microbiome induces local and systemic mechanisms in crop plants to cope with continuous changes to the environment. This synergism (plant-microbe) in the agroecosystem induces complex mechanisms within the plant cellular system (Figure 1). Interestingly, the continuous change in climatic conditions has paved the way for a better understanding of plant cellular complexity; researchers are constantly ruminating on questions associated with the physiological, molecular, and biochemical processes related to plant-microbe interplay (Glick, 2020; Akanmu et al., 2021).

Because of the growing concern about climate change, it is important to explicitly explicate the synergy between plant-soil-microbe about protection against abiotic stressors. Understanding the changes in different abiotic stresses induced by either anthropogenic or natural means is crucial to reducing the negative effects of environmental stress as it impacts agricultural productivity (Jalil and Ansari, 2019). A report by the Food and Agriculture Organization (FAO) of the United Nations on the challenges limiting global food productivity argued that one of the major problems faced by the scientific community in the effort to increase crop production is unwanted abiotic stressors (FAO, 2009). As such, there is a need to address the challenges associated with plant growth sustainably. These include eco-friendly technological processes and the efficient use of bioproducts to address the constraints posed by environmental stresses (FAO, 2009).

Several abiotic factors can limit plant growth and development including low or high temperature, heavy metal toxicity, soil alkalinity or acidity, drought, flooding and salinity (Emamverdian et al., 2015; Pasala et al., 2016; Jalil and Ansari, 2019). Abnormal soil acidity can lead to nutrient deficiency in plants thereby reducing essential physiological attributes needed to improve plant growth and development (Jalil and Ansari, 2019; Akinola and Babalola, 2020). Similarly, salt treatment induces toxicity in plant tissues, leading to osmotic imbalance and stress which hinders plant growth. In addition, abiotic stressors increase the production of ROS and induce phytotoxicity by negatively impacting protein structure and functions (Baral and Izaguirre-Mayoral, 2017; Mukhtar et al., 2018; Komaresofla et al., 2019).

Naturally, plant cell organelles *viz.*, chloroplasts, peroxisomes and mitochondria help in producing ROS, with hydrogen peroxide and oxygen radicals being produced in the mitochondria. Hydrogen peroxide and oxygen are produced in the chloroplast (Jalil and Ansari,

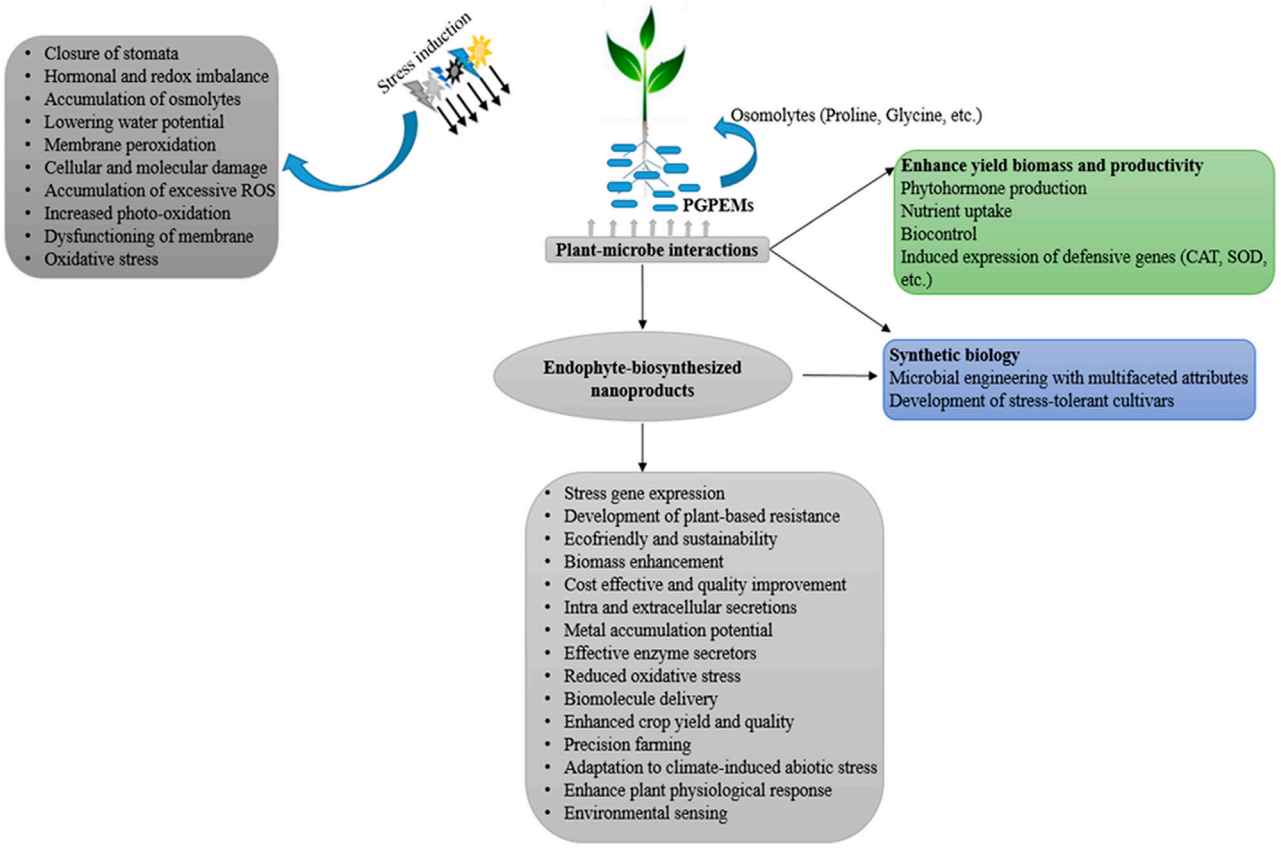


FIGURE 1
Concept of endophyte interactions and biosynthesized nanoproducts to alleviate abiotic stress and enhance crop yield.

2019). Using peroxidase dismutase, the peroxides are transformed into hydrogen peroxide (H_2O_2). The oxidation process involved in the conversion of xanthine and hypoxanthine to uric acid is achieved in the peroxisomal matrix using xanthine oxidase to generate oxygen radicals (Halliwell and Gutteridge, 2015; Jalil and Ansari, 2019). These radicals destroy cell biomolecules, such as DNA, carbohydrates, lipids, and proteins, resulting in cell death.

Plants can rapidly acclimatize to an abrupt change in the environment, such as unwanted abiotic conditions. A shift in the soil condition alters plant metabolic equilibrium and causes plant cells to modify genetic and metabolic processes (Tuteja and Mahajan, 2007; Tuteja and Sopory, 2008; Simontacchi et al., 2015). Plants then activate defense mechanisms needed to relieve unwanted stress conditions, reprogramming metabolic processes within the plant cell, thus facilitating bio-physicochemical relief of abiotic stress conditions (Massad et al., 2012; Mickelbart et al., 2015; Yolcu et al., 2016).

Due to uncertainty surrounding the mechanism of action of metallic NPs, different hypothetical mechanisms were frequently mentioned in different studies. These include that:

a) NPs aggregate and dissolve the cell membrane, resulting in the alteration of cell permeability and dissolution of the PMF—Proton motive force (McQuillan, 2010; Singh et al., 2019).
b) ROS—Reactive oxygen species that help in the destruction of the cellular structure are produced by metallic NPs and ions (Singh et al., 2019).
c) Absorption of metal ions by cells helps in the degradation of intracellular ATP and the disruption of DNA synthesis (Singh et al., 2019).

Oxidation reactions attributed to metallic ions in cells induce responses such as ROS—due to cell signal differentiation and cell death (Mueller et al., 2005). The integral components of ROS include peroxomonocarbonate ($HOOCO_2^-$), peroxynitrate (O_2NOO^-), peroxynitrite ($ONOO^-$), nitric compounds, hypochlorite and hypochlorous acids, peroxyl (RO_2^-), and hydroperoxyl (HO_2^-), and other oxygen-related compounds (Wu et al., 2014). With the catalysis of superoxidase dismutase (SOD), oxygen ions have a short lifespan due to instant reduction. NADPH—nicotinamide adenine

dinucleotide phosphate oxidase in the mitochondria induces lipid peroxidation of the cell membrane (Singh et al., 2019). SOD initiates the complete conversion of oxygen into hydrogen peroxide. Physiologically, different detoxifying enzymes *viz*., glutathione peroxidase, catalase, SOD and antioxidants (flavonoids, vitamin E and ascorbic acids) modulate intracellular stages. Meanwhile, ROS activated by NPs of either CuO, ZnO or Ag plays a crucial role in genotoxicity. Oxidative stress degraded genetic materials are associated with different biological mechanisms *viz*., mutagenesis. Stress activation due to oxidative species results in nanotoxicity and the accumulation of oxidative stress leading to DNA destruction (Fu et al., 2014). The destruction of DNA because of OS; involves the breakage of single and double-stranded sugar bases, the generation of basic sites and DNA-protein crosslinks. Closely, hydroxyl radicals cause rapid damage to cells, whereas, from a distance, less-reactive ROS may interact easily (Fu et al., 2014).

Microbe-induced abiotic stress tolerance

An adaptation used in the process of abiotic stress tolerance is often referred to as induced systemic tolerance/resistance (IST/ISR). The intrinsic genetic and metabolic potential of microbes contribute immensely to the relief of plants from abiotic stresses (Gopalakrishnan et al., 2015). The role of endosphere and rhizosphere inhabitants belonging to different genera *viz*., *Cyanobacteria* (Singh et al., 2011), *Trichoderma* (Pandey et al., 2016; Igiehon and Babalola, 2021), *Burkholderia* (Naveed et al., 2014a; Naveed et al., 2014b), *Methylobacterium* (Meena et al., 2012), *Bradyrhizobium* (Tittabutr et al., 2013), *Enterobacter* (Sorty et al., 2016), *Bacillus* (Ashraf et al., 2004; Sorty et al., 2016), *Pantoea* (Sorty et al., 2016), *Rhizobium* (Igiehon and Babalola, 2021; Igiehon et al., 2021), *Azospirillum* (Omar et al., 2009), *Azotobacter*, and *Pseudomonas* (Ndeddy Aka and Babalola, 2016) have functional traits useful in improving plant growth under abiotic stresses. The functional role of *Trichoderma harzianum* in alleviating soil stresses through the upregulation of genes such as malonialdehyde, dehydrin, and aquaporin genes, has been reported by Pandey et al. (2016) on different serotypes of rice. Also, the synthesis of exopolysaccharides, antioxidants, protein defensins and phytohormones may be induced using plant growth-promoting rhizobacteria. Most of these functions are effective against drought and other abiotic stressors (Kaushal and Wani, 2016). Therefore, the effective productivity monitoring parameters, *viz*., screening, selection and inoculation of stress-mitigating microbes, can be helpful as a viable option to increase crop productivity to solve the problem of a growing world population with insufficient food (Akinola and Babalola, 2021). *Trichoderma harzianum* inoculation enhances the oil content of *Brassica juncea* inhibited by salinity stress and improves the plant's physiological traits, such as reducing sodium ion uptake, enhancing osmolyte synthesis, antioxidant accumulation, and facilitating the uptake of essential plant nutrients (Ahmad et al., 2015). Similarly, ACC deaminase production was shown to be responsible for the upregulation of monodehydroascorbate reductase in *B. juncea* (Brotman et al., 2013). Also, the addition of *Acinetobacter* sp. and *Pseudomonas* sp. have been used to increase the production of ACC deaminase and indole-3-acetic acid (IAA) in oat and barley grown in salinity-stressed soil (Chang et al., 2014). *Streptomyces* sp. strain PGPA39 has also been used to alleviate salinity stress in tomato plants (Palaniyandi et al., 2014). In *Arabidopsis*, wheat, and maize plants, *Burkholderia sp*., has been used to relieve plants and soil of salt and drought stresses (Naveed et al. (2014a); Naveed et al. (2014b); Pinedo et al. (2015).

There are a large number of microorganisms within proximity to plant tissues and across the vicinity of plant roots because the plant root exudates provide diverse metabolites and nutrients which attract beneficial microorganisms. These metabolites are crucial to the microbial presence surrounding and attached to plants (Akinola et al., 2021a; Akinola and Babalola, 2021) with chemoattraction being associated with microbial movement toward these compounds (Meena et al., 2017). While utilizing these plant exudates, plant growth-beneficial microorganisms associated with the plant endosphere induce both direct and indirect mechanisms, such as biocontrol agents, phytostimulation, and biofertilization (Hayat et al., 2010; Akinola and Babalola, 2020).

Indirect mechanisms of plant growth promotion include the production of antimicrobial agents, hydrogen cyanide (HCN), and antibiotics, which exert antagonistic effects against plant pathogens. Direct mechanisms include nitrogen fixation, stimulation of plant hormone synthesis, solubilization of potassium and phosphorus, synthesis of siderophores which facilitate iron uptake, and sequestration of zinc and other micro-and macronutrients from the soil (Meena et al., 2017). In addition, many plant-associated microbes also induce systemic resistance against various phytopathogens triggered by plant secondary metabolites (Meena et al., 2017; Omomowo and Babalola, 2019). Apart from bacteria, mycorrhizal fungi are also good to plant growth promoters. These include both vesicular-arbuscular mycorrhiza (VAM) and other ectomycorrhizal fungi (Akinola and Babalola, 2021). These fungi use their extensive hyphal networking to increase plant nutrient uptake. For instance, in studies by Sun et al. (2010) and Baltruschat et al. (2008), an endophytic fungus—*Piriformospora indica* was used to improve drought and salinity tolerance in Chinese cabbage and barley, respectively. These processes were achieved by improving both physiological traits and the level of plant antioxidants. At some point, microbes activate systemic or local stress responses in plants under abiotic stress. In other instances, they activate direct

TABLE 1 Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Wheat		*Bacillus pumilus* (FAB10)		Salinity	Enhanced wheat growth with improvement in photosynthesis, plant tissue proline content, and transpiration	Ansari et al. (2019)
Paddy plants		*Curtobacterium albidum* (SRV4)		Salinity	Improved plant proline content, membrane solubilization index, and photosynthetic pigment efficiency	Vimal et al. (2019)
Wheat		*Bacillus megaterium* + *B. licheniformis* + Fulvic acid		Alkalinity	Improved plant growth, reduction in soil cadmium, increase in organic matter	Li et al. (2019)
Guinea grass (*Megathyrsus maximus*)		*Bacillus* spp.		Drought	Increased accumulation of proline and glutathione reductase activity	Moreno-Galván et al. (2020)
Maize (*Zea mays* L.)		*Azotobacter salinestris*, *A. chroococum*		Drought	Increase in shoot dry weight, chlorophyll content, plant height and N, P, Fe concentration	Shirinbayan et al. (2019)
Lettuce *Latuca sativa*		*Curtobacterium herbarum* (CAH5)		Drought	Reduction in oxidative stress and lipid peroxidation	Silambarasan et al. (2019)
Common ice-plant (*Mesembryanthemum crystallinum* L.)		*Streptomyces diastaticus* WZ902 (LC390202), *Bacillus subtilis subsp. Inaquosorum* LM03-B (LC390203)		Salinity	Increased plant growth, and elongated roots. ACC deaminase activity, phosphorus solubilization, and siderophore production	Mahmood et al. (2019)
Sorghum and sudan grass seedlings on red mud	*Trichoderma asperellum* RM-28			Sodic/saline-Alkalinity	Decreased pH and EC of red mud, and improved plant chlorophyll content, growth, and oxidative stress	Anam et al. (2019)
Salicornia sp		*Staphylococcus* sp. (rhizosphere strain) + *Staph.* sp. (endophytic strain)		Salinity	Enhanced growth and high salt tolerance with both strains. Increased phosphate solubilization and IAA production	Komaresofla et al. (2019)
Thale cress *Arabidopsis thaliana*		*Pantoea stewartii* JZ2, *Bacillus* sp. JZ34, *Microbacterium barkeri* JZ37, *Arthrobacter* sp. JZ12, *Cellulomonas* sp. JZ18		Salinity	Endophytic bacteria from the desert help reduce Na^+/K^+ ratio and increase plant shoot and root biomass	Eida et al. (2019)
Sulla carnosa		*Actinobacter* sp. (Br3) + *Pseudomonas putuda* (Br18) + *Curtobacterium* sp. (Br20)		Salinity	Enhanced soluble sugar, oxidative enzyme activities, ameliorated induced soil salinity and increased plant growth	Hmaeid et al. (2019)
Wheat (*Triticum aestivum*)		1-aminocyclopropane-1-carboxylate dismutase (ACCD)-producing *Klebsiella* spp. (8IJA, 27IJA)		Salinity	Increase in plant biomass and superoxidase dismutase activity	Acuña et al. (2019)
Maize (*Zea mays* L.)	*Glomus tortuosum*			Salinity	Increased crop output, chlorophyll content, and rubisco activity	Xu et al. (2018)
Finger millet (*Eleusine coracana L. Gaertn*)		*Pseudomonas* spp.		Drought	Improved growth performance and foliar nutrient content and increased antioxidant properties	Chandra et al. (2018)

(Continued on following page)

TABLE 1 (*Continued*) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Ice plant (*Aizoaceae* spp.)		*Mesembryanthemum crystallinum*		Salinity	Increase in rubisco activity, crop output, and chlorophyll content	Zhang et al. (2018)
White clover (*Trifolium repens*)		*Azospirillum brasilense*		Salinity	Polyphenols and phenol production	Khalid et al. (2017)
Lettuce (*Latuca sativa*)		*Curtobacterium herbarum* (CAH5)		Drought and Aluminium stress	Increased plant root and shoot growth, enhanced plant growth under 4-nitroaniline	Silambarasan and Vangnai (2017)
Maize (*Zea mays* L.)		*Pseudomonas putida* (FBKV2)		Drought	Increase in root length and dry biomass	Vurukonda et al. (2016)
Mung beans (*Vigna radiata*)		*Bacillus drentensis*, *Enterobacter cloacae*		Salinity	Increase in plant height, seed yield, dry biomass, chlorophyll content, water absorption rate, transpiration, and salt tolerance	Mahmood et al. (2016)
Tomato (*Solanum lycopersicum*)		*Arthrobacter* strains (TF1, TF7), *Bacillus megaterium* (TF2, TF3)		Salinity	Increase in seedling length, vigor index, dry weight, and tomato seed germination	Fan et al. (2016)
Maize (*Zea mays* L.)		*Chryseobacterium humi* ECP37 + *Pseudomonas reactans* EDP28		Salinity	Increased seedling and plant yield	Moreira et al. (2016)
Maize (*Zea mays* L.)	Glomus etunicatum +	*Methylobacterium oryzae* CBMB20			Improved crop yield after the *in vivo* application of organisms	Lee et al. (2015)
Garden thyme (*Thymus vulgaris*)		*Enterobacter* sp. + *Bacillus* sp. + *Bacillus thuringensis* + agrowaste		Drought	Optimal nutrition and better physiological traits compared to control	Armada et al. (2015a)
French lavender (*Lavandula dentate*), Common sage (*Salvia officinalis*), Lavender-cotton (*Santolina chamaecyparissus*)						
Maize (*Zea mays* L.)	Consortium of AMF	*Bacillus thuringensis*		Drought	Increased plant growth, photosynthesis efficiency, decreased oxidative damage to lipids, increased accumulation of proline and nutrient	Armada et al. (2015b)
Chicken pea (*Cicer arietinum*) cultivars BG-3629, BG-1003		*Pseudomonas putida*		Drought	Conferred drought tolerance by improving several biochemical and physiological parameters	Tiwari et al. (2016)
Mung beans (*Vigna radiata*)		*Pseudomonas putida* (SB21)		Acidity	The large increase in plant growth	Saluja et al. (2014)
Mung beans (*Vigna radiata*)		*Comamonas* spp. (SB20)		Alkalinity	Increase in plant yield after exposure to alkaline soil	Saluja et al. (2014)
White clover (*Trifolium repens*)	Arbuscular mycorrhiza fungi (AMF) +	Combination of any two of *Bacillus thuringensis*, *Rhizophagus intraradices*, *Pseudomonas putida*		Drought	Increased root and shoot weight with high superoxidase dismutase (SOD) activity	Ortiz et al. (2015)
Common bean (*Phaseolus vulgaris*)		*Pseudomonas fluorescens*		Salinity	Na^+ exclusion, proline production, increased SOD, catalase activity and shoot biomass	Younesi and Moradi (2014)

(Continued on following page)

TABLE 1 (*Continued*) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Barley (*Hordeum vulgare*), Oats (*Avena sativa*)		*Pseudomonas* sp., *Acinetobacter* spp.		Salinity	Increased IAA and ACC deaminase production	Chang et al. (2014)
Rice sensitive to salt (GJ-17)		*Bacillus pumilus*, *Pseudomonas pseudoalcaligenes*		Salinity	Increased SOD activity and reduced lipid peroxidase	Jha and Subramanian (2014)
Tomato (*Solanum lycopersicum*)		*Streptomyces* sp. (PGPA39)		Salinity	Phosphate solubilization, increased plant yield, IAA production, and ACC deaminase activity	Palaniyandi et al. (2014)
Mung beans (*Vigna radiata* L)		*Pseudomonas* sp. + *Rhizobium* sp		Salinity	Increased ACC deaminase activity and IAA production	Ahmad et al. (2013)
Wheat (*Triticum aestivum*)		*Serratia ficaria*, *Enterobacter cloacae*, *Pseudomonas fluorescens*, *P. putida*		Salinity	Improved nutrient uptake and enhanced plant growth	Nadeem et al. (2013)
Rice (*Oryza sativa*)		*Bacillus amyloliquefaciens* NBRISN13 (SN13)		Salinity	Increased colonization of osmoprotectant utilizing microbes to induce salt tolerance in rice	Nautiyal et al. (2013)
Wheat (*T. aestivum*)		*Halobacillus* spp *Bacillus halodenitrificans*		Salinity	Increase in dry weight and root length of the plant	Ramadoss et al. (2013)
Tomato (*Solanum lycopersicum*)		*Bacillus pumilis*, *Bacillus subtilis*		Salinity	High PGP traits, vigor index, and ability to tolerate saline soil	Damodaran et al. (2013)
Wheat (*T. aestivum*)		*Streptomyces* sp		Salinity	Increase in N, P, Fe, and Mn of the wheat shoots and alleviation of salt inhibition	Sadeghi et al. (2018)
Rice (*Oryza sativa*)		*Bacillus* sp., *Alcaligenes* sp., *Ochrobactrum* sp		Salinity	Increased germination, root, shoot growth, and chlorophyll content. ACC deaminase reduces ethylene production under salt stress	Bal et al. (2013)
Groundnut (*Arachis hypogaea* L.)		*Haererohalobacter* sp. (JG-11), *Bravibacterium casei* (JG-08), *Brachybacterium saurashtrense* (JG-06)		Salinity	Increase in phosphorus, nitrogen content, High Ca^{2+} and balanced K^{+}/Na^{+} ratio. ACC deaminase activity	Shukla et al. (2012)
		Raoultella planticola Rs-2		Salinity	ACC deaminase activity and high plant yield	Wu et al. (2012)
Mung bean (*Vigna radiata*)		*Rhizobium phaseoli* + PGPR (*Pseudomonas fluorescens* (MK20), *P. syringae* MK1)		Salinity	Increased efficiency of water use and ACC deaminase activity	Ahmad et al. (2012b)
Wheat (*T. aestivum*)		*Bacillus* sp. (SKU-3), *Paenibacillus* sp. (SKU-11)		Salinity	Exopolysaccharides produced by test organisms mitigate soil salinity	Upadhyay et al. (2011)
Sunflower treated with NaCl		*Pseudomonas fluorescens* biotype F, *P. fluorescens* CECT378^{T}		Salinity	Balanced K^{+}/Na^{+} ratio, siderophore, and IAA production	Shilev et al. (2012)
Wheat (*T. aestivum*)		*Pseudomonas extremorientalis* (TSAU6), *P. aureantiaca* (TSAU22), *P. extremorientalis* (TSAU20)		Salinity	Production of phytohormones such as gibberellin, auxin, zeatin, and alleviation of salinity inhibition	Egamberdieva (2009)
Soybean (*Glycine max*)		*P. putida* (62BN)		Acidity	Reduction in cadmium concentration and increased plant growth in acidic soil	Rani et al. (2009)
Soybean (*Glycine max*)		*P. monteilli* (97AN)		Alkalinity	Increased plant growth and amelioration of soil alkalinity	Rani et al. (2009)

(Continued on following page)

TABLE 1 (*Continued*) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
Wheat seedling		Exopolysaccharides producing bacterial strains *viz.* *Aeromonas hydrophila/caviae* (MAS-765), *Bacillus insolitus* (MAS17), *Bacillus* sp. (MAS617, MAS620, MAS820)		Salinity	Increased physiological properties (root, shoot, and yield) in a saline environment and reduced Na + uptake by the plant	Ashraf et al. (2004)
Indian mustard (*Brassica juncea* L.) Barley (*Hordeum vulgare*)	*Trichoderma harzianum* *Piriformospora indica*			Salinity	An antioxidative defense system was used to mitigate the effect of NaCl on plant	Ahmad et al. (2015)
				Salinity	Microorganism induces desaturation of fatty acids in leaves, attenuated NaCl-induced lipid peroxidation and metabolic heat efflux useful in salt tolerance	Baltruschat et al. (2008)
Arabidopsis thaliana	*Trichoderma* spp.			Salinity	Activation of antioxidative compounds *viz.* ACC deaminase for tolerance against salt stress	Brotman et al. (2013)
Soybean (*Glycine max*)	AMF	*Rhizobium* spp		Drought	The synergy between AMF and *Rhizobium* spp. Relieve plants of drought stress by increasing the level of plant proline	Igiehon and Babalola (2021)
Rice (*Oryza sativa* L)		*Bacillus pumilus*		Salinity and heavy metal	The bacterium reduces the antioxidative activity of the plant due to the limited uptake of Na^+	Khan et al. (2016)
Rice (*Oryza sativa* L)	*Trichoderma harzianum* Th-56			Drought	*T. harzianum* modulates the activation of essential compounds such as lipid, peroxidase, SOD, and proline, needed to improve drought tolerance in tice	Pandey et al. (2016)
Micro Tom Tomato		*Streptomyces* sp. PGPA 39		Salinity	Reduction in leaf proline content increased chlorophyll content and plant biomass after inoculating the plant with *Streptomyces* sp	Palaniyandi et al. (2014)
Piptatherum miliaceum L. *Thymus vulgaris* Letc.	AMF	*Bacillus thuringensis*		Drought	Decreased stomatal conductance, electrolyte leakage, proline activity, increased water content, and nutrient uptake	Ortiz et al. (2015)
Brassica juncea		*Pseudomonas aeruginosa, Bacillus subtilis*, *Alcaligenes faecalis*		Heavy metal	Organisms reduce the uptake, toxic effect of heavy metals and also increase plant growth	Ndeddy Aka and Babalola (2016)
Maize (*Zea mays* L)		Endophytes *Burkholderia phytofirmans* (PsJN), *Enterobacter* sp. FD17		Drought	Endophytes relieve the effect of drought by increasing root-shoot biomass, chlorophyll content, photosynthesis, leaf area, and other physiological traits	Naveed et al. (2014b)
Wheat		*Burkholderia phytofirmans* PsJN		Drought	*B. phytofirmans* increases ionic balance, antioxidant level, nutrient uptake, and	Naveed et al. (2014a)

(Continued on following page)

TABLE 1 (*Continued*) Examples from the recent literature of the effect of plant growth-promoting microbes in the relief of plant stress.

Crop type	Adopted organism(s)			Stress	Inference	References
	Fungi	Bacteria	Archaea			
					protein concentration in grains	
Legume		*Bradyrhizobium, Rhizobacteria* containing stress-induced ACC deaminase		High temperature, Drought, and salinity	Synergism between used organisms mitigated different plant stressors by adjusting the expression of ACC deaminase to varying levels of stress conditions	Tittabutr et al. (2013)
Chinese cabbage	*Piriformospora indica*			Drought	Plastid-localized CAS proteins, drought-related genes and antioxidant enzymes were stimulated	Sun et al. (2010)
Rice (*Oryza sativa* L.)		*Pseudomonas putida* MTCC102		Nutrient deficiency	*P. putida* strain relieved the stress of iron deficiency	Sharma et al. (2013)
Rice (*Oryza sativa* L.)		*Pseudomonas* strains PF1, TDK1		Salinity	*Pseudomonas* strains relieved the plant of salt stress, increased physiological parameters, such as root and shoot length, dry weight, and plant height	Sen and Chandrasekhar (2014)
Arabidopsis thaliana		*Burkholderia phytofirmans* PsJN		Salinity	*B. phytofirmans* induces long-term transcriptional and metabolic changes in plants, suggesting the need to understand spatiotemporal mechanisms associated with the process	Pinedo et al. (2015)
Wheat (*Triticum aestivum* L.)		*Sinorhizobium* strains, *Rhizobium* sp., *Pseudomonas* sp., *Enterobacter* sp., *Acinetobacter* sp., *Bacillus, Pantoea* sp		Salinity	Plant growth-promoting bacteria isolated from halophytic weeds help germination and seedling wheat growth under saline stress	Sorty et al. (2016)
Chinese cabbage	*Piriformospora indica*			Drought	The upregulation of the expression level of drought-related genes, *viz.* RD290A, ANACO72, CBLI, and DREB2A in the leaves of Chinese cabbage help relieve plants of imposed drought stress	Sun et al. (2010)
Barley (*Hordeum vulgare* L.)		*Hartmannibacter diazotrophicus* E19^T		Salinity	*H. diazotrophicus* increased the root and shoot ratio of barley under salt stress. This growth promotion was associated with ACC-deaminase production	Suarez et al. (2015)

responses to support plant growth and development. This complex and multipronged action of soil microbes makes them a vital and viable choice for disease suppression and abiotic stress control in plants (Franken, 2012; Meena et al., 2017).

Several mechanisms have highlighted the enormous benefit of plant-associated microbiomes (Kushwaha et al., 2020; Glick and Gamalero, 2021; Adeleke and Babalola, 2022). The microbes found in the plant root environment typically belong to the genera *Pseudomonas*, *Klebsiella*, *Aeromonas*, *Azotobacter*, *Enterobacter*, *Bacillus*, *Azospirillum*, and *Achromobacter* (Ortiz et al., 2015; Kaushal and Wani, 2016; Sorty et al., 2016; Babalola et al., 2021; Fasusi et al., 2021) (Table 1).

All rhizosphere and endosphere bacteria with the ability to maintain plant growth under different adverse soil conditions are referred to as plant growth-promoting bacteria (PGPB) (Agri

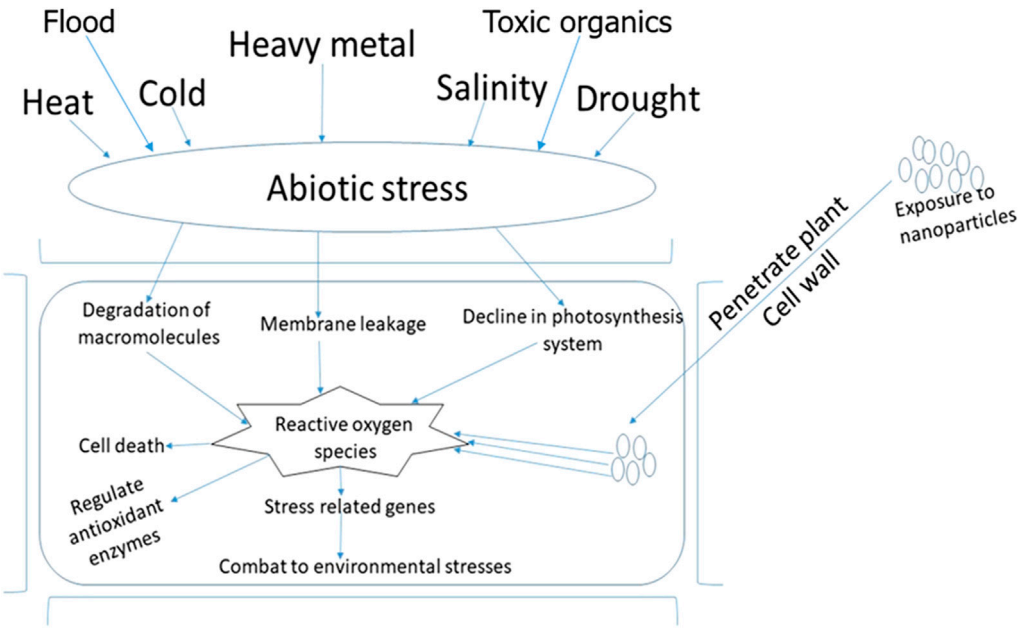


FIGURE 2
The use of nanotechnology to suppress abiotic stress conditions in a plant cell.

et al., 2022). There are other mechanisms plant microbes use to promote plant growth and development. IAA is produced to improve plant root development (Meena et al., 2017) where auxins initiate root growth and cell elongation. However, the high production of auxin may negatively affect root growth (Sorty et al., 2016; Akinola and Babalola, 2020). High auxin secretion also has drawbacks because of the increased ethylene production. In addition, the enzyme ACC deaminase is a key component in lowering the stress ethylene that results from both biotic and abiotic stress (Glick, 2004).

The mechanisms mentioned above have been reported in rhizosphere bacteria and fungi with enhanced phytohormones production for sustainable plant growth (Belimov et al., 2007; Ojuederie et al., 2019; Akinola et al., 2021c). Other studies have employed rhizobiomes to mitigate environmental stresses and improve the growth of crop plants in maize (Rojas-Tapias et al., 2012; Akinola et al., 2021a; Chaudhary A. et al., 2021), rice (Sharma et al., 2013), soybean (Sen and Chandrasekhar, 2014), and barley (Suarez et al., 2015).

The use of nanomaterials to relieve abiotic plant stresses

Plants possess several mechanisms needed to cope with unwanted soil conditions, including heat stress, drought, flooding, salinity, and chilling. Several researchers have studied molecular and cellular plant responses to abiotic stress (Gepstein and Glick, 2013; Ali and Glick, 2019; Santoyo et al., 2021a). Primarily, plants respond to abiotic stress using methods, such as an increase in MAPK (mitogen-activated protein kinase), abscisic acid, ROS, increased intracellular messenger *viz*., polyphosphate, inositol and raised Ca^{2+} in the cytoplasm as shown in Figure 2.

Meanwhile, stress relief responses, such as regulation of the expression of specific stress genes, and the proteins involved in the protection from cellular damage are involved in the advanced level of plant response. In addition, secondary metabolites ensure physiological processes to reduce abiotic stress conditions by activating the biosynthesis of polyamines signal transduction, ROS-induced photosystem protection and stabilizing cellular structure (Oh et al., 2009; Jalil and Ansari, 2019).

In mitigating soil stresses, the plant cell wall helps in plant adaptation and guides against stress perception. Induced peroxidases modify plant cell walls, which bring together oxidative stress and ROS when in contact with plant stressors (Rouet et al., 2006; Daudi et al., 2012). When plants encounter oxidative stress, immediate defense responses, such as the regulation of gene expression, enzyme production, phenylpropanoid aggregation, and ROS are produced (Daudi et al., 2012; Jalil and Ansari, 2019).

Although plants develop various mechanisms to initiate responses against adverse conditions. Nevertheless, their responses may differ even among the same plant species. Consequently, augmentation of stress tolerance in plants and identification of tolerant plant material remains conservative and

ecofriendly methods towards sustainable agricultural practices and crop production (Akinola et al., 2022; Chaudhary et al., 2022). Nanoscience is an emerging multi-disciplinary area that involved the use of nanomaterials in different fields at the nano-level. The most promising application of nanoscience could be exploited in agroecosystem practices, food processing and packaging materials. In the current scenario, nanomaterials can be used as a tool to effectively promote plant growth and also ameliorate plant stressors (Saxena et al., 2016; Chaudhary et al., 2021b).

A lot has been done on the use of nanotechnological approaches to stress responses (Shabnam et al., 2014; Tripathi et al., 2015; Singh and Lee, 2016). The effect of NPs on sustainable plant growth and development is concentration-dependent, which also increases antioxidant enzyme activity. For example, in a study to assess the effect of TiO_2 NPs on onion seedlings, TiO_2 NPs increased the activity of the superoxidase dismutase enzyme (Laware and Raskar, 2014). Meanwhile, a drastic change in the physiological traits of the onion plant was noticed with an increased concentration of TiO_2 NPs (Laware and Raskar, 2014). Under these conditions, the activities of the catalase and amylase enzymes decreased at lower concentrations of TiO_2. In another study by Changmei et al. (2002), SiO_2 and TiO_2 NPs showed significant positive effects on the growth and sprouting of *Glycine max* seedlings.

Effect of NPs on heavy metal stressed plants

Contamination of the plant-soil environment by metallic ions is a severe menace to sustainable agricultural practices worldwide. Heavy metal stress increases plant toxicity, thus leading to retarded plant growth (Chibuike and Obiora, 2014; Jalil and Ansari, 2019). This happens due to decreased enzymatic activities induced by a continuous decrease in essential nutrients available in the soil (Sharma et al., 2012). Furthermore, heavy metal ions induce ROS production affecting the plant's physiological properties; *viz*., membrane permeability reduction, cell structure deformation, and degradation of available plant cell protein. To relieve the constraints attributed to heavy metal stress, plants induce defense mechanisms including the production of polyphosphates, organic acids, and metal chelates, which all reduce the influx of metal ions and activate the synthesis of antioxidants to lower ROS production. The activation of these defense mechanisms ensures resistance against heavy metal stress. Moreover, the use of synthesized NPs can reduce the burden of phytotoxicity induced by heavy metals on plants (Sharma et al., 2012; Gunjan and Zaidi, 2014; Tripathi et al., 2015).

Because of the small size and surface area of synthesized NPs, they can easily penetrate plant cells and retain a high affinity for metallic ions. In a study by Worms et al. (2012), it was reported that quantum dots (i.e., the nanoparticles of a semiconductor) reduce Pb and Cu accessibility to plant cells. The report of Singh and Lee (2016) showed TiO_2 NPs reduce Cd toxicity and improve physiological traits, *viz*., plant growth, and photosynthetic rate. The study of Li and Huang (2014) with *Brassica juncea* revealed the effect of hydroxyapatite NPs in the relief of cadmium toxicity. Similarly, synthesized SiNPs helped to reduce chromium toxicity in peas (Tripathi et al., 2015). Shabnam et al. (2014) also discovered that the treatment of cowpea with AuNPs induces a reduction of Au ions to a nontoxic form by phenolic compounds of cowpea seeds (Table 2).

Effect of NPs on heat stress

Exposing a plant to an extreme temperature for a long period results in retarded plant growth and development. Heat stress reduces photosynthetic and chlorophyll content, membrane ion leakage, protein degradation, and lipid depletion. This is because an increase in ROS generation induces oxidative stress (Wahid, 2007; Karuppanapandian et al., 2011; Prasad et al., 2011). Haghighi et al. (2014) reported the effect of low concentrations SeNPs in reducing heat stress by stimulating the photosynthetic ability of plants, increasing hydration, and improving plant growth.

Anti-oxidative properties of the plant have also been improved at low SeNPs levels, while high concentrations of SeNPs induce oxidative stress (Haghighi et al., 2014). Plants induce the production of molecular chaperones and heat shock proteins during heat stress to resist oxidative stress (Hasanuzzaman et al., 2013; Hasanuzzaman et al., 2014).

Furthermore, carbon nanotubes, such as HSP90 have been used to upregulate genes involved in heat shock protein synthesis. A study by Zhao et al. (2012) showed that the exposure of maize to CeO_2NPs upregulates HSP70 and generates large amounts of hydrogen peroxide.

Effect of NPs on salinity stress

Salinity is an important abiotic stressor that deteriorates and limits the output of food crops. Owing to the susceptibility of most plants (i.e., lycophyte category) to salt stress, the majority of plant products are negatively affected, thereby reducing their economic value (Munns and Tester, 2008; Akinola and Babalola, 2020). Salinity stress hinders both physiological and biochemical processes associated with the sprouting of the plant.

Salinity causes one or more of the following: specific ionic toxicity, nutritional imbalance, and a reduced osmotic potential (Jalil and Ansari, 2019). In addition, some other critical physiological processes, such as lipid metabolism, protein synthesis, and photosynthesis, are often negatively affected (Parida and Das, 2005). The use of nano-based-fertilization

TABLE 2 Some recent reports of the effect of nanotechnology in alleviating plant stressors.

Nanoparticle	Characterization	Plant stress	Size of the nanoparticle	Test plant	Inference	References
CuNPs	SEM, XRD	Drought	30 nm–40 nm	Maize (*Zea mays* L.)	CuNPs increased carotenoid, chlorophyll, and anthocyanin levels in maize grown under drought stress. Also, reactive oxygen species (ROS) decreased as a result of the activities of scavenging enzymes	Van Nguyen et al. (2022)
MgNPs	SEM, XRD	Lead-induced	≈20 nm	*Daucus carota*	MgNPs help to detoxify ROS to mitigate Pb-induced stress and improve plant growth and nutrient uptake	Faiz et al. (2022)
Chitosan-Selenium NPs (Cs-SeNPs)	XRD, SEM, TEM	Salinity	≈50 nm	Bitter melon (*Momordica charantia*)	Cs-SeNPs alleviated the effect of salinity stress by reducing Na^+ aggregation, MDA and H_2O_2 oxidants and increased relative water content, K^+, proline concentration and antioxidant enzyme activity in plant	Sheikhalipour et al. (2021)
CeNPs	XRD, SEM	Salinity	10 nm	Rice (*Oryza sativa* L.)	CeNPs enhanced nitric oxide production by activating the transcription of *NIA2*-encoding nitrate reductase and controlling dephosphorylation of its protein which resulted in NO production and plant tolerance to salt	Zhou et al. (2021)
FeNPs	FTIR, XRD, SEM, TEM, EDS	Drought and Cadmium toxicity	18 nm–94 nm	Rice (*Oryza sativa* L.)	FeNPs decreased ROS and improved plant biomass, nutrient acquisition, photosynthesis efficiency, and other plant physiological traits. More also, Cd transporter genes (*OsLCT1*, *OsHMA2*, *OsHMA3*) were curtailed in FeNPs-treated rice plant	Ahmed et al. (2021)
SiNPs	XRD, SEM, TEM	Salinity	< 50 nm	Lentil (*Lens culinaris* Medik.)	SiNPs improved the physiological traits *viz.* root length, shoot length, seedling fresh and dry weight of lentil under salinity stress	Sabaghnia and Janmohammadi (2015)
ZnNPs	SEM, XRD	Drought	10 nm–30 nm	Soybean (*Glycine max*) seeds	ZnNPs were effective on seedling growth in water stress conditions	Sedghi et al. (2013)
AgNPs + 2, 4-dichlorophenoxyacetic acid	XRD, SEM	Oxidative	10 nm–40 nm	*Vigna radiata* L	The synergistic effect of AgNPs and 2, 4-dichlorophenoxyacetic acid inhibited senescence in plants under oxidative stress	Karuppanapandian et al. (2011)
TiNPs	SEM, XRD	Cold	7 nm–40 nm	*Cicer arietinum* L	TiNPs increased cold tolerance *via* an improved redox status of plant	Mohammadi et al. (2013)
SiNPs	SEM, UV-Vis, XRD	Heavy metal	10 nm–30 nm	*Pisum sativum* L	SiNPs protected plants against phytotoxicity induced by chromium and improved plant growth	Tripathi et al. (2015)
CeNPs	SEM, XRD	Heat shock and lipid peroxidation	10 nm ± 1 nm	*Zea mays* L	Improved plant growth under heat shock	Zhao et al. (2012)
TiNPs	SEM, XRD, TEM	Heavy metal	< 100 nm	*Glycine max*	TiNPs increased Cd uptake and minimize stress induced by Cd on soybean	Singh and Lee (2016)

(Continued on following page)

TABLE 2 (*Continued*) Some recent reports of the effect of nanotechnology in alleviating plant stressors.

Nanoparticle	Characterization	Plant stress	Size of the nanoparticle	Test plant	Inference	References
SiNPs	XRD, SEM, TEM	Salinity	20 nm–30 nm	Basil (*Ocimum basilicum*)	Significantly increased the morphological and physiological traits of plants under salt stress	Kalteh et al. (2018)
Single-walled carbon nanotubes (SWNTs)	ICP-MS, SEM	Drought	10 nm–20 nm	*Arabidopsis thaliana*	Plant nanotubes augmented photosynthetic and biochemical sensing	Giraldo et al. (2014)
TiNPs	SEM, TEM	Drought	20 nm–30 nm	Wheat	TiNPs increased the agronomic traits of plants under drought stress	Jaberzadeh et al. (2013)
TiNPs	SEM, XRD	Cold	7 nm–40 nm	*Cicer arietinum* L	TiNPs induced positive physiological effects on plant cells	Hasanpour et al. (2015)
SeNPs	XRD, SEM	High and low tempt	20 nm–30 nm	*Lycopersicum esculentum*	SeNPs helped to improve plant growth under high and low-temperature stress	Haghighi et al. (2014)
Hydroxyapatite (HAP) NPs	SEM, TEM	Heavy metal (Cd)	10 nm–40 nm	*Brassica chinensis* L. (bok choy)	HAPNP reduced Cd uptake and other effects of Cd-contaminated soil	Li and Huang (2014)
SiNPs	XRD, ICP-MS, SEM	Drought	10 nm–30 nm	Hawthorn (*Crataegus* sp.)	Increased plant biomass, xylem water potential, and malondialdehyde (MDA) content	Ashkavand et al. (2015)
SiNPs	TEM	Drought	10 nm–15 nm	Wheat grass (*Agropyron elongatum* L.)	SiO_2NPs significantly increased seed germination of tall wheat grass	Azimi et al. (2014)
TiNPs	TEM, SEM	Drought	≈21 nm	Onion (*Allium cepa*)	TiNPs enhanced seed germination and seedling growth. It also increased the activities of hydrolytic and antioxidant enzymes, amylase, protease, and SOD	Laware and Raskar (2014)
AgNPs	XRD, SEM	Salinity, cold, Heat and Drought	10 nm–30 nm	*A. thaliana*	AgNPs are a novel and eco-friendly method to control multiple abiotic stressors	Kohan-Baghkheirati and Geisler-Lee (2015)

Key (definition of abbreviations): SEM, scanning electron microscope, XRD—X-Ray Diffraction Crystallography, TEM, Transmission Electron Microscopy; FTIR, Fourier-Transform Infrared Spectroscopy; EDS, Energy Dispersive Spectroscopy, UV-Vis—Ultraviolet-Visible Infrared Spectrophotometry, ICP-MS, Inductively Coupled Plasma Mass Spectrometry; MDA, Malonaldehyde.

processes proffers solutions to relieve unwanted plant stresses and enhance the efficient use of plant resources. Less than 50% of applied chemical pesticides and fertilizers are used by the plant; the remainder often increases soil toxicity. This problem and many other growth-impeding factors may be effectively resolved using nanoscience (Martínez-Ballesta et al., 2016). For instance, the use of SiNPs and Si-fertilizer has a sustainable effect on the morphological and physiology of basil plants (*Ocimum basilicum*) under salinity stress. The results of this study suggested that the change in the physiological traits may be a result of tolerance induction in the basil plant, which helps to mitigate the effect of salt stress (Kalteh et al., 2018). Many other studies have shown that SiO_2NPs can relieve the effect of salinity stress. For example, Haghighi et al. (2014) and Sabaghnia and Janmohammadi (2015) showed the positive effects of SiNPs on *Lens culinaris* Medik. Under salinity stress, SiNPs was able to induce a significant increase in the growth of *Lens culinaris* Medik seedlings and the germination of seeds. Introducing SiNPs not only enhances early seedling growth and seed germination but also improves other growth features associated with the plant under salinity stress. In the same study by Haghighi et al. (2014) on tomatoes, SiO_2NPs decreased ionic toxicity of the stressor leading to a substantial increase in the shoot, root fresh and dry weight of tomato plants under salt stress. Gao et al. (2006) showed the effect of SiO_2NPs on maize plants after long exposure to salinity stress. Applying SiO_2NPs enhanced the sprouting of the plant (Savvas et al., 2009), as shown in Table 2. The mechanism of action of silica nanoparticles reduces the Na^+ ion concentration in the plant. As a result, limited Na^+ ion is available for absorption by plant tissues. Since salinity stress increases Na^+ ion uptake and osmotic potential, the process of contamination is reduced using SiO_2NPs because of this mechanism of action (Raven, 1983).

In addition, multi-walled carbon nanotubes (MCN) have been tested against salinity-stressed broccoli plants (Martínez-Ballesta et al. (2016). The MCN-treated plants exhibited increased assimilation of CO_2, aquaporin transduction, increased water uptake and modified the broccoli root plasma membrane which increased the sprouting of the plant.

Effect of NPs on chilling stress

Low temperatures can destroy plant cells because of ion leakage and permeability distortion of the plant cell membrane. This chilling stress leads to a reduction in plant growth and germination (Bhattacharya, 2022; Petruccelli et al., 2022) with tolerance to chilling varying between different plant species. The greater the damage to plant membranes, the more deleterious the effect of chilling stress on the plant (Rawat et al., 2020). In addition, photosynthesis and its biochemical components are greatly affected by chilling stress because low temperature damages the photosystems, inhibiting properties associated with light absorption, such as increasing Rubisco degradation, CO_2 assimilation, transpiration rate, and reducing the chlorophyll content (Jajoo and Mathur, 2021; Sherin et al., 2022). To ensure the relief of plants from chilling stress, NPs are used to enhance photosystem activities by inhibiting ROS production, increasing the activities of the chloroplast, and improving the production of Rubisco enzymes (Ayyaz et al., 2022; Chandel et al., 2022).

TiO_2NPs activate processes needed to enhance the synthesis of chlorophyll and the expression of the Rubisco binding protein gene, improve leaf pigment, antioxidant enzyme synthesis, and decrease the effect of chilling stress by reducing plant cell damage and ion leakage (Asadi and Cheniany, 2022; Sardar et al., 2022; Zare et al., 2022). Low-temperature stress upregulates the expression of *MeAPX2* and *ZnSOD/MeCu* genes, which increases glutathione reductase, dehydroascorbate reductase, and monodehydroascorbate activities that remove ROS. It also helps to reduce oxidative stress (Sonkar et al., 2021). The use of TiO_2NPs to reduce chilling stress has restructured plant biochemical physiognomies whenever plant cells are exposed to low-temperature environments (El-Gazzar et al., 2020; Elsheerya et al., 2020; Nasr et al., 2021).

Effect of NPs on drought stress

Soil drought is an abiotic stress limiting crop productivity in arid and semi-arid regions (Gamalero and Glick, 2022). Several studies have highlighted the effects of silicon NPs on drought-induced plant stress. For instance, SiNPs have been used to relieve the impact of drought stress on hawthorns (*Crataegus sp.*) (Ashkavand et al., 2015). The aforementioned study was conducted using different concentrations of SiNPs, depending on the severity of the stress. Biochemical and physiological responses differ in plant seedlings based on the positive effect of SiNPs on carbohydrate contents, proline, leaf pigments, membrane leakage, water content, malondialdehyde, and photosynthetic parameters (Ashkavand et al., 2015). A study was conducted to test the effect of SiNPs on two different sorghum (*Sorghum bicolor* (L.) Moench) cultivars with different drought tolerance susceptibility patterns, maintaining the photosynthetic rate and reducing the root-to-shoot ratio. This showed that SiNPs was able to augment plant water uptake efficacy (Hattori et al., 2005). Also, a low concentration of sodium silicate was used to mitigate the effect of drought stress on wheat (Pei et al., 2010). The silicon content of the compound was able to maintain the leaf potential in water absorption, improve the leaf chlorophyll content, and enhance shoot growth. Although the mechanism of action of this compound is yet to be determined, silicon compounds have been reported to be involved in the reduction of plant membrane lipid peroxidation.

In soybean, ZnONPs have been reported to boost the resilience of soybean plants to drought stress (Sedghi et al., 2013). This study revealed that the application of ZnONPs helped in the germination of soybean in a drought-stressed plant; an effect attributed to the role of Zn in the improvement of seed viability and sprouting of plant seeds in Zn deficient areas (Degenhardt and Gimmler, 2000).

Iron is an essential nutrient needed for plant growth and development; an iron-deficient plant shows physiological change, *viz*., chlorosis and reduced metabolism (Jalil and Ansari, 2019). Micronutrients can be used to relieve the effects of drought stress in some plants. Davar et al. (2014) showed the impact of exogenous FeNPs in the flowering and fruiting stages of a plant under drought stress. In addition, to reduce the adverse effects of drought stress, TiO_2NPs have been applied to the leaves of wheat to improve agronomic and physiological features, such as gluten, starch, photosynthetic activities, biomass, harvest index, final yield and plant weight (Jaberzadeh et al., 2013).

Plant microbes in agriculture to address future food scarcity

Some bacteria and fungi can colonize the internal tissues of their host plants without causing any detrimental effects (Adeleke and Babalola, 2021b). Various bacterial and fungal endophytes produce plant growth traits, such as siderophores, nitrogen fixation, phosphate solubilization, antibiotic production and induced systemic resistance to various environmental stresses (Santoyo et al., 2016; Adeleke et al., 2021).

Plant roots absorb water and minerals from the soil, then translocate them to other plant parts (Liu et al., 2021). In addition, the plant produces copious amounts of exudates such as amino acids, organic acids, and sugars into the soil which are utilized by soil microbes and contribute to the

TABLE 3 Various endophytic microbes inhabiting crop plants and their functions.

Endophyte	Plant(s)	Functions	References
Burkholderia seminalis strain 869T2	*Arabidopsis*, loose-leaf lettuce, romaine lettuce, red-leaf lettuce, and Chinese amaranth	Plant growth promotion, auxin production, siderophore synthesis, and phosphate solubilization	Hwang et al. (2021)
Cyanobacteria (*Nostoc punctiforme* PCC 73102)	Rice (*Oryza sativa*)	When these organisms are inoculated into the roots of rice, they produce heterocysts and nitrogenase activity that contributes to plant growth under a limited nitrogen supply	Álvarez et al. (2020)
Firmicutes	Tomato (*Solanum lycopersicum*)	These endophytes dominate different cultivars of tomato promoting resistance against *Ralstonia solanacearum*	Sahu et al. (2020)
Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria	Sugarcane (*Saccharum officinarum*)	These organisms were isolated from sugarcane leaves, sheaths, and roots. They contributed to plant growth promotion	Teheran-Sierra et al. (2021)
Klebsiella MK2R2, *Bacillus* B2L2, *Enterobacter* E1S2	Maize (*Zea mays*)	These endophytic organisms have the potential to improve the growth of maize and nitrogen fertilization	Mowafy et al. (2021)
Pseudomonas protegens MP12	Grapevine (*Vitis vinifera*)	This organism colonizes inner grapevine tissues, and contributes to antifungal ability, preventing mycelial growth of certain grapevine phytopathogens	Andreolli et al. (2021)
Rhizobium (*Bacillus siamensis*)	Chickpea plants (*Cicer arietinum* L.)	This rhizobium had various PGP features including nitrogen fixation, phosphate solubilization, ACC deaminase, IAA production, synthesis of hydroxamate-type siderophores	Gorai et al. (2021)

microbial biomass in the root environment (Lyu et al., 2021). Also, seeds produce low molecular weight organic exudates into the surrounding soil during germination. Several endophytes have been reported to be present in the endosphere (He et al., 2021).

Endophytic relationships with the host plants can be symbiotic or pathogenic. Often, essential and uncommon organic substances are secreted by endophytes that assist in providing various functions, not only for soil health but also as a solution to plant stress challenges. Endophytes can often protect plants from phytopathogens and abiotic stresses (Table 3).

The impact of abiotic stressors on plant growth and soil health can be major or minor depending on the prevailing environmental conditions (Sachdev et al., 2021). Abiotic stresses negatively affect crop production and microbial diversity (Chouhan et al., 2021). Various mechanisms employed by endophytic microorganisms induce systemic resistance (ISR) or abiotic stress tolerance in plants (Gupta et al., 2021). Therefore, there is a need to restructure modern agricultural systems to include recent developments in endosphere biology (Santoyo et al., 2021b). Some studies have explained the role of endophytic bacteria in agricultural systems under abiotic stresses in combating future food scarcity. For instance, *B. amyloliquefaciens* RWL-1 producing ABA can enhance rice yield in soil with a high salt concentration (Ganie et al., 2021). This bacterium produces essential amino acids and salicylic acid which assist rice growth in salinity/drought conditions (Thepbandit et al., 2021). The endophytic fungus, *Bipolaris sp.*, produces gibberellins which contribute to the growth of *Glycine max* (Lubna et al., 2022). *Sphingomonas sp.* LK11 is an endophyte from leguminous plants that also synthesizes gibberellins which enhance tomato growth and the plant chlorophyll content (Adeleke and Babalola, 2021a).

Various reports revealed the presence of IAA-producing endophytic bacteria (Rashid et al., 2012; Panigrahi et al., 2020; Turbat et al., 2020). *Burkholderia kururiensis* is an endophyte that stimulates the expression of IAA genes, especially in the roots of transgenic rice, thereby contributing to rice growth (Zhou et al., 2020).

Some endophytes are halotolerant, which can be isolated from the weed *Psoralea corylifolia* to assess their PGP activity in wheat. The growth of wheat plants can be improved with the aid of an extract from the bacterial isolates during the production of IAA under saline-stress conditions (Amini Hajiabadi et al., 2021). The identification of various strains embedded in weeds revealed various genera including *Acinetobacter, Enterobacter, Marinobacterium, Pseudomonas, Rhizobium*, and *Sinorhizobium* (AlSharari et al., 2022). The hormone cytokinin is also produced by some endophytic bacteria, according to Eid et al. (2021). *Pseudomonas resinovorans* and *Paenibacillus polymyxa* isolated from *Gynura procumbens* are good examples of endophytic bacteria producing cytokinin (Eid et al., 2021). From a bacterial culture, the obtained extracts were tested *in vitro* and inoculated into the cotyledon of cucumber to observe their cytokinin activity.

A strain of *Sinorhizobium meliloti* engineered to overproduce cytokinin by transferring the *Agrobacterium tumefaciens ipt* gene into the bacterium, and a strain of *Pseudomonas spp.*, that protected alfalfa plants from drought-stressed conditions (Oleńska et al., 2020), these two bacteria were inoculated together or separately, in the cultivation of sorghum (*Sorghum bicolor*). The results revealed that the two strains inoculated together reduced the requirement for chemical nitrogen fertilizer

TABLE 4 The biological activities of nanoparticle-synthesizing endophytic microbes against plant pathogens.

Endophytic organisms	Plant pathogens	Microbial activity	References
Silver (Ag) Nanoparticle			
Alternaria alternate	Bacillus cereus, Klebsiella pneumoniae, Pseudomonas aeruginosa, E.coli, Staphylococcus aureus, Proteus mirabilis	Antibacterial and antioxidant	Govindappa et al. (2022)
Micromonospora sp. SH121 (Mm-AgNPs)	Bacillus cereus, Enterococcus faecalis, Enterococcus hirae, Escherichia coli, Klebsiella pneumoniae, Proteus vulgaris, Pseudomonas putida, Staphylococcus epidermidis, Streptococcus pneumoniae, Aspergillus flavus	Antimicrobial, antibiofilm, and anticancer	Mazmancı et al. (2022)
Streptomyces species	Bacterial and fungal agents	Biosynthesis and Antibacterial	ALqahtani et al. (2022)
Phoma sp. (MN995524), Chaetomium globosum (MN995493), and Chaetomium sp. (MN995550)	Klebsiella pneumonia	Antibacterial activities	Sonbol et al. (2022)
Trichoderma atroviride	Pathogenic bacteria and fungi	Antibacterial, anticandidal, and antifungal effects	Abdel-Azeem et al. (2020)
Pseudomonas poae	Fusarium graminearum head blight pathogen	Antifungal	Ibrahim et al. (2020)
Rhizobium pusense (MS-1), Bacillus cereus MS-2, Bacillus flexus (MS-3), Methylophilus flavus (MS-4), Pseudomonas aeruginosa (MS-5)	Bacillus thuringiensis, Azotobacter chroococcum (CL13), Escherichia coli, Pseudomonas putida (ECL5), Bacillus licheniformis (R-1), Rhizobium sp. (CV1)	Antibacterial activity	Singh et al. (2022b)
Talaromyces purpureogenus	Listeria monocytogenes, Escherichia coli, Shigella dysenteriae, Salmonella typhi	Antibacterial activity	Sharma et al. (2022)
Serratia marcescens, Burkholderia cepacia	Aspergillus niger, A. fumigatus, Fusarium oxysporum, Pythium sp., Rosellinia sp	Antifungal activity	Mittal et al. (2021)
Terminalia arjuna	Escherichia coli MTCC1687, Pseudomonas aeruginosa ATCC9027, Staphylococcus aureus ATCC6538	Antibacterial activity	Singh et al. (2022a)
Penicillium cinnamopurpureum	Bacillus subtilis (MTCC-121), Pseudomonas aeruginosa (MCC-3097), Staphylococcus aureus (MCC-2043), Escherichia coli (MCC-3099)	Antibacterial activity	Dinesh et al. (2022)
Phoma glomerata, Phoma herbarium, Fusarium semitectum, Trichoderma, Candida albicans	Candida albicans, Pseudomonas aeruginosa, E. coli, Bipolaris sorokiniana, Magnaporthe grisea	Antibacterial, antifungal, and insecticidal activity	Shinde et al. (2022)
Gold (Au) Nanoparticle			
Phoma sp	Rhizoctonia solani AG1-IA, Xanthomonas oryzae	Antifungal and antibacterial activity	Soltani Nejad et al. (2022)
Pseudomonas aeruginosa	Vigna unguiculata	Plant growth enhancement/ promotion	Panichikkal and Krishnankutty, (2022)
Aspergillus terreus	Fusarium oxysporum, Rhizoctonia solani	Antimicrobial, antioxidant, and antifungal activity	Mishra et al. (2022)
Alternaria alternate, Fusarium species	Cervical carcinoma (HeLa), breast carcinoma (MCF-7), non-small cell lung carcinoma (H1975), hepatocellular carcinoma cell line (Hep G2)	Anticancer activity	Ravi et al. (2022)
Aspergillus sp., Alternaria sp	Escherichia coli, Staphylococcus aureus	Antibacterial, antifungal, and antitumor activities	Mostafa et al. (2022)
Lysinibacillus odyssey	Staphylococcus epidermidis Staphylococcus aureus, Streptococcus pyogenes, Enterococcus faecalis, Bacillus subtilis	Dose-dependent antioxidant and antibacterial activity	Cherian et al. (2022)
Zinc-oxide (ZnO) nanoparticles			
Aspergillus niger	Staphylococcus aureus	Antibacterial activity	Abdelkader et al. (2022)
Enterobacter hormaechei	Klebsiella pneumoniae (ATCC: 4617), Escherichia coli (ATCC: 15224), Pseudomonas aeruginosa (ATCC: 9721), Bacillus subtilis (ATCC: 6633), Staphylococcus epidermidis (ATCC: 14990) Aspergillus fumigatus, Aspergillus niger, Aspergillus flavus, Fusarium solani, Mucor mycosis	Antifungal, antibacterial, and antioxidant potential	Saqib et al. (2022)
Trichoderma viride	Staphylococcus aureus, Bacillus spp., Pseudomonas aeruginosa, Klebsiella spp., Acinetobacter baumannii, Candida albicans	Antimicrobial and antioxidant activities	Kaur et al. (2022)

to a low level and significantly improved the cultivation of sorghum. The procedure also enhanced the colonization effectiveness of both bacteria in the roots of rice plants (Abbaszadeh-Dahaji et al., 2020). In summary, endophytes can play a major role in modulating phytohormone levels in plants, thereby contributing to plant growth and managing various stress conditions.

Symbiotic nitrogen fixation reduces atmospheric nitrogen by the action of the leguminous plants in association with nitrogen-fixing bacteria, increasing the plant's nutritional value (Rana et al., 2020). Several years ago, the only known nitrogen-fixing bacteria in legume nodules were rhizobia. However, numerous non-rhizobial bacterial species have been found in legume root nodules. Hanaka et al. (2021) reported how an endophytic bacteria isolated from the soybean, *Bacillus mojavensis,* exhibited biocontrol activity against the soybean pathogenic fungus, *Rhizoctonia solani*. These endophytic microorganisms have antagonistic activity against soil-borne pathogens and possess the ability to enhance the growth of soybean plants. The *B. mojavensis* strain produced ammonia, HCN, and siderophores. It also contributed to chitinase activity and solubilization of phosphate (Hanaka et al., 2021). The inoculation of this endophyte onto soybean seeds can help control various pathogens.

The introduction of nanotechnology in agriculture is a developing sector in agriculture despite several applications, and the true possibilities are yet to be obtained. Nanotechnology constitutes certain substances with unusual features that are revealed either as a result of the quantum confinement effects or the production of certain reactive surfaces that are at a nanoscale (Umapathy et al., 2022). The nanoscale degree when compared with the macroscopic level, reveals the properties of the material that are special as a result of the reduced size, shape of nanomaterials, and greater surface area-to-weight ratio. Nanomaterials or nanoparticles (NPs) have beneficial properties, with high reactivity, modified bioactivity, and surface effects (Bruchiel-Spanier et al., 2022). NPs are produced by either a single element like silver (Au) or gold (Au) or by a mixture of elements, which are observed in those constituting oxides like titanium oxide (TiO_2), silicon oxide (SiO_2), and zinc oxide (ZnO) (Behl et al., 2022). Gold and silver NPs regarded as inorganic NPs, are relevant as a result of their application. Although, few studies have shown how the NPs are manufactured from endophytes (Fadiji et al., 2022a; Kaur et al., 2022; Saqib et al., 2022), thus suggesting possible means for continuous studies on endophytic nanoparticles.

Various approaches including biological, chemical, and physical approaches are made use of in the production of NP, yet, the process of biosynthesis is environmentally friendly, free of chemical derivatives that are hazardous to humans, animals, and the environment. These chemicals have been used recently to reduce the potential of applying chemicals in the biomedical and food processing industries. Several procedures involving intracellular and extracellular for the biological synthesis of nanomaterials coexist in nature. In this field, the study is still understudied (Qian et al., 2022). The production of environmentally friendly, and non-toxic biological materials for manufacturing NPs would result in supporting the production of natural materials with the aid of living organisms (Fadiji et al., 2022a).

NPs produced from metal-based are manufactured by microorganisms through extracellular and intracellular mechanisms (Franco et al., 2022). The process of electrostatic induction takes place in metallic ions between negative and positive charges intracellularly in the cell wall of the microorganisms, followed by the decrease of the metal ions to their metallic form. Cell disruption is a constitutional prerequisite to acquiring pure NPs (Fadiji et al., 2022a). The biomass extracts from the cell, or culture supernatant when added to the solution of metals produce NPs outside the cell of the microorganisms (extracellularly) (Jadoun et al., 2022). Reductases are produced and liberated into the culture medium by cofactors, with microbial cells that execute this procedure. Endophytic microbes have been suggested as biofactories for the synthesis of metal-based NPs with agricultural and therapeutic applications. These microbes are embedded in plants intercellularly, producing a symbiotic link (Roy et al., 2022). The advantage confers on the plant by the endophytes is to improve health status *via* various mechanisms, like the release of antimicrobial (antibacterial and antifungal) compounds and the secretion of growth-promoting metabolites (Shahid et al., 2022).

In plant tissues, endophytic microbes accommodating them can produce nanoparticles, which are advantageous to the host plant by promoting plant growth or reducing the prevalence of diseases (Koné et al., 2022). Endophytes can resist metals occurring in the environment to alleviate toxicity and stress in the host plant, as well as improve their beneficial association and adaption over other microbes inhabiting the ecosystem (Mathur and Ulanova, 2022). The potential of endophytes to take away metals can be applied to manufacture metal-based NPs *via* extracellular and intracellular processes (Table 4). Typical examples were obtained in the production of AgNPs, which have a spherical shape and a mean size of 22 nm–45 nm, which can be manufactured intracellularly employing the supernatant of Ag-resistant *Bacillus safensis* TEN12 (Ahmed et al., 2020). Zinc oxide (ZnO) NPs sized 2 nm–9 nm, were produced extracellularly by the zinc-tolerant endophyte *Curvularia geniculata* (Ahmed et al., 2020). Gürsoy et al. (2021) reported how gold nanoparticles (AuNPs) sized 20 nm–40 nm were produced intracellularly in the cell wall and cytoplasm of *Chlorella sorokiniana*. Cobalt oxide nanoparticles (CoONPs), which are spherical at 20 nm in diameter, were produced extracellularly by the *A. nidulans* that are CoO-tolerant (Ahmed et al., 2020). *Aspergillus nidulans* are endophytes, which reveal the potential of the CoO-tolerant produced spherical CoONPs with a diameter of 20 nm through an

extracellular tract (Fadiji et al., 2022a). Endophytic microorganisms can produce some biological active materials with a broad gap of structural and biological potential, which can be employed to examine the health and promote plant growth and are significant in improving the sustainability of agriculture (Kumar and Nautiyal, 2022). Fungi and bacteria isolated from parts of plants can be cultured in the laboratory under the most desirable growth conditions to synthesize NPs with the needed characteristics for application in the agricultural sector (Elnahal et al., 2022).

Fate of NPs

The use of NPs for agroecosystem practices could be a very complicated matrix and information on the fate of nanomaterials in the soil is inadequate. After applying NPs to the soil, they are absorbed in the plant tissue directly. Such interaction could either increase or decrease the bioavailability and toxicity of NPs depending on the physicochemical properties of the soil. However, the potency of NPs is most dependent on the type of crop and the properties of the soil *viz*., microbial community, clay content, ionic strength, pH, salinity, organic matter, etc., (Reddy et al., 2016; Thiagarajan and Ramasubbu, 2021).

Effect of microbial community

Plant endophyte and the microbial community helps in the transformation of NPs. They help to recycle nutrients, effectively decomposition of organic compounds and conserve soil quality. The introduction of nanomaterials could affect microbial inhabitation which invariably reduces plant productivity (Jacoby et al., 2017; Chavan et al., 2020). The effect of NPs on the rhizosphere bacteria of butter crunch lettuce was reported by Kibbey and Strevett (2019). NPs and rhizosphere bacteria react together *via* electrostatic interactions that affect the surface properties of bacteria, which disallow easy attachment to the root surfaces of the plant. They also reported that fluctuations in soil mineral nutrients (P, Fe, Mn, etc.) were a result of spiked biosolid amendment of soil with NPs, which affects soil microbial load. Withal, NPs were also reported to have affected the sequestration of plant nutrients and other agroecosystem processes as reported by Bellani et al. (2020).

At times, NPs may also inhibit the colonization of plant growth promoters when combined with other nutrients. This deleterious effect was reported by Liu et al. (2020). Here, the negative effect associated with the combination of TiO_2NPs with Cu_2 $(OH)_2$ CO_3 was reported. The synergy between TiO_2NPs and Cu_2 $(OH)_2$ CO_3 boosted photocatalytic disinfection processes that disabled the effect of microorganisms such as *Fusarium graminearum* and *E. coli* within a short time of application (Liu et al., 2020).

Effect of clay content

Another important component that determines the fate of NPs is the clay content of the soil. The high the clay content of the soil, the decreased mobility of NPs because both the physical straining and electrostatic interactions would be increased. However, the soil retention capacity depends mainly on the clay to NPs ratio. The higher the ratio, the better the soil retention capacity (Shah et al., 2016). Metals are easily retained in the soil when there is an increase in the clay content. And as such reduces the uptake of metallic ions by the plant. This simply indicates the low toxicity of metallic NPs (Larue et al., 2018; Thiagarajan and Ramasubbu, 2021).

Effect of natural organic matter

NOM influences the stability and aggregation of NPs within the soil. NOM includes mobile and reactive organic fractions *viz*. hydrocarbons, amino acids, hydrophilic acids, fatty acids, fulvic, and humic acids. NOM is produced through the disintegration of animal and plant remains in the soil. Sludge-amended soil and NOM have been reported to cover 10.9% and 8.9% of soil, respectively. Meanwhile, the physicochemical properties of NPs and features of proximal soil are usually influenced after the adsorption of NOM (Bakshi et al., 2019). A recent study by Zhang et al. (2020) showed the stability of TiO_2NPs when introduced to a paddy field with high organic matter. In another study that demonstrated the effect of a high concentration of NOM on the bioaccumulation of NPs, the ability of NOM to retrain NPs could be attributed to the change in the surface area of soil as a result of an increase in the concentration of NOM. The interaction of NPs with NOM alters the binding property of the soil to improve the steric repulsion between nanomaterials by aggregating and retaining them in the soil. Asides, the reaction of NPs and NOM depends greatly on their particle sizes through hydrophobic interaction (Lee et al., 2011).

Conclusion

Globally, crop improvement and productivity are faced with diverse abiotic stress challenges. To avert this problem, the use of nanomaterials from endophytic microbes has the potential to mitigate the effects of abiotic stresses affecting plants by stimulating plant defense mechanisms. Beneficial endophytic microbes as bioinoculants can be effectively harnessed for various ecological purposes such as abiotic stress reduction, nutrient absorption, enhancing photosynthesis, increasing plant growth parameters, and obviating agrochemical use. Additionally, the nanomaterial synthesizing endophytic microbes promise to improve crop productivity sustainably.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Funding

This research was funded by the National Research Foundation of South Africa (UID: 123634; 132595).

Acknowledgments

National Research Foundation of South Africa and The World Academy of Science (NRF-TWAS) African Renaissance is acknowledged for a Doctoral scholarship stipend to BA (UID: 116100). SA and AA are grateful to North-West University, South Africa, for the postgraduate bursary. OB recognizes NRF for grants (UID: 123634; 132595) that support work in her research group.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

Abbaszadeh-Dahaji, P., Masalehi, F., and Akhgar, A. (2020). Improved growth and nutrition of sorghum (*Sorghum bicolor*) plants in a low-fertility calcareous soil treated with plant growth–promoting rhizobacteria and Fe-edta. *J. Soil Sci. Plant Nutr.* 20, 31–42. doi:10.1007/s42729-019-00098-9

Abd-Alla, M. H., Nafady, N. A., Bashandy, S. R., and Hassan, A. A. (2019). Mitigation of effect of salt stress on the nodulation, nitrogen fixation and growth of chickpea (*Cicer arietinum* L.) by triple microbial inoculation. *Rhizosphere* 10, 100148. doi:10.1016/j.rhisph.2019.100148

Abdel-Azeem, A., Nada, A., O'donovan, A., Kumar Thakur, V., and Elkelish, A. (2020). Mycogenic silver nanoparticles from endophytic *Trichoderma atroviride* with antimicrobial activity. *J. Renew. Mat.* 8, 171–185. doi:10.32604/jrm.2020.08960

Abdel-Aziz, S. M., Prasad, R., Hamed, A. A., and Abdelraof, M. (2018). "Fungal nanoparticles: A novel tool for a green biotechnology?," in *Fungal nanobionics: Principles and applications* (Springer), 61–87.

Abdelkader, D. H., Negm, W. A., Elekhnawy, E., Eliwa, D., Aldosari, B. N., and Almurshedi, A. S. (2022). Zinc oxide nanoparticles as potential delivery carrier: Green synthesis by *Aspergillus niger* endophytic fungus, characterization, and *in vitro*/*in vivo* antibacterial activity. *Pharm. (Basel).* 15, 1057. doi:10.3390/ph15091057

Aboyewa, J. A., Sibuyi, N. R., Meyer, M., and Oguntibeju, O. O. (2021). Green synthesis of metallic nanoparticles using some selected medicinal plants from southern Africa and their biological applications. *Plants* 10, 1929. doi:10.3390/plants10091929

Acuña, J. J., Campos, M., De La Luz Mora, M., Jaisi, D. P., and Jorquera, M. A. (2019). ACCD-producing rhizobacteria from an Andean Altiplano native plant (*Parastrephia quadrangularis)* and their potential to alleviate salt stress in wheat seedlings. *Appl. Soil Ecol.* 136, 184–190. doi:10.1016/j.apsoil.2019.01.005

Adeleke, B. S., Ayilara, M. S., Akinola, S. A., and Babalola, O. O. (2022). Biocontrol mechanisms of endophytic fungi. *Egypt. J. Biol. Pest Control* 32, 46–17. doi:10.1186/s41938-022-00547-1

Adeleke, B. S., and Babalola, O. O. (2021a). Biotechnological overview of agriculturally important endophytic fungi. *Hortic. Environ. Biotechnol.* 62, 507–520. doi:10.1007/s13580-021-00334-1

Adeleke, B. S., Babalola, O. O., and Glick, B. R. (2021). Plant growth-promoting root-colonizing bacterial endophytes. *Rhizosphere* 20, 100433. doi:10.1016/j.rhisph.2021.100433

Adeleke, B. S., and Babalola, O. O. (2022). Meta-omics of endophytic microbes in agricultural biotechnology. *Biocatal. Agric. Biotechnol.* 42, 102332. doi:10.1016/j.bcab.2022.102332

Adeleke, B. S., and Babalola, O. O. (2021b). Pharmacological potential of fungal endophytes associated with medicinal plants: A review. *J. Fungi (Basel).* 7, 147. doi:10.3390/jof7020147

Agri, U., Chaudhary, P., Sharma, A., and Kukreti, B. (2022). Physiological response of maize plants and its rhizospheric microbiome under the influence of potential bioinoculants and nanochitosan. *Plant Soil* 474, 451–468. doi:10.1007/s11104-022-05351-2

Ahmad, F., Siddiqui, M. A., Babalola, O. O., and Wu, H.-F. (2012a). Biofunctionalization of nanoparticle assisted mass spectrometry as biosensors for rapid detection of plant associated bacteria. *Biosens. Bioelectron. X.* 35, 235–242. doi:10.1016/j.bios.2012.02.055

Ahmad, M., Zahir, Z. A., Asghar, H. N., and Arshad, M. J. a. O. M. (2012b). The combined application of rhizobial strains and plant growth promoting rhizobacteria improves growth and productivity of mung bean (*Vigna radiata* L.) under salt-stressed conditions. *Ann. Microbiol.* 62, 1321–1330. doi:10.1007/s13213-011-0380-9

Ahmad, M., Zahir, Z. A., Nazli, F., Akram, F., Arshad, M., and Khalid, M. J. B. J. O. M. (2013). Effectiveness of halo-tolerant, auxin producing *Pseudomonas* and *Rhizobium* strains to improve osmotic stress tolerance in mung bean (*Vigna radiata* L.). *Braz. J. Microbiol.* 44, 1341–1348. doi:10.1590/s1517-83822013000400045

Ahmad, P., Hashem, A., Abd-Allah, E. F., Alqarawi, A., John, R., Egamberdieva, D., et al. (2015). Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L) through antioxidative defense system. *Front. Plant Sci.* 6, 868. doi:10.3389/fpls.2015.00868

Ahmadpour, K. S., Salari, S., and Ghasemi, N. A. P. (2021). Comparison of antifungal and cytotoxicity activities of titanium dioxide and zinc oxide nanoparticles with amphotericin B against different Candida species: *In vitro* evaluation. *J. Clin. Lab. Anal.* 35, 23577. doi:10.1002/jcla.23577

Ahmed, B., Cao, B., Mishra, B., Boyanov, M. I., Kemner, K. M., Fredrickson, J. K., et al. (2012). Immobilization of U (VI) from oxic groundwater by Hanford 300 Area sediments and effects of Columbia River water. *Water Res.* 46, 3989–3998. doi:10.1016/j.watres.2012.05.027

Ahmed, F., and Rodrigues, D. F. (2013). Investigation of acute effects of graphene oxide on wastewater microbial community: A case study. *J. Hazard. Mat.* 256, 33–39. doi:10.1016/j.jhazmat.2013.03.064

Ahmed, T., Noman, M., Manzoor, N., Shahid, M., Abdullah, M., Ali, L., et al. (2021). Nanoparticle-based amelioration of drought stress and cadmium toxicity in rice via triggering the stress responsive genetic mechanisms and nutrient acquisition. *Ecotoxicol. Environ. Saf.* 209, 111829. doi:10.1016/j.ecoenv.2020.111829

Ahmed, T., Shahid, M., Noman, M., Bilal Khan Niazi, M., Zubair, M., Almatroudi, A., et al. (2020). Bioprospecting a native silver-resistant *Bacillus safensis* strain for green synthesis and subsequent antibacterial and anticancer activities of silver nanoparticles. *J. Adv. Res.* 24, 475–483. doi:10.1016/j.jare.2020.05.011

Ajilogba, C. F., Babalola, O. O., and Nikoro, D. (2021). "Nanotechnology as vehicle for biocontrol of plant diseases in crop production," in *Food security and safety: Africa's Perspective*. Editor O. O. Babalola (Hardcover: eBook), 709–724. 978-3-030-50672-8978-3-030-50671-1.

Akanmu, A. O., Babalola, O. O., Venturi, V., Ayilara, M. S., Adeleke, B. S., Amoo, A. E., et al. (2021). Plant disease management: Leveraging on the plant-microbe-soil interface in the biorational use of organic amendments. *Front. Plant Sci.* 12, 700507. doi:10.3389/fpls.2021.700507

Akinola, S. A., Adeyemo, R. O., and Adebayo, I. A. (2022). "Overview and emergence of nanobiotechnology in plants," in *Diverse applications of nanotechnology in the biological sciences* (Apple Academic Press), 173–197.

Akinola, S. A., Ayangbenro, A. S., and Babalola, O. O. (2021c). Metagenomic insight into the community structure of maize-rhizosphere bacteria as predicted by different environmental factors and their functioning within plant proximity. *Microorganisms* 9, 1419. doi:10.3390/microorganisms9071419

Akinola, S. A., Ayangbenro, A. S., and Babalola, O. O. (2021a). The diverse functional genes of maize rhizosphere microbiota assessed using shotgun metagenomics. *J. Sci. Food Agric.* 101, 3193–3201. doi:10.1002/jsfa.10948

Akinola, S. A., Ayangbenro, A. S., and Babalola, O. O. (2021b). The immense functional attributes of maize rhizosphere microbiome: A shotgun sequencing approach. *Agriculture* 11, 118. doi:10.3390/agriculture11020118

Akinola, S. A., and Babalola, O. O. (2021). The fungal and archaeal community within plant rhizosphere: A review on their contribution to crop safety. *J. Plant Nutr.* 44, 600–618. doi:10.1080/01904167.2020.1845376

Akinola, S. A., and Babalola, O. O. (2020). The importance of adverse soil microbiomes in the light of omics: Implications for food safety. *Plant Soil Environ.* 66, 421–430. doi:10.17221/118/2020-pse

Ali, S., and Glick, B. R. (2019). "Plant–bacterial interactions in management of plant growth under abiotic stresses," in *New and future developments in microbial biotechnology and bioengineering* (Elsevier), 21–45.

Alqahtani, M. S., Hozzein, W. N., and Alharbi, S. A. (2022). Biosynthesis and antibacterial activity of silver nanoparticles using medicinal plants associated endophytic bacteria from in Riyadh Region Saudi Arabia. *Sch. Acad. J. Biosci.* 4, 68–76. doi:10.36347/sajb.2022.v10i04.001

Alsharari, S. S., Galal, F. H., and Seufi, A. M. (2022). Composition and diversity of the culturable endophytic community of six stress-tolerant dessert plants grown in stressful soil in a hot dry desert region. *J. Fungi (Basel).* 8, 241. doi:10.3390/jof8030241

Álvarez, C., Navarro, J. A., Molina-Heredia, F. P., and Mariscal, V. (2020). Endophytic colonization of rice (*Oryza sativa* L.) by the symbiotic strain *Nostoc punctiforme* PCC 73102. *Mol. Plant. Microbe. Interact.* 33, 1040–1045. doi:10.1094/mpmi-01-20-0015-sc

Alvarez, L. H., and Cervantes, F. J. (2012). Assessing the impact of alumina nanoparticles in an anaerobic consortium: Methanogenic and humus reducing activity. *Appl. Microbiol. Biotechnol.* 95, 1323–1331. doi:10.1007/s00253-011-3759-4

Amini Hajiabadi, A., Mosleh Arani, A., Ghasemi, S., Rad, M. H., Etesami, H., Shabazi Manshadi, S., et al. (2021). Mining the rhizosphere of halophytic rangeland plants for halotolerant bacteria to improve growth and yield of salinity-stressed wheat. *Plant Physiol. biochem.* 163, 139–153. doi:10.1016/j.plaphy.2021.03.059

Anam, G. B., Reddy, M. S., and Ahn, Y.-H. (2019). Characterization of *Trichoderma asperellum* RM-28 for its sodic/saline-alkali tolerance and plant growth promoting activities to alleviate toxicity of red mud. *Sci. Total Environ.* 662, 462–469. doi:10.1016/j.scitotenv.2019.01.279

Andreolli, M., Zapparoli, G., Lampis, S., Santi, C., Angelini, E., and Bertazzon, N. (2021). *In vivo* endophytic, rhizospheric and epiphytic colonization of *Vitis vinifera* by the plant-growth promoting and antifungal strain *Pseudomonas protegens* MP12. *Microorganisms* 9, 234. doi:10.3390/microorganisms9020234

Ansari, F. A., Ahmad, I., and Pichtel, J. (2019). Growth stimulation and alleviation of salinity stress to wheat by the biofilm forming *Bacillus pumilus* strain FAB10. *Appl. Soil Ecol.* 143, 45–54. doi:10.1016/j.apsoil.2019.05.023

Armada, E., Azcón, R., López-Castillo, O. M., Calvo-Polanco, M., and Ruiz-Lozano, J. M. (2015a). Autochthonous arbuscular mycorrhizal fungi and *Bacillus thuringiensis* from a degraded Mediterranean area can be used to improve physiological traits and performance of a plant of agronomic interest under drought conditions. *Plant Physiol. biochem.* 90, 64–74. doi:10.1016/j.plaphy.2015.03.004

Armada, E., Barea, J.-M., Castillo, P., Roldán, A., and Azcón, R. J. a. S. E. (2015b). Characterization and management of autochthonous bacterial strains from semiarid soils of Spain and their interactions with fermented agrowastes to improve drought tolerance in native shrub species. *Appl. Soil Ecol.* 96, 306–318. doi:10.1016/j.apsoil.2015.08.008

Asadi, A., and Cheniany, M. (2022). Enhancing effect of titanium dioxide nanoparticles on growth, phenolic metabolites production and antioxidant potential of *Ziziphora clinopodioides* Lam. *Russ. J. Plant Physiol.* 69, 74. doi:10.1134/s1021443722040021

Ashkavand, P., Tabari, M., Zarafshar, M., Tomaskova, I., and Struve, D. (2015). Effect of SiO2 nanoparticles on drought resistance in hawthorn seedlings. *For. Res. Pap.* 76, 350–359. doi:10.1515/frp-2015-0034

Ashraf, M., Hasnain, S., Berge, O., and Mahmood, T. (2004). Inoculating wheat seedlings with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. *Biol. Fertil. Soils* 40, 157–162. doi:10.1007/s00374-004-0766-y

Audah, K. A. (2019). *Nanotechnology: Applications in energy, drug and food*. Springer, 249–265.Drug discovery: A biodiversity perspective.

Ayyaz, A., Fang, R., Ma, J., Hannan, F., Huang, Q., Athar, H., et al. (2022). Calcium nanoparticles (Ca-NPs) improve drought stress tolerance in Brassica napus by modulating the photosystem II, nutrient acquisition and antioxidant performance. *NanoImpact* 28, 100423. doi:10.1016/j.impact.2022.100423

Azimi, R., Borzelabad, M. J., Feizi, H., and Azimi, A. (2014). Interaction of SiO_2 nanoparticles with seed prechilling on germination and early seedling growth of tall wheatgrass (*Agropyron elongatum* L.). *Pol. J. Chem. Technol.* 16, 25–29. doi:10.2478/pjct-2014-0045

Babalola, O. O., Fasusi, O. A., Amoo, A. E., and Ayangbenro, A. S. (2021). Complete genome sequence of a plant growth-promoting rhizobacterium, *Bacillus* sp. strain OA1, isolated from soybeans. *Biocatal. Agric. Biotechnol.* 36, 102121. doi:10.1016/j.bcab.2021.102121

Baker, S., Kavitha, K. S., Yashavantha Rao, H. C., Rakshith, D., Harini, B. P., Kumar, K., et al. (2015a). Bacterial endo-symbiont inhabiting *Tridax procumbens* L. and their antimicrobial potential. *Chin. J. Biol.* 2015, 1–6. doi:10.1155/2015/309267

Baker, S., Kumar, K. M., Santosh, P., Rakshith, D., and Satish, S. (2015b). Extracellular synthesis of silver nanoparticles by novel *Pseudomonas veronii* AS41G inhabiting *Annona squamosa* L. and their bactericidal activity. *Spectrochimica Acta Part A Mol. Biomol. Spectrosc.* 136, 1434–1440. doi:10.1016/j.saa.2014.10.033

Bakshi, M., Liné, C., Bedolla, D. E., Stein, R. J., Kaegi, R., Sarret, G., et al. (2019). Assessing the impacts of sewage sludge amendment containing nano-TiO_2 on tomato plants: A life cycle study. *J. Hazard. Mat.* 369, 191–198. doi:10.1016/j.jhazmat.2019.02.036

Bal, H. B., Nayak, L., Das, S., and Adhya, T. K. (2013). Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. *Plant Soil* 366, 93–105. doi:10.1007/s11104-012-1402-5

Baltruschat, H., Fodor, J., Harrach, B. D., Niemczyk, E., Barna, B., Gullner, G., et al. (2008). Salt tolerance of barley induced by the root endophyte *Piriformospora indica* is associated with a strong increase in antioxidants. *New Phytol.* 180, 501–510. doi:10.1111/j.1469-8137.2008.02583.x

Baral, B., and Izaguirre-Mayoral, M. L. (2017). "Purine-derived ureides under drought and salinity," in *Advances in agronomy* (Elsevier), 167–204.

Battin, T. J., Kammer, F. V., Weilhartner, A., Ottofuelling, S., and Hofmann, T. (2009). Nanostructured TiO_2: Transport behavior and effects on aquatic microbial communities under environmental conditions. *Environ. Sci. Technol.* 43, 8098–8104. doi:10.1021/es9017046

Behl, T., Kaur, I., Sehgal, A., Singh, S., Sharma, N., Bhatia, S., et al. (2022). The dichotomy of nanotechnology as the cutting edge of agriculture: Nano-farming as an asset versus nanotoxicity. *Chemosphere* 288, 132533. doi:10.1016/j.chemosphere.2021.132533

Belimov, A., Dodd, I., Safronova, V., Hontzeas, N., and Davies, W. (2007). *Pseudomonas brassicacearum* strain Am3 containing 1-aminocyclopropane-1-carboxylate deaminase can show both pathogenic and growth-promoting properties in its interaction with tomato. *J. Exp. Bot.* 58, 1485–1495. doi:10.1093/jxb/erm010

Bellani, L., Siracusa, G., Giorgetti, L., Di Gregorio, S., Castiglione, M. R., Spanò, C., et al. (2020). TiO2 nanoparticles in a biosolid-amended soil and their implication in soil nutrients, microorganisms and *Pisum sativum* nutrition. *Ecotoxicol. Environ. Saf.* 190, 110095. doi:10.1016/j.ecoenv.2019.110095

Bhattacharya, A. (2022). "Low temperature stress and plant-water relationship: A review," in *Physiological processes in plants under low temperature stress* (Singapore: Springer), 107–197.

Brotman, Y., Landau, U., Cuadros-Inostroza, Á., Takayuki, T., Fernie, A. R., Chet, I., et al. (2013). *Trichoderma*-plant root colonization: Escaping early plant defense

responses and activation of the antioxidant machinery for saline stress tolerance. *PLoS Pathog.* 9, e1003221. doi:10.1371/journal.ppat.1003221

Bruchiel-Spanier, N., Betsis, S., Naim, G., and Mandler, D. (2022). Electrochemical and electrophoretic coatings of medical implants by nanomaterials. *J. Solid State Electrochem.* 26, 1871–1896. doi:10.1007/s10008-022-05235-6

Cao, B., Majors, P. D., Ahmed, B., Renslow, R. S., Silvia, C. P., Shi, L., et al. (2012). Biofilm shows spatially stratified metabolic responses to contaminant exposure. *Environ. Microbiol.* 14, 2901–2910. doi:10.1111/j.1462-2920.2012.02850.x

Chandel, S. S., Shree, B., Mondal, K., and Mali, S. (2022). "Mechanism of nanoparticles-mediated alleviating biotic and abiotic stresses in agricultural crops: Recent advances and future perspectives," in *The Role of nanoparticles in plant nutrition under soil pollution. Sustainable plant nutrition in a changing world*. Editors V. D. Rajput, K. K. Verma, N. Sharma, and T. Minkina (Cham: Springer), 117–139.

Chandra, D., Srivastava, R., Glick, B. R., and Sharma, A. K. J. P. (2018). Drought-tolerant Pseudomonas spp. improve the growth performance of finger millet (*Eleusine coracana* (L.) Gaertn.) under non-stressed and drought-stressed conditions. *Pedosphere* 28, 227–240. doi:10.1016/s1002-0160(18)60013-x

Chang, P., Gerhardt, K. E., Huang, X.-D., Yu, X.-M., Glick, B. R., Gerwing, P. D., et al. (2014). Plant growth-promoting bacteria facilitate the growth of barley and oats in salt-impacted soil: Implications for phytoremediation of saline soils. *Int. J. Phytoremediation* 16, 1133–1147. doi:10.1080/15226514.2013.821447

Changmei, L., Chaoying, Z., Junqiang, W., Guorong, W., and Mingxuan, T. (2002). Research of the effect of nanometer materials on germination and growth enhancement of *Glycine max* and its mechanism. *Soybean Sci.* 21, 168–171.

Chaudhary, A., Chaudhary, P., Upadhyay, A., Kumar, A., and Singh, A. (2021a). Effect of *Gypsum* on plant growth promoting rhizobacteria. *Environ. Ecol.* 39, 1248–1256.

Chaudhary, P., Chaudhary, A., Bhatt, P., Kumar, G., Khatoon, H., Rani, A., et al. (2022). Assessment of soil health indicators under the influence of nanocompounds and *Bacillus* spp. in field condition. *Front. Environ. Sci.* 9, 769871. doi:10.3389/fenvs.2021.769871

Chaudhary, P., Chaudhary, A., Khati, P., and Kumar, G. (2021b). Nanotechnology and its role in improvement of crop production for sustainable agriculture. *Krishi Sci.* 2, 22–24.

Chaudhary, P., Khati, P., Chaudhary, A., Gangola, S., Kumar, R., and Sharma, A. (2021c). Bioinoculation using indigenous *Bacillus* spp. improves growth and yield of *Zea mays* under the influence of nanozeolite. *3 Biotech.* 11, 11. doi:10.1007/s13205-020-02561-2

Chavan, S., and Nadanathangam, V. (2019). Effects of nanoparticles on plant growth-promoting bacteria in Indian agricultural soil. *Agron. (Basel).* 9, 140. doi:10.3390/agronomy9030140

Chavan, S., Sarangdhar, V., and Nadanathangam, V. (2020). Toxicological effects of TiO_2 nanoparticles on plant growth promoting soil bacteria. *Emerg. Contam.* 6, 87–92. doi:10.1016/j.emcon.2020.01.003

Cherian, T., Maity, D., Rajendra Kumar, R. T., Balasubramani, G., Ragavendran, C., Yalla, S., et al. (2022). Green chemistry based gold nanoparticles synthesis using the marine bacterium *Lysinibacillus odysseyi* PBCW2 and their multitudinous activities. *Nanomaterials* 12, 2940. doi:10.3390/nano12172940

Chibuike, G. U., and Obiora, S. C. (2014). Heavy metal polluted soils: Effect on plants and bioremediation methods. *Appl. Environ. Soil Sci.* 2014, 1–12. doi:10.1155/2014/752708

Chouhan, G. K., Verma, J. P., Jaiswal, D. K., Mukherjee, A., Singh, S., De Araujo Pereira, A. P., et al. (2021). Phytomicrobiome for promoting sustainable agriculture and food security: Opportunities, challenges, and solutions. *Microbiol. Res.* 248, 126763. doi:10.1016/j.micres.2021.126763

Damodaran, T., Sharma, D., Mishra, V., Jha, S., Kannan, R., Sah, V., et al. (2013). Isolation of salt tolerant endophyticand rhizospheric bacteria by natural selection and screening for promising plant growth promoting rhizobacteria [PGPR] and growth vigour in tomato under sodic soil. *Afr. J. Microbiol. Res.* 7, 5082–5089.

Das, P., Williams, C. J., Fulthorpe, R. R., Hoque, M. E., Metcalfe, C. D., and Xenopoulos, M. A. (2012). Changes in bacterial community structure after exposure to silver nanoparticles in natural waters. *Environ. Sci. Technol.* 46, 9120–9128. doi:10.1021/es3019918

Daudi, A., Cheng, Z., O'brien, J. A., Mammarella, N., Khan, S., Ausubel, F. M., et al. (2012). The apoplastic oxidative burst peroxidase in *Arabidopsis* is a major component of pattern-triggered immunity. *Plant Cell* 24, 275–287. doi:10.1105/tpc.111.093039

Davar, Z. F., Roozbahani, A., and Hosnamidi, A. (2014). Evaluation the effect of water stress and foliar application of Fe nanoparticles on yield, yield components and oil percentage of safflower (*Carthamus tinctorious* L.) *Int. J. Adv. Biol. Biomed. Res.* 2, 1150–1159.

Degenhardt, B., and Gimmler, H. (2000). Cell wall adaptations to multiple environmental stresses in maize roots. *J. Exp. Bot.* 51, 595–603. doi:10.1093/jexbot/51.344.595

Devi, L. S., and Joshi, S. (2015). Ultrastructures of silver nanoparticles biosynthesized using endophytic fungi. *J. Microsc. Ultrastruct.* 3, 29–37. doi:10.1016/j.jmau.2014.10.004

Dimkpa, C. O., Mclean, J. E., Britt, D. W., and Anderson, A. J. (2012). CuO and ZnO nanoparticles differently affect the secretion of fluorescent siderophores in the beneficial root colonizer, *Pseudomonas chlororaphis* O6. *Nanotoxicology* 6, 635–642. doi:10.3109/17435390.2011.598246

Dinesh, B., Monisha, N., Shalini, H. R., Prathap, G. K., Poyya, J., Shantaram, M., et al. (2022). Antibacterial activity of silver nanoparticles synthesized using endophytic fungus - *Penicillium cinnamopurpureum*. *Spectrosc. Lett.* 55, 20–34. doi:10.1080/00387010.2021.2010764

Ding, Y., Peng, N., Du, Y., Ji, L., and Cao, B. (2014). Disruption of putrescine biosynthesis in *Shewanella oneidensis* enhances biofilm cohesiveness and performance in Cr (VI) immobilization. *Appl. Environ. Microbiol.* 80, 1498–1506. doi:10.1128/aem.03461-13

Dutta, G., and Sugumaran, A. (2021). Bioengineered zinc oxide nanoparticles: Chemical, green, biological fabrication methods and its potential biomedical applications. *J. Drug Deliv. Sci. Technol.* 66, 102853. doi:10.1016/j.jddst.2021.102853

Egamberdieva, D. J. (2009). Alleviation of salt stress by plant growth regulators and IAA producing bacteria in wheat. *Acta Physiol. Plant.* 31, 861–864. doi:10.1007/s11738-009-0297-0

Eid, A. M., Fouda, A., Abdel-Rahman, M. A., Salem, S. S., Elsaied, A., Oelmüller, R., et al. (2021). Harnessing bacterial endophytes for promotion of plant growth and biotechnological applications: An overview. *Plants (Basel).* 10, 935. doi:10.3390/plants10050935

Eida, A. A., Alzubaidy, H. S., De Zélicourt, A., Synek, L., Alsharif, W., Lafi, F. F., et al. (2019). Phylogenetically diverse endophytic bacteria from desert plants induce transcriptional changes of tissue-specific ion transporters and salinity stress in *Arabidopsis thaliana*. *Plant Sci.* 280, 228–240. doi:10.1016/j.plantsci.2018.12.002

El-Gazzar, N., Almaary, K., Ismail, A., and Polizzi, G. (2020). Influence of *Funneliformismosseae* enhanced with titanium dioxide nanoparticles (TiO_2NPs) on *Phaseolus vulgaris* L. under salinity stress. *PLoS One* 15, e0243491. doi:10.1371/journal.pone.0243491

Elemike, E. E., Uzoh, I. M., Onwudiwe, D. C., and Babalola, O. O. (2019). The role of nanotechnology in the fortification of plant nutrients and improvement of crop production. *Appl. Sci. (Basel).* 9, 499. doi:10.3390/app9030499

Elnahal, A. S. M., El-Saadony, M. T., Saad, A. M., Desoky, E.-S. M., El-Tahan, A. M., Rady, M. M., et al. (2022). The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: A review. *Eur. J. Plant Pathol.* 162, 759–792. doi:10.1007/s10658-021-02393-7

Elsheerya, N. I., Sunoja, V. S. J., Wena, Y., Zhua, J. J., Muralidharana, G., and Cao, K. F. (2020). Foliar application of nanoparticles mitigates the chilling effect on photosynthesis and photoprotection in sugarcane. *Plant Physiol. biochem.* 149, 50–60. doi:10.1016/j.plaphy.2020.01.035

Emamverdian, A., Ding, Y., Mokhberdoran, F., and Xie, Y. (2015). Heavy metal stress and some mechanisms of plant defense response. *Sci. World J.* 2015, 1–18. doi:10.1155/2015/756120

Fabrega, J., Zhang, R., Renshaw, J. C., Liu, W.-T., and Lead, J. R. (2011). Impact of silver nanoparticles on natural marine biofilm bacteria. *Chemosphere* 85, 961–966. doi:10.1016/j.chemosphere.2011.06.066

Fadiji, A. E., Mortimer, P. E., Xu, J., Ebenso, E. E., and Babalola, O. O. (2022a). Biosynthesis of nanoparticles using endophytes: A novel approach for enhancing plant growth and sustainable agriculture. *Sustainability* 14, 10839. doi:10.3390/su141710839

Fadiji, A. E., Onwudiwe, D. C., Mthiyane, D. M. N. B., and Oluranti, O. (2022b). Harnessing the known and unknown impact of nanotechnology on enhancing food security and reducing postharvest losses: Constraints and future prospects. *Agron. (Basel).* 12, 1657. doi:10.3390/agronomy12071657

Faiz, S., Yasin, N. A., Khan, W. U., Shah, A. A., Akram, W., Ahmad, A., et al. (2022). Role of magnesium oxide nanoparticles in the mitigation of lead-induced stress in daucus carota: Modulation in polyamines and antioxidant enzymes. *Int. J. Phytoremediation* 24, 364–372. doi:10.1080/15226514.2021.1949263

Fan, P., Chen, D., He, Y., Zhou, Q., Tian, Y., and Gao, L. J. I. J. O. P. (2016). Alleviating salt stress in tomato seedlings using Arthrobacter and Bacillus megaterium isolated from the rhizosphere of wild plants grown on saline–alkaline lands. *Int. J. Phytoremediation* 18, 1113–1121. doi:10.1080/15226514.2016.1183583

FAO (2009). *Food Agriculture Organization of the United Nations. High level expert forum—how to feed the world in 2050*. Italy: Office of the Director, Agricultural Development Economics Division Rome.

Fasusi, O. A., Amoo, A. E., and Babalola, O. O. (2021). Characterization of plant growth-promoting rhizobacterial isolates associated with food plants in South Africa. *Antonie Leeuwenhoek* 114, 1683–1708. doi:10.1007/s10482-021-01633-4

Flemming, H., and Wingender, J. (2010). The biofilm matrix. *Nat. Rev. Microbiol.* 8, 623–633. doi:10.1038/nrmicro2415

Franco, D., Calabrese, G., Guglielmino, S. P. P., and Conoci, S. (2022). Metal-based nanoparticles: Antibacterial mechanisms and biomedical application. *Microorganisms* 10, 1778. doi:10.3390/microorganisms10091778

Franken, P. (2012). The plant strengthening root endophyte *Piriformospora indica*: Potential application and the biology behind. *Appl. Microbiol. Biotechnol.* 96, 1455–1464. doi:10.1007/s00253-012-4506-1

Frenk, S., Ben-Moshe, T., Dror, I., Berkowitz, B., and Minz, D. (2013). Effect of metal oxide nanoparticles on microbial community structure and function in two different soil types. *PloS One* 8, e84441. doi:10.1371/journal.pone.0084441

Fu, P. P., Xia, Q., Hwang, H.-M., Ray, P. C., and Yu, H. (2014). Mechanisms of nanotoxicity: Generation of reactive oxygen species. *J. Food Drug Anal.* 22, 64–75. doi:10.1016/j.jfda.2014.01.005

Gamalero, E., and Glick, B. R. (2022). Recent advances in bacterial amelioration of plant drought and salt stress. *Biology* 11, 437. doi:10.3390/biology11030437

Gangadoo, S., Xu, C., Cozzolino, D., Latham, K., Della Gaspera, E., Chapman, J., et al. (2022). Probing nanoscale interactions of antimicrobial zinc oxide quantum dots on bacterial and fungal cell surfaces. *Adv. Mat. Interfaces* 9, 2101484. doi:10.1002/admi.202101484

Ganie, S. A., Bhat, J. A., and Devoto, A. (2021). The influence of endophytes on rice fitness under environmental stresses. *Plant Mol. Biol.* 109, 447–467. doi:10.1007/s11103-021-01219-8

Gao, X., Zou, C., Wang, L., and Zhang, F. (2006). Silicon decreases transpiration rate and conductance from stomata of maize plants. *J. Plant Nutr.* 29, 1637–1647. doi:10.1080/01904160600851494

Gepstein, S., and Glick, B. R. (2013). Strategies to ameliorate abiotic stress-induced plant senescence. *Plant Mol. Biol.* 82, 623–633. doi:10.1007/s11103-013-0038-z

Giraldo, J. P., Landry, M. P., Faltermeier, S. M., Mcnicholas, T. P., Iverson, N. M., Boghossian, A. A., et al. (2014). Plant nanobionics approach to augment photosynthesis and biochemical sensing. *Nat. Mat.* 13, 400–408. doi:10.1038/nmat3890

Glick, B. R. (2004). Bacterial ACC deaminase and the alleviation of plant stress. *Adv. Appl. Microbiol.* 56, 291–312. doi:10.1016/S0065-2164(04)56009-4

Glick, B. R. (2020). *Beneficial plant-bacterial interactions*. 2nd Edition. Heidelberg: Springer, 383.

Glick, B. R., and Gamalero, E. (2021). Recent developments in the study of plant microbiomes. *Microorganisms* 9, 1533. doi:10.3390/microorganisms9071533

Gopalakrishnan, S., Sathya, A., Vijayabharathi, R., Varshney, R. K., Gowda, C., and Krishnamurthy, L. (2015). Plant growth promoting rhizobia: Challenges and opportunities. *3 Biotech.* 5, 355–377. doi:10.1007/s13205-014-0241-x

Gorai, P. S., Ghosh, R., Mandal, S., Ghosh, S., Chatterjee, S., Gond, S. K., et al. (2021). *Bacillus siamensis* CNE6- a multifaceted plant growth promoting endophyte of *Cicer arietinum* L. having broad spectrum antifungal activities and host colonizing potential. *Microbiol. Res.* 252, 126859. doi:10.1016/j.micres.2021.126859

Govindappa, M., Manasa, D., Vinaykiya, V., Dutta, S., Pawar, R., and Raghavendra, V. B. (2022). Screening of antibacterial and antioxidant activity of biogenically synthesized silver nanoparticles from *alternaria alternata*, endophytic fungus of *Dendrophthoe falcata*-a Parasitic Plant. *Bionanoscience* 12, 128–141. doi:10.1007/s12668-021-00932-4

Gunjan, B., and Zaidi, M. (2014). Impact of gold nanoparticles on physiological and biochemical characteristics of *Brassica juncea*. *J. Plant Biochem. Physiol.* 2, 1000133.

Gupta, S., Schillaci, M., Walker, R., Smith, P. M. C., Watt, M., and Roessner, U. (2021). Alleviation of salinity stress in plants by endophytic plant-fungal symbiosis: Current knowledge, perspectives and future directions. *Plant Soil* 461, 219–244. doi:10.1007/s11104-020-04618-w

Gürsoy, N., Yilmaz Öztürk, B., and Dağ, İ. (2021). Synthesis of intracellular and extracellular gold nanoparticles with a green machine and its antifungal activity. *Turk. J. Biol.* 45, 196–213. doi:10.3906/biy-2010-64

Haghighi, M., Abolghasemi, R., and Da Silva, J. a. T. (2014). Low and high temperature stress affect the growth characteristics of tomato in hydroponic culture with Se and nano-Se amendment. *Sci. Hortic.* 178, 231–240. doi:10.1016/j.scienta.2014.09.006

Halliwell, B., and Gutteridge, J. M. (2015). *Free radicals in biology and medicine*. USA: Oxford University Press.

Hanaka, A., Ozimek, E., Reszczyńska, E., Jaroszuk-Ściseł, J., and Stolarz, M. (2021). Plant tolerance to drought stress in the presence of supporting bacteria and fungi: An efficient strategy in horticulture. *Horticulturae* 7, 390. doi:10.3390/horticulturae7100390

Hasanpour, H., Maali-Amir, R., and Zeinali, H. (2015). Effect of TiO_2 nanoparticles on metabolic limitations to photosynthesis under cold in chickpea. *Russ. J. Plant Physiol.* 62, 779–787. doi:10.1134/s1021443715060096

Hasanuzzaman, M., Bhuyan, M., Anee, T. I., Parvin, K., Nahar, K., Mahmud, J. A., et al. (2019). Regulation of ascorbate-glutathione pathway in mitigating oxidative damage in plants under abiotic stress. *Antioxidants* 8, 384. doi:10.3390/antiox8090384

Hasanuzzaman, M., Nahar, K., and Fujita, M. (2013). "Extreme temperature responses, oxidative stress and antioxidant defense in plants," in *Abiotic stress-plant responses and applications in agriculture*. Editors K. Vahdat and C. Leslie (Rijeka: InTech), 169–205. doi:10.5772/54833

Hasanuzzaman, M., Nahar, K., and Fujita, M. (2014). "Silicon and selenium: Two vital trace elements that confer abiotic stress tolerance to plants," in *Emerging technologies and management of crop stress tolerance* (Elsevier), 377–422.

Hattori, T., Inanaga, S., Araki, H., An, P., Morita, S., Luxová, M., et al. (2005). Application of silicon enhanced drought tolerance in *Sorghum bicolor*. *Physiol. Plant.* 123, 459–466. doi:10.1111/j.1399-3054.2005.00481.x

Hayat, R., Ali, S., Amara, U., Khalid, R., and Ahmed, I. (2010). Soil beneficial bacteria and their role in plant growth promotion: A review. *Ann. Microbiol.* 60, 579–598. doi:10.1007/s13213-010-0117-1

He, C., Zeng, Q., Chen, Y., Chen, C., Wang, W., Hou, J., et al. (2021). Colonization by dark septate endophytes improves the growth and rhizosphere soil microbiome of licorice plants under different water treatments. *Appl. Soil Ecol.* 166, 103993. doi:10.1016/j.apsoil.2021.103993

He, L., Liu, Y., Mustapha, A., and Lin, M. (2011). Antifungal activity of zinc oxide nanoparticles against *Botrytis cinerea* and *Penicillium expansum*. *Microbiol. Res.* 166, 207–215. doi:10.1016/j.micres.2010.03.003

Hmaeid, N., Wali, M., Mahmoud, O. M.-B., Pueyo, J. J., Ghnaya, T., and Abdelly, C. (2019). Efficient rhizobacteria promote growth and alleviate NaCl-induced stress in the plant species *Sulla carnosa*. *Appl. Soil Ecol.* 133, 104–113. doi:10.1016/j.apsoil.2018.09.011

Hulikere, M. M., and Joshi, C. G. (2019). Characterization, antioxidant and antimicrobial activity of silver nanoparticles synthesized using marine endophytic fungus-*Cladosporium cladosporioides*. *Process Biochem.* 82, 199–204. doi:10.1016/j.procbio.2019.04.011

Hwang, H. H., Chien, P. R., Huang, F. C., Hung, S. H., Kuo, C. H., Deng, W. L., et al. (2021). A plant endophytic bacterium, *Burkholderia seminalis* strain 869T2, promotes plant growth in *Arabidopsis*, Pak Choi, Chinese Amaranth, Lettuces, and other vegetables. *Microorganisms* 9, 1703. doi:10.3390/microorganisms9081703

Ibrahim, E., Zhang, M., Zhang, Y., Hossain, A., Qiu, W., Chen, Y., et al. (2020). Green-synthesization of silver nanoparticles using endophytic bacteria isolated from garlic and its antifungal activity against Wheat *Fusarium* head blight pathogen *Fusarium graminearum*. *Nanomaterials* 10, 219. doi:10.3390/nano10020219

Igiehon, N. O., Babalola, O. O., Cheseto, X., and Torto, B. (2021). Effects of rhizobia and arbuscular mycorrhizal fungi on yield, size distribution and fatty acid of soybean seeds grown under drought stress. *Microbiol. Res.* 242, 126640. doi:10.1016/j.micres.2020.126640

Igiehon, O. N., and Babalola, O. O. (2021). Rhizobium and mycorrhizal fungal species improved soybean yield under drought stress conditions. *Curr. Microbiol.* 78, 1615–1627. doi:10.1007/s00284-021-02432-w

Imade, E. E., Ajiboye, T. O., Fadiji, A. E., Onwudiwe, D. C., and Babalola, O. O. (2022). Green synthesis of zinc oxide nanoparticles using plantain peel extracts and the evaluation of their antibacterial activity. *Sci. Afr.* 16, e01152. doi:10.1016/j.sciaf.2022.e01152

Iravani, S., Korbekandi, H., Mirmohammadi, S. V., and Zolfaghari, B. (2014). Synthesis of silver nanoparticles: Chemical, physical and biological methods. *Res. Pharm. Sci.* 9, 385–406.

Ishida, K., Cipriano, T. F., Rocha, G. M., Weissmüller, G., Gomes, F., Miranda, K., et al. (2013). Silver nanoparticle production by the fungus *Fusarium oxysporum*: Nanoparticle characterisation and analysis of antifungal activity against pathogenic yeasts. *Mem. Inst. Oswaldo Cruz* 109, 220–228. doi:10.1590/0074-0276130269

Jaberzadeh, A., Moaveni, P., Moghadam, H. R. T., and Zahedi, H. (2013). Influence of bulk and nanoparticles titanium foliar application on some agronomic traits, seed gluten and starch contents of wheat subjected to water deficit stress. *Not. Bot. Horti Agrobot. Cluj. Napoca.* 41, 201–207. doi:10.15835/nbha4119093

Jacoby, R., Peukert, M., Succurro, A., Koprivova, A., and Kopriva, S. (2017). The role of soil microorganisms in plant mineral nutrition—Current knowledge and future directions. *Front. Plant Sci.* 8, 1617. doi:10.3389/fpls.2017.01617

Jadoun, S., Chauhan, N. P. S., Zarrintaj, P., Barani, M., Varma, R. S., Chinnam, S., et al. (2022). Synthesis of nanoparticles using microorganisms and their applications: A review. *Environ. Chem. Lett.* 20, 3153–3197. doi:10.1007/s10311-022-01444-7

Jajoo, A., and Mathur, S. (2021). Role of arbuscular mycorrhizal fungi as an underground saviuor for protecting plants from abiotic stresses. *Physiol. Mol. Biol. Plants* 27, 2589–2603. doi:10.1007/s12298-021-01091-2

Jalil, S. U., and Ansari, M. I. (2019). Nanoparticles and abiotic stress tolerance in plants: Synthesis, action, and signaling mechanisms. *Plant Signal. Mol.* 2019, 549–561.

Jha, Y., and Subramanian, R. B. (2014). PGPR regulate caspase-like activity, programmed cell death, and antioxidant enzyme activity in paddy under salinity. *Physiol. Mol. Biol. Plants* 20, 201–207. doi:10.1007/s12298-014-0224-8

Jin, L., Son, Y., Deforest, J. L., Kang, Y. J., Kim, W., and Chung, H. (2014). Single-walled carbon nanotubes alter soil microbial community composition. *Sci. Total Environ.* 466, 533–538. doi:10.1016/j.scitotenv.2013.07.035

Kalteh, M., Alipour, Z. T., Ashraf, S., Marashi Aliabadi, M., and Falah Nosratabadi, A. (2018). Effect of silica nanoparticles on basil (*Ocimum basilicum*) under salinity stress. *J. Chem. Health Risks.* 4, 49–55.

Kang, S., Herzberg, M., Rodrigues, D. F., and Elimelech, M. (2008). Antibacterial effects of carbon nanotubes: Size does matter. *Langmuir* 24, 6409–6413. doi:10.1021/la800951v

Karuppanapandian, T., Wang, H. W., Prabakaran, N., Jeyalakshmi, K., Kwon, M., Manoharan, K., et al. (2011). 2, 4-dichlorophenoxyacetic acid-induced leaf senescence in mung bean (*Vigna radiata* L. *Wilczek*) and senescence inhibition by co-treatment with silver nanoparticles. *Plant Physiol. biochem.* 49, 168–177. doi:10.1016/j.plaphy.2010.11.007

Kaur, T., Bala, M., Kumar, G., and Vyas, A. (2022). Biosynthesis of zinc oxide nanoparticles via endophyte *Trichoderma viride* and evaluation of their antimicrobial and antioxidant properties. *Arch. Microbiol.* 204, 620. doi:10.1007/s00203-022-03218-9

Kaushal, M., and Wani, S. P. (2016). Plant-growth-promoting rhizobacteria: Drought stress alleviators to ameliorate crop production in drylands. *Ann. Microbiol.* 66, 35–42. doi:10.1007/s13213-015-1112-3

Khalid, M., Bilal, M., Hassani, D., Iqbal, H., Wang, H., and Huang, D. J. B. S. (2017). Mitigation of salt stress in white clover (*Trifolium repens*) by *Azospirillum brasilense* and its inoculation effect. *Bot. Stud.* 58, 5. doi:10.1186/s40529-016-0160-8

Khan, A., Zhao, X. Q., Javed, M. T., Khan, K. S., Bano, A., Shen, R. F., et al. (2016). *Bacillus pumilus* enhances tolerance in rice (*Oryza sativa* L.) to combined stresses of NaCl and high boron due to limited uptake of Na+. *Environ. Exp. Bot.* 124, 120–129. doi:10.1016/j.envexpbot.2015.12.011

Khati, P., Pankaj, P., Nisha, B., Kumar, R., and Sharma, A. (2018). Effect of nanozeolite and plant growth promoting rhizobacteria on maize. *3 Biotech.* 8, 141. doi:10.1007/s13205-018-1142-1

Khatoon, U. T., Rao, G. N., Mohan, M. K., Ramanaviciene, A., and Ramanavicius, A. (2018). Comparative study of antifungal activity of silver and gold nanoparticles synthesized by facile chemical approach. *J. Environ. Chem. Eng.* 6, 5837–5844. doi:10.1016/j.jece.2018.08.009

Kibbey, T. C., and Strevett, K. A. (2019). The effect of nanoparticles on soil and rhizosphere bacteria and plant growth in lettuce seedlings. *Chemosphere* 221, 703–707. doi:10.1016/j.chemosphere.2019.01.091

Kim, K.-J., Sung, W. S., Suh, B. K., Moon, S.-K., Choi, J.-S., Kim, J. G., et al. (2009). Antifungal activity and mode of action of silver nano-particles on *Candida albicans*. *Biometals* 22, 235–242. doi:10.1007/s10534-008-9159-2

Kohan-Baghkheirati, E., and Geisler-Lee, J. (2015). Gene expression, protein function and pathways of *Arabidopsis thaliana* responding to silver nanoparticles in comparison to silver ions, cold, salt, drought, and heat. *Nanomaterials* 5, 436–467. doi:10.3390/nano5020436

Komaresofla, B. R., Alikhani, H. A., Etesami, H., and Khoshkholgh-Sima, N. A. (2019). Improved growth and salinity tolerance of the halophyte *Salicornia* sp. by co–inoculation with endophytic and rhizosphere bacteria. *Appl. Soil Ecol.* 138, 160–170. doi:10.1016/j.apsoil.2019.02.022

Koné, Y., Alves, E., Silveira, P. R., Ferreira, A. N., De Medeiros, F. H. V., and Cruz-Magalhães, V. (2022). Control of blast disease caused by *Pyricularia oryzae* with *Epicoccum nigrum* and microscopic studies of their interaction with rice plants under greenhouse conditions. *Biol. Control* 167, 104840. doi:10.1016/j.biocontrol.2022.104840

Kumar, A., Patel, J. S., Meena, V. S., and Srivastava, R. (2019). Recent advances of PGPR based approaches for stress tolerance in plants for sustainable agriculture. *Biocatal. Agric. Biotechnol.* 20, 101271. doi:10.1016/j.bcab.2019.101271

Kumar, R., Sahoo, S., Joanni, E., Singh, R. K., Tan, W. K., Kar, K. K., et al. (2021). Recent progress on carbon-based composite materials for microwave electromagnetic interference shielding. *Carbon* 177, 304–331. doi:10.1016/j.carbon.2021.02.091

Kumar, V., and Nautiyal, C. S. (2022). Plant abiotic and biotic stress alleviation: From an endophytic microbial perspective. *Curr. Microbiol.* 79, 311. doi:10.1007/s00284-022-03012-2

Kumari, S., Sharma, A., Chaudhary, P., and Khati, P. (2020). Management of plant vigor and soil health using two agriusable nanocompounds and plant growth promotory rhizobacteria in Fenugreek. *3 Biotech.* 10, 461. doi:10.1007/s13205-020-02448-2

Kushwaha, P., Kashyap, P. L., Bhardwaj, A. K., Kuppusamy, P., Srivastava, A. K., and Tiwari, R. K. (2020). Bacterial endophyte mediated plant tolerance to salinity: Growth responses and mechanisms of action. *World J. Microbiol. Biotechnol.* 36, 26. doi:10.1007/s11274-020-2804-9

Larue, C., Baratange, C., Vantelon, D., Khodja, H., Surblé, S., Elger, A., et al. (2018). Influence of soil type on TiO_2 nanoparticle fate in an agro-ecosystem. *Sci. Total Environ.* 630, 609–617. doi:10.1016/j.scitotenv.2018.02.264

Laware, S., and Raskar, S. (2014). Effect of titanium dioxide nanoparticles on hydrolytic and antioxidant enzymes during seed germination in onion. *Int. J. Curr. Microbiol. App. Sci.* 3, 749–760.

Lee, S., Kim, K., Shon, H., Kim, S. D., and Cho, J. (2011). Biotoxicity of nanoparticles: Effect of natural organic matter. *J. Nanopart. Res.* 13, 3051–3061. doi:10.1007/s11051-010-0204-z

Lee, Y., Krishnamoorthy, R., Selvakumar, G., Kim, K., and Sa, T. (2015). Alleviation of salt stress in maize plant by co-inoculation of arbuscular mycorrhizal fungi and *Methylobacterium oryzae* CBMB20. *J. Korean Soc. Appl. Biol. Chem.* 58, 533–540. doi:10.1007/s13765-015-0072-4

Li, D., Cui, F., Zhao, Z., Liu, D., Xu, Y., Li, H., et al. (2014). The impact of titanium dioxide nanoparticles on biological nitrogen removal from wastewater and bacterial community shifts in activated sludge. *Biodegradation* 25, 167–177. doi:10.1007/s10532-013-9648-z

Li, J., Zhang, P., Ye, J., Zhang, G., and Cai, Y. (2019). Simultaneous *in-situ* remediation and fertilization of Cd-contaminated weak-alkaline farmland for wheat production. *J. Environ. Manage.* 250, 109528. doi:10.1016/j.jenvman.2019.109528

Li, Z., and Huang, J. (2014). Effects of nanoparticle hydroxyapatite on growth and antioxidant system in pakchoi (*Brassica chinensis* L.) from cadmium-contaminated soil. *J. Nanomater.* 2014, 470962.

Liang, Z., Das, A., and Hu, Z. (2010). Bacterial response to a shock load of nanosilver in an activated sludge treatment system. *Water Res.* 44, 5432–5438. doi:10.1016/j.watres.2010.06.060

Liu, B., Mu, L., Zhang, J., Han, X., and Shi, H. (2020). $TiO_2/Cu_2(OH)_2CO_3$ nanocomposite as efficient antimicrobials for inactivation of crop pathogens in agriculture. *Mater. Sci. Eng. C* 107, 110344. doi:10.1016/j.msec.2019.110344

Liu, H. Q., Lu, X. B., Li, Z. H., Tian, C. Y., and Song, J. (2021). The role of root-associated microbes in growth stimulation of plants under saline conditions. *Land Degrad. Dev.* 32, 3471–3486. doi:10.1002/ldr.3955

Liu, X., Jin, X., Cao, B., and Tang, C. Y. (2014). Bactericidal activity of silver nanoparticles in environmentally relevant freshwater matrices: Influences of organic matter and chelating agent. *J. Environ. Chem. Eng.* 2, 525–531. doi:10.1016/j.jece.2013.10.008

Lowry, G. V., Gregory, K. B., Apte, S. C., and Lead, J. R. (2012). Transformations of nanomaterials in the environment. *Environ. Sci. Technol.* 7, 6893–6899.

LubnaKhan, M. A., Asaf, S., Jan, R., Waqas, M., Kim, K.-M., et al. (2022). Endophytic fungus *Bipolaris* sp. CSL-1 induces salt tolerance in *Glycine max*. L via modulating its endogenous hormones, antioxidative system and gene expression. *J. Plant Interact.* 17, 319–332. doi:10.1080/17429145.2022.2036836

Lyu, D., Msimbira, L. A., Nazari, M., Antar, M., Pagé, A., Shah, A., et al. (2021). The coevolution of plants and microbes underpins sustainable agriculture. *Microorganisms* 9, 1036. doi:10.3390/microorganisms9051036

Mahmood, A., Amaya, R., Turgay, O. C., Yaprak, A. E., Taniguchi, T., and Kataoka, R. (2019). High salt tolerant plant growth promoting rhizobacteria from the common ice-plant *Mesembryanthemum crystallinum* L. *Rhizosphere* 9, 10–17. doi:10.1016/j.rhisph.2018.10.004

Mahmood, S., Daur, I., Al-Solaimani, S. G., Ahmad, S., Madkour, M. H., Yasir, M., et al. (2016). Plant growth promoting rhizobacteria and silicon synergistically enhance salinity tolerance of mung bean. *Front. Plant Sci.* 7, 876. doi:10.3389/fpls.2016.00876

Mallmann, E. J. J., Cunha, F. A., Castro, B. N., Maciel, A. M., Menezes, E. A., and Fechine, P. B. A. (2015). Antifungal activity of silver nanoparticles obtained by green synthesis. *Rev. Inst. Med. Trop. S. Paulo* 57, 165–167. doi:10.1590/s0036-46652015000200011

Martínez-Ballesta, M., Zapata, L., Chalbi, N., and Carvajal, M. (2016). Multiwalled carbon nanotubes enter broccoli cells enhancing growth and water uptake of plants exposed to salinity. *J. Nanobiotechnol.* 14, 42–14. doi:10.1186/s12951-016-0199-4

Masoumizadeh, M., Madani, M., Fatahian, S., and Shakib, P. (2022). Effect of silver nanoparticles (AgNPs) on *Candida albicans, Candida dubliniensis* and *Candida guilliermondii*. *Curr. Drug Ther.* 17, 50–55. doi:10.2174/1574885517666220221093456

Masrahi, A., Vandevoort, A. R., and Arai, Y. (2014). Effects of silver nanoparticle on soil-nitrification processes. *Arch. Environ. Contam. Toxicol.* 66, 504–513. doi:10.1007/s00244-013-9994-1

Massad, T. J., Dyer, L. A., and Vega C, G. (2012). Costs of defense and a test of the carbon-nutrient balance and growth-differentiation balance hypotheses for two co-occurring classes of plant defense. *PLoS One* 7, e47554. doi:10.1371/journal.pone.0047554

Mathur, V., and Ulanova, D. (2022). Microbial metabolites beneficial to plant hosts across ecosystems. *Microb. Ecol.* doi:10.1007/s00248-022-02073-x

Mazmancı, B., Könen Adıgüzel, S., Sadak, Y. S., Yetkin, D., Ay, H., and Adıgüzel, A. O. (2022). Antimicrobial, antibiofilm, and anticancer potential of silver nanoparticles synthesized using pigment-producing *Micromonospora* sp. SH121. *Prep. Biochem. Biotechnol.*, 1–13. doi:10.1080/10826068.2022.2101001

Mcquillan, J. (2010). Bacterial nanoparticle interactions. PhD thesis. Exeter: University of Exeter, 211.

Mcquillan, J. S., and Shaw, A. M. (2014). Differential gene regulation in the Ag nanoparticle and Ag+-induced silver stress response in *Escherichia coli:* A full transcriptomic profile. *Nanotoxicology* 8, 177–184. doi:10.3109/17435390.2013.870243

Meena, K. K., Kumar, M., Kalyuzhnaya, M. G., Yandigeri, M. S., Singh, D. P., Saxena, A. K., et al. (2012). Epiphytic pink-pigmented methylotrophic bacteria enhance germination and seedling growth of wheat (*Triticum aestivum*) by producing phytohormone. *Ant. Van Leeuwenhoek* 101, 777–786. doi:10.1007/s10482-011-9692-9

Meena, K. K., Sorty, A. M., Bitla, U. M., Choudhary, K., Gupta, P., Pareek, A., et al. (2017). Abiotic stress responses and microbe-mediated mitigation in plants: The omics strategies. *Front. Plant Sci.* 8, 172. doi:10.3389/fpls.2017.00172

Mickelbart, M. V., Hasegawa, P. M., and Bailey-Serres, J. (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nat. Rev. Genet.* 16, 237–251. doi:10.1038/nrg3901

Mishra, R. C., Kalra, R., Dilawari, R., Goel, M., and Barrow, C. J. (2022). Biosynthesis of *Aspergillus terreus* mediated gold nanoparticle: Antimicrobial, antioxidant, antifungal and *in vitro* cytotoxicity studies. *Materials* 15, 3877. doi:10.3390/ma15113877

Mittal, D., Kumar, A., Balasubramaniam, B., Thakur, R., Singh Siwal, S., Saini, V., et al. (2021). Synthesis of Biogenic silver nanoparticles using plant growth-promoting bacteria: Potential use as biocontrol agent against phytopathogens. *Biomat. Polym. Horiz.* 1, 22–31. doi:10.37819/bph.001.01.0130

Mohammadi, R., Maali-Amiri, R., and Abbasi, A. (2013). Effect of TiO_2 nanoparticles on chickpea response to cold stress. *Biol. Trace Elem. Res.* 152, 403–410. doi:10.1007/s12011-013-9631-x

Mohanty, A., Wu, Y., and Cao, B. (2014). Impacts of engineered nanomaterials on microbial community structure and function in natural and engineered ecosystems. *Appl. Microbiol. Biotechnol.* 98, 8457–8468. doi:10.1007/s00253-014-6000-4

Moreira, H., Pereira, S. I., Marques, A. P., Rangel, A. O., Castro, P. M. J. E. S., and Research, P. (2016). Mine land valorization through energy maize production enhanced by the application of plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi. *Environ. Sci. Pollut. Res.* 23, 6940–6950. doi:10.1007/s11356-015-5914-4

Moreno-Galván, A. E., Cortés-Patiño, S., Romero-Perdomo, F., Uribe-Vélez, D., Bashan, Y., and Bonilla, R. R. (2020). Proline accumulation and glutathione reductase activity induced by drought-tolerant rhizobacteria as potential mechanisms to alleviate drought stress in Guinea grass. *Appl. Soil Ecol.* 147, 103367. doi:10.1016/j.apsoil.2019.103367

Mostafa, E. M., Abdelgawad, M. A., Musa, A., Alotaibi, N. H., Elkomy, M. H., Ghoneim, M. M., et al. (2022). Chitosan silver and gold nanoparticle formation using endophytic fungi as powerful antimicrobial and anti-biofilm potentialities. *Antibiotics* 11, 668. doi:10.3390/antibiotics11050668

Mowafy, A. M., Fawzy, M. M., Gebreil, A., and Elsayed, A. (2021). Endophytic *Bacillus, Enterobacter,* and *Klebsiella* enhance the growth and yield of maize. *Acta Agric. Scand. Sect. B —. Soil & Plant Sci.* 71, 237–246. doi:10.1080/09064710.2021.1880621

Mueller, C. F., Laude, K., Mcnally, J. S., and Harrison, D. G. (2005). Redox mechanisms in blood vessels. *Arterioscler. Thromb. Vasc. Biol.* 25, 274–278. doi:10.1161/01.atv.0000149143.04821.eb

Mukhtar, S., Mirza, B. S., Mehnaz, S., Mirza, M. S., Mclean, J., and Malik, K. A. (2018). Impact of soil salinity on the microbial structure of halophyte rhizosphere microbiome. *World J. Microbiol. Biotechnol.* 34, 136. doi:10.1007/s11274-018-2509-5

Munns, R., and Tester, M. (2008). Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.* 59, 651–681. doi:10.1146/annurev.arplant.59.032607.092911

Nadeem, S. M., Zahir, Z. A., Naveed, M., and Nawaz, S. J. a. O. M. (2013). Mitigation of salinity-induced negative impact on the growth and yield of wheat by plant growth-promoting rhizobacteria in naturally saline conditions. *Ann. Microbiol.* 63, 225–232. doi:10.1007/s13213-012-0465-0

Nagy, A., Harrison, A., Sabbani, S., Munson, R. S., Jr, Dutta, P. K., and Waldman, W. J. (2011). Silver nanoparticles embedded in zeolite membranes: Release of silver ions and mechanism of antibacterial action. *Int. J. Nanomedicine* 6, 1833–1852. doi:10.2147/ijn.s24019

Nasr, F., Pateiro, M., Rabiei, V., Razavi, F., Formaneck, S., Gohari, G., et al. (2021). Chitosan-phenylalanine nanoparticles (Cs-Phe Nps) extend the postharvest life of Persimmon (*Diospyros kaki*) fruits under chilling stress. *Coatings* 11, 819. doi:10.3390/coatings11070819

Nasrollahi, A., Pourshamsian, K., and Mansourkiaee, P. (2011). Antifungal activity of silver nanoparticles on some of fungi. *Int. J. Nano Dimens.* 1, 233–239.

Nautiyal, C. S., Srivastava, S., Chauhan, P. S., Seem, K., Mishra, A., and Sopory, S. K. (2013). Plant growth-promoting bacteria *Bacillus amyloliquefaciens* NBRISN13 modulates gene expression profile of leaf and rhizosphere community in rice during salt stress. *Plant Physiol. biochem.* 66, 1–9. doi:10.1016/j.plaphy.2013.01.020

Naveed, M., Hussain, M. B., Zahir, Z. A., Mitter, B., and Sessitsch, A. (2014a). Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. *Plant Growth Regul.* 73, 121–131. doi:10.1007/s10725-013-9874-8

Naveed, M., Mitter, B., Reichenauer, T. G., Wieczorek, K., and Sessitsch, A. (2014b). Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* PsJN and *Enterobacter* sp. FD17. *Environ. Exp. Bot.* 97, 30–39. doi:10.1016/j.envexpbot.2013.09.014

Ndeddy Aka, R. J., and Babalola, O. O. (2016). Effect of bacterial inoculation of strains of *Pseudomonas aeruginosa, Alcaligenes feacalis* and *Bacillus subtilis* on germination, growth and heavy metal (Cd, Cr, and Ni) uptake of *Brassica juncea*. *Int. J. Phytoremediation* 18, 200–209. doi:10.1080/15226514.2015.1073671

Neethu, S., Midhun, S. J., Sunil, M., Soumya, S., Radhakrishnan, E., and Jyothis, M. (2018). Efficient visible light induced synthesis of silver nanoparticles by *Penicillium polonicum* ARA 10 isolated from *Chetomorpha antennina* and its antibacterial efficacy against *Salmonella enterica serovar Typhimurium*. *J. Photochem. Photobiol. B Biol.* 180, 175–185. doi:10.1016/j.jphotobiol.2018.02.005

Noukelag, S. K., Mewa-Ngongang, M., Ngqoloda, S., Kotsedi, L., Razanamahandry, L. C., Ntwampe, S. K. O., et al. (2022). *Influence of synthesis method on structural, morphological, magnetic, and antimicrobial properties of Fe-Ag nanoparticles*. *J. Inorg. Organomet. Polym. Mat.* doi:10.1007/s10904-022-02493-9

Nyberg, L., Turco, R. F., and Nies, L. (2008). Assessing the impact of nanomaterials on anaerobic microbial communities. *Environ. Sci. Technol.* 42, 1938–1943. doi:10.1021/es072018g

Oh, M.-M., Trick, H. N., and Rajashekar, C. (2009). Secondary metabolism and antioxidants are involved in environmental adaptation and stress tolerance in lettuce. *J. Plant Physiol.* 166, 180–191. doi:10.1016/j.jplph.2008.04.015

Ojuederie, O. B., Olanrewaju, O. S., and Babalola, O. O. (2019). Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agron. (Basel).* 9, 712. doi:10.3390/agronomy9110712

Oleńska, E., Małek, W., Wójcik, M., Swiecicka, I., Thijs, S., and Vangronsveld, J. (2020). Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: A methodical review. *Sci. Total Environ.* 743, 140682. doi:10.1016/j.scitotenv.2020.140682

Omar, M., Osman, M., Kasim, W., and El-Daim, A. (2009). "Improvement of salt tolerance mechanisms of barley cultivated under salt stress using Azospirillum brasilense," in *Salinity and water stress* (Springer), 133–147.

Omomowo, O. I., and Babalola, O. O. (2019). Bacterial and fungal endophytes: Tiny giants with immense beneficial potential for plant growth and sustainable agricultural productivity. *Microorganisms* 7, 481. doi:10.3390/microorganisms7110481

Ortiz, N., Armada, E., Duque, E., Roldán, A., and Azcón, R. (2015). Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: Effectiveness of autochthonous or allochthonous strains. *J. Plant Physiol.* 174, 87–96. doi:10.1016/j.jplph.2014.08.019

Ovais, M., Khalil, A. T., Islam, N. U., Ahmad, I., Ayaz, M., Saravanan, M., et al. (2018). Role of plant phytochemicals and microbial enzymes in biosynthesis of

metallic nanoparticles. *Appl. Microbiol. Biotechnol.* 102, 6799–6814. doi:10.1007/s00253-018-9146-7

Palaniyandi, S., Damodharan, K., Yang, S., and Suh, J. (2014). *Streptomyces* sp. strain PGPA39 alleviates salt stress and promotes growth of 'Micro Tom'tomato plants. *J. Appl. Microbiol.* 117, 766–773. doi:10.1111/jam.12563

Pandey, G. (2018). Challenges and future prospects of agri-nanotechnology for sustainable agriculture in India. *Environ. Technol. Innov.* 11, 299–307. doi:10.1016/j.eti.2018.06.012

Pandey, V., Ansari, M. W., Tula, S., Yadav, S., Sahoo, R. K., Shukla, N., et al. (2016). Dose-dependent response of *Trichoderma harzianum* in improving drought tolerance in rice genotypes. *Planta* 243, 1251–1264. doi:10.1007/s00425-016-2482-x

Panichikkal, J., and Krishnankutty, R. E. (2022). Chitosan and gold nanoparticles supplementation for augmentation of indole-3-acetic acid production by rhizospheric *Pseudomonas aeruginosa* and plant growth enhancement. *Curr. Microbiol.* 79, 185. doi:10.1007/s00284-022-02850-4

Panigrahi, S., Mohanty, S., and Rath, C. C. (2020). Characterization of endophytic bacteria *Enterobacter cloacae* MG00145 isolated from *Ocimum sanctum* with indole acetic acid (IAA) production and plant growth promoting capabilities against selected crops. *S. Afr. J. Bot.* 134, 17–26. doi:10.1016/j.sajb.2019.09.017

Parida, A., and Das, A. (2005). Salt tolerance and salinity effects on plants: A review. *Ecotoxicol. Environ. Saf.* 60, 324–349. doi:10.1016/j.ecoenv.2004.06.010

Park, H.-J., Kim, J. Y., Kim, J., Lee, J.-H., Hahn, J.-S., Gu, M. B., et al. (2009). Silver-ion-mediated reactive oxygen species generation affecting bactericidal activity. *Water Res.* 43, 1027–1032. doi:10.1016/j.watres.2008.12.002

Pasala, R. K., Khan, M. I. R., Minhas, P. S., Sultana, R., Per, T., Deokate, P., et al. (2016). Can plant bioregulators minimize the crop productivity losses caused by drought, heat stress and salinity? An integrated review. *J. Appl. Bot. Food.* 89, 113–125.

Pawlett, M., Ritz, K., Dorey, R. A., Rocks, S., Ramsden, J., and Harris, J. A. (2013). The impact of zero-valent iron nanoparticles upon soil microbial communities is context dependent. *Environ. Sci. Pollut. Res.* 20, 1041–1049. doi:10.1007/s11356-012-1196-2

Pei, Z., Ming, D., Liu, D., Wan, G., Geng, X., Gong, H., et al. (2010). Silicon improves the tolerance to water-deficit stress induced by polyethylene glycol in wheat (*Triticum aestivum* L.) seedlings. *J. Plant Growth Regul.* 29, 106–115. doi:10.1007/s00344-009-9120-9

Pelletier, D. A., Suresh, A. K., Holton, G. A., Mckeown, C. K., Wang, W., Gu, B., et al. (2010). Effects of engineered cerium oxide nanoparticles on bacterial growth and viability. *Appl. Environ. Microbiol.* 76, 7981–7989. doi:10.1128/aem.00650-10

Petruccelli, R., Bartolini, G., Ganino, T., Zelasco, S., Lombardo, L., Perri, E., et al. (2022). Cold stress, freezing adaptation, varietal susceptibility of *Olea europaea* L.: A review. *Plants (Basel).* 11, 1367. doi:10.3390/plants11101367

Pinedo, I., Ledger, T., Greve, M., and Poupin, M. J. (2015). *Burkholderia phytofirmans* PsJN induces long-term metabolic and transcriptional changes involved in *Arabidopsis thaliana* salt tolerance. *Front. Plant Sci.* 6, 466. doi:10.3389/fpls.2015.00466

Prasad, P., Pisipati, S., Momčilović, I., and Ristic, Z. (2011). Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. *J. Agron. Crop Sci.* 197, 430–441. doi:10.1111/j.1439-037x.2011.00477.x

Premachandra, D., Hudek, L., Enez, A., Ballard, R., Barnett, S., Franco, C. M., et al. (2020). Assessment of the capacity of beneficial bacterial inoculants to enhance canola (*Brassica napus* L.) growth under low water activity. *Agron. (Basel).* 10, 1449. doi:10.3390/agronomy10091449

Prucek, R., Tuček, J., Kilianová, M., Panáček, A., Kvítek, L., Filip, J., et al. (2011). The targeted antibacterial and antifungal properties of magnetic nanocomposite of iron oxide and silver nanoparticles. *Biomaterials* 32, 4704–4713. doi:10.1016/j.biomaterials.2011.03.039

Qian, D., Liu, H., Hu, F., Song, S., and Chen, Y. (2022). Extracellular electron transfer-dependent Cr(VI)/sulfate reduction mediated by iron sulfide nanoparticles. *J. Biosci. Bioeng.* 134, 153–161. doi:10.1016/j.jbiosc.2022.05.005

Qian, Y., Yu, H., He, D., Yang, H., Wang, W., Wan, X., et al. (2013). Biosynthesis of silver nanoparticles by the endophytic fungus *Epicoccum nigrum* and their activity against pathogenic fungi. *Bioprocess Biosyst. Eng.* 36, 1613–1619. doi:10.1007/s00449-013-0937-z

Radzig, M., Nadtochenko, V., Koksharova, O., Kiwi, J., Lipasova, V., and Khmel, I. (2013). Antibacterial effects of silver nanoparticles on gram-negative bacteria: Influence on the growth and biofilms formation, mechanisms of action. *Colloids Surfaces B Biointerfaces* 102, 300–306. doi:10.1016/j.colsurfb.2012.07.039

Rahi, D. K., and Parmar, A. S. (2014). Mycosynthesis of silver nanoparticles by an endophytic *Penicillium* species of *Aloe vera* root, evaluation of their antibacterial and antibiotic enhancing activity. *Int. J. Nanomater. Biostructures.* 6, 160–166.

Rahman, S., Rahman, L., Khalil, A. T., Ali, N., Zia, D., Ali, M., et al. (2019). Endophyte-mediated synthesis of silver nanoparticles and their biological applications. *Appl. Microbiol. Biotechnol.* 103, 2551–2569. doi:10.1007/s00253-019-09661-x

Ramadoss, D., Lakkineni, V. K., Bose, P., Ali, S., and Annapurna, K. J. S. (2013). Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. *SpringerPlus* 2, 6. doi:10.1186/2193-1801-2-6

Ramalingmam, P., Muthukrishnan, S., and Thangaraj, P. (2015). Biosynthesis of silver nanoparticles using an endophytic fungus, *Curvularia lunata* and its antimicrobial potential. *J. Nanosci. Nanoeng.* 1, 241–247.

Rana, K. L., Kour, D., Kaur, T., Devi, R., Yadav, A. N., Yadav, N., et al. (2020). Endophytic microbes: Biodiversity, plant growth-promoting mechanisms and potential applications for agricultural sustainability. *Antonie Leeuwenhoek* 113, 1075–1107. doi:10.1007/s10482-020-01429-y

Rani, A., Souche, Y. S., and Goel, R. (2009). Comparative assessment of *in situ* bioremediation potential of cadmium resistant acidophilic *Pseudomonas putida* 62BN and alkalophilic *Pseudomonas monteilli* 97AN strains on soybean. *Int. Biodeterior. Biodegrad.* 63, 62–66. doi:10.1016/j.ibiod.2008.07.002

Rashid, S., Charles, T. C., and Glick, B. R. (2012). Isolation and characterization of new plant growth-promoting bacterial endophytes. *Appl. Soil Ecol.* 61, 217–224. doi:10.1016/j.apsoil.2011.09.011

Raven, J. A. (1983). The transport and function of silicon in plants. *Biol. Rev.* 58, 179–207. doi:10.1111/j.1469-185x.1983.tb00385.x

Ravi, P., Somu, P., Acharya, D., Gomez, L. A., Thathapudi, J. J., Ramachandra, Y. L., et al. (2022). Isolation and phytochemical screening of endophytic fungi isolated from medicinal plant *Mappia foetida* and evaluation of its *in vitro* cytotoxicity in cancer. *Appl. Biochem. Biotechnol.* 194, 4570–4586. doi:10.1007/s12010-022-03929-1

Rawat, N., Sneh, L., and Singla-Pareek, A. P. (2020). Membrane dynamics during individual and combined abiotic stresses in plants and tools to study the same. *Physiol. Plant.* 171, 653–676.

Reddy, P. V. L., Hernandez-Viezcas, J., Peralta-Videa, J., and Gardea-Torresdey, J. (2016). Lessons learned: Are engineered nanomaterials toxic to terrestrial plants? *Sci. Total Environ.* 568, 470–479. doi:10.1016/j.scitotenv.2016.06.042

Rehman, H., Ali, W., Khan, N. Z., Aasim, M., Khan, T., and Khan, A. L. (2022). *Delphinium uncinatum* mediated biosynthesis of zinc oxide nanoparticles and *in-vitro* evaluation of their antioxidant, cytotoxic, antimicrobial, anti-diabetic, anti-inflammatory, and anti-aging activities. *Saudi J. Biol. Sci.* 30, 103485. doi:10.1016/j.sjbs.2022.103485

Rojas-Tapias, D., Moreno-Galván, A., Pardo-Díaz, S., Obando, M., Rivera, D., and Bonilla, R. (2012). Effect of inoculation with plant growth-promoting bacteria (PGPB) on amelioration of saline stress in maize (*Zea mays*). *Appl. Soil Ecol.* 61, 264–272. doi:10.1016/j.apsoil.2012.01.006

Rouet, M., Mathieu, Y., Barbier-Brygoo, H., and Laurière, C. (2006). Characterization of active oxygen-producing proteins in response to hypo-osmolarity in tobacco and *arabidopsis* cell suspensions: Identification of a cell wall peroxidase. *J. Exp. Bot.* 57, 1323–1332. doi:10.1093/jxb/erj107

Roy, A., Pandit, C., Gacem, A., Alqahtani, M. S., Bilal, M., Islam, S., et al. (2022). Biologically derived gold nanoparticles and their applications. *Bioinorg. Chem. Appl.* 2022, 1–13. doi:10.1155/2022/8184217

Sabaghnia, N., and Janmohammadi, M. (2015). "Effect of nano-silicon particles application on salinity tolerance in early growth of some lentil genotypes," in *Annales universitatis mariae curie-sklodowska, sectio C–biologia*, 39.

Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., and Hasanuzzaman, M. (2021). Abiotic stress and reactive oxygen species: Generation, signaling, and defense mechanisms. *Antioxidants* 10, 277. doi:10.3390/antiox10020277

Sadeghi, A., Karimi, E., Dahaji, P. A., Javid, M. G., Dalvand, Y., and Askari, H. (2018). Plant growth promoting activity of an auxin and siderophore producing isolate of *Streptomyces* under saline soil conditions. *World J. Microbiol. Biotechnol.* 34, 16. doi:10.1007/s11274-017-2393-4

Sadek, M. E., Shabana, Y. M., Sayed-Ahmed, K., and Abou-Tabl, A. H. (2022). Antifungal activities of sulfur and copper nanoparticles against cucumber postharvest diseases caused by *Botrytis cinerea* and *Sclerotinia sclerotiorum*. *J. Fungi (Basel).* 8, 412. doi:10.3390/jof8040412

Sahu, P. K., Thomas, P., Singh, S., and Gupta, A. (2020). Taxonomic and functional diversity of cultivable endophytes with respect to the fitness of cultivars against *Ralstonia solanacearum*. *J. Plant Dis. Prot. (2006).* 127, 667–676. doi:10.1007/s41348-020-00320-2

Saluja, B., Sharma, V. J. S., and Journal, S. (2014). Cadmium resistance mechanism in acidophilic and alkalophilic bacterial isolates and their application in bioremediation of metal-contaminated soil. *Soil Sediment Contam. Int. J.* 23, 1–17. doi:10.1080/15320383.2013.772094

Santhoshkumar, J., Sowmya, B., Kumar, S. V., and Rajeshkumar, S. (2019). Toxicology evaluation and antidermatophytic activity of silver nanoparticles synthesized using leaf extract of *Passiflora caerulea*. *S. Afr. J. Chem. Eng.* 29, 17–23. doi:10.1016/j.sajce.2019.04.001

Santoyo, G., Gamalero, E., and Glick, B. R. (2021a). Mycorrhizal-bacterial amelioration of plant abiotic and biotic stress. *Front. Sustain. Food Syst.* 5, 672881. doi:10.3389/fsufs.2021.672881

Santoyo, G., Guzmán-Guzmán, P., Parra-Cota, F. I., Santos-Villalobos, S. D. L., Orozco-Mosqueda, M. D. C., and Glick, B. R. (2021b). Plant growth stimulation by microbial consortia. *Agron. (Basel).* 11, 219. doi:10.3390/agronomy11020219

Santoyo, G., Moreno-Hagelsieb, G., Del Carmen Orozco-Mosqueda, M., and Glick, B. R. (2016). Plant growth-promoting bacterial endophytes. *Microbiol. Res.* 183, 92–99. doi:10.1016/j.micres.2015.11.008

Saqib, S., Nazeer, A., Ali, M., Zaman, W., Younas, M., Shahzad, A., et al. (2022). Catalytic potential of endophytes facilitates synthesis of biometallic zinc oxide nanoparticles for agricultural application. *BioMetals* 35, 967–985. doi:10.1007/s10534-022-00417-1

Sardar, R., Ahmed, S., and Yasin, N. A. (2022). Titanium dioxide nanoparticles mitigate cadmium toxicity in Coriandrum sativum L. through modulating antioxidant system, stress markers and reducing cadmium uptake. *Environ. Pollut.* 292, 118373. doi:10.1016/j.envpol.2021.118373

Savvas, D., Giotis, D., Chatzieustratiou, E., Bakea, M., and Patakioutas, G. (2009). Silicon supply in soilless cultivations of zucchini alleviates stress induced by salinity and powdery mildew infections. *Environ. Exp. Bot.* 65, 11–17. doi:10.1016/j.envexpbot.2008.07.004

Saxena, R., Tomar, R. S., and Kumar, M. (2016). Exploring nanobiotechnology to mitigate abiotic stress in crop plants. *J. Pharm. Sci. Res.* 8, 974.

Sedghi, M., Hadi, M., and Toluie, S. G. (2013). Effect of nano zinc oxide on the germination parameters of soybean seeds under drought stress. *Ser. Biol.* 16, 73.

Sen, S., and Chandrasekhar, C. (2014). Effect of PGPR on growth promotion of rice (*Oryza sativa* L.) under salt stress. *Asian J. Plant Sci. Res.* 4, 62–67.

Shabnam, N., Pardha-Saradhi, P., and Sharmila, P. (2014). Phenolics impart Au^{3+}-stress tolerance to cowpea by generating nanoparticles. *PLoS One* 9, e85242. doi:10.1371/journal.pone.0085242

Shah, V., Luxton, T. P., Walker, V. K., Brumfield, T., Yost, J., Shah, S., et al. (2016). Fate and impact of zero-valent copper nanoparticles on geographically-distinct soils. *Sci. Total Environ.* 573, 661–670. doi:10.1016/j.scitotenv.2016.08.114

Shahid, M., Zeyad, M. T., Syed, A., Singh, U. B., Mohamed, A., Bahkali, A. H., et al. (2022). Stress-tolerant endophytic isolate *Priestia aryabhattai* BPR-9 modulates physio-biochemical mechanisms in wheat (*Triticum aestivum* L.) for enhanced salt tolerance. *Int. J. Environ. Res. Public Health* 19, 10883. doi:10.3390/ijerph191710883

Sharma, A., Sagar, A., Rana, J., and Rani, R. (2022). Green synthesis of silver nanoparticles and its antibacterial activity using fungus *Talaromyces purpureogenus* isolated from *Taxus baccata* Linn. *Micro Nano Syst. Lett.* 10, 2–12. doi:10.1186/s40486-022-00144-9

Sharma, A., Shankhdhar, D., and Shankhdhar, S. (2013). Enhancing grain iron content of rice by the application of plant growth promoting rhizobacteria. *Plant Soil Environ.* 59, 89–94. doi:10.17221/683/2012-pse

Sharma, P., Jha, A. B., Dubey, R. S., and Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J. Bot.* 2012, 1–26. doi:10.1155/2012/217037

Sheikhalipour, M., Esmaielpour, B., Behnamian, M., Gohari, G., Giglou, M. T., Vachova, P., et al. (2021). Chitosan–selenium nanoparticle (Cs–Se NP) foliar spray alleviates salt stress in bitter melon. *Nanomaterials* 11, 684. doi:10.3390/nano11030684

Sherin, G., Raj-Aswathi, K. P., and Puthur, J. T. (2022). Photosynthetic functions in plants subjected to stresses are positively influenced by priming. *Plant Stress* 4, 100079. doi:10.1016/j.stress.2022.100079

Shilev, S., Sancho, E. D., and Benlloch-González, M. J. (2012). Rhizospheric bacteria alleviate salt-produced stress in sunflower. *J. Environ. Manage.* 95, S37–S41. doi:10.1016/j.jenvman.2010.07.019

Shinde, B. H., Inamdar, S. N., Nalawade, S. A., and Chaudhari, S. B. (2022). A systematic review on antifungal and insecticidal applications of biosynthesized metal nanoparticles. *Mater. Today Proc.* doi:10.1016/j.matpr.2022.09.548

Shirinbayan, S., Khosravi, H., and Malakouti, M. J. (2019). Alleviation of drought stress in maize (*Zea mays*) by inoculation with *Azotobacter* strains isolated from semi-arid regions. *Appl. Soil Ecol.* 133, 138–145. doi:10.1016/j.apsoil.2018.09.015

Shukla, P. S., Agarwal, P. K., and Jha, B. J. J. O. P. G. R. (2012). Improved salinity tolerance of *Arachis hypogaea* (L.) by the interaction of halotolerant plant-growth-promoting rhizobacteria. *J. Plant Growth Regul.* 31, 195–206. doi:10.1007/s00344-011-9231-y

Silambarasan, S., Logeswari, P., Valentine, A., and Cornejo, P. (2019). Role of *Curtobacterium herbarum* strain CAH5 on aluminum bioaccumulation and enhancement of *Lactuca sativa* growth under aluminum and drought stresses. *Ecotoxicol. Environ. Saf.* 183, 109573. doi:10.1016/j.ecoenv.2019.109573

Silambarasan, S., and Vangnai, A. S. (2017). Plant-growth promoting *Candida* sp. AVGB4 with capability of 4-nitroaniline biodegradation under drought stress. *Ecotoxicol. Environ. Saf.* 139, 472–480. doi:10.1016/j.ecoenv.2017.02.018

Simontacchi, M., Galatro, A., Ramos-Artuso, F., and Santa-María, G. E. (2015). Plant survival in a changing environment: The role of nitric oxide in plant responses to abiotic stress. *Front. Plant Sci.* 6, 977. doi:10.3389/fpls.2015.00977

Singh, D. P., Prabha, R., Yandigeri, M. S., and Arora, D. K. (2011). Cyanobacteria-mediated phenylpropanoids and phytohormones in rice (*Oryza sativa*) enhance plant growth and stress tolerance. *Ant. Van Leeuwenhoek* 100, 557–568. doi:10.1007/s10482-011-9611-0

Singh, D., Rathod, V., Ninganagouda, S., Herimath, J., and Kulkarni, P. (2013). Biosynthesis of silver nanoparticle by endophytic fungi *Pencillium* sp. isolated from *Curcuma longa* (turmeric) and its antibacterial activity against pathogenic gram negative bacteria. *J. Pharm. Res.* 7, 448–453. doi:10.1016/j.jopr.2013.06.003

Singh, J., and Lee, B.-K. (2016). Influence of nano-TiO_2 particles on the bioaccumulation of Cd in soybean plants (*Glycine max*): A possible mechanism for the removal of Cd from the contaminated soil. *J. Environ. Manage.* 170, 88–96. doi:10.1016/j.jenvman.2016.01.015

Singh, J., Perumal, V., Singh, U., Tripathi, D. K., and Sharma, S. (2022a). Green synthesis of silver nanoparticles from bark extract of *terminalia arjuna* and their application as next generation antibacterial agents. *Curr. Nanosci.* 18, 743–757. doi:10.2174/1573413718666220221102909

Singh, J., Vishwakarma, K., Ramawat, N., Rai, P., Singh, V. K., Mishra, R. K., et al. (2019). Nanomaterials and microbes' interactions: A contemporary overview. *3 Biotech.* 9, 68–14. doi:10.1007/s13205-019-1576-0

Singh, M., Qureshi, K. A., Jaremko, M., Rajput, M., Singh, S. K., KaushalendraPandey, K. D., et al. (2022b). Bioprospects of endophytic bacteria in plant growth promotion and ag-nanoparticle biosynthesis. *Plants (Basel).* 11, 1787. doi:10.3390/plants11141787

Soliman, A. M., Abdel-Latif, W., Shehata, I. H., Fouda, A., Abdo, A. M., and Ahmed, Y. M. (2021). Green approach to overcome the resistance pattern of *Candida* spp. using biosynthesized silver nanoparticles fabricated by *Penicillium chrysogenum* F9. *Biol. Trace Elem. Res.* 199, 800–811. doi:10.1007/s12011-020-02188-7

Soltani Nejad, M., Samandari Najafabadi, N., Aghighi, S., Pakina, E., and Zargar, M. (2022). Evaluation of *Phoma* sp. biomass as an endophytic fungus for synthesis of extracellular gold nanoparticles with antibacterial and antifungal properties. *Molecules* 27, 1181. doi:10.3390/molecules27041181

Sonawane, H., Shelke, D., Chambhare, M., Dixit, N., Math, S., Sen, S., et al. (2022). Fungi-derived agriculturally important nanoparticles and their application in crop stress management–Prospects and environmental risks. *Environ. Res.* 212, 113543. doi:10.1016/j.envres.2022.113543

Sonbol, H., Mohammed, A., and Korany, S. M. (2022). Soil fungi as biomediator in silver nanoparticles formation and antimicrobial efficacy. *Int. J. Nanomedicine* 17, 2843–2863. doi:10.2147/ijn.s356724

Sonkar, S., Pandey, B., Rathore, S. S., Sharma, L., and Singh, A. K. (2021). "Applications of nanobiotechnology in overcoming temperature stress," in *Nanobiotechnology*. Editors J. M. Al-Khayri, M. I. Ansari, and A. K. Singh (Cham: Springer), 417–435.

Sorty, A. M., Meena, K. K., Choudhary, K., Bitla, U. M., Minhas, P., and Krishnani, K. (2016). Effect of plant growth promoting bacteria associated with halophytic weed (*Psoralea corylifolia* L) on germination and seedling growth of wheat under saline conditions. *Appl. Biochem. Biotechnol.* 180, 872–882. doi:10.1007/s12010-016-2139-z

Suarez, C., Cardinale, M., Ratering, S., Steffens, D., Jung, S., Montoya, A. M. Z., et al. (2015). Plant growth-promoting effects of *Hartmannibacter diazotrophicus* on summer barley (*Hordeum vulgare* L.) under salt stress. *Appl. Soil Ecol.* 95, 23–30. doi:10.1016/j.apsoil.2015.04.017

Sun, C., Johnson, J. M., Cai, D., Sherameti, I., Oelmüller, R., and Lou, B. (2010). *Piriformospora indica* confers drought tolerance in Chinese cabbage leaves by stimulating antioxidant enzymes, the expression of drought-related genes and the plastid-localized CAS protein. *J. Plant Physiol.* 167, 1009–1017. doi:10.1016/j.jplph.2010.02.013

Sunkar, S., and Nachiyar, C. V. (2012a). Biogenesis of antibacterial silver nanoparticles using the endophytic bacterium *Bacillus cereus* isolated from *Garcinia xanthochymus*. *Asian pac. J. Trop. Biomed.* 2, 953–959. doi:10.1016/s2221-1691(13)60006-4

Sunkar, S., and Nachiyar, C. V. (2012b). Microbial synthesis and characterization of silver nanoparticles using the endophytic bacterium *Bacillus cereus*: A novel source in the benign synthesis. *Glob. J. Med. Res.* 12, 43–50.

Teheran-Sierra, L. G., Funnicelli, M. I. G., De Carvalho, L. a. L., Ferro, M. I. T., Soares, M. A., and Pinheiro, D. G. (2021). Bacterial communities associated with sugarcane under different agricultural management exhibit a diversity of plant growth-promoting traits and evidence of synergistic effect. *Microbiol. Res.* 247, 126729. doi:10.1016/j.micres.2021.126729

Thepbandit, W., Papathoti, N. K., Daddam, J. R., Thumanu, K., Siriwong, S., Thanh, T. L., et al. (2021). Identification of salicylic acid mechanism against leaf blight disease in *Oryza sativa* by SR-FTIR microspectroscopic and docking studies. *Pathogens* 10, 652. doi:10.3390/pathogens10060652

Thiagarajan, V., and Ramasubbu, S. (2021). Fate and behaviour of TiO_2 nanoparticles in the Soil: Their impact on staple food crops. *Water Air Soil Pollut.* 232, 274–318. doi:10.1007/s11270-021-05219-8

Thomas, T. T, D., and Puthur, J. T. (2017). UV radiation priming: A means of amplifying the inherent potential for abiotic stress tolerance in crop plants. *Environ. Exp. Bot.* 138, 57–66. doi:10.1016/j.envexpbot.2017.03.003

Tittabutr, P., Piromyou, P., Longtonglang, A., Noisa-Ngiam, R., Boonkerd, N., and Teaumroong, N. (2013). Alleviation of the effect of environmental stresses using co-inoculation of mungbean by *Bradyrhizobium* and rhizobacteria containing stress-induced ACC deaminase enzyme. *Soil Sci. Plant Nutr.* 59, 559–571. doi:10.1080/00380768.2013.804391

Tiwari, S., Lata, C., Chauhan, P. S., and Nautiyal, C. S. (2016). *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. *Plant Physiol. biochem.* 99, 108–117. doi:10.1016/j.plaphy.2015.11.001

Tripathi, D. K., Singh, V. P., Prasad, S. M., Chauhan, D. K., and Dubey, N. K. (2015). Silicon nanoparticles (SiNp) alleviate chromium (VI) phytotoxicity in *Pisum sativum* (L.) seedlings. *Plant Physiol. biochem.* 96, 189–198. doi:10.1016/j.plaphy.2015.07.026

Turbat, A., Rakk, D., Vigneshwari, A., Kocsubé, S., Thu, H., Szepesi, Á., et al. (2020). Characterization of the plant growth-promoting activities of endophytic fungi isolated from *Sophora flavescens*. *Microorganisms* 8, 683. doi:10.3390/microorganisms8050683

Tuteja, N., and Mahajan, S. (2007). Calcium signaling network in plants: An overview. *Plant Signal. Behav.* 2, 79–85. doi:10.4161/psb.2.2.4176

Tuteja, N., and Sopory, S. K. (2008). Chemical signaling under abiotic stress environment in plants. *Plant Signal. Behav.* 3, 525–536. doi:10.4161/psb.3.8.6186

Umapathy, V. R., Natarajan, P. M., Sumathijones, C., Swamikannu, B., Johnson, W. M. S., Alagarsamy, V., et al. (2022). Current trends and future perspectives on dental nanomaterials – an overview of nanotechnology strategies in dentistry. *J. King Saud Univ. - Sci.* 34, 102231. doi:10.1016/j.jksus.2022.102231

Upadhyay, S., Singh, J., and Singh, D. P. (2011). Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. *Pedosphere* 21, 214–222. doi:10.1016/s1002-0160(11)60120-3

Van Nguyen, D., Nguyen, H. M., Le, N. T., Nguyen, K. H., Nguyen, H. T., Le, H. M., et al. (2022). Copper nanoparticle application enhances plant growth and grain yield in maize under drought stress conditions. *J. Plant Growth Regul.* 41, 364–375. doi:10.1007/s00344-021-10301-w

Varshney, R. K., Bansal, K. C., Aggarwal, P. K., Datta, S. K., and Craufurd, P. Q. (2011). Agricultural biotechnology for crop improvement in a variable climate: Hope or hype? *Trends Plant Sci.* 16, 363–371. doi:10.1016/j.tplants.2011.03.004

Vimal, S. R., Patel, V. K., and Singh, J. S. (2019). Plant growth promoting *Curtobacterium albidum* strain SRV4: An agriculturally important microbe to alleviate salinity stress in paddy plants. *Ecol. Indic.* 105, 553–562. doi:10.1016/j.ecolind.2018.05.014

Vurukonda, S. S. K. P., Vardharajula, S., Shrivastava, M., and Skz, A. J. R. (2016). Multifunctional *Pseudomonas putida* strain FBKV2 from arid rhizosphere soil and its growth promotional effects on maize under drought stress. *Rhizosphere* 1, 4–13. doi:10.1016/j.rhisph.2016.07.005

Wahid, A. (2007). Physiological implications of metabolite biosynthesis for net assimilation and heat-stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. *J. Plant Res.* 120, 219–228. doi:10.1007/s10265-006-0040-5

Wang, C. Y., Makvandi, P., Zare, E. N., Tay, F. R., and Niu, L. N. (2020). Advances in antimicrobial organic and inorganic nanocompounds in biomedicine. *Adv. Ther. (Weinh).* 3, 2000024. doi:10.1002/adtp.202000024

Worms, I. A., Boltzman, J., Garcia, M., and Slaveykova, V. I. (2012). Cell-wall-dependent effect of carboxyl-CdSe/ZnS quantum dots on lead and copper availability to green microalgae. *Environ. Pollut.* 167, 27–33. doi:10.1016/j.envpol.2012.03.030

Wu, H., Yin, J.-J., Wamer, W. G., Zeng, M., and Lo, Y. M. (2014). Reactive oxygen species-related activities of nano-iron metal and nano-iron oxides. *J. Food Drug Anal.* 22, 86–94. doi:10.1016/j.jfda.2014.01.007

Wu, Z., Yue, H., Lu, J., and Li, C. J. (2012). Characterization of rhizobacterial strain Rs-2 with ACC deaminase activity and its performance in promoting cotton growth under salinity stress. *World J. Microbiol. Biotechnol.* 28, 2383–2393. doi:10.1007/s11274-012-1047-9

Xu, H., Lu, Y., and Tong, S. (2018). Effects of arbuscular mycorrhizal fungi on photosynthesis and chlorophyll fluorescence of maize seedlings under salt stress. *Emir. J. Food Agric.* 30, 199–204. doi:10.9755/ejfa.2018.v30.i3.1642

Yadav, A. N. (2017). Agriculturally important microbiomes: Biodiversity and multifarious PGP attributes for amelioration of diverse abiotic stresses in crops for sustainable agriculture. *Biomed. J. Sci. Tech. Res.* 1, 861–864. doi:10.26717/bjstr.2017.01.000321

Yang, Y., Chen, Q., Wall, J. D., and Hu, Z. (2012a). Potential nanosilver impact on anaerobic digestion at moderate silver concentrations. *Water Res.* 46, 1176–1184. doi:10.1016/j.watres.2011.12.024

Yang, Y., Mathieu, J. M., Chattopadhyay, S., Miller, J. T., Wu, T., Shibata, T., et al. (2012b). Defense mechanisms of *Pseudomonas aeruginosa* PAO1 against quantum dots and their released heavy metals. *ACS Nano* 6, 6091–6098. doi:10.1021/nn3011619

Yashavantha Rao, H. C., Nagendra-Prasad, M. N., Prasad, A., Harini, B. P., Azmath, P., Rakshith, D., et al. (2016). Biomimetic synthesis of silver nanoparticles using endosymbiotic bacterium inhabiting *Euphorbia hirta* L. and their bactericidal potential. *Scientifica* 2016, 9020239. doi:10.1155/2016/9020239

Yolcu, S., Ozdemir, F., Güler, A., and Bor, M. (2016). Histone acetylation influences the transcriptional activation of POX in *Beta vulgaris* L. and *Beta maritima* L. under salt stress. *Plant Physiol. biochem.* 100, 37–46. doi:10.1016/j.plaphy.2015.12.019

Younesi, O., and Moradi, A. J. A. (2014). Effects of plant growth-promoting rhizobacterium (PGPR) and arbuscular mycorrhizal fungus (AMF) on antioxidant enzyme activities in salt-stressed bean (*Phaseolus vulgaris* L.) *Agriculture* 60, 10–21. doi:10.2478/agri-2014-0002

Zare, A. S., Ganjeali, A., Kakhki, M. R. V., Cheniany, M., and Mashreghi, M. (2022). Plant elicitation and TiO2 nanoparticles application as an effective strategy for improving the growth, biochemical properties, and essential oil of peppermint. *Physiol. Mol. Biol. Plants* 28, 1391–1406.

Zhang, J., Wang, P., Tian, H., Jiang, H., Wang, Y., and Yan, C. J. S. (2018). Identification of interior salt-tolerant bacteria from ice plant *Mesembryanthemum crystallinum* and evaluation of their promoting effects. *Symbiosis* 76, 243–252. doi:10.1007/s13199-018-0551-6

Zhang, R., Tu, C., Zhang, H., and Luo, Y. (2020). Stability and transport of titanium dioxide nanoparticles in three variable-charge soils. *J. Soils Sediments* 20, 1395–1403. doi:10.1007/s11368-019-02509-x

Zhao, L., Peng, B., Hernandez-Viezcas, J. A., Rico, C., Sun, Y., Peralta-Videa, J. R., et al. (2012). Stress response and tolerance of Zea mays to CeO2 nanoparticles: Cross talk among H2O2, heat shock protein, and lipid peroxidation. *ACS Nano* 6, 9615–9622. doi:10.1021/nn302975u

Zhou, H., Wu, H., Zhang, F., Su, Y., Guan, W., Xie, Y., et al. (2021). Molecular basis of cerium oxide nanoparticle enhancement of rice salt tolerance and yield. *Environ. Sci. Nano* 8, 3294–3311. doi:10.1039/d1en00390a

Zhou, J., Li, P., Meng, D., Gu, Y., Zheng, Z., Yin, H., et al. (2020). Isolation, characterization and inoculation of Cd tolerant rice endophytes and their impacts on rice under Cd contaminated environment. *Environ. Pollut.* 260, 113990. doi:10.1016/j.envpol.2020.113990

Zulfiqar, F., Navarro, M., Ashraf, M., Akram, N. A., and Munné-Bosch, S. (2019). Nanofertilizer use for sustainable agriculture: Advantages and limitations. *Plant Sci.* 289, 110270. doi:10.1016/j.plantsci.2019.110270

frontiers | Frontiers in Microbiology

TYPE Review
PUBLISHED 16 February 2023
DOI 10.3389/fmicb.2023.1040901

OPEN ACCESS

EDITED BY
Parul Chaudhary,
National Dairy Research Institute (ICAR), India

REVIEWED BY
Remember Roger Adjei,
University of Energy and Natural Resources, Ghana
Anuj Chaudhary,
Shobhit University,
India

*CORRESPONDENCE
Olubukola O. Babalola
✉ olubukola.babalola@nwu.ac.za

SPECIALTY SECTION
This article was submitted to Microbiotechnology, a section of the journal Frontiers in Microbiology

RECEIVED 09 September 2022
ACCEPTED 17 January 2023
PUBLISHED 16 February 2023

CITATION
Ayilara MS, Adeleke BS, Akinola SA, Fayose CA, Adeyemi UT, Gbadegesin LA, Omole RK, Johnson RM, Uthman QO and Babalola OO (2023) Biopesticides as a promising alternative to synthetic pesticides: A case for microbial pesticides, phytopesticides, and nanobiopesticides.
Front. Microbiol. 14:1040901.
doi: 10.3389/fmicb.2023.1040901

Biopesticides as a promising alternative to synthetic pesticides: A case for microbial pesticides, phytopesticides, and nanobiopesticides

Modupe S. Ayilara[1,2], Bartholomew S. Adeleke[1,3], Saheed A. Akinola[1,4], Chris A. Fayose[5], Uswat T. Adeyemi[6], Lanre A. Gbadegesin[7], Richard K. Omole[8,9], Remilekun M. Johnson[8], Qudus O. Uthman[10] and Olubukola O. Babalola[1]*

[1]Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa, [2]Department of Biological Sciences, Kings University, Ode-Omu, Nigeria, [3]Department of Biological Sciences, Microbiology Unit, School of Science, Olusegun Agagu University of Science and Technology, Okitipupa, Nigeria, [4]Department of Microbiology and Parasitology, School of Medicine and Pharmacy, College of Medicine and Health Sciences, University of Rwanda, Butare, Rwanda, [5]Department of Agricultural Technology, Ekiti State Polytechnic, Isan-Ekiti, Nigeria, [6]Department of Agricultural Economics and Farm Management, Faculty of Agriculture, University of Ilorin, Ilorin, Nigeria, [7]Institute of Mountain Hazards and Environment, University of Chinese Academy of Sciences, Chengdu, China, [8]Department of Microbiology, Obafemi Awolowo University, Ile-Ife, Nigeria, [9]Microbiology Unit, Department of Applied Sciences, Osun State College of Technology, Esa-Oke, Nigeria, [10]Soil, Water and Ecosystem Sciences, University of Florida, Gainesville, FL, United States

Over the years, synthetic pesticides like herbicides, algicides, miticides, bactericides, fumigants, termiticides, repellents, insecticides, molluscicides, nematicides, and pheromones have been used to improve crop yield. When pesticides are used, the over-application and excess discharge into water bodies during rainfall often lead to death of fish and other aquatic life. Even when the fishes still live, their consumption by humans may lead to the biomagnification of chemicals in the body system and can cause deadly diseases, such as cancer, kidney diseases, diabetes, liver dysfunction, eczema, neurological destruction, cardiovascular diseases, and so on. Equally, synthetic pesticides harm the soil texture, soil microbes, animals, and plants. The dangers associated with the use of synthetic pesticides have necessitated the need for alternative use of organic pesticides (biopesticides), which are cheaper, environment friendly, and sustainable. Biopesticides can be sourced from microbes (e.g., metabolites), plants (e.g., from their exudates, essential oil, and extracts from bark, root, and leaves), and nanoparticles of biological origin (e.g., silver and gold nanoparticles). Unlike synthetic pesticides, microbial pesticides are specific in action, can be easily sourced without the need for expensive chemicals, and are environmentally sustainable without residual effects. Phytopesticides have myriad of phytochemical compounds that make them exhibit various mechanisms of action, likewise, they are not associated with the release of greenhouse gases and are of lesser risks to human health compared to the available synthetic pesticides. Nanobiopesticides have higher pesticidal activity, targeted or controlled release with top-notch biocompatibility and biodegradability. In this review, we examined the different types of pesticides, the merits, and demerits of synthetic pesticides and biopesticides, but more importantly, we x-rayed appropriate and sustainable approaches to improve the acceptability and commercial usage of microbial pesticides, phytopesticides, and nanobiopesticides for plant nutrition, crop protection/yield, animal/human health promotion, and their possible incorporation into the integrated pest management system.

KEYWORDS
nanoparticles, biopesticides, synthetic pesticides, soil health, pesticides

1. Introduction

From antiquity, the use of synthetic (chemical) pesticides to control crop pests for improved crop production is known (Anani et al., 2020). Synthetic pesticides are made from chemicals and carriers, such as polymers (Rakhimol et al., 2020), which are specific for different pests. They range from those employed in the control of weeds (herbicides), algae (algicides), fungi (fungicide), mites or ticks (miticides/acaricides), bacteria (bactericides), rodents (rodenticide), termites (termiticides), insects (insecticides), molluscs (molluscicides), and nematodes (nematicides), which form the basis of their classification (Anakwue, 2019). Another mode of pesticide classification can be based on their active ingredients, which include organochlorines, dichlorvos, diazinon, diamide, chlorpyrifos, etc. Although synthetic pesticides have positive effects on crop yield and productivity, they also have some negative impacts on soil biodiversity, animals, aquatic life, and humans (Farooq et al., 2019). Synthetic pesticides usually render the soil brittle, reduce soil respiration, and lessen the activities of some macroorganisms in the soil, such as earthworms (Pertile et al., 2020; Pelosi et al., 2021). They also reduce the characteristics of animal offspring, animal immunity to diseases, vitality, and the success of mating in animals (Syromyatnikov et al., 2020). They negatively affect soil microorganisms by limiting their biological services in the production of certain plant growth-promoting traits, such as siderophores, nitrogen, indole-3-acetic, etc. (Kumar and Kumar, 2019). When synthetic pesticides get into the environment through different means, such as vapormovements, indiscriminate disposal, droplet drift, erosion, and leaching, some non-targeted plants are encountered, thus resulting in a decline in the plant's photosynthetic ability and seed production (Hashimi et al., 2020). The intrusion of pesticides into the water bodies during runoff can lead to the death of aquatic life and water pollution. Also, the accumulation of pesticides in the water bodies can be transitional from the aquatic lives to the animals and humans, and their biomagnification can result in deadly diseases, such as cancer, kidney diseases, skin rashes, diabetes, etc. (Jayaraj et al., 2017; Sabarwal et al., 2018; Manfo et al., 2020). However, biopesticides have emerged and have been very useful in the control of pests with lot of merits.

Biopesticides are cheap, environment-friendly, specific in their mode of action, sustainable, do not leave residues, and are not associated with the release of greenhouse gases (Borges et al., 2021). These biopesticides can be in the form of phytopesticides (plant origin; Idris et al., 2022), microbial pesticides (microbial origin; Harish et al., 2021), and nanobiopesticides (nanoparticles produced from biological agents; Abdollahdokht et al., 2022; Pan et al., 2023). Unlike synthetic pesticides, microbial pesticides are specific in action, can be easily sourced without the need for expensive chemicals, and are environmentally sustainable without residual effects (Harish et al., 2021; Hummadi et al., 2021). Phytopesticides have myriad of phytochemical compounds that make them exhibit various mechanisms of action, likewise, they are not associated with the release of greenhouse gases and are of lesser risks to human health compared to the available synthetic pesticides (Malahlela et al., 2021; Idris et al., 2022). Nanobiopesticides have higher pesticidal activity, targeted or controlled release with top-notch biocompatibility, and biodegradability compared to the synthetic pesticides (Abdollahdokht et al., 2022; Pan et al., 2023). Biopesticides act through different mechanisms, which include the inhibition and destruction of the plasma membrane and protein translation of pathogens/pests. Although, a few drawbacks have reduced their acceptability and commercial utilization, yet, biopesticides are highly specific in their target, have a short shelf life, are less persistent in the soil environment, and originate from sustainable raw materials, unlike synthetic pesticides (Kumar et al., 2021). Some of the merits of biopesticides mentioned above could also serve as their demerits. For example, the specificity in their target toward pest could be a demerit if the desire is to control many pests simultaneously. Also, their short shelf life means they are easily degradable and persist less in the environment, but this turns to a demerit if the goal is to completely eliminate the existing pests and prevent the growth of the pests that will come after the application of the biopesticides. The critical assessment of these merits and demerits, and the possible measures to improve on these seeming drawbacks has become very important. Therefore, this review examined the types, effects, advantages, and disadvantages of both synthetic and biopesticides. Also, different measures to improve on biopesticides (that is, microbial pesticides, phytopesticides, and nanobiopesticides) for possible incorporation into the integrated pest management system to reduce yield and quality loss were adequately discussed.

2. Classification of pesticides

Pesticides can be classified based on their active ingredients, functions, and sources. According to their active ingredients, pesticides are classified into organochlorines, propanil, and so on (Table 1). In terms of their functions, they can be classified into herbicides, fungicides, algicides, rodenticides, and so on (Figure 1). However, according to their sources, pesticides are classified into synthetic pesticides and biopesticides. Many pesticides, which include carbofuran, carbendazim, dichlorvos, anthraquinone, dinocap, paraquat, methomyl, aldicarb, and diuron have been banned for use in a lot of countries due to their toxicity to humans (Boucaud-Maitre et al., 2019). These banned pesticides are usually preferred by farmers because they are more affordable and more available compared to unbanned pesticides (Kehinde and Tijani, 2021). It is therefore important for World Health Organization (WHO), Food and Agriculture Organization (FAO), and other regulatory bodies to impose a ban on such products worldwide and also sanction companies that produce them.

2.1. Classification of pesticides according to their functions

Pesticides can be classified according to the functions they perform. For instance, algicides (acaricides) destroy algae on different surfaces (Zheng et al., 2018), and antifeedants prevent the destruction of plants

TABLE 1 Classification of pesticides according to their active ingredients.

Biopesticides (Brand name)	Active ingredient	Pest controlled	Mode of action	References
Endosulfan	Organochlorines	Silkworm and Armyworm	It alters the enzymatic function and the electrophysiological properties of the nerve cell.	Anikwe et al. (2021); Indratin et al. (2021)
Mancozeb	Metal–organic compounds	*Phytophthora infestans*	It disrupts the biochemical processes within the cells of pests by interfering with the enzymes containing sulphydryl groups.	Sari and Lubis (2021)
Diazol	Diazinon	*B. invadens*	It inhibits the enzyme acetylcholinesterase (AChE), which hydrolyzes the neurotransmitter acetylcholine (ACh) in cholinergic synapses and neuromuscular junctions.	Abdullahi et al. (2020)
DDForce	Dichlorvos	*Phytophthora capsici*	It inhibits the neural acetylcholinesterase enzyme.	Aba et al. (2018); Okoroiwu and Iwara (2018)
Aldicarb	Carbamic and thiocarbamide derivatives	Thrips (*Frankliniella* sp.)	It inhibits the cholinesterase enzyme.	Allen et al. (2018)
Lefenuron	Urea derivatives	Dicotyledonous weed and broom corn plantation cereal	It interferes with the deposition synthesis, and polymerization, of chitin.	Abraham and Vasantha (2020); Ghelichpour et al. (2020); Surma et al. (2021)
Pyrinex Lorsban	Chlorpyrifos Chlorpyrifos	*B. invadens* Citrus peel miner larvae	It inhibits the cholinesterase enzyme.	Abdullahi et al. (2020); Maurer et al. (2018)
Sniper	Diamide	*S. exigua,* mosquitoes	It causes the misregulation of the ryanodine receptors (RyRs) in insects.	Ebuehi et al. (2017); Rabelo et al. (2020)
Cydim super	Cypermethrin+dimethoate	*B. invadens*	It modulates the sodium channel.	Abdullahi et al. (2020)
Talstar	Pyrethroid	*Agrotis ipsilon,* Tropical sob webworm	It modulates the sodium channel.	Rabelo et al. (2020); Campos et al. (2022)
Pendillin	Pendimenthalin	Weed	It inhibits root and shoots growth.	Dugje et al. (2020)
Laraforce	Lamdacyhalothrin	Insect	It disrupts gating by disrupting the gating mechanism of sodium channels.	Oso and Awe (2019)
Regalia	Chlorothalonil	Downy mildew and powdery mildew	It deactivates and reduces glutathione.	Jones et al. (2020); Scariot et al. (2022)
Deltapaz	Deltamethrin	*B. invadens*	It interferes with the normal production and conduction of nerve signals in the nervous system.	Abdullahi et al. (2020)
Alachlor	Chloroacetanilide	*B. stearothermophilus*	It blocks the synthesis of lipids and isoprenoids.	Pereira et al. (2021)
Roundup	Glycophosphate	Broomrape	It blocks the activity of the 5-enol-pyruvyl-shikimate-3-phosphate synthase (EPSPS) enzyme	Kanissery et al. (2019); Elsakhawy et al. (2020)
Dinocap	Phenol and nitrophenol derivatives	*Podosphaera pannosa*	It causes renal toxicity.	Kumar and Chandel (2018)
Caocobre	Copper-containing compounds	Cocoa black pod disease	It inhibits enzymes and disrupts the pest's cellular proteins.	Husak (2015); Tsufac et al. (2020)
Paraeforce	Paraquat	Weed	It inhibits photosynthesis.	Imoloame (2021)
Aminforce	2,4-D Amine SL	Weed	It interferes with the hormones of the pest.	Dogara et al. (2022)
Butaforce	Butachlor	*Bufo regularis* tadpole	It inhibits cell division in pests.	Ejilibe et al. (2019)
Atrazine	Atrazine	Weed	It interferes with photosynthesis.	Sumekar et al. (2022)
Ronstar	Oxidiaxone	Weed	It inhibits the protoporhyrinogen oxidase (PPO) enzyme.	Dugje et al. (2020)

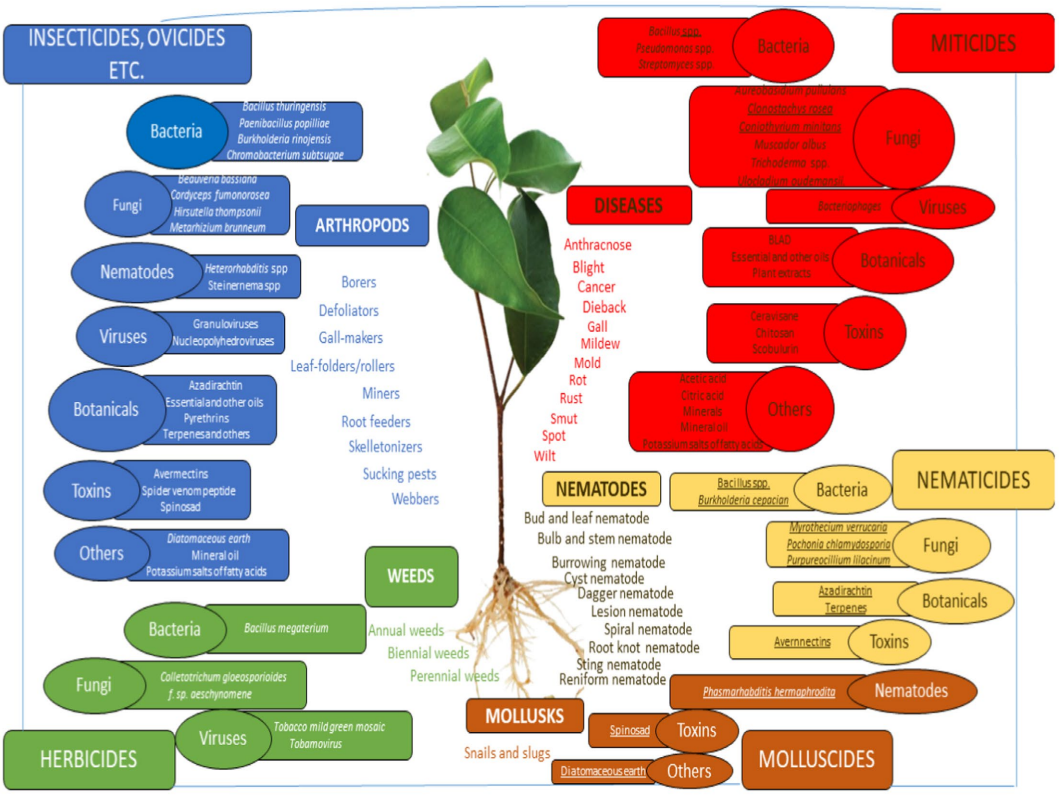


FIGURE 1
Classification of Bio-pesticides and their target pests.

or harvested and preserved crops by other pests which could feed on them (Peprah-Yamoah et al., 2022). Herbicides prevent the growth of weeds and eliminate them (Loddo et al., 2019), while miticides are used to kill termites or ticks that destroy crops (Murcia-Morales et al., 2021). Similarly, bactericides and fungicides get rid of harmful bacteria and fungi, respectively, or inhibit their growth without tampering with the beneficial ones (Ullah and Dijkstra, 2019; Akanmu et al., 2021). Fumigants exhibit broad-spectrum activity against fungi, insects, and bacteria (Fang et al., 2020). Termiticides suppress the activities of termites on the soil (Singh et al., 2020). Repellents are used to repel insect pests and birds. Acaricides are used to control arachnids (Benelli, 2022) and insecticides help to destroy insects that affect plants, animals, and humans (Matsuda et al., 2020). Equally, the effective use of nematicides in the control of nematodes, rodenticides in the control of mice and other rodents, and molluscicides in the control of molluscs have been documented (Horgan and Kudavidanage, 2020; Figure 1). Attractants lure and attract pests to a trap or bait (Souto et al., 2021). Insect growth regulators disrupt the molting, maturity from pupal stage to adult, or other life processes of insects (Jindra and Bittova, 2020).

2.2. Classification of pesticides according to their sources

Pesticides are classified into chemical and biological pesticides according to their source. Chemical pesticides are very effective and rapid in the control of pests. They are made from inorganic or synthetic salts, such as sulfur, copper sulfate, lime, and ferrous sulfate. Their chemical compositions are simple and highly soluble in water, which makes them easily absorbable by pests, thereby enhancing their activity and durability in the environment (Kim et al., 2017; Abubakar et al., 2020).

Biological pesticides (biopesticides) are substances produced from biological agents that manage pests in agriculture to enhance crop production (Samada and Tambunan, 2020). They can be sourced from microorganisms, plants, or nanoparticles (Kidd et al., 2017; Samada and Tambunan, 2020; Adeleke et al., 2022d). Microbes release certain metabolites, which protect plants from pests and are useful as microbial pesticides (Samada and Tambunan, 2020). Active compounds from plants used as phytopesticides include phenols, alkaloids, and terpenes (Abubakar et al., 2020). Generally, nanoparticles can be produced from chemical or biological agents (mainly plants or microbes; Omole et al., 2018). Nanoparticles of biological origins that are used as pesticides are termed nanobiopesticides and are also very important as plant protectants (Pan et al., 2023). Nanobiopesticides have found application as pesticidal agents in agriculture because of their excellent physicochemical characteristics like size, reactivity, surface area, and so on. Besides, nanobiopesticides have unambiguous biological interactions with plants, as well as clear transport and fate in the environment (Bratovcic et al., 2021; Kumar et al., 2022; Pan et al., 2023).

2.3. Adverse effects of synthetic pesticides

Synthetic pesticides are faced with drawbacks, which include the cost of purchase and production, persistence in the soil, pest resistance, impacts on health and the environment, economic harm to organic producers due to pesticide drift, disposal of contaminated crops,

removal of stockpiles of unused pesticides as well as regular containers, and the disposal of expired/unused products, which can affect organic farms or innocent populace (Hicks et al., 2018; Essiedu et al., 2020).

A large portion of pesticides when applied on the soil for agricultural purposes remains non-degradable. Hence, they are more persistent in the environment and leach to underground and surface water, thus leading to loss of biodiversity and pollution. Of all the pesticides applied on the soil, about 98% affect organisms that are not targeted. For instance, in Europe, pesticides decrease soil respiration by 35%, reduce insect biomass by 70%, and decrease the number of farm birds by 50%; and in America and Europe, it reduces the honeybee population by 30% (Ali et al., 2021). Research by Tongo et al. (2022) revealed Aldrin pesticide as a major pesticide detected in the Ikpoba river in the Southern part of Nigeria. Although, other chemicals, such as diazinon, endrin, glyphosate, aldrin, endosulfan I, heptachlor, heptachlor epoxide, and carbofuran present with the tendencies of being biomagnified need proper monitoring. Furthermore, pesticides (e.g., carbamate and organophosphate) have been reported to negatively affect soil's nutrients, as they chelate some important metal ions, thus making them unavailable for plant uptake (Kaur et al., 2017). Likewise, plant photosynthesis, reproduction, and seed production can be adversely affected by pesticides (Hashimi et al., 2020).

Residues of pesticides in food crops can be consumed directly by humans or used in the production of animal feeds (Choudhary et al., 2018). This can come to play when pesticides are applied toward harvesting (Jallow et al., 2017). Biomagnification of pesticides occurs in animals when they feed on accidentally or deliberately contaminated harvested food crops or forage. Topical pesticides are applied on food crops to control parasites, and through other means, such as disposal, spraying, and formulations of pesticides (Choudhary et al., 2018). Pesticide accumulation in the granular tissues of animals can lead to the death of cells, necrosis (causing a reduced hormone production), ovarian follicles (resulting in a reduced progesterone level), reduced oestrogen production, reduced libido, and a reduced sperm concentration and quality in male animals (Li et al., 2022).

Accumulation of pesticides in birds (e.g., bald eagles, ospreys, grebes, cormorants, seagulls, pelicans, and peregrine falcons) living in pesticide-polluted areas can lead to reproduction problems (Garces et al., 2020). Pesticides lead to crossed bill deformity in birds. For example, a high concentration of DDT pesticides led to crossed-bill deformity in a wild bald eagle (Garces et al., 2020). In reptiles inhabiting areas close to rivers where water from agricultural farms is washed, deformities could be observed. For example, snapping turtles living in Erie and Lake Ontario in Canada were found to have deformities, such as deformed jaws, limbs, cranium, carapaces, nostrils, and tails, enlarged yolk sacs, dwarfism, missing eyes, unhatched eggs, and these were traced to chemical pesticides contamination (Garces et al., 2020). In soils, the reduction in the function and population of fungi, actinomycetes, and bacteria has been linked to the usage of three pesticides, namely glyphosate, malathion, and alphacypermethrin (Kumar et al., 2019). All the negative effects of synthetic pesticides lead to the loss of biodiversity and genetic conservation in animals. Furthermore, it also alters soil biodiversity and health, by affecting the microbial functions in the soil, which directly or indirectly enhances soil nutrients and plant health.

Consumption of vegetables, food crops, fruits, milk, and meat from animals that contain high pesticide residue can lead to different diseases in humans (Omoyajowo et al., 2018; Li et al., 2022). Onwujiogu et al. (2022) found pesticides in Bambara groundnut quantity, which is beyond the Maximum Residual Limit (MRL) recommended by the WHO and could pose a threat to the health of humans, especially children who feed on them. Omoyajowo et al. (2018) also experimented to unravel the level of pesticides in three fruits and realized that the pesticide level of watermelon was above the MRL level specified by the WHO/FAO, which equally poses a health threat to the consumers. Similarly, pesticides are used to protect harvested food crops, vegetables, and fruits and those used for other purposes aside that which they are manufactured. For instance, the use of calcium carbide to ripen fruits poses health threats to humans. Calcium carbide contains calcium arsenide and calcium phosphide, and when reacts with water, forms arsine and phosphide, thus leading to headache, vomiting, dizziness, nausea, unconsciousness, and fatigue in humans (Andrew et al., 2018). Equally, ethepon, a pesticide used to hasten the ripening of fruits, vegetables, and cereals exhibited hepatocyte properties when tested on albino rats (Bhadoria et al., 2018).

Furthermore, in humans, biomagnification of pesticides through food (such as fish), drinking water, skin pores (while spraying), post-harvest crop preservation, and inhalation, give rise to diseases, such as cancer, Parkinson's diseases, eye irritation, diabetes, kidney diseases, hypertension, skin rashes, liver dysfunction, eczema, birth defects, Alzheimer's diseases, neurological destruction, cardiovascular diseases, and endocrine disorder (Damalas and Koutroubas, 2016; Jayaraj et al., 2017; Sabarwal et al., 2018; Manfo et al., 2020). Likewise, high pesticides level can lead to about 25–30% increase in mental ailments, and a 50% increase in severe brain cancer, leukaemia, lymphoma, and cancer.

3. Biopesticides as an alternative to synthetic pesticides

Due to the drawbacks of synthetic pesticides, an alternative means of pest control is being encouraged, which is the use of biopesticides (Ojuederie et al., 2021; Ayilara et al., 2022b; Figure 2). Biopesticides are effective and safer means of controlling pests, they have a mild effect on the environment compared to their synthetic counterpart, and they are specific in their target, hence preventing bioaccumulation (Saberi et al., 2020; Kumar et al., 2021). Biopesticides are made from natural substances, such as plants, microbes, and nanoparticles of biological origin, thus, making them a sustainable means of pest control (Kumar et al., 2021).

Some successes have been recorded in the use of biopesticides in the control of some pests to which chemical pesticides are being applied (Table 2).

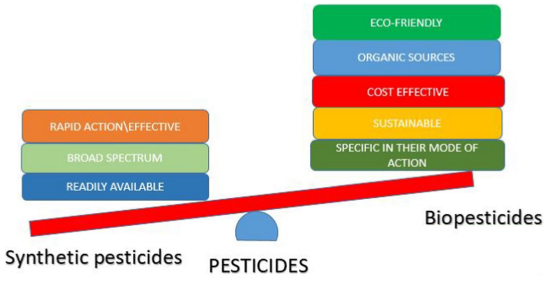


FIGURE 2
Comparison of the advantages of synthetic pesticides and biopesticides.

TABLE 2 Different Biopesticides and the pest they control.

Microbial pesticides	Entomopathogenic viruses	Target insects and pests	References
	Nucleopolyhedroviruses	*Lepidoptera*	Harish et al. (2021)
	Imported cabbageworm (PiraGV) NPV (AucaMNPV)	*Artogeia (Pieris) rapae*	Singh et al. (2019)
	Potato tuber moth GV (PhopGV)	Phthorimaea operculella	Singh et al. (2019)
	Entomopathogenic fungi		
	Paecilomyces lilacinus	Soil nematodes	Moreno-Gavíra et al. (2020)
	Beauveria bassiana	Whitefly	McGuire and Northfield (2020)
	Hirsutella thompsonii	Spider mites and whitefly	Saranya et al. (2021)
	Isaria fumosorosea	Termites, grasshoppers, caterpillars, and beetles	Gautam (2020)
	Metarhizium brunneum	Nematodes (pathogens)	Hummadi et al. (2021)
	Paecilomyces fumosoroseus	Insects and mealy bugs	Abbas (2020)
	Verticillium lecanii	Nematodes, mites & thrips, scale insects, mealy bugs, etc.	Pathania et al. (2022)
	Myrothecium verrucaria	Nematodes	Hagag (2021)
	Lagenidium giganteum	Pest mosquito species	Kaczmarek and Boguś (2021)
	Entomopathogenic bacteria		
	B. thuringiensis	Elm Leaf Beetle,Alfalfa weevil	Saberi et al. (2020)
	Beauveria bassiana	Whitefly	McGuire and Northfield (2020)
	B. thuringensis var. *israelensis*	Fungus gnats, black flies, larvae of mosquitoes	Lee et al. (2021)
	B. sphaericus, *B. lentimorbus*, and *B. popilliae*	Larvae of Aedes spp., Culiseta, Psorophora, and Culex mosquitoes	Falqueto et al. (2021)
	Entomopathogenic nematodes		
	Heterorhabdits taysearae	*Bactrocera dorsalis*	Godjo et al. (2018)
	Steinernema carpocapsae, Heterorhabditis bacteriophora,	Larvae of cabbage white butterfly	Aioub et al. (2021)
	Steinernema feltiae		
	Steinernema carpocapsa,		
	Steinernema riobrave,	Armyworm	Gozel and Gozel (2021)
	Steinernema feltiae		
	Steinernema carpocapsae,		
	S. bicornutum,	Leafminers	Abbas (2022)
	Heterorhabditis indica and		
	H. bacteriophora.		
	Steinernema carpocapsae		
		Potato tuber moth	Ebrahimi et al. (2022)
Nanobiopesticides			
	Nano-sized particles		
	Mesocyclops longisetus-derived nanoparticles	*Culex quinquefasciatus*	Narware et al. (2019)
	Mesocyclops scalpelliformis-derived nanoparticles	*Culex quinquefasciatus*	Rodrigues et al. (2019)
	Silver nanobiopesticide	*Alternaria solani, A. alternata*	Narware et al. (2019)
	Silver nanoparticles	*Xanthomonas axonopodis pv. citri, X. oryzae pv. oryzae* and *Ustilaginoidea virens*	Roseline et al. (2019)
	Gold nanoparticles	*Culex quinquefasciatus, Anopheles stephensi* and *Aedes aegypti*	
			Kovendan et al. (2018)
Phytopesticides			
	Plants		
	Lantana camara	Eggs of root-knot nematode- *Meloidogyne incognita*	Malahlela et al. (2021)

(Continued)

TABLE 2 (Continued)

Microbial pesticides	Entomopathogenic viruses	Target insects and pests	References
	Azadirachta indica	*Colletotrichum coccodes*	Opeyemi et al. (2018)
	Jimson weed, Camelina and *White hellebore*	*Colorado beetle*	Basiev et al. (2019)
	Andropogon nardus	*S. rolfsii and Pestalotia sp*	
	Atalantia guillauminii, Eucalyptus procera	*Tenebrionid pests*	Idris et al. (2022)
	Siparuna guianensis	*Lepidoptera sp.*	
			Lourenço et al. (2018)

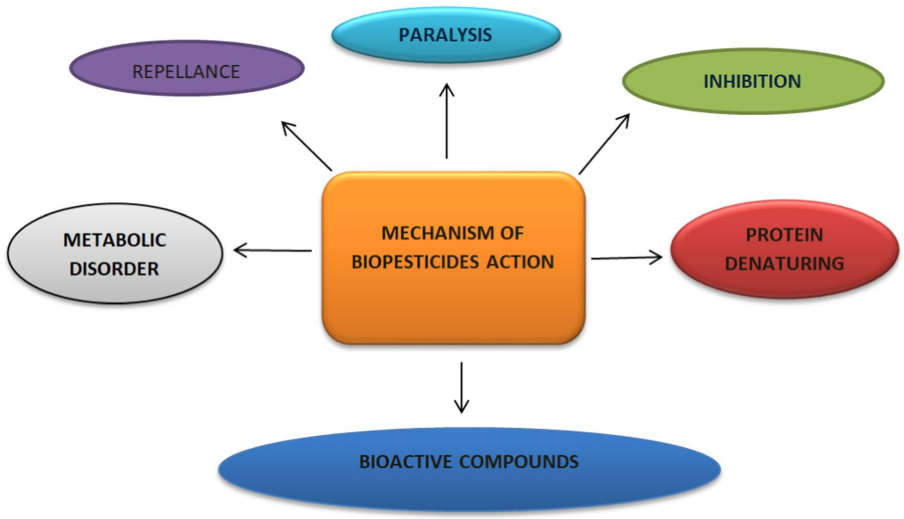


FIGURE 3
Mechanism of action of biopesticides.

The effectiveness of biopesticides in pest management comes from various modes of action, which include actions that regulate gut disruption, pest growth, and pest metabolism. Biopesticides work by denaturing protein, causing metabolic disorder and paralysis, activating target-poisoning mechanisms, exhibiting multisite inhibitory actions, and releasing neuromuscular toxins and bioactive compounds (Figure 3; Sparks and Nauen, 2015; Dar et al., 2021; Fenibo et al., 2021). These multiple actions offer biopesticides the capacity to alter the course of pest resistance as compared to chemical pesticides. Studies have indicated that biopesticides are eco-friendly, possess low toxicity properties, are biodegradable, and specific in action with little or no negative impact on non-target organisms (Deravel et al., 2014; Kalpana and Anil, 2021), Unlike biopesticides, conventional pesticides are a major source of environmental pollution, which promotes pest resistance with high post-harvest contamination and bioaccumulation in food crops (Fenibo et al., 2021).

However, there are various limitations to the full adoption, development, and use of biopesticides in agriculture. Biopesticides are often ranked as having low efficacy and a slower rate in the control of pests and diseases (Damalas and Koutroubas, 2016; Delgado-Carrillo et al., 2018). Commercial biopesticide products are highly expensive and not readily available in the global market. In addition to the problem of commercialization, biopesticides also face quality control problems and concise shelf-life (Arthurs and Dara, 2019).

Many farmers also worry about dosage recommendations and fear the evaluation of new pest species that may be resistant to the existing biopesticides (Stevenson et al., 2017). The advantages and disadvantages of biopesticides are summarized in Table 3. Biopesticides have also been classified into three groups based on their extraction source and the constituting molecule/compound. The three groups include; (i) Microbial Biopesticides; (ii) Biochemical Pesticides; and (iii) GMO-Based Biopesticides. The source characteristics and the consisting molecules of biopesticide influence the mechanisms by which biopesticides protect the crops from the attack of pathogens. For example, fungicides and bactericides derived from microorganisms act by inhibiting or disrupting the process of protein translation, or cause a major disruption in plasma membrane permeability, thus leading to cell death, while some may prevent glucose formation in target pathogens (Parker and Sperandio, 2009; Svidritskiy, et al., 2013; Gwinn, 2018).

3.1. Microbial pesticides

Microbial pesticides consist of substances derived from microorganisms like bacteria, fungi, viruses, protozoa, and algae, which are used in the control of pests (Adeleke et al., 2022c). Microbes use the toxic metabolites produced to destroy and prevent the growth of pests. Microbial pesticides are applied to the environment through different

TABLE 3 Advantages and disadvantages of biopesticides.

Pesticides	Advantages	Disadvantages	References
Microbial pesticides	They are specific in their mode of action, have a short residual effect, they are environment friendly, are made from different species, which ensures sustainability in their production, are cost-effective, and it is easy to make a mass production *in vitro*. They are not associated with the emission of greenhouse gases.	They have short shelf lives, there is a challenge with their stability in different environments, and there are uncertainties regarding the exposure rate/level and duration. They are easily degraded and their effects last for a short period. In many countries, the regulations for their registration are very stringent which reduces their availability.	Borges et al. (2021); Kumar et al. (2021); Llamas et al. (2021); Adeleke et al. (2022c)
Plant pesticides	They are cost-effective and sustainable compared to synthetic alternatives. They can be derived from different plant species.	They are specific; thus may not be able to control more than one pest at a time. Therefore, any plant that has the potential to be affected by more than one pest may require more than one phytopesticide. Their quality is dependent on the quality of the raw materials used; therefore, the plant materials used must be harvested during the time of the day when the plant phytochemicals are active. There might be issues with the consistency of products because the concentration and constituents of plant phytochemicals change across different geographical and ecological locations. Their registration and registration procedure are tedious.	Damalas and Koutroubas (2020); Souto et al. (2021)
Nanobiopesticides	They are cheaper, more stable, and sustainable compared to their chemical counterparts; they have no residual effects and are not associated with greenhouse gases emission.	The dosage of nanoparticles in the environment might be difficult to control because they are small in size and because many nanoparticles, which are occurring naturally might be identical to the ones introduced to the environment. They are more active in the laboratory, and not much work has been done on their field application. The procedure for their regulations is tedious and time-consuming and they have a slow mode of action.	Chaudhary and Sharma (2019); Damalas and Koutroubas (2020); Sabry (2020); Saleh (2020); Adeleke et al. (2022a)

techniques, such as emulsion, electrospraying system, fluidized bed, spray drying, extrusion, lyophilization, spray cooling, and coacervation (De Oliveira et al., 2021). The major categories of microbes used as biopesticides include bacteria genera, *Chromobacterium, Pseudomonas,* and *Yersinia*, fungal genera *Beauveria, Paecilomyces, Verticillium, Hirsutella, Metarhizium*, and *Lecanicillium* and nematodes belonging to the genera *Steinernema* and *Heterorhabditis* (Chang et al., 2003; Kumar et al., 2021; Adeleke et al., 2022b).

A fungi species, *Trichoderma* sp. has been reported to prevent the activity of numerous fungi inhabiting the soil that cause root rot, black gram, and green gram in chickpeas, and groundnut (Samada and Tambunan, 2020). Likewise, *Beauveria bassiana* and *M. brunneum* have been reported in the control of thrips, beetles, weevil, aphids, whiteflies, and mites infestation in ornamental crops, fruits, and vegetables (Dara, 2017; Arthurs and Dara, 2019). Other examples of microbial pesticides are listed in Table 2.

Of all the bacterial pesticides, *Bacillus thuringiensis* (Bt) is well-known and have been made into products available for commercial purpose (Ujvary, 2010; Ruiu, 2018). *Bacillus thuringiensis* is a Gram-positive bacteria that acts as an insecticide by producing exudates, such as poisonous parasporal crystals and endospores which when consumed by insects get dissolved in their midgut by the alkaline environment and release delta-endotoxin, a protein that has a lethal effect on insects (Xiao and Wu, 2019). *Bacillus* thuringiensis is used to reduce pest infestation in plants, such as cabbage and potato, and is capable of controlling lepidopterans in different plants (Berini et al., 2018; Samada and Tambunan, 2020). As good as the positive effects of commercially available Bt sounds, they come with some drawbacks which include quick deactivation when exposed to light, short activity time, slow lethal rate, and low awareness and sensitivity to the environment (Xiao and Wu, 2019). The short life and environmental sensitivity of microbial pesticides, which reduce their awareness and usage are the major challenges associated with their use (Pathak et al., 2017). For instance, baculoviruses only survive in their host and cannot reproduce outside their host; hence, they cannot be used outside their host (Borges et al., 2021). Their host may have an adverse environmental impact on the environment, and their use might be dangerous.

Fungi are also used to control plant pests. An example is the mycoinsecticide, which is a microbial insecticide whose active ingredient is a living fungus that exhibits an antagonistic effect on insects or other arthropod pests, with some strains releasing metabolites while inside the pest that may also injure or kill it (Zaki et al., 2020). Only a few rare fungal strains have been developed as commercial mycoinsecticides, hence, the technology is still in its early stages. Attachments, germination, penetration, invasion, replication, and host death are the six general phases of action for mycoinsecticides (Zaki et al., 2020).

Spores can land on and attach to the target host's cuticle when the formulated product is diluted and applied according to label instructions. Adhesion is primarily achieved through hydrophobic interactions between the cuticle and the spore. The number of spores attached to the host's body determines their efficacy. The spore germinates in response to chemical cues on the cuticle and then develops an aspersorium, which is the penetration structure. The fungus penetrates the layers of the cuticle through a combination of mechanical pressure and enzyme degradation (Zaki et al., 2020).

Generally, microbial pesticides exert no adverse effects on the environment, producers, and consumers of agricultural products because their ingredients are generally considered safe and are target-specific (Guven et al., 2021). In addition, their usage lower greenhouse gas emissions compared to chemical pesticides (Llamas et al., 2021). Furthermore, there is a wide variety of organisms from which microbial biopesticides can be derived to solve the problem of resistance and ensures sustainability. Since different microbes used as biopesticides might require different storage condition, it might be cumbersome for sellers, producers, marketers, and end users to cope with their storage and transportation. Hence, more research is needed to ensure a sustainable and extended shelf-ability of microbial pesticides.

3.2. Phytopesticides

Essential oil and extract from different parts of plants have been successfully used to control plant diseases (Ayilara et al., 2022a). They attract, repel, prevent respiration, detect host plants from specific pests, destroy the eggs and larvae of pests, and destroy pests from feeding on plants (Tripathi et al., 2009; Halder et al., 2013; Ali et al., 2017). Essential oil from *Coleus aromaticus* Benth., *Hyptis suaveolens* (L.), *Azadirachta indica, Ageratum conyzoides* L., and *Achillea* sp., have been reported to control the infestation of *Tribolium castaneum* (Herbst), a red flour beetle that destroys many crop species (Singh et al., 2014; Jaleel et al., 2015; Upadhyay et al., 2018). Other plant parts, such as bark, flowers, roots, leaves, peels, seeds, and buds can be used to control different plant pathogens (Tongnuanchan and Benjakul, 2014).

Plant families that have been reported to contain bioactive compounds with activity against important crop pests include Myrtaceae, Lauraceae, Rutaceae, Lamiaceae, Asteraceae, Apiaceae, Cupressaceae, Poaceae, Zingiberaceae, Piperaceae, Liliaceae, Apocynaceae, Solanaceae, Caesalpinaceae, and Sapotaceae (Gakuubi et al., 2016). They are easily available which makes them inexpensive and can be easily incorporated into agricultural production systems. Secondary metabolites, such as steroids, alkaloids, tannins, terpenes, phenols, flavonoids, and resins are commonly found in botanical pesticides and have shown antifungal, antibacterial, antioxidant, or insecticidal properties (Ahmad et al., 2017). The specific compounds found in certain plant species make them effective against a specific category of pests and also determine their mode of action on the target pests (Lengai et al., 2020). Botanical pesticides contain bioactive compounds that act in a variety of ways against pests, such as insects, fungi, bacteria, nematodes, and plant host cells infected with viral pathogens (Lengai et al., 2020). Depending on the botanical compound and pest, the modes of action may include repellence, inhibition, protein denaturation, and other effects. Pesticides derived from pyrethrum target insect nerve cells, thus causing paralysis and death. Also, neem-based pesticides with antifeedant and repellent properties, induce moulting abnormalities, hinder oviposition, and disrupt the endocrine system (Lengai et al., 2020).

Pesticides from plants have been well-reported to interfere with the normal metabolism of insect pests, which include the octopamine and acetylcholinesterase pathways (Polsinelli et al., 2010; Pang et al., 2012; Dassanayake et al., 2021). Acetylcholinesterase is an enzyme used by insects in their neuronal communication and neuromuscular functions and can be toxic to insects by destroying the membrane of the postsynaptic junction and the current of the nerve. Octapamine on the other hand is a hormone involved in neuromodulation and neurotransmission in insects and can impair the muscle juncture and homeostasis of the body fluids of insects (Dassanayake et al., 2021). Equally, plant pesticides can prevent cell wall biosynthesis, cell membrane structure, ATPases function, quorum sensing, efflux pumps, and biofilm formation (Lang and Buchbauer, 2012; Hu et al., 2017). Extracts from four weed plants, namely *Lippia javanica*, *Tithonia diversifolia*, *Vernonia amygdalina,* and *ephrosia vogelii*, in Tanzania were used to control insects in common bean (Mkenda et al., 2015). Similarly, Lovatto et al. (2004) carried out an experiment where nine different aqueous plant extracts from the leaves, fruits, and flowers of nine plants were used to repel and kill *Brevicoryne brassicae*. *Solanum pseudocapsicum* L., and *Solanum guaraniticum* A were reported to be the most effective.

3.3. Nanobiopesticides

Nanobiopesticides can be defined as biological protection products that are developed using nanotechnology to enhance efficacy and reduce an environmental load of pesticides (Chaudhary et al., 2021b,d). Nanobiopesticides are formulated from nanomaterials and applied specially fixed on a hybrid substrate, encapsulated in a matrix or functionalized nanocarriers for external stimuli or enzyme-mediated triggers (Agostini et al., 2012; Khati et al., 2018; Kumari et al., 2020; Agri et al., 2021, 2022; Chaudhary et al., 2022; Pan et al., 2023). They are nanostructures with two or three dimensions used for carrying agrochemical ingredients and can help increase water solubility and bioavailability, and protect agrochemicals against environmental degradation. It also helps revolutionize the control of pathogens, weeds, and insects in crops (Yadav et al., 2020). They are available in different forms, such as nano-gel, nano-encapsulation, nano-fibres, nano-sphere, etc. (Rajna and Paschapur, 2019; Pan et al., 2023).

Nanoparticles in recent years are being reported to be very helpful in agriculture (Omole et al., 2018). They have been used as active ingredients and carriers to stabilize many agrochemicals and their products from them include nanofertilizers, nanopesticides, etc. (Chaudhary and Sharma, 2019; Chaudhary et al., 2021a). For instance, pesticides from nanomaterials, such as magnesium oxide, magnesium hydroxide, copper oxide, and zinc oxide derived from aqueous extracts of *Chamaemelum nobile* flowers, *Punica granatum* peels, green peach aphid (GPA) and *Olea europaea* leaves have been reported in the control of insects (Grillo et al., 2021; Konappa et al., 2021). Also, silver nanoparticles derived from the leaf extract of *Euphorbia hirta* have been explored in the control of the causative agent of cotton bollworm, *Helicoverpa armigera* (Devi et al., 2014). The ability of copper oxide nanoparticles and zinc oxide nanoparticles to control *Alternaria citri*, a causative agent of citrus black rot disease in the plant has as well been reported (Lasso-Robledo et al., 2022). In addition, Sardar et al. (2022) used combined and individual zinc oxide and copper oxide to control citrus black rot disease in a potato dextrose medium. The fungal and insecticidal effects of copper nanoparticles have been demonstrated against *Tribolium castaneum,* a pest that affects grain (El-Saadony et al., 2020). The major interactions which occur between plants and nanoparticles have been studied using different techniques, which include fluorescence spectroscopy, microscopy, and magnetic resonance imaging (Chhipa, 2019). The effectiveness of nanobiopesticides can be determined by the composition, surface charge, concentration, size, and chemical and physical changes (Chhipa, 2019).

The critical role of nanoformulations in reducing active ingredient degradation, improving water solubility equilibrium, and increasing the biological availability of active ingredients is well understood, and this has helped in avoiding endemic pest infestation, plant injury, and economic loss by lowering the quality and quantity of agricultural products and foods (Syafrudin et al., 2021; Chaudhary et al., 2021a,c).

Because of their small size and larger surface area, nanopesticides' chemical properties differ significantly from conventional pesticides, and these properties can be used to develop an efficient assemble of a structure with several advantages, such as the possibility of better interaction and mode of action at a target site of the desired pest. Nano-sized products exhibit greater selectivity without impairing compound bioactivity against the target pathogen. Their increased toxicity can also increase pest penetration (Priya et al., 2018). Nanoparticle application reduces drifting and leaching issues and allows for the use of a smaller amount of active compound per area, as long as the formulation can provide optimal concentration delivery for the target insecticide for longer periods. There are several methods for creating pesticide nanoproducts, such as nanoemulsions, nanocapsules, and inorganic engineered nanoparticles (such as metal oxides, metals, and clays), and can be further developed to improve the efficacy of existing pesticides, reduce their environmental toxicity, or both.

On a general note, biopesticides have been reported to be capable of controlling pests but their sole use for sustainable agriculture may not be realistic, majorly because they are not readily available in many locations and their mode of action can be very slow. Hence, they should be incorporated with the existing synthetic pesticides and be applied majorly close to the harvest period of crops since residual chemicals observed in plants are those majorly applied close to harvest periods. Furthermore, this will help to maintain suitable agriculture, pending the improvements of biopesticides.

3.4. Molecular mechanisms of the application of biopesticides

It is very important to understand the molecular mechanisms underlying the action of biopesticides at each stage of action to ensure better control strategies over pests. Understanding the biopesticides mechanisms of action against insect pests at the molecular level will allow for synergistic approaches among biopesticides, which have different mechanisms of action without an overlapping mechanism. This will also give allowance for the exploration of different toxic molecules present in biopesticides that can enlarge the pesticidal arsenal of these biopesticides. The widely used biopesticides and their mechanisms of action at the biochemical level have been described. However, the entomopathogenic fungus, *Beauveria bassiana* has gained wide acceptance and can be used as a model to describe the molecular mechanism of biopesticides' application.

Beauveria bassiana is an example of an entomopathogenic fungus that has been widely used as biopesticide because it is highly efficacious against a lot of arthropod hosts (Boomsma et al., 2014). However, to understand their effectiveness and sustainability against pests, there is a need to fully evaluate their molecular mechanism of pathogenicity beyond the conventional approach. The mechanism of pathogenicity of *B. bassiana* begins with adhesion to the host pest, penetration of cuticle, and colonization of the pest heaemocoel (Wojda et al., 2009).

The hydrophobins-coated aerial conidia of *B. bassiana* allow its hydrophobic interaction with the cuticles of insects (Holder and Keyhani, 2005). This hydrophobicity of the *B. bassiana* aerial conidia can be influenced by the role that several genes expressed by *B. bassiana* play in lipid homeostasis. It has been revealed by transcriptomics analyses that there is an upregulation of gene expressions for hydrophobins and *Metarhizium* adhesion-like protein 1, 2 (MAD 1, MAD2) by *B. bassiana* which are crucial for its hydrophobic attachment to the cuticle of insect (Wang and St Leger, 2007). The transportation and storage of lipids in the conidia, and maintenance of the lipid homeostasis of *B. bassiana* is possible when mammalian-like perilipin 1 (MPL1) genes are over-expressed (Chen et al., 2018). The role that the MPL1 gene plays is crucial because its deletion causes a reduction in the turgor pressure of the appressoria impairing the adhesiveness of *B. bassiana* (Wang and Leger, 2007). Also, the surface sensing and signaling for the germination of conidia and formation of appressoria is made possible by CFEM-domain-containing genes in *B. bassiana* (Sabnam and Barman, 2017). Proteomics has also revealed that *B. bassiana* secretes sphingomyelin phosphodiesterase, which allows it to disrupt the membrane of the host insect upon contact with the cuticles of the insect (Santi et al., 2019).

Once *B. bassiana* completed adhesion to the host insect, its conidia germinate and develop appressoria to allow penetration into the cuticle of the host. The penetration efficiency of *B. bassiana* usually increased when the structural outlook of the appressorium allows the synergistic functioning of enzymatic digestion and mechanical pressure (Singh et al., 2017). The hyphae of *B. bassiana* germinate in the exoskeleton of the insect as the penetration proceeds and *B. bassiana* produces secondary hyphae inside the cuticle. The hyphae switch to blastospores (motile, more hydrophilic, and better evade the insect's host immunity) when exposed to hyperosmotic environment in the haemocoel (Ortiz-Urquiza and Keyhani, 2016). Through transcriptomics, it has been reported that chitin synthase is responsible for chitin production, and β-1,3-glucanases soften the cell wall to allow germination, while several cell wall protein-conferring genes give the cell wall of *B. bassiana* its building blocks (Tartar et al., 2005; Mouyna et al., 2013; Chen et al., 2018). Genes necessary for the cell body differentiation in *B. bassiana* include osmosensor Mos1, signaling-related genes, and mitogen-activated-protein kinases (MAPKs) like protein kinase A (PKA; Chen et al., 2018; Zhou et al., 2019). For penetration into the cuticle of the host insect, notable proteases, lipases, chitinases, and carboxypeptidases have been reported and these include subtilisin-like protease (Pr) isoform 1A (Pr1A) and 1B (Pr1B), cytochrome P450s (CYPs) and GH18 family chitinases (Lai et al., 2017).

In response to the penetration into the cuticle of the insect, the insect activates melanization and produces antimicrobial peptides (AMPs), reactive oxygen species (ROS), and protease inhibitors (Ortiz-Urquiza and Keyhani, 2016). Stress management and immune-evasion-related genes are upregulated to overcome the host insect defense mechanisms. Glutathione S-transferases (GSTs), catalases, peroxidases, superoxide dismutase (SODs), thioredoxins, and oxidoreductases are anti-oxidative enzyme-producing genes over-expressed in *B. bassiana* (Lai et al., 2017). Heat shock proteins (HSPs) are expressed to maintain internal cellular integrity against diverse types of stress (Santi et al., 2019). Another mechanism used by *B. bassiana* is the production of secondary metabolites that are toxic to the insect cell. These metabolites include oosporeins, beauvericin, isarolides, beauverolides, tenellins, and bassianolide (Chandler, 2017). The biosynthesis of oosporein happens in the haemocoel and it is mediated by the over-expression of polyketide synthase (PKS) gene (Lai et al., 2017). It is interesting to note that a greater amount of beauverolides secreted by *B. bassiana* usually occur

when live insect tissues are present than in the presence of dead insect tissues (de Bekker et al., 2013). With these fantastic mechanisms of action, *B. bassiana* stands out among the entomopathogenic fungi, thus making it an attractive and widely used biopesticide against a lot of arthropod hosts.

Lastly, it is good to note that the complex mechanism of pathogenesis exhibited by *B. bassiana* cannot be fully understood by a singular omics approach, there is a need to examine the total expressions of different proteins, secondary metabolites, and their genes at every infection stage. Hence, researchers in different fields of omics need to collaborate to work with the same parameters to have a holistic view of the mechanism of action of different biopesticides.

4. Integrated pest management system

Integrated Pest Management (IPM) system refers to the mechanism of controlling pests using different techniques, such as habitat manipulation, biological and chemical control measures, use of pest-resistant varieties, and the modification of cultural practices. These techniques can be merged to ensure the long-term protection of plants (Deguine et al., 2021). For instance, IPM has been used in the control of *Tuta absoluta*, a deadly pest that affects tomatoes globally, and has developed resistance to insecticides (Desneux et al., 2021). Here, the synthetic pesticides and biological pesticides include the release and conservation of sex pheromones and arthropod natural enemies (Desneux et al., 2021). The use of IPM has been reported to be cost-effective and reduces the loss of crop yield (Hagstrum and Flinn, 2018). Currently, the adoption of IPM is limited owing to several factors, which include awareness, user preference, production industry, technology, policy, and culture (Deguine et al., 2021). It is, therefore, necessary to increase awareness of the inclusion of biological pesticides from microorganisms, plants, and nanobiopesticides in IPM. The awareness of many people about IPM will be an advantage to encourage producers to produce more of it, enhance its adoption and encourage researchers to carry out more research on it.

5. Future prospects and conclusion

A lot of crops are lost yearly to pest, but the emergence of synthetic pesticides have helped to reduce the loss. Nevertheless, the adverse effects of synthetic pesticides limit their use; thus, promoting the use of biological pesticides. Since biopesticides have proven as good alternative to chemical pesticides, it will be very important to explore them for maximum use in agriculture. The demand and availability of biopesticides are very poor, hence discouraging the producers and the users, respectively. Therefore, making grants or capital available for researchers, entrepreneurs, producers, and marketers will help to enhance the production and availability of biopesticides.

The shelf-life of biopesticides is short, as they require special temperatures and conditions for survival during transportation and storage. Hence, more research to unravel the mechanisms to make biopesticides more stable and improve their shelf-life will go a long way in increasing their efficiency.

The fact that biopesticides have no residual effects on the environment could serve as an advantage and a disadvantage. An advantage because it will not remain long enough to be dangerous to the plants, humans, and animals (which is one of the major demerits of synthetic pesticides), and it is a disadvantage because it will only protect crops as long as it has contacts with the pests, and pests that infest after their application would not be affected and might need another application, thus leading to a higher cost implication and labor for farmers. Consequently, more research should be carried out to incorporate bio-carriers and other sustainable methods, which can be used to enhance the persistence of biopesticides in the environment. Since biopesticides are highly specific in their mode of action, chemical reactions may occur if more than a biopesticide is applied to a crop that is affected by different pests. Hence, it is important to carry out more research on the compatibility of different biopesticides, which are likely to be used together on the same crop. Furthermore, most research carried out on biopesticides was focused on yield and not the nutritional quality of the crops, an insight into the nutritional quality of biopesticides will enhance their use.

The Maximum Residual Limit for pesticides in local markets (not only for food crops that would be exported) should be enforced and awareness should be created on the effectiveness of biopesticides so that farmers can explore them. In addition, a mobile meter, device, or strip could be developed, made affordable and easily available to enhance the easy and rapid detection of pesticide levels in food crops. This will help farmers to take caution and also help the populace to avoid feeding on crops with a Maximum Residual Limit greater than the WHO specified value. Awareness of the effects of the indiscriminate use and health effects of biopesticides in humans will also help to promote a good environment and health. Due to the numerous challenges still encountered with the use of biopesticides, the sole use of biopesticides might not be feasible. Therefore, their incorporation with the existing synthetic pesticides will be a better means of preventing crops from pests and ensuring sustainable agriculture.

Author contributions

MA, BA, and SA conceived the idea and were involved in the writing of the manuscript. CF, UA, LG, RO, RJ, and QU contributed to the writing of the manuscript. MA, BA, and RO revised the manuscript. OB reviewed and edited the final draft of the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This study was funded through research grants from the National Research Foundation, South Africa (UID: 123634 and 132595).

Acknowledgments

OB appreciates the research grants from the National Research Foundation, South Africa.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Aba, S., Eze, S., Ishieze, P., Omeje, T., and Ugwuoke, K. (2018). Controlling phytophthora blight of cucumber (*Cucumis sativus*) in a derived savannah, using different spray intervals of a registered fungicide. *Plant Pathol. Quar.* 8, 122–130. doi: 10.5943/ppq/8/2/3

Abbas, M. S. T. (2020). Interactions between entomopathogenic fungi and entomophagous insects. *Adv. Entomol.* 08, 130–146. doi: 10.4236/ae.2020.83010

Abbas, M. S. T. (2022). Pathogenicity of entomopathogenic nematodes to dipteran leaf miners, house flies and mushroom flies. *Egypt. J. Biol. Pest Control* 32, 1–9. doi: 10.1186/s41938-022-00566-y

Abdollahdokht, D., Gao, Y., Faramarz, S., Poustforoosh, A., Abbasi, M., Asadikaram, G., et al. (2022). Conventional agrochemicals towards nano-biopesticides: an overview on recent advances. *Chem. Biol. Technol. Agric.* 9:13. doi: 10.1186/s40538-021-00281-0

Abdullahi, G., Obeng-Ofori, D., Afreh-Nuamah, K., and Billah, M. (2020). Acute and residual concentration-dependent toxicities of some selected insecticides to adult *Bactrocera invadens* drew, Tsuruta and white (*Diptera*: Tephritidae). *J. Basic Appl. Zool.* 81, 1–10. doi: 10.1186/s41936-020-00144-4

Abraham, D. A., and Vasantha, V. S. (2020). Hollow polypyrrole composite synthesis for detection of trace-level toxic herbicide. *ACS Omega* 5, 21458–21467. doi: 10.1021/acsomega.0c01870

Abubakar, Y., Tijjani, H., Egbuna, C., Adetunji, C. O., Kala, S., Kryeziu, T. L., et al. (2020). "Pesticides, history, and classification" in *Natural Remedies for Pest, Disease and Weed Control*. eds. E. Chukwuebuka and S. Barbara (Netherlands: Elsevier), 29–42.

Adeleke, B. S., Akinola, S. A., Adedayo, A. A., Glick, B. R., and Babalola, O. O. (2022a). Synergistic relationship of endophyte-nanomaterials to alleviate abiotic stress in plants. *Front. Environ. Sci.* 10:1015897. doi: 10.3389/fenvs.2022.1015897

Adeleke, B. S., Ayangbenro, A. S., and Babalola, O. O. (2022b). *In vitro* screening of sunflower associated endophytic bacteria with plant growth-promoting traits. *Front. Sustain. Food Syst.* 6:903114. doi: 10.3389/fsufs.2022.903114

Adeleke, B. S., Ayilara, M. S., Akinola, S. A., and Babalola, O. O. (2022c). Biocontrol mechanisms of endophytic fungi. *Egypt. J. Biol. Pest Control* 32, 1–17. doi: 10.1186/s41938-022-00547-1

Adeleke, B. S., Fadiji, A. E., Ayilara, M. S., Igiehon, O. N., Nwachukwu, B. C., and Babalola, O. O. (2022d). Strategies to enhance the use of endophytes as bioinoculants in agriculture. *Horticulturae* 8:498. doi: 10.3390/horticulturae8060498

Agostini, A., Mondragón, L., Coll, C., Aznar, E., Marcos, M. D., Martínez-Máñez, R., et al. (2012). Dual enzyme-triggered controlled release on capped nanometric silica mesoporous supports. *Chemistry Open* 1, 17–20. doi: 10.1002/open.201200003

Agri, U., Chaudhary, P., and Sharma, A. (2021). In vitro compatibility evaluation of agriusable nanochitosan on beneficial plant growth-promoting rhizobacteria and maize plant. *Nat Acad. Sci. Lett.* 44, 555–559. doi: 10.1007/s40009-021-01047-w

Agri, U., Chaudhary, P., Sharma, A., and Kukreti, B. (2022). Physiological response of maize plants and its rhizospheric microbiome under the influence of potential bioinoculants and nanochitosan. *Plant Soil* 474, 451–468. doi: 10.1007/s11104-022-05351-2

Ahmad, W., Singh, S., and Kumar, S. (2017). Phytochemical screening and antimicrobial study of *Euphorbia hirta* extracts. *J. Med. Plant Study* 5, 183–186.

Aioub, A. A., El-Ashry, R. M., Hashem, A. S., Elesawy, A. E., and Elsobki, A. E. (2021). Compatibility of entomopathogenic nematodes with insecticides against the cabbage white butterfly, *Pieris rapae* L.(Lepidoptera: Pieridae). *Egypt. J. Biol. Pest Control* 31, 1–12. doi: 10.1186/s41938-021-00498-z

Akanmu, A. O., Babalola, O. O., Venturi, V., Ayilara, M. S., Adeleke, B. S., Amoo, A. E., et al. (2021). Plant disease management: leveraging on the plant-microbe-soil interface in the biorational use of organic amendments. *Front. Plant Sci.* 12:700507. doi: 10.3389/fpls.2021.700507

Ali, A. M., Mohamed, D. S., Shaurub, E., and Elsayed, A. M. (2017). Antifeedant activity and some biochemical effects of garlic and lemon essential oils on Spodoptera littoralis (Boisduval)(Lepidoptera: Noctuidae). *J. Entomol. Zool. Stud.* 5, 1476–1482.

Ali, S., Ullah, M. I., Sajjad, A., Shakeel, Q., and Hussain, A. (2021). "Environmental and health effects of pesticide residues" in *Sustainable Agriculture Reviews*. eds. Inamuddin, M. I. Ahamed and E. Lichtfouse (New York, NY: Springer), 311–336.

Allen, K. C., Luttrell, R. G., Sappington, T. W., Hesler, L. S., and Papiernik, S. K. (2018). Frequency and abundance of selected early-season insect pests of cotton. *J. Integr. Pest Manag.* 9, 1–20. doi: 10.1093/jipm/pmy010

Anakwue, R. (2019). Cardiotoxicity of pesticides: are Africans at risk? *Cardiovasc. Toxicol.* 19, 95–104. doi: 10.1007/s12012-018-9486-7

Anani, O. A., Mishra, R. R., Mishra, P., Enuneku, A. A., Anani, G. A., and Adetunji, C. O. (2020). "Effects of toxicant from pesticides on food security: current developments" in *Innovations in Food Technology*. eds. P. Mishra, R. R. Mishra and C. O. Adetunji (New York, NY: Springer), 313–321.

Andrew, G. S., Simon, U. T., John, A. U., Godwin, O. O., Alexander, N. I., and Ikagu, Y. M. (2018). Studies on changes in some haematological and plasma biochemical parameters in wistar rats fed on diets containing calcium carbide ripened mango fruits. *Int. J. Food Sci. Nutr. Eng.* 8, 27–36. doi: 10.5923/j.food.20180802.02

Anikwe, J. C., Okelana, F. A., Mokwunye, I. U., and Oyedokun, A. Y. (2021). History and recent development of pesticide usage on cocoa in Nigeria. *Afric. J. Gen. Agric.* 5, 211–219.

Arthurs, S., and Dara, S. K. (2019). Microbial biopesticides for invertebrate pests and their markets in the United States. *J. Invertebr. Pathol.* 165, 13–21. doi: 10.1016/j.jip.2018.01.008

Ayilara, M. S., Abberton, M., Oyatomi, O. A., Babalola, O. O., and Odeyemi, O. (2022a). Potentials of underutilized legumes in food security. *Front. Soil Sci.* 2:1020193. doi: 10.3389/fsoil.2022.1020193

Ayilara, M. S., Adeleke, B. S., and Babalola, O. O. (2022b). Bioprospecting and challenges of plant microbiome research for sustainable agriculture, a review on soybean endophytic bacteria. *Microb. Ecol.* 2022, 1–23. doi: 10.1007/s00248-022-02136-z

Basiev, S., Bekmurzov, A., Bekuzarova, S., Dulaev, T., Sokolova, L., Bolieva, Z., et al. (2019). Phytoinsecticides to fight against Colorado beetle. *KnE Life Sci.* 2022, 562–569. doi: 10.18502/kls.v4i14.5643

Benelli, G. (2022). Insecticide, acaricide, repellent and antimicrobial development. *Molecules* 27:386. doi: 10.3390/molecules27020386

Berini, F., Katz, C., Gruzdev, N., Casartelli, M., Tettamanti, G., and Marinelli, F. (2018). Microbial and viral chitinases: attractive biopesticides for integrated pest management. *Biotechnol. Adv.* 36, 818–838. doi: 10.1016/j.biotechadv.2018.01.002

Bhadoria, P., Nagar, M., Bharihoke, V., and Bhadoria, A. S. (2018). Ethephon, an organophosphorous, a fruit and vegetable ripener: has potential hepatotoxic effects? *J. Fam. Med. Primary Care* 7:179. doi: 10.4103/jfmpc.jfmpc_422_16

Boomsma, J. J., Jensen, A. B., Meyling, N. V., and Eilenberg, J. (2014). Evolutionary interaction networks of insect pathogenic fungi. *Annu. Rev. Entomol.* 59, 467–485. doi: 10.1146/annurev-ento-011613-162054

Borges, S., Alkassab, A. T., Collison, E., Hinarejos, S., Jones, B., McVey, E., et al. (2021). Overview of the testing and assessment of effects of microbial pesticides on bees: strengths, challenges and perspectives. *Apidologie* 52, 1256–1277. doi: 10.1007/s13592-021-00900-7

Boucaud-Maitre, D., Rambourg, M.-O., Sinno-Tellier, S., Puskarczyk, E., Pineau, X., Kammerer, M., et al. (2019). Human exposure to banned pesticides reported to the French poison control centers: 2012–2016. *Environ. Toxicol. Pharmacol.* 69, 51–56. doi: 10.1016/j.etap.2019.03.017

Bratovcic, A., Hikal, W. M., Said-Al Ahl, H. A. H., Tkachenko, K. G., Baeshen, R. S., Sabra, A. S., et al. (2021). Nanopesticides and Nanofertilizers and agricultural development: scopes, advances and applications. *OJE* 11, 301–316. doi: 10.4236/oje.2021.114022

Campos, J. N. D., Rabelo, M. M., Bann, P. L., Unruh, J. B., and de Paula-Moraes, S. V. (2022). Insecticide efficacy against tropical sod webworm in concentration-mortality bioassay, 2021. *Arthropod. Manag. Tests* 47:tsac009. doi: 10.1093/amt/tsac009

Chandler, D. (2017). "Basic and applied research on entomopathogenic fungi" in *Microbial Control of Insect and Mite Pests*. ed. L. A. Lacey (Amsterdam: Elsevier), 69–89.

Chang, J. H., Choi, J. Y., Jin, B. R., Roh, J. Y., Olszewski, J. A., Seo, S. J., et al. (2003). An improved baculovirus insecticide producing occlusion bodies that contain bacillus thuringiensis insect toxin. *J. Invertebr. Pathol.* 84, 30–37. doi: 10.1016/S0022-2011(03)00121-6

Chaudhary, P., Chaudhary, A., Bhatt, P., Kumar, G., Khatoon, H., Rani, A., et al. (2022). Assessment of soil health indicators under the influence of nanocompounds and *bacillus* spp. in field condition. Frontiers in environmental. *Science* 9:648. doi: 10.3389/fenvs.2021.769871

Chaudhary, P., Chaudhary, A., Parveen, H., Rani, A., Kumar, G., Kumar, R., et al. (2021a). Impact of nanophos in agriculture to improve functional bacterial community and crop productivity. *BMC Plant Biol.* 21, 1–12. doi: 10.1186/s12870-021-03298-7

Chaudhary, P., Khati, P., Chaudhary, A., Gangola, S., Kumar, R., and Sharma, A. (2021b). Bioinoculation using indigenous *bacillus* spp. improves growth and yield of *Zea mays* under the influence of nanozeolite. *Biotechnology* 11, 1–12. doi: 10.1007/s13205-020-02561-2

Chaudhary, P., Khati, P., Chaudhary, A., Maithani, D., Kumar, G., and Sharma, A. (2021c). Cultivable and metagenomic approach to study the combined impact of nanogypsum and *Pseudomonas taiwanensis* on maize plant health and its rhizospheric microbiome. *PLoS One* 16:e0250574. doi: 10.1371/journal.pone.0250574

Chaudhary, P., and Sharma, A. (2019). Response of nanogypsum on the performance of plant growth promotory bacteria recovered from nanocompound infested agriculture field. *Environ. Ecol.* 37, 363–372.

Chaudhary, P., Sharma, A., Chaudhary, A., Khati, P., Gangola, S., and Maithani, D. (2021d). Illumina based high throughput analysis of microbial diversity of maize rhizosphere treated with nanocompounds and bacillus sp. *Appl. Soil Ecol.* 159:103836. doi: 10.1016/j.apsoil.2020.103836

Chen, A., Wang, Y., Shao, Y., Zhou, Q., Chen, S., Wu, Y., et al. (2018). Genes involved in Beauveria bassiana infection to galleria mellonella. *Arch. Microbiol.* 200, 541–552. doi: 10.1007/s00203-017-1456-0

Chhipa, H. (2019). "Applications of nanotechnology in agriculture" in *Methods in Microbiology*. eds. V. Gurtler, A. S. Ball and S. Soni (Amsterdam: Elsevier), 115–142.

Choudhary, S., Yamini, N. R., Yadav, S. K., Kamboj, M., and Sharma, A. (2018). A review: pesticide residue: cause of many animal health problems. *J. Entomol. Zool. Stud.* 6, 330–333.

Damalas, C. A., and Koutroubas, S. D. (2016). Farmers' exposure to pesticides: toxicity types and ways of prevention. *Toxics* 4, 1–10. doi: 10.3390/toxics4010001

Damalas, C. A., and Koutroubas, S. D. (2020). "Botanical pesticides for eco-friendly pest management: drawbacks and limitations" in *Pesticides in Crop Production: Physiological Biochemical Action*, vol. 10, 181–193.

Dar, S. A., Wani, S. H., Mir, M., Showkat, A., Dolkar, T., and Dawa, T. (2021). Biopesticides: mode of action, efficacy and scope in pest management. *J. Adv. Res. Biochem. Pharmacol.* 4, 1–8.

Dara, S. (2017). "Microbial control of arthropod pests in small fruits and vegetables in temperate climate" in *Microbial Control of Insect and Mite Pests*. ed. L. A. Lacey (Amsterdam: Elsevier), 209–221.

Dassanayake, M. K., Chong, C. H., Khoo, T.-J., Figiel, A., Szumny, A., and Choo, C. M. (2021). Synergistic field crop pest management properties of plant-derived essential oils in combination with synthetic pesticides and bioactive molecules: a review. *Foods* 10:2016. doi: 10.3390/foods10092016

de Bekker, C., Smith, P. B., Patterson, A. D., and Hughes, D. P. (2013). Metabolomics reveals the heterogeneous secretome of two entomopathogenic fungi to *ex vivo* cultured insect tissues. *PLoS One* 8:e70609. doi: 10.1371/journal.pone.0070609

De Oliveira, J. L., Fraceto, L. F., Bravo, A., and Polanczyk, R. A. (2021). Encapsulation strategies for *bacillus thuringiensis*: from now to the future. *J. Agric. Food Chem.* 69, 4564–4577. doi: 10.1021/acs.jafc.0c07118

Deguine, J.-P., Aubertot, J.-N., Flor, R. J., Lescourret, F., Wyckhuys, K. A., and Ratnadass, A. (2021). Integrated pest management: good intentions, hard realities. *Agron. Sustain. Dev.* 41, 1–35. doi: 10.1007/s13593-021-00689-w

Delgado-Carrillo, O., Martén-Rodríguez, S., Ashworth, L., Aguilar, R., Lopezaraiza-Mikel, M., and Quesada, M. (2018). Temporal variation in pollination services to Cucurbita moschata is determined by bee gender and diversity. *Ecosphere* 9:e02506. doi: 10.1002/ecs2.2506

Deravel, J., Krier, F., and Jacques, P. (2014). Biopesticides, a complementary and alternative approach to the use of agrochemicals. A review. *Biotechnologie, Agronomie, Société et Environnement* 18, 220–232.

Desneux, N., Han, P., Mansour, R., Arnó, J., Brévault, T., Campos, M. R., et al. (2021). Integrated pest management of *Tuta absoluta*: practical implementations across different world regions. *J. Pest. Sci.* 1, 1–23. doi: 10.1007/S10340-021-01442-8

Devi, G. D., Murugan, K., and Selvam, C. P. (2014). Green synthesis of silver nanoparticles using Euphorbia hirta (Euphorbiaceae) leaf extract against crop pest of cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae). *J. Biopest.* 7:54.

Dogara, A. M., Hamad, S. W., Halliru, B. S., Wada, N., and Dalorima, T. (2022). Influences of different concentrations of herbicides on the growth and yield of maize as well as their effects on the associated weeds in North-Western Nigeria. *Passer J. Basic Appl. Sci.* 4, 31–36. doi: 10.24271/psr.2021.309284.1097

Dugje, I., Menkir, A., Kamai, N., Aminu, D., Kamara, A., Odo, P., et al. (2020). Participatory evaluation of provitamin a-rich maize (*Zea mays* L.) hybrids in savanna zones of Northeast Nigeria. *Abuja J. Agric. Environ.* 1, 133–154.

Ebrahimi, L., Sheikhigarjan, A., and Ghazavi, M. (2022). Entomopathogenic nematodes for control of potato tuber moth Phthorimaea operculella [Zeller], (Lepidoptera: Gelechiidae) in infested tubers. *Int. J. Pest Manag.* 2022, 1–8. doi: 10.1080/09670874.2022.2058709

Ebuehi, O. A., Oluwatosin, R., and Olufemi, A.-O. (2017). Sniper-organophosphate pesticide exposure induces neurotoxicity and biochemical agitation in male Sprague-Dawley rats. *Int. J. Adv. Biotechnol. Res.* 1, 20–25. doi: 10.33545/26174693.2017.v1.i2a.99

Ejilibe, C. O., Nwamba, H. O., Atama, I. C., Chiamaka, L. A., Aguzie, I. O., Madu, J. C., et al. (2019). Biochemical responses of Bufo regularis (Reuss, 1833) tadpole exposed to Butaforce® and Termex® pesticides. *Pak. J. Zool.* 51, 1–6. doi: 10.17582/journal.pjz/2019.51.6.2175.2180

El-Saadony, M. T., Abd El-Hack, M. E., Taha, A. E., Fouda, M. M., Ajarem, J. S., Maodaa, S. N., et al. (2020). Ecofriendly synthesis and insecticidal application of copper nanoparticles against the storage pest Tribolium castaneum. *Nano* 10:587. doi: 10.3390/nano10030587

Elsakhawy, T., Alkahtani, M. D., Sharshar, A. A., Attia, K. A., Hafez, Y. M., and Abdelaal, K. A. (2020). Efficacy of mushroom metabolites (Pleurotus ostreatus) as a natural product for the suppression of broomrape growth (*Orobanche crenata* Forsk) in faba bean plants. *Plan. Theory* 9, 1–18. doi: 10.3390/plants9101265

Essiedu, J. A., Adepoju, F. O., and Ivantsova, M. N. (2020). Benefits and limitations in using biopesticides: a review. *AIP Conf. Proc.* 2313:080002. doi: 10.1063/5.0032223

Falqueto, S. A., Pitaluga, B. F., de Sousa, J. R., Targanski, S. K., Campos, M. G., de Oliveira Mendes, T. A., et al. (2021). *Bacillus* spp. metabolites are effective in eradicating *Aedes aegypti* (Diptera: Culicidae) larvae with low toxicity to non-target species. *J. Invertebr. Pathol.* 179:107525. doi: 10.1016/j.jip.2020.107525

Fang, W., Wang, X., Huang, B., Zhang, D., Liu, J., Zhu, J., et al. (2020). Comparative analysis of the effects of five soil fumigants on the abundance of denitrifying microbes and changes in bacterial community composition. *Ecotoxicol. Environ. Saf.* 187:109850. doi: 10.1016/j.ecoenv.2019.109850

Farooq, M. A., Arif, M. J., Gogi, M. D., Nawaz, A., and Atta, B. (2019). Comparative efficacy of different pesticide residue mitigation modules in mango. *Am. J. Biomed. Sci. Res.* 4, 214–219. doi: 10.34297/AJBSR.2019.04.000801

Fenibo, E. O., Ijoma, G. N., and Matambo, T. (2021). Biopesticides in sustainable agriculture: A critical sustainable development driver governed by green chemistry principles. *Front. Sus. Food Syst.* 5:619058. doi: 10.3389/fsufs.2021.619058

Gakuubi, M. M., Wanzala, W., Wagacha, J. M., and Dossaji, S. F. (2016). Bioactive properties of *Tagetes minuta* L. (Asteraceae) essential oils: a review. *Am. J. Essent. Oil Nat. Products* 2, 27–36.

Garces, A., Pires, I., and Rodrigues, P. (2020). Teratological effects of pesticides in vertebrates: a review. *J. Environ. Sci. Health A* 55, 75–89. doi: 10.1080/03601234.2019.1660562

Gautam, U.K. (2020). Effect of the entomopathogenic fungus Isaria fumosorosea on physiological processes in insects. Faculty of Science, University of South Bohemia in České Budějovice

Ghelichpour, M., Mirghaed, A. T., Hoseini, S. M., and Jimenez, A. P. (2020). Plasma antioxidant and hepatic enzymes activity, thyroid hormones alterations and health status of liver tissue in common carp (*Cyprinus carpio*) exposed to lufenuron. *Aquaculture* 516:734634. doi: 10.1016/j.aquaculture.2019.734634

Godjo, A., Zadji, L., Decraemer, W., Willems, A., and Afouda, L. (2018). Pathogenicity of indigenous entomopathogenic nematodes from Benin against mango fruit fly (*Bactrocera dorsalis*) under laboratory conditions. *Biol. Control* 117, 68–77. doi: 10.1016/j.biocontrol.2017.10.009

Gozel, U., and Gozel, C. (2021). Entomopathogenic nematodes in Pest management. Integrated Pest management. *Environ. Sound Pest Manag.* 55:63894. doi: 10.5772/63894

Grillo, R., Fraceto, L. F., Amorim, M. J., Scott-Fordsmand, J. J., Schoonjans, R., and Chaudhry, Q. (2021). Ecotoxicological and regulatory aspects of environmental sustainability of nanopesticides. *J. Hazard. Mater.* 404:124148. doi: 10.1016/j.jhazmat.2020.124148

Guven, O., Aydin, T., Karaca, I., and Butt, T. (2021). Biopesticides offer an environmentally friendly solution for control of pine processionary moth (*Thaumetopoea wilkinsoni* tams) larvae and pupae in urban areas. *Biocontrol Sci. Tech.* 31, 35–52. doi: 10.1080/09583157.2020.1826905

Gwinn, K. D. (2018). Bioactive natural products in plant disease control. *Studies in Natural Products Chemistry* 56, 229–246. doi: 10.1016/B978-0-444-64058-1.00007-8

Hagag, E. S. (2021). Evaluation of metabolites of *Myrothecium verrucaria* as biological nematicide against root-knot nematode, *Meloidogyne incognita in vitro* and *in vivo* on sugar beet plants. *J. Plant Protect. Pathol.* 12, 47–53. doi: 10.21608/jppp.2021.52745.1007

Hagstrum, D. W., and Flinn, P. W. (2018). "Integrated pest management" in *Integrated Management of Insects in Stored Products*. eds. B. Subramanyam and D. W. Hagstrum (Florida: CRC Press), 399–407.

Halder, J., Rai, A., and Kodandaram, M. (2013). Compatibility of neem oil and different entomopathogens for the management of major vegetable sucking pests. *Nat Acad. Sci. Lett.* 36, 19–25. doi: 10.1007/s40009-012-0091-1

Harish, S., Murugan, M., Kannan, M., Parthasarathy, S., Prabhukarthikeyan, S., and Elango, K. (2021). "Entomopathogenic viruses" in *Microbial Approaches for Insect Pest Management*. ed. Omkar (New York, NY: Springer), 1–57.

Hashimi, M. H., Hashimi, R., and Ryan, Q. (2020). Toxic effects of pesticides on humans, plants, animals, pollinators and beneficial organisms. *Asian Plant Res. J.* 5, 37–47. doi: 10.9734/aprj/2020/v5i430114

Hicks, H. L., Comont, D., Coutts, S. R., Crook, L., Hull, R., Norris, K., et al. (2018). The factors driving evolved herbicide resistance at a national scale. *Nature Ecol. Evol.* 2, 529–536. doi: 10.1038/s41559-018-0470-1

Holder, D. J., and Keyhani, N. O. (2005). Adhesion of the entomopathogenic fungus *Beauveria* (Cordyceps) *bassiana* to substrata. *Appl. Environ. Microbiol.* 71, 5260–5266. doi: 10.1128/AEM.71.9.5260-5266.2005

Horgan, F. G., and Kudavidanage, E. P. (2020). Use and avoidance of pesticides as responses by farmers to change impacts in rice ecosystems of southern Sri Lanka. *Environ. Manag.* 65, 787–803. doi: 10.1007/s00267-020-01272-x

Hu, Y., Zhang, J., Kong, W., Zhao, G., and Yang, M. (2017). Mechanisms of antifungal and anti-aflatoxigenic properties of essential oil derived from turmeric (*Curcuma longa* L.) on *aspergillus flavus*. *Food Chem.* 220, 1–8. doi: 10.1016/j.foodchem.2016.09.179

Hummadi, E. H., Dearden, A., Generalovic, T., Clunie, B., Harrott, A., Cetin, Y., et al. (2021). Volatile organic compounds of *Metarhizium brunneum* influence the efficacy of entomopathogenic nematodes in insect control. *Biol. Control* 155:104527. doi: 10.1016/j.biocontrol.2020.104527

Husak, V. (2015). Copper and copper-containing pesticides: metabolism, toxicity and oxidative stress. *J. Vasyl Stefanyk Precarp. Nat. Univ. Ser. Soc. Hum. Sci.* 2, 39–51. doi: 10.15330/jpnu.2.1.38-50

Idris, H., Suryani, E., Gustia, H., and Ramadhan, A. I. J. R. I. E. (2022). The effect of various essential oil and solvent additives on the botanical pesticide of *Piper aduncum* essential oil on formulation antifungal activity. *Results Eng.* 16:100644. doi: 10.1016/j.rineng.2022.100644

Imoloame, E. O. (2021). Agronomic and economic performance of maize (*Zea mays* L.) as influenced by seed bed configuration and weed control treatments. *Open Agriculture* 6, 445–455. doi: 10.1515/opag-2021-0030

Indratin, Poniman, Sukarjo, and Helmi, M. (2021). Distribution of endosulfan insecticide residues on intensive shallot agriculture farming in Brebes regency, Indonesia. *IOP Conf. Ser. Earth Environ. Sci.* 648:012080. doi: 10.1088/1755-1315/648/1/012080

Jaleel, W., Saeed, Q., Saeed, S., Ansari, T., Naqqash, M. N., Iqbal, N., et al. (2015). Efficacy and time mortality of *Tribolium castaneum* (Herbst)(Coleoptera: Tenebrionidae) by some essential oils through contact and fumigant methods. *Appl. Sci. Bus. Econom.* 2, 1–7.

Jallow, M. F., Awadh, D. G., Albaho, M. S., Devi, V. Y., and Ahmad, N. (2017). Monitoring of pesticide residues in commonly used fruits and vegetables in Kuwait. *Int. J. Environ. Res. Public Health* 14:833. doi: 10.3390/ijerph14080833

Jayaraj, R., Megha, P., and Sreedev, P. (2017). Organochlorine pesticides their toxic effects on living organisms and their fate in the environment. *Interdiscip. Toxicol.* 9, 90–100. doi: 10.1515/intox-2016-0012

Jindra, M., and Bittova, L. (2020). The juvenile hormone receptor as a target of juvenoid "insect growth regulators". *Arch. Insect Biochem. Physiol.* 103:e21615. doi: 10.1002/arch.21615

Jones, J. G., Korir, R. C., Walter, T. L., and Everts, K. L. (2020). Reducing chlorothalonil use in fungicide spray programs for powdery mildew, anthracnose, and gummy stem blight in melons. *Plant Dis.* 104, 3213–3220. doi: 10.1094/PDIS-04-20-0712-RE

Kaczmarek, A., and Boguś, M. I. (2021). Fungi of entomopathogenic potential in Chytridiomycota and Blastocladiomycota, and in fungal allies of the Oomycota and microsporidia. *IMA fungus* 12, 1–13. doi: 10.1186/s43008-021-00074-y

Kalpana, T., and Anil, T. (2021). A review of biopesticides and their plant phytochemicals information. *Ann. Romanian Soc. Cell Biol.* 25, 3576–3588.

Kanissery, R., Gairhe, B., Kadyampakeni, D., Batuman, O., and Alferez, F. (2019). Glyphosate: its environmental persistence and impact on crop health and nutrition. *Plan. Theory* 8:499. doi: 10.3390/plants8110499

Kaur, S., Kumar, V., Chawla, M., Cavallo, L., Poater, A., and Upadhyay, N. (2017). Pesticides curbing soil fertility: effect of complexation of free metal ions. *Front. Chem.* 5:43. doi: 10.3389/fchem.2017.00043

Kehinde, A. D., and Tijani, A. A. (2021). Effects of access to livelihood capitals on adoption of European Union (EU) approved pesticides among cocoa producing households in Osun state. *Agri. Trop. Subtrop.* 54, 57–70. doi: 10.2478/ats-2021-0007

Khati, P., Bhatt, P., Kumar, R., and Sharma, A. (2018). Effect of nanozeolite and plant growth promoting rhizobacteria on maize. *Biotech* 8, 1–12. doi: 10.1007/s13205-018-1142-1

Kidd, P. S., Alvarez-Lopez, V., Becerra-Castro, C., Cabello-Conejo, M., and Prieto-Fernandez, A. (2017). Potential role of plant-associated bacteria in plant metal uptake and implications in phytotechnologies. *Adv. Bot. Res.* 83, 87–126. doi: 10.1016/bs.abr.2016.12.004

Kim, K.-H., Kabir, E., and Jahan, S. A. (2017). Exposure to pesticides and the associated human health effects. *Sci. Total Environ.* 575, 525–535. doi: 10.1016/j.scitotenv.2016.09.009

Konappa, N., Krishnamurthy, S., Arakere, U. C., Chowdappa, S., Akbarbasha, R., and Ramachandrappa, N. S. (2021). "Nanofertilizers and nanopesticides: recent trends, future prospects in agriculture" in *Advances in Nano-Fertilizers Nano-Pesticides in Agriculture*. ed. P. Opender Koul (Amsterdam: Woodhead Publishing Series in Food Science), 281–330.

Kovendan, K., Chandramohan, B., Govindarajan, M., Jebanesan, A., Kamalakannan, S., Vincent, S., et al. (2018). Orchids as sources of novel nanoinsecticides? Efficacy of *Bacillus sphaericus* and Zeuxine gracilis-fabricated silver nanoparticles against dengue, malaria and filariasis mosquito vectors. *J. Clust. Sci.* 29, 345–357. doi: 10.1007/s10876-018-1331-4

Kumar, V., and Chandel, S. (2018). Effect of different fungicides against Podosphaera pannosa causing rose powdery mildew under greenhouse conditions. *J. Crop Weed* 14, 168–173.

Kumar, V., and Kumar, P. (2019). "Pesticides in agriculture and environment: impacts on human health" in *Contaminants in Agriculture Environment: Health Risks Remediation, Vol. 1*. eds. V. Kumar, R. Kumar, J. Singh and P. Kumar (India: ture and Environmental Science Academy), 76–95.

Kumar, R., Kumar, N., Rajput, V. D., Mandzhieva, S., Minkina, T., Saharan, B. S., et al. (2022). Advances in biopolymeric Nanopesticides: a new eco-friendly/eco-protective perspective in precision agriculture. *Nano* 12:3964. doi: 10.3390/nano12223964

Kumar, J., Ramlal, A., Mallick, D., and Mishra, V. (2021). An overview of some biopesticides and their importance in plant protection for commercial acceptance. *Plan. Theory* 10:1185. doi: 10.3390/plants10061185

Kumar, V., Singh, S., and Upadhyay, N. (2019). Effects of organophosphate pesticides on siderophore producing soils microorganisms. *Biocatal. Agric. Biotechnol.* 21:101359. doi: 10.1016/j.bcab.2019.101359

Kumari, S., Sharma, A., Chaudhary, P., and Khati, P. (2020). Management of plant vigor and soil health using two agriusable nanocompounds and plant growth promotory rhizobacteria in fenugreek. *Biotech* 10:461. doi: 10.1007/s13205-020-02448-2

Lai, Y., Chen, H., Wei, G., Wang, G., Li, F., and Wang, S. (2017). In vivo gene expression profiling of the entomopathogenic fungus *Beauveria bassiana* elucidates its infection stratagems in Anopheles mosquito. *Sci. China Life Sci.* 60, 839–851. doi: 10.1007/s11427-017-9101-3

Lang, G., and Buchbauer, G. (2012). A review on recent research results (2008–2010) on essential oils as antimicrobials and antifungals. A review. *Flavour Fragr. J.* 27, 13–39. doi: 10.1002/ffj.2082

Lasso-Robledo, J. L., Torres, B., and Peralta-Videa, J. R. (2022). Do all cu nanoparticles have similar applications in nano-enabled agriculture? *Plant Nano Biol.* 1:100006. doi: 10.1016/j.plana.2022.100006

Lee, Y. K., Jin, N. Y., Kim, H. J., Yu, Y. M., Yasunaga-Aoki, C., and Youn, Y. N. (2021). Investigation and characteristics of novel biological control agents for controlling dipteran pests. *J. Faculty Agric.* 66, 183–190.

Lengai, G. M., Muthomi, J. W., and Mbega, E. R. (2020). Phytochemical activity and role of botanical pesticides in pest management for sustainable agricultural crop production. *Sci. Afric.* 7:e00239. doi: 10.1016/j.sciaf.2019.e00239

Li, Z., Xiong, J., and Fantke, P. (2022). Screening of pesticide distributions in foods of animal origin: a matrix-based approach for biotransfer factor modeling of grazing mammals. *Environ Sci Process Impacts* 24, 609–624. doi: 10.1039/d1em00454a

Llamas, B., Suarez-Rodriguez, M. C., Gonzalez-Lopez, C. V., Mora, P., and Acien, F. G. (2021). Techno-economic analysis of microalgae related processes for CO_2 bio-fixation. *Algal Res.* 57:102339. doi: 10.1016/j.algal.2021.102339

Loddo, D., Scarabel, L., Sattin, M., Pederzoli, A., Morsiani, C., Canestrale, R., et al. (2019). Combination of herbicide band application and inter-row cultivation provides sustainable weed control in maize. *Agronomy* 10:20. doi: 10.3390/agronomy10010020

Lourenço, A. M., Haddi, K., Ribeiro, B. M., Corrêia, R. F., Tomé, H. V., Santos-Amaya, O., et al. (2018). Essential oil of Siparuna guianensis as an alternative tool for improved lepidopteran control and resistance management practices. *Sci. Rep.* 8, 1–13. doi: 10.1038/s41598-018-25721-0

Lovatto, P. B., Goetze, M., and Thomé, G. C. H. (2004). Extracts effect of wild plants of the Solanaceae family on Brevicoryne brassicae control in cabbage (Brassica oleracea var. acephala). *Cienc. Rural* 34, 971–978. doi: 10.1590/S0103-84782004000400001

Malahlela, M., Thibane, V. S., and Mudau, F. N. (2021). Nematocidal activity of fermented extracts from *Lantana camara* plant parts against *Meloidogyne javanica* on tomato. *Int. J. Veg. Sci.* 27, 20–28. doi: 10.1080/19315260.2019.1697981

Manfo, F. P. T., Mboe, S. A., Nantia, E. A., Ngoula, F., Telefo, P. B., Moundipa, P. F., et al. (2020). Evaluation of the effects of agro pesticides use on liver and kidney function in farmers from Buea. *J. Toxicol.* 2020:2305764. doi: 10.1155/2020/2305764

Matsuda, K., Ihara, M., and Sattelle, D. B. (2020). Neonicotinoid insecticides: molecular targets, resistance, and toxicity. *Annu. Rev. Pharmacol. Toxicol.* 60, 241–255. doi: 10.1146/annurev-pharmtox-010818-021747

Maurer, M., Kerns, D., and Tellez, T. (2018). Citrus Peel miner Marmara salictella monitoring techniques and control measures 1996-971. *Citrus Decid. Fruit Nut Res. Rep.* 1, 1–8.

McGuire, A. V., and Northfield, T. D. (2020). Tropical occurrence and agricultural importance of *Beauveria bassiana* and *Metarhizium anisopliae*. *Front. Sustain. Food Syst.* 4:6. doi: 10.3389/fsufs.2020.00006

Mkenda, P., Mwanauta, R., Stevenson, P. C., Ndakidemi, P., Mtei, K., and Belmain, S. R. (2015). Extracts from field margin weeds provide economically viable and environmentally benign pest control compared to synthetic pesticides. *PLoS One* 10:e0143530. doi: 10.1371/journal.pone.0143530

Moreno-Gavíra, A., Huertas, V., Diánez, F., Sánchez-Montesinos, B., and Santos, M. (2020). *Paecilomyces* and its importance in the biological control of agricultural pests and diseases. *Plan. Theory* 9:1746. doi: 10.3390/plants9121746

Mouyna, I., Hartl, L., and Latgé, J.-P. (2013). β-1, 3-glucan modifying enzymes in aspergillus fumigatus. *Front. Microbiol.* 4:81. doi: 10.3389/fmicb.2013.00081

Murcia-Morales, M., Díaz-Galiano, F. J., Guitérrez-Tirado, I., Flores, J. M., Van der Steen, J. J., and Fernández-Alba, A. R. (2021). Dissipation and cross-contamination of miticides in apiculture. Evaluation by APIStrip-based sampling. *Chemosphere* 280:130783. doi: 10.1016/j.chemosphere.2021.130783

Narware, J., Yadav, R., Keswani, C., Singh, S., and Singh, H. (2019). "Silver nanoparticle-based biopesticides for phytopathogens: scope and potential in agriculture" in *Nano-Biopesticides Today and Future Perspectives*. ed. K. Opender (Amsterdam: Elsevier), 303–314.

Ojuederie, O. B., Chukwuneme, C. F., Samuel, O., Olanrewaju, M. A., Adegboyega, T. T., and Babalola, O. O. (2021). Contribution of microbial inoculants in sustainable maintenance of human health, including test methods and evaluation of safety of microbial pesticide microorganisms. *Biopestic. Bot. Microorgan. Improv. Agric. Hum. Health* 1, 207–240.

Okoroiwu, H. U., and Iwara, I. A. (2018). Dichlorvos toxicity: a public health perspective. *Interdiscip. Toxicol.* 11:129. doi: 10.2478/intox-2018-0009

Omole, R. K., Torimiro, N., Alayande, S. O., and Ajenifuja, E. (2018). Silver nanoparticles synthesized from *Bacillus subtilis* for detection of deterioration in the post-harvest spoilage of fruit. *Sustain. Chem. Pharm.* 10, 33–40. doi: 10.1016/j.scp.2018.08.005

Omoyajowo, K., Njok, K., Amiolemen, S., Ogidan, J., Adenekan, O., Olaniyan, K., et al. (2018). Assessment of pesticide residue levels in common fruits consumed in Lagos state, Nigeria. *LASU J. Res. Rev. Sci.* 2018, 56–62.

Onwujiogu, V. C., Abugu, H. O., and Okoye, C. O. (2022). Health risk assessment of pesticide residue in freshly harvested *Vigna subtserranea* (Bambara nut) in Nsukka south eastern Nigeria. *Environ. Monit. Assess.* 194, 1–15. doi: 10.1007/s10661-022-10201-w

Opeyemi, B. S., Temidayo, B. R., Babalola, Y. O., Emmanuel, I. B., Ojubolamo, M. T., and Folake, A. B. (2018). Biological control of anthracnose disease of tomato using ethanolic extracts of *Azadirachta indica* and *Nicotiana tabacum*. *Int. Ann. Sci.* 4, 20–26. doi: 10.21467/ias.4.1.20-26

Ortiz-Urquiza, A., and Keyhani, N. (2016). Molecular genetics of *Beauveria bassiana* infection of insects. *Adv. Genet.* 94, 165–249. doi: 10.1016/bs.adgen.2015.11.003

Oso, A., and Awe, G. (2019). Effects of different water regimes and spacing on insect pest infestation and efficacy of control measures in cucumber (*Cucumis sativus*). *J. Exp. Agric. Int.* 41, 1–8. doi: 10.9734/jeai/2019/v41i530415

Pan, X., Guo, X., Zhai, T., Zhang, D., Rao, W., Cao, F., et al. (2023). Nanobiopesticides in sustainable agriculture: developments, challenges, and perspectives. *Environ. Sci. Nano*. 10, 41–61. doi: 10.1039/D2EN00605G

Pang, Y.-P., Brimijoin, S., Ragsdale, D. W., Yan Zhu, K., and Suranyi, R. (2012). Novel and viable acetylcholinesterase target site for developing effective and environmentally safe insecticides. *Curr. Drug Targets* 13, 471–482. doi: 10.2174/138945012799499703

Parker, C. T., and Sperandio, V. (2009). Cell-to-cell signalling during pathogenesis. *Cellular Microbiology* 11, 363–369. doi: 10.1111/j.1462-5822.2008.01272.x

Pathak, D., Yadav, R., and Kumar, M. (2017). "Microbial pesticides: development, prospects and popularization in India" in *Plant-microbe interactions in agro-ecological perspectives*. eds. D. Singh, H. Singh and R. Prabha (US: Springer), 455–471.

Pathania, A., Dutta, J., and Mhatre, P. H. (2022). *In-vitro* efficacy of *Verticillium lecanii* (Zimm.) Viegas against Estonian cyst nematode, Cactodera estonica. *Indian Phytopathol.* 75, 1167–1171. doi: 10.1007/s42360-022-00526-4

Pelosi, C., Bertrand, C., Daniele, G., Coeurdassier, M., Benoit, P., Nélieu, S., et al. (2021). Residues of currently used pesticides in soils and earthworms: a silent threat? *Agric. Ecosyst. Environ.* 305:107167. doi: 10.1016/j.agee.2020.107167

Peprah-Yamoah, E., Afrifa-Yamoah, E., Ofori, H., and Adua, E. (2022). Antifeedant potency of *Mentha spicata* aqueous extracts against fall armyworm (*Spodoptera frugiperda*). *Res. Square* 1, 1–15. doi: 10.21203/rs.3.rs-1314042/v1

Pereira, S. P., Santos, S. M., Fernandes, M. A., Deus, C. M., Martins, J. D., de Lima, M. C. P., et al. (2021). Improving pollutants environmental risk assessment using a multi model toxicity determination with *in vitro*, bacterial, animal and plant model systems: the case of the herbicide alachlor. *Environ. Pollut.* 286, 117239–117211. doi: 10.1016/j.envpol.2021.117239

Pertile, M., Antunes, J. E. L., Araujo, F. F., Mendes, L. W., Van den Brink, P. J., and Araujo, A. S. F. (2020). Responses of soil microbial biomass and enzyme activity to herbicides imazethapyr and flumioxazin. *Sci. Rep.* 10, 1–9. doi: 10.1038/s41598-020-64648-3

Polsinelli, G. A., Singh, S. K., Mishra, R. K., Suranyi, R., Ragsdale, D. W., Pang, Y.-P., et al. (2010). Insect-specific irreversible inhibitors of acetylcholinesterase in pests including the bed bug, the eastern yellowjacket, German and American cockroaches, and the confused flour beetle. *Chem. Biol. Interact.* 187, 142–147. doi: 10.1016/j.cbi.2010.01.036

Priya, S., Sarvendra, K., Vinod, K.S., and Kapil, A.C. (2018). Nanopesticides: Manage food security and environmental pollution. Available at: https://www.biotecharticles.com/Agriculture-Article/Nanopesticides-Manage-Food-Security-and-Environmental-Pollution-4391.html (Accessed April 10, 2022).

Rabelo, M. M., Paula-Moraes, S. V., Pereira, E. J. G., and Siegfried, B. D. (2020). Contrasting susceptibility of lepidopteran pests to diamide and pyrethroid insecticides in a region of overwintering and migratory intersection. *Pest Manag. Sci.* 76, 4240–4247. doi: 10.1002/ps.5984

Rajna, S., and Paschapur, A. (2019). Nanopesticides: its scope and utility in pest management. *Indian Farmer* 6, 17–21.

Rakhimol, K., Thomas, S., Volova, T., and Jayachandran, K. (2020). *Controlled Release of Pesticides for Sustainable Agriculture*. New York, NY: Springer.

Rodrigues, D., Costa-Pinto, A. R., Sousa, S., Vasconcelos, M. W., Pintado, M. M., Pereira, L., et al. (2019). *Sargassum muticum* and *Osmundea pinnatifida* enzymatic extracts: chemical, structural, and cytotoxic characterization. *Mar. Drugs* 17:209. doi: 10.3390/md17040209

Roseline, T. A., Murugan, M., Sudhakar, M., and Arunkumar, K. (2019). Nanopesticidal potential of silver nanocomposites synthesized from the aqueous extracts of red seaweeds. *Environ. Technol. Innov.* 13, 82–93. doi: 10.1016/j.eti.2018.10.005

Ruiu, L. (2018). Microbial biopesticides in agroecosystems. *Agronomy* 8:235. doi: 10.3390/agronomy8110235

Sabarwal, A., Kumar, K., and Singh, R. P. (2018). Hazardous effects of chemical pesticides on human health–cancer and other associated disorders. *Environ. Toxicol. Pharmacol.* 63, 103–114. doi: 10.1016/j.etap.2018.08.018

Saberi, F., Marzban, R., Ardjmand, M., Shariati, F. P., and Tavakoli, O. (2020). Optimization of culture media to enhance the ability of local *bacillus thuringiensis* var. *tenebrionis*. Journal of the Saudi society of. *Agric. Sci.* 19, 468–475. doi: 10.1016/j.jssas.2020.08.004

Sabnam, N., and Barman, S. R. (2017). WISH, a novel CFEM GPCR is indispensable for surface sensing, asexual and pathogenic differentiation in rice blast fungus. *Fungal Genet. Biol.* 105, 37–51. doi: 10.1016/j.fgb.2017.05.006

Sabry, A.-K. H. (2020). Role of nanopesticides in agricultural development. *Intellect. Prop. Issues Nanotechnol.* 2020, 107–120. doi: 10.1201/9781003052104-7

Saleh, T. A. (2020). Trends in the sample preparation and analysis of nanomaterials as environmental contaminants. *Trends Environ. Analy. Chem.* 28:e00101. doi: 10.1016/j.teac.2020.e00101

Samada, L. H., and Tambunan, U. S. F. (2020). Biopesticides as promising alternatives to chemical pesticides: a review of their current and future status. *Online J. Biol. Sci.* 20, 66–76. doi: 10.3844/ojbsci.2020.66.76

Santi, L., Coutinho-Rodrigues, C. J., Berger, M., Klein, L. A., De Souza, E. M., Rosa, R. L., et al. (2019). Secretomic analysis of *Beauveria bassiana* related to cattle tick, *Rhipicephalus microplus*, infection. *Folia Microbiol.* 64, 361–372. doi: 10.1007/s12223-018-0659-3

Saranya, S., Ramaraju, K., and Jeyarani, S. (2021). Ovicidal action of different fungal pathogens against two spotted spider mite, *Tetranychus urticae* (Koch) under laboratory conditions. *J. Biol. Control.* 35, 37–40. doi: 10.18311/jbc/2021/27410

Sardar, M., Ahmed, W., Al Ayoubi, S., Nisa, S., Bibi, Y., Sabir, M., et al. (2022). Fungicidal synergistic effect of biogenically synthesized zinc oxide and copper oxide nanoparticles against *Alternaria citri* causing citrus black rot disease. *Saudi J. Biol. Sci.* 29, 88–95. doi: 10.1016/j.sjbs.2021.08.067

Sari, A., and Lubis, L. (2021). The effectiveness of contact fungicides mancozeb in controlling potato leaf blight disease (Phytophthora infestans (Mont) de Barry) in Karo District in the wet month and in the laboratory. *IOP Conf. Ser. IOP Publ. Earth Environ. Sci.* 782:042022. doi: 10.1088/1755-1315/782/4/042022

Scariot, F. J., Delamare, A. P. L., and Echeverrigaray, S. (2022). The effect of chlorothalonil on Saccharomyces cerevisiae under alcoholic fermentation. *Pestic. Biochem. Physiol.* 182, 1–8. doi: 10.1016/j.pestbp.2021.105032

Singh, A., Bhardwaj, R., and Singh, I. K. (2019). "Biocontrol agents: potential of biopesticides for integrated pest management" in *Biofertilizers for Sustainable Agriculture and Environment*. eds. B. Giri, R. Prasad, Q. S. Wu and A. Varma (New York, NY: Springer), 413–433.

Singh, S., Bhuva, B. V., Solanki, V. H., Patel, K. N., and Patel, K. (2020). Persistence and downward movement of four termiticides in three representative soils of Gujarat under laboratory conditions. *J. Entomol. Zool. Studi.* 8, 1803–1811.

Singh, P., Prakash, B., and Dubey, N. (2014). Insecticidal activity of Ageratum conyzoides L., *Coleus aromaticus* Benth. And *Hyptis suaveolens* (L.) Poit essential oils as fumigant against storage grain insect *Tribolium castaneum* Herbst. *J. Food Sci. Technol.* 51, 2210–2215. doi: 10.1007/s13197-012-0698-8

Singh, D., Raina, T. K., and Singh, J. (2017). Entomopathogenic fungi: an effective biocontrol agent for management of insect populations naturally. *J. Pharm. Sci.* 9:833.

Souto, A. L., Sylvestre, M., Tölke, E. D., Tavares, J. F., Barbosa-Filho, J. M., and Cebrián-Torrejón, G. (2021). Plant-derived pesticides as an alternative to pest management and sustainable agricultural production: prospects, applications and challenges. *Molecules* 26:4835. doi: 10.3390/molecules26164835

Sparks, T. C., and Nauen, R. (2015). IRAC: Mode of action classification and insecticide resistance management. *Pest. Biochem. Physiol.* 121, 122–128. doi: 10.1016/j.pestbp.2014.11.014

Stevenson, P. C., Isman, M. B., and Belmain, S. R. (2017). Pesticidal plants in Africa: A global vision of new biological control products from local uses. *Industrial Crops and Products* 110, 2–9. doi: 10.1016/j.indcrop.2017.08.034

Sumekar, Y., Widayat, D., Umiyati, U., and Fitri, A. (2022). Persistence and effectiveness of atrazine herbicide in sweet corn (*Zea mays* saccharata Sturt) cultivation with different organic ingredients in doses. *Research square* 1, 1–13. doi: 10.21203/rs.3.rs-1677256/v1

Surma, M., Sadowska-Rociek, A., and Cieślik, E. (2021). Application of quechers method for the determination of phenylurea herbicides in beetroot by HPLC with uv-Vis detection. *J. Microbiol. Biotechnol. Food Sci.* 2021, 145–147. doi: 10.15414/jmbfs.2015.4.special3.145-147

Svidritskiy, E., Ling, C., Ermolenko, D. N., and Korostelev, A. A. (2013). Blasticidin S inhibits translation by trapping deformed tRNA on the ribosome. *Proceedings of the National Academy of Sciences* 110, 12283–12288. doi: 10.1073/pnas.1304922110

Syafrudin, M., Kristanti, R. A., Yuniarto, A., Hadibarata, T., Rhee, J., Al-Onazi, W. A., et al. (2021). Pesticides in drinking water—a review. *Int. J. Environ. Res. Public Health* 18:468. doi: 10.3390/ijerph18020468

Syromyatnikov, M. Y., Isuwa, M. M., Savinkova, O. V., Derevshchikova, M. I., and Popov, V. N. (2020). The effect of pesticides on the microbiome of animals. *Agriculture* 10, 1–14. doi: 10.3390/agriculture10030079

Tartar, A., Shapiro, A. M., Scharf, D. W., and Boucias, D. G. (2005). Differential expression of chitin synthase (CHS) and glucan synthase (FKS) genes correlates with the formation of a modified, thinner cell wall in in vivo-produced Beauveria bassiana cells. *Mycopathologia* 160, 303–314. doi: 10.1007/s11046-005-0134-y

Tongnuanchan, P., and Benjakul, S. (2014). Essential oils: extraction, bioactivities, and their uses for food preservation. *J. Food Sci.* 79, R1231–R1249. doi: 10.1111/1750-3841.12492

Tongo, I., Onokpasa, A., Emerure, F., Balogun, P., Enuneku, A., Erhunmwunse, N., et al. (2022). Levels, bioaccumulation and biomagnification of pesticide residues in a tropical freshwater food web. *Int. J. Environ. Sci. Technol.* 19, 1467–1482. doi: 10.1007/s13762-021-03212-6

Tripathi, A., Upadhyay, S., Bhuiyan, M., and Bhattacharya, P. (2009). A review on prospects of essential oils as biopesticide in insect-pest management. *Pharmacog. Phytotherap.* 1, 052–063. doi: 10.5897/JPP.9000003

Tsufac, A. R., Awazi, N. P., and Yerima, B. P. K. (2020). Determinants and policy ramifications of cocoa farmers' use of agrochemicals in cocoa-based (*Theobroma cacao*) agroforestry systems in Cameroon. *J. Exp. Agric. Int.* 42, 26–37. doi: 10.9734/jeai/2020/v42i1030611

Ujvary, I. (2010). "Pest control agents from natural products" in *Hayes' Handbook of Pesticide Toxicology*. ed. B. T. Ikem (Massachusetts: Elsevier), 119–229.

Ullah, M. R., and Dijkstra, F. A. (2019). Fungicide and bactericide effects on carbon and nitrogen cycling in soils: a meta-analysis. *Soil Systems* 3:23. doi: 10.3390/soilsystems3020023

Upadhyay, N., Dwivedy, A. K., Kumar, M., Prakash, B., and Dubey, N. K. (2018). Essential oils as eco-friendly alternatives to synthetic pesticides for the control of *Tribolium castaneum* (Herbst)(Coleoptera: Tenebrionidae). *J. Essent. Oil Bear. Plants* 21, 282–297. doi: 10.1080/0972060X.2018.1459875

Wang, C., and Leger, R. J. S. (2007). The Metarhizium anisopliae perilipin homolog MPL1 regulates lipid metabolism, appressorial turgor pressure, and virulence. *J. Biol. Chem.* 282, 21110–21115. doi: 10.1074/jbc.M609592200

Wang, C., and St Leger, R. (2007). The MAD1 adhesin of Metarhizium anisopliae links adhesion with blastospore production and virulence to insects, and the MAD2 adhesin enables attachment to plants. *Eukaryot. Cell* 6, 808–816. doi: 10.1128/EC.00409-06

Wojda, I., Kowalski, P., and Jakubowicz, T. (2009). Humoral immune response of galleria mellonella larvae after infection by Beauveria bassiana under optimal and heat-shock conditions. *J. Insect Physiol.* 55, 525–531. doi: 10.1016/j.jinsphys.2009.01.014

Xiao, Y., and Wu, K. (2019). Recent progress on the interaction between insects and *bacillus thuringiensis* crops. *Philos. Trans. R. Soc. B* 374:20180316. doi: 10.1098/rstb.2018.0316

Yadav, R. K., Singh, N., Singh, A., Yadav, V., Bano, C., and Khare, S. (2020). Expanding the horizons of nanotechnology in agriculture: recent advances, challenges and future perspectives. *Vegetos* 33, 203–221. doi: 10.1007/s42535-019-00090-9

Zaki, O., Weekers, F., Thonart, P., Tesch, E., Kuenemann, P., and Jacques, P. (2020). Limiting factors of mycopesticide development. *Biol. Control* 144:104220. doi: 10.1016/j.biocontrol.2020.104220

Zheng, N., Ding, N., Gao, P., Han, M., Liu, X., Wang, J., et al. (2018). Diverse algicidal bacteria associated with harmful bloom-forming *Karenia mikimotoi* in estuarine soil and seawater. *Sci. Total Environ.* 631, 1415–1420. doi: 10.1016/j.scitotenv.2018.03.035

Zhou, Q., Shao, Y., Chen, A., Li, W., Wang, J., and Wang, Y. (2019). In vivo transcriptomic analysis of Beauveria bassiana reveals differences in infection strategies in *galleria mellonella* and *Plutella xylostella*. *Pest Manag. Sci.* 75, 1443–1452. doi: 10.1002/ps.5266

frontiers | Frontiers in Microbiology

TYPE Review
PUBLISHED 03 May 2023
DOI 10.3389/fmicb.2023.1133968

OPEN ACCESS

EDITED BY
Parul Chaudhary,
National Dairy Research Institute (ICAR),
India

REVIEWED BY
Bartholomew Saanu Adeleke,
Olusegun Agagu University of Science and Technology,
Nigeria
Anuj Chaudhary,
Shobhit University,
India
Geeta Bhandari,
Swami Rama Himalayan University,
India

*CORRESPONDENCE
Viabhav Kumar Upadhayay
✉ viabhav.amu@gmail.com
Manoj Kumar Chitara
✉ manojchitara01@gmail.com

†These authors have contributed equally to this work and share first authorship

SPECIALTY SECTION
This article was submitted to Microbiotechnology, a section of the journal Frontiers in Microbiology

RECEIVED 29 December 2022
ACCEPTED 06 March 2023
PUBLISHED 03 May 2023

CITATION
Upadhayay VK, Chitara MK, Mishra D, Jha MN, Jaiswal A, Kumari G, Ghosh S, Patel VK, Naitam MG, Singh AK, Pareek N, Taj G, Maithani D, Kumar A, Dasila H and Sharma A (2023) Synergistic impact of nanomaterials and plant probiotics in agriculture: A tale of two-way strategy for long-term sustainability.
Front. Microbiol. 14:1133968.
doi: 10.3389/fmicb.2023.1133968

Synergistic impact of nanomaterials and plant probiotics in agriculture: A tale of two-way strategy for long-term sustainability

Viabhav Kumar Upadhayay[1*†], Manoj Kumar Chitara[2*†], Dhruv Mishra[3], Manindra Nath Jha[1], Aman Jaiswal[1], Geeta Kumari[1], Saipayan Ghosh[4], Vivek Kumar Patel[5], Mayur G. Naitam[1], Ashish Kumar Singh[6], Navneet Pareek[7], Gohar Taj[8], Damini Maithani[9], Ankit Kumar[10], Hemant Dasila[11] and Adita Sharma[12]

[1]Department of Microbiology, College of Basic Sciences & Humanities, Dr. Rajendra Prasad Central Agricultural University, Samastipur, Bihar, India, [2]Department of Plant Pathology, College of Agriculture, A.N.D University of Agriculture and Technology, Ayodhya, Uttar Pradesh, India, [3]Department of Biological Sciences, College of Basic Sciences and Humanities, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India, [4]Department of Horticulture, PGCA, Dr. Rajendra Prasad Central Agricultural University, Samastipur, Bihar, India, [5]Department of Plant Pathology, PGCA, Dr. Rajendra Prasad Central Agricultural University, Samastipur, Bihar, India, [6]Department of Biotechnology and Synthetic Biology, Center of Innovative and Applied Bioprocessing, Sector 81, Mohali, India, [7]Department of Soil Science, College of Agriculture, G. B. Pant University of Agriculture and Technology, Pantnagar, India, [8]Department of Molecular Biology & Genetic Engineering, College of Basic Sciences and Humanities, GBPUA&; T, Pantnagar, Uttarakhand, India, [9]School of Biotechnology, IFTM University, Moradabad, India, [10]Department of Horticulture, College of Agriculture, G. B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India, [11]Department of Microbiology, Akal College of Basic Sciences, Eternal University, Sirmaur, Himachal Pradesh, India, [12]College of Fisheries, Dholi, Dr. Rajendra Prasad Central Agricultural University, Muzaffarpur, Bihar, India

Modern agriculture is primarily focused on the massive production of cereals and other food-based crops in a sustainable manner in order to fulfill the food demands of an ever-increasing global population. However, intensive agricultural practices, rampant use of agrochemicals, and other environmental factors result in soil fertility degradation, environmental pollution, disruption of soil biodiversity, pest resistance, and a decline in crop yields. Thus, experts are shifting their focus to other eco-friendly and safer methods of fertilization in order to ensure agricultural sustainability. Indeed, the importance of plant growth-promoting microorganisms, also determined as "plant probiotics (PPs)," has gained widespread recognition, and their usage as biofertilizers is being actively promoted as a means of mitigating the harmful effects of agrochemicals. As bio-elicitors, PPs promote plant growth and colonize soil or plant tissues when administered in soil, seeds, or plant surface and are used as an alternative means to avoid heavy use of agrochemicals. In the past few years, the use of nanotechnology has also brought a revolution in agriculture due to the application of various nanomaterials (NMs) or nano-based fertilizers to increase crop productivity. Given the beneficial properties of PPs and NMs, these two can be used in tandem to maximize benefits. However, the use of combinations of NMs and PPs, or their synergistic use, is in its infancy but has exhibited better crop-modulating effects in terms of improvement in crop productivity, mitigation of environmental stress (drought, salinity, etc.), restoration of soil fertility, and strengthening of the bioeconomy. In addition, a proper assessment of nanomaterials is necessary before their application, and

a safer dose of NMs should be applicable without showing any toxic impact on the environment and soil microbial communities. The combo of NMs and PPs can also be encapsulated within a suitable carrier, and this method aids in the controlled and targeted delivery of entrapped components and also increases the shelf life of PPs. However, this review highlights the functional annotation of the combined impact of NMs and PPs on sustainable agricultural production in an eco-friendly manner.

KEYWORDS

nanomaterials, plant probiotics, sustainable agriculture, soil fertility, bioeconomy

1. Introduction

Numerous tactics dealing with the improvement of crop production are essentially required to meet the basic food needs of the rapidly growing human population. The sector of agriculture affected by climate change, where increasing phenomena of abiotic stresses such as drought, salinity, cold, flooding, and biotic stress (attacks by pathogens such as bacteria, fungi, oomycetes, nematodes, and herbivores) negatively affect agricultural production (Shahzad et al., 2021; Upadhayay et al., 2023). In addition, the agrochemicals showed a significant increase in crop yield in the last few decades (Lin et al., 2019), but later harmful effects from the over-application of chemical fertilizers became apparent (Upadhayay et al., 2022a,b). It led to the degradation of soil quality, disturbance of soil microbial ecology, pollution of soil and water bodies, and harmful effects on human health due to residues of pesticides and herbicides (Singh et al., 2020; Tripathi et al., 2020; Boregowda et al., 2022). Moreover, the transition to organic agriculture, particularly the use of biofertilizers, provided an environmentally friendly alternative to chemical-based agriculture, as well as improved crop yield and soil quality (Asghar et al., 2022; Elnahal et al., 2022). The term "plant probiotics (PPs)" can be used to decode a distinct group of microbial strains with all the necessary characteristics to be classified as biofertilizers that influence plant growth through both direct and indirect mechanisms (microbes that show beneficial attributes for plants in terms of growth and yield; Sarbani and Yahaya, 2022; Rai et al., 2023). The rhizosphere and the inner regions of plant tissues each serve as a special hub for their respective microbial communities, the rhizomicrobiome (Jiang G. et al., 2022), and the endophytomicrobiome (Pandey et al., 2022). This microbiome is a rich source of plant probiotics due to the multitude of traits it possesses, such as the solubilization of nutrients (Khan et al., 2022), nitrogen fixation (Abdelkhalek et al., 2022), production of plant hormones [indole-3-acetic acid (IAA); Nazli et al., 2020], ammonia (Upadhayay et al., 2022b), anti-pathogenic compounds (Mathur et al., 2019), hydrogen cyanide (HCN; Kashyap et al., 2021), exopolysaccharides (Latif et al., 2022), siderophore (Mushtaq et al., 2022), and lytic enzymes (Reddy et al., 2022). Plant probiotics enhance nutrient uptake and provide protection for plants from environmental stresses, such as biotic and abiotic stresses, and also improve plant health (Kenawy et al., 2021; Pandey et al., 2022). Plant probiotics with varying plant growth-stimulating capabilities provide advantages such as improved crop productivity and food security (Arif et al., 2020; Ghoghari et al., 2022). In contemporary times, the use of nanotechnology in developing countries is gaining more attention, especially in the field of agriculture (Neme et al., 2021). Due to their greater surface area and solubility, nanomaterials are regarded as superior to conventional agrochemicals when used as nanofertilizers in agriculture (Fen et al., 2022). Nanofertilizers improve the nutrient uptake efficiency of plants, diminish the detrimental effects of environmental stresses, and increase crop productivity (Guleria et al., 2022). It is possible to use a combination of the selective plant probiotics that have been shown to be compatible with the nanoparticles of interest (Khati et al., 2017, 2018; Agri et al., 2021; Chaudhary et al., 2021a,b,c). NMs and PPs together hold a great promise for sustainable agriculture as better alternatives to agrochemicals and are becoming a popular concept in the agricultural sector. This idea of efficient fertilization can be preferred over chemical-based fertilization because of its higher efficacy in resource utilization, sustained and slow release of nutrients, increase in crop productivity with a lesser dose of fertilizer, and least negative impacts on soil. Moreover, the use of NMs and PPs is economically feasible and poses lesser toxicity to the environment. According to the literature, the "cocktail" of NMs and PPs can be considered a "nanobiofertilizer (NBF)," because it has the effectiveness of both components (i.e., NMs and PPs) and aids in the slow and controlled release of nutrients, improves nutrient use efficiency, and results in a significant increase in crop yield (Kumari and Singh, 2020).

The microbial part of this cocktail contributes benefits to the plant system due to its wide array of plant growth-stimulating traits such as the solubilization of nutrients, nitrogen fixation, production of plant hormones, EPS, siderophore, and anti-pathogenic compounds. The improvement in soil fertility, functional enzymatic activities, NPK content, organic carbon content, and soil microbial biomass are reflected under the influence of the effective microbial component. On the contrary, the second and most effective segment, "NMs," maximize the benefits and contributes to plant growth through the controlled and sustained release of nutrients, a reduction in the fixation of nutrients in the soil, an increase in the bio-availability of nutrients to plants, making plants more tolerant to environmental stress, and the protection of plants from pests. The combination of nanomaterials and plant probiotics can be applied to plants in a variety of ways, including seed treatment, seedling treatment, foliar application, soil application, and other methods. Nanotechnology advancements have also led to the encapsulation of plant probiotic strains within the appropriate nanomaterials (Panichikkal et al., 2019, 2021; Akhtar et al., 2022) or the encapsulation of both NMs and PPs within a suitable carrier (Moradi Pour et al., 2022), depending on the choice of experiments. This concept maintains the efficacy and shelf life of the

microbial component (PPs) as well as the controlled and sustained supply of both NMs and PPs. This two-pronged strategy increases nutrient availability directly through the use of nanomaterials, while also stimulating plant growth through effective microbial treatment. The use of such a combination of effective doses of NMs and PPs has the potential to create a big difference in the agricultural sector, which will eventually be fruitful in providing benefits of sustainable agricultural production and as well as food security (Kumari et al., 2021; Agri et al., 2022; Akhtar et al., 2022). The present review illustrates the impact of the combined use of NM and PP, as an effective but two-way strategy, on food crops in terms of increased crop production, reducing the detrimental effects of environmental stress, improving soil fertility, and strengthening the bioeconomy.

2. Compendious outline of nanomaterials

Nanomaterials are naturally or artificially synthesized exceptionally tiny molecules ranging from 1 to 100 nm in size (Rehman and Pandey, 2022). The smaller size and high surface-to-volume ratio of nanomaterials give them distinct and advantageous properties in different scientific fields compared to their bulk analog (Yang et al., 2022). The NM has unique physiochemical properties and flexible scaffolds, making them functional with biomolecules and unique compared to other materials (Muthukumaran et al., 2022). Furthermore, it has been demonstrated that some NMs, such as magnetic (Armenia et al., 2022), gold (Jiang et al., 2017), polymeric (Kamaly et al., 2016), or hybrid NMs (Ferreira Soares et al., 2020), may react to external stimuli, leading to a spatiotemporally regulated release of macromolecules. In the last few decades, synthetic NMs have been efficiently used in pharmacology and medicine, especially for therapeutic or diagnostic applications (Zain et al., 2022). These NMs or nanoparticles are carbon-based, inorganic, or organic. Inorganic nanoparticles have numerous scientific uses and are metallic or metal oxides. Constructive or destructive processes can synthesize these nanomaterials using nearly all metals (Upadhayay et al., 2019). Among the different elements, Cd, Au, Al, Co, Zn, Pb, Fe, Cu, and Ag are frequently used to synthesize nanoparticles (Ali et al., 2022). It was reported that the metal oxide-based nanoparticles alter the nature of their analog metals (Sanzari et al., 2019). For example, iron (Fe) containing nanoparticles (NPs) rapidly oxidized to Fe oxide in the presence of oxygen (O) at room temperature, making them more reactive and efficient compared to their parent iron nanoparticles (Sanzari et al., 2019; Ezealigo et al., 2021). There are different types of commonly manufactured nanoparticles, such as "silicon dioxide (SiO_2)," "zinc oxide (ZnO)," "cerium oxide (CeO_2)," "aluminium oxide (Al_2O_3)," "titanium oxide (TiO_2)," and "magnetite (Fe_3O_4)" which contain metal oxides (Fuskele and Sarviya, 2017). Some nanoparticles, *viz.*, liposomes, dendrimers, ferritin, and micelles, are organic nanoparticles and eco-friendly in nature (Sanzari et al., 2019; Upadhayay et al., 2019).

In addition, "carbon-based" refers to another critical group of nanoparticles, further classified into fullerenes, graphene, carbon nanotubes (CNTs), carbon nanofibers, and carbon black (Ramar and Balraj, 2022). Occasionally, the term "activated carbon in nanosize" is also used for carbon-based nanoparticles (Upadhayay et al., 2019). The "bottom-up" strategy and the "top-down" approach have been suggested as two crucial strategies for the synthesis of NPs (Gutiérrez-Cruz et al., 2022). Among them, the bottom-up method is occasionally referred to as the constructive method because it involves the steady construction of a structure that starts from the atomic level and progresses up to the nanoparticle level (Upadhayay et al., 2019). Different methods such as chemical vapor deposition (CVD), biosynthesis, sol–gel, pyrolysis, and spinning are the bottom-up approach for nanoparticle synthesis. The term "biosynthesis" refers to a sustainable process that uses plant, bacterial, and fungal extracts coupled with precursors to create nanoparticles (Sanzari et al., 2019).

On the other hand, the bulk material is broken down into nanometric-sized particles using the "top-down method" or "destructive process (Yin et al., 2021)." Different strategies frequently used for the development of nanoparticles include laser ablation, thermal decomposition, nanolithography, sputtering, and mechanical milling (Sanzari et al., 2019; Upadhayay et al., 2019). Currently, polymeric nanoparticles have sought lots of attention due to their ease of synthesis, biocompatibility, and responsiveness to stimuli (Zu et al., 2021).

However, core or shell nanoparticles are also available in different combinations of materials used, which are organic/organic, inorganic/organic, and inorganic/inorganic materials. The shell of nanoparticles is selected based on ultimate applications and use (Sanzari et al., 2019). For example, it was proposed that polymeric shells enhance nanoparticle biocompatibility (Sharifianjazi et al., 2021). It has also been possible to create NPs with a nanostructured shell. Mesoporous silica nanoparticles (NPs) are nanoparticles with a mesoporous structure and a highly functionalizable surface (Zhang et al., 2022). In nanotechnology, a novel class of NMs known as nanogels (NGs) is gaining more attention due to its colloidal stability, bioconjugation, good physicochemical qualities, and stimuli sensitivity such as temperature and pH (Dalir Abdolahinia et al., 2022). Nanogels are made up of natural or synthetic polymer chains that are nano-sized ionic as well as non-ionic hydrogels. The NGs are highly porous that have high water content, i.e., 70–90% of the whole structure with high load capacity (Sanzari et al., 2019). A few examples of the nanogels are poly (vinyl alcohol), poly (ethyleneimine), chitosan, poly (ethylene oxide), poly (vinylpyrrolidone), alginate, poly (vinylpyrrolidone), and among them, the most frequent NGs is N-isopropyl acrylamide (Pinelli et al., 2022). Hybrid NGs are classified as (i) "nanomaterial–nanogel," which incorporates nano-sized materials such as "magnetic" or "carbonaceous" NPs and (ii) "polymer–nanogel composites," which include "interpenetrated networks (IPNs)," "copolymer," and "core-shell particles" (Eslami et al., 2019; Sanzari et al., 2019).

3. Nanomaterials in agriculture: A way of smart delivery of nano-based fertilizers

The agricultural sector is highly dependent on climatic conditions, but in recent years, climate change has become a major concern of our human civilization (Qin et al., 2020; Kasperson et al., 2022). The adverse effects of climate change manifested as excessive rainfall, drought, extreme cold, heat wave, pest resurgence, and disease outbreaks caused the biological change in the crop life cycle, resulting in reduced grain yield, which directly affects food security on a global scale (Chitara et al., 2017; Liliane and Charles, 2020). Experts are

focusing on the development of cutting-edge technologies in the agricultural sector in order to mitigate the detrimental effects of climate change (Shahzad et al., 2021) and emphasizing the synthesis of various nano-based products and the assessment of safer doses of nano-based products prior to their application. Moreover, nano-based fertilizers can provide an economically feasible and ecologically safe option for sustainable crop production under climate change scenarios.

Nanotechnology-based synthetic fertilizer applications in agricultural crop production are becoming popular strategies due to their beneficial role in increasing crop productivity, improving nutrient use efficiency, and reducing the impact of environmental constraints on crops (Beig et al., 2022). There are certain types of NMs *viz.* inorganic-based NMs, carbon-based NMs, organic-based NMs, and composite-based NMs have been used in agricultural crop production. Using all these NMs, researchers developed site-specific, targeted nanofertilizers, nanoherbicides, nanopesticides, nanofungicides, and nanoinsecticides, which have to prove themselves as highly efficient nano-based agrochemicals (Bana et al., 2020; Qazi and Dar, 2020; Ahmed et al., 2021; Okey-Onyesolu et al., 2021). Targeted application of nanofertilizers to crops improves nutrient use efficiency and prevents nutrient losses, as well as reducing the over-application of fertilizers can also help reduce fertilizer toxicity, which is followed by many farmers (Hofmann et al., 2020; Mejias et al., 2021). In addition to the application of nano fertilizers, nano herbicides are also used in weed control. Weed also hampers the agricultural dry matter accumulation due to their high competitiveness with the main crop for nutrients and space. Thus, with the help of nanotechnology, more competent nano-based herbicides have been developed that give better results compared to commercially available conventional herbicides (Abigail and Chidambaram, 2017; Balah and Pudake, 2019). Conventional herbicides only kill the top of the leaves, resulting in weed regrowth, but in the case of nanoherbicide application, the targets for killing are the root of the weed. After the roots have died, the weed plants are unable to resist regrowth.

Applications of NMs-based nano-pesticides are helpful in the control of a wide variety of pests that affect crops. In general, the conventional application of pesticides to crops increases cultivation costs and causes environmental pollution (Hajji-Hedfi and Chhipa, 2021). Nano-based pesticides have increased retention capacity with high efficacy, durability, good dispersion, and wettability, which makes them a potent pesticide compared to conventional pesticides, as well as their low dose release, which increases effectiveness and reduces environmental losses, soil degradation, and toxicity (Kumar et al., 2019; Vignardi et al., 2020). Some examples of nano-pesticides are Karate® ZEON against soybeans, rice, and cotton pests; and stomach poison for insects sold as Gutbuster. Similarly, nanomaterial-based nanofungicides and antimicrobial compounds are also helpful in plant disease management. Due to its large surface area to volume ratio, it increases their contact with the microbes and easily penetrates into the microbial cell, making excellent contact for nano-fungicides. Applications of nanofungicides provide targeted delivery, improved bioavailability as a result of increased solubility and penetrability, lower dosages, and decreased dose-dependent toxic effects (Ul Haq and Ijaz, 2019). Recently, metal-based NPs such as Ag, Au, Cu, Cd, Al, Se, Zn, Ce, Ti, and Fe synthesized with plant extract have gained in popularity, and they are all effective in the control of phytopathogens (Hernández-Díaz et al., 2021). Many researchers have demonstrated AgNPs as potent nanometal-based pesticides with antibacterial and antifungal activity, successfully used in controlling plant diseases (Khan et al., 2021; Tariq et al., 2022).

The application of NMs such as nanochitosan, nanogypsum, nanourea, carbon nanotubes, and nanophosphorus also showed their important roles in disease suppression, improvement in soil functions and structure, enhancement in photosynthetic efficiency, and crop production. *Meloidogyne incognita* densities alone or in the presence of TMV were reduced by nano-chitosan by 45.89 to 66.61%, while root gall density was reduced by 10.63 to 67.8% (Khalil et al., 2022). The combined use of nanogypsum and *Pseudomonas taiwanensis* on maize improves the structure and function of the soil, which has a beneficial influence on plant health without generating toxicity (Chaudhary et al., 2021c). The foliar application of nano-urea to pearl millet plants improved plant growth metrics, dry matter accumulation, chlorophyll content, and NPK content (Sharma S. K. et al., 2022). Carbon nanotubes have potent antibacterial properties as well as induced defense activation after application to tomato crops infested with *Alternaria solani* (González-García et al., 2021). The administration of the nanophosphorous (nP) *via* foliar application to plants growing in P-deficient soil increased plant growth and yield attributing metrics, leaf integrity, chlorophyll content, P contents of leaf and seed, and improved anatomical topographies (Abou-Sreea et al., 2022). Table 1 depicts a recent scenario deciphering the beneficial effects of various NMs on plants. In addition, Table 2 shows some of the commercially available fertilizers based on NMs with their ingredients (Elemike et al., 2019; Pirzadah et al., 2020; Avila-Quezada et al., 2022).

4. Molecular insights on NMs for plant growth and development

The advancement of NMs in terms of plant growth is further embellished by illustrating their molecular mechanisms, which are particularly well understood at the level of relative gene expression. Several high-throughput studies have been conducted to investigate the effects of NMs on specific gene expression patterns, whether upregulation or downregulation, for a variety of plant activities such as seed germination, photosynthesis, and abiotic and biotic stress tolerance. Application of ZnO NPs (25 mg/L) recorded the maximum level of photosynthetic pigments due to the higher expression of photosynthesis-related genes ("CHLI," "LHCa/b," and "RSSU"; Mardi et al., 2022). The effect of silica nanoparticles observed in terms of improvement of wheat growth under filed conditions and upregulation of genes related to plant hormones ("TIR1" for IAA; "PYR/PYL," "PP2C," "SnRK2," and "ABF" for abscisic acid), sugar metabolism (α-glucosidase, SUS, SPC), and chlorophyll ("CHLH," "CAO," and "POR"; Li et al., 2023). Foliar application of manganese ferrite NMs (10 mg/L) induced early flowering in tomatoes by upregulating the flowering induction gene *SFT*. A similar study also reported the upregulation of genes associated with gibberellin biosynthesis (GA20ox2, GA20ox3, and SIGAST; Yue et al., 2022). Among the genes involved in the photosynthetic process in *Brassica chinensis* L., ferredoxin-NADP reductase (PetH) was highly expressed under various concentrations (0.7, 7, and 70 mg/kg) of CeO_2 NPs, while photosystem II lipoprotein (Psb27) was downregulated under varying levels of NPs (7, 70, and 350 mg/kg; Hong et al., 2023). One of the most important mechanisms for plant survival under stress conditions is the expression and regulation of abiotic stress-responsive genes (Sahil et al.,

TABLE 1 Beneficial effects of different nanomaterials on plants.

Nano- materials	Concentration	Crop	Beneficial role	Reference
Nano selenium	100 mg/L	Tomato (*Solanum lycopersicum* L.)	• Enhanced yield and quality of tomato fruits • Increase in soluble solids content • Activation of antioxidant enzymes such as CAT, POX, and PPO under saline stress	Saffan et al. (2022)
	-do-	Banana	• Enhancement in the growth, photosynthetic pigments and improvement in fluorescence	Shalaby et al. (2022)
Nano- Copper	-do-	Wheat (*Triticum aestivum* L.)	• Amelioration of DNA damage and DNA Methylation	Hosseinpour et al. (2022)
	69.4 µM (4.444 mg/L)	Maize	• Increase in plant growth and grain yield	Van Nguyen et al. (2022)
Nano-chitosan	100 and 200 µg/ml	Potato (*Solanum tuberosum*)	• Controlling bacterial wilt caused by *Ralstonia solanacearum*	Khairy et al. (2022)
Zinc- nanoparticle	40–160 mg/kg (soil application), 10-40 ppm (foliar application)	maize	• Enhancement in the growth and extract yield of maize cultivated in Zn-deficient soils	Azam et al. (2022)
Nano-urea	500 and 1,000 mg/L	*Vigna radiata* L.	• Reduction in nitrate (NO_3-N) leaching • Significant enhancement in the protein content, free radical scavenging activity and phenolic content • Increment in morphological growth as well as crop biomass	Sharma A. et al. (2022)
Zinc- and magnesium-doped hydroxyapatite-urea nanohybrids	50 and 25%	Wheat (*Triticum aestivum*)	• Improvement in the wheat growth and yield. • Enhancement in the nutritional element uptake and grain protein and phospholipid levels	Sharma B. et al. (2022)
Nano- gypsum	240 kg/ha	Spinach	• Mitigation of salinity-sodicity effects and enhancement in the spinach growth in saline-sodic soil	Salama et al. (2022)
Nanophosphorus	0.1 g/L	Fenugreek	• Increase in deficit irrigation stress tolerance • Enhancement in plant growth and productivity by increasing water use efficiency, osmo-regulatory compounds (especially, soluble sugars and proline) and activation of antioxidant enzymes	Abou-Sreea et al. (2022)

2021). NMs, however, showed a positive impact in terms of improving plant tolerance by upregulating the expression of genes involved in plant survival under stress conditions. Chitosan NPs upregulated drought-responsive genes such as "*HsfA1a*," "*SlAREB1*," "*LeNCED1*," and "*LePIP1*" in *Solanum lycopersicum* (Mohamed and Abdel-Hakeem, 2023). The genes involved in drought tolerance, such as "*P5CS*," "*CAT1*," and "*DREB2*," related to "proline biosynthesis," "catalase activity," and "dehydration-responsive element-binding proteins," respectively, were highly expressed in wheat by the application of zinc oxide NPs to mitigate the drastic effect of drought in plants (Raeisi Sadati et al., 2022). Recently, Subotić et al. (2022) reported higher expression of aquaporin genes (*PIP1;3*, *PIP1;5*, and *PIP2;4*) related to water and solute transportation across the plant membrane in tomatoes by exposing them to a nanosubstance, i.e., hyper-harmonized hydroxyl-modified fullerene (3HFWC). Phytochemicals, such as alkaloids, have defensible importance in plants under stress conditions, and their biosynthesis is increased under drought conditions (Amirifar et al., 2022). The further addition of nanomaterials can enhance the level of biosynthesis of phytochemicals in plants. The study of Ali et al. (2021) observed the upregulation of key genes such as *STR* (strictosidine synthase), *PRX1* (peroxidase 1), *GS* (geissoschizine synthase), and *DAT* (deacetylvindoline-4-O-acetyltransferase) involved in the biosynthesis of alkaloids under the response of chitosan NMs in drought stress. In tomato plants, Rahmatizadeh et al. (2021) showed the effect of

TABLE 2 List of some approved and commercially available nanomaterials-based fertilizers.

Name of fertilizer	Constituents	Name of manufacturer
Nano-Urea (Liquid)	4% total N (w/v)	Indian Farmers Fertiliser Cooperative Ltd., India
Plant nutrition powder (green nano)	N (0.5%), P_2O_5 (0.7%), K_2O (3.9%), Ca (2.0%), Mg (0.2%), S (0.8%), Fe (1.0%), Mn (49 ppm), Cu (17 ppm), and Zn (12 ppm)	Green Organic World Co., Ltd., Thailand
Nano Fertilizer (Eco Star; 5) gm	N (8.2%), K_2O (2.3%), organic matter (75.9%), and C:N (5.4)	Shan Maw Myae Trading Co., Ltd., India
Nano Ultra-Fertilizer (500) g	Organic matter (5.5%), T-N (10%), T-P_2O_5 (9%), T-K_2O (14%), AC-P_2O_5 (8%), CA-K_2O (14%), and CA-MgO, (3%)	SMTET Eco-technologies Co., Ltd. Taiwan
Nano Calcium (Magic Green; 1) kg	$CaCO_3$ (77.9%), $MgCO_3$ (7.4%), SiO2 (7.47%), K (0.2%), Na (0.03%), P (0.02%), Fe (7.4 ppm), Al_2O_3 (6.3 ppm), Sr. (804 ppm) sulfate (278 ppm), Ba (174 ppm), Mn (172 ppm), and Zn (10 ppm)	AC International Network Co., Ltd., Germany
Biozar Nano-Fertilizer	Combination of organic materials, micronutrients, and macromolecules	Fanavar NanoPazhoohesh Markazi Company, Iran
TAG NANO (NPK, PhoS, Zinc, Cal, etc.) fertilizers	Proteino-lacto-gluconate chelated with micronutrients, vitamins, probiotics, seaweed extracts, humic acid	Tropical Agrosystem India (P) Ltd., India
PPC Nano (120) mL	M protein (19.6%), Na_2O, (0.3%), K_2O (2.1%), $(NH_4)_2SO_4$ (1.7%), and diluent (76%)	WAI International Development Co., Ltd., Malaysia
Zinc oxide (ZnO)- universal additive agent (1–50 nm)	ZnO (99.9%)	Land Green & Technology Co., Ltd., Taiwan
Nano green	Extracts of corn, grain, soybeans, potatoes, coconut, and palm	Nano Green Sciences, Inc., India
Nano max NPK fertilizer	Multiple organic acids chelated with major nutrients, amino acids, organic carbon, organic micro nutrients/ trace elements, vitamins, and probiotic	JU Agri Sciences Pvt. Ltd., Janakpuri, New Delhi, India
Nano-Ag Answer®	Total nitrogen (1.0%), available phosphate (0.1%), soluble potash (5.5%.), and other ingredients (93.4%)	Urth Agriculture, USA

nano-SiO_2 (50 mg/L) as a possible mediator, stimulating the expression of "*LeNRAMP3*" and "*LeFER*." The overexpression of these genes might enhance the nutritional status of Cd-stressed tomato plants, indicating that the *LeFER* transporter plays a vital role in alleviating the impact of Cd stress. Furthermore, the resultant upregulation of the several genes associated with various functions under the response of NMs is illustrated in Table 3.

5. Plant probiotics: Unraveling a long story in a nutshell

Current agricultural production cannot guarantee a consistent food supply for the rapidly expanding global population over the next 50 years. In addition, changes in dietary preferences and the increasing demand for the production of a wide variety of crop-based food products, etc., are imposing massive pressure on the production of crops at a huge scale. In recent decades, excessive amounts of chemical-based fertilizers and pesticides have been used to improve agricultural output on a vast scale; this was also a necessary step in order to solve the food crisis. Indeed, agrochemicals have changed the scenario of the agricultural world in terms of accessing multiple crop yields even under environmental stress conditions, but they have also left negative environmental footprints (Mitra et al., 2021; Tazunoki et al., 2022). Soil quality degradation, disturbance of local soil microbial ecology, health hazards from chemical residues of agrochemicals, and contamination of local water bodies are the adverse consequences of heavy reliance on agro-based chemicals (Mandal et al., 2020; Meena et al., 2020; Tazunoki et al., 2022). In the contemporary world, due to the tremendous awareness of the negative impacts of agrochemicals on organic farming and other chemical-free practices, people's interest is shifting to reducing dependence on chemical-based products (Nithya et al., 2022). Fortunately, the concept of using plant growth-promoting microbes as biofertilizers/biopesticides is favorable as a green technology for sustainable agriculture (Khan et al., 2019; Elnahal et al., 2022). Plant growth-promoting microbes are actually effective or beneficial microorganisms that confer beneficial attributes to the host plants (Massa et al., 2022; Chaudhary et al., 2022c). Like human probiotics, a specialized set of microbial strains responsible for gut health, the term "plant probiotics" has recently become trendy to denote beneficial microorganisms that are necessary for the wellbeing of host plants (Carro and Nouioui, 2017; Menéndez and Paço, 2020; Sarbani and Yahaya, 2022). Therefore, plant probiotics and plant growth-promoting microorganisms (bacteria, fungi, etc.) are somewhat synonymous with each other and are part of a complex microbial community that either colonizes the rhizosphere (rhizomicrobiome; Ravichandran et al., 2022) or

TABLE 3 Upregulation of genes associated with functional attributes in plants under the influence of nanomaterials.

Nanomaterial (s)	Plant	Functional attributes	Upregulation of related gene(s)	Reference
Mesoporous silica NPs (50 μg/ml)	*Arabidopsis thaliana*	Chlorophyll and carotenoid biosynthesis	CAO (chlorophyll a oxygenase), CHLM (Magnesium-protoporphyrin), CHLG (chlorophyll synthase), CHLD (Mg-chelatase subunit D), PDS3 (phytoene desaturase), GGPS (geranylgeranyl pyrophosphate synthase), IPI (isopentenyl pyrophosphate: dimethyllallyl pyrophosphate isomerase) and LYC (lycopene cyclase)	Lu et al. (2020)
ZnO NPs (20 mg/L)	Rapeseed (*Brassica napus* L.)	Salinity stress alleviation	ARP (auxin responsive proteins)	Hezaveh et al. (2019)
Selenium NP (4 and 40 mg/L) + nitric oxide (NO; 25 μM)	Chicory (*Cichorium intybus* L.)	Production of valuable secondary metabolites and improvement in defence system	Phenylalanine ammonia-lyase (*PAL*), hydroxycinnamoyl-CoA quinate transferase (*HCT1*), and hydroxycinnamoyl-CoA Quinate/shikimate hydroxycinnamoyl transferase (*HQT1*) genes	Abedi et al. (2021)
Silicon NPs (2 mM) + methyl jasmonate (MeJA; 0.5 mM)	Strawberry cv. Paros	Better response of plant to salinity stress	*cAPX*, *DREB*, *MnSOD*, and *GST* genes	Moradi et al. (2022)
Fe_3O_4 NPs (100 μg/ml)	*Nicotiana benthamiana*	Enhancement in plant resistance against TMV	SA responsive PR (pathogenicity related proteins) genes (*PR1* and *PR2*)	Cai et al. (2020)
AgNPs (0.2 and 0.5 mg/L)	Rice seeds	Improvement in water uptake ability of aged rice during germination	Aquaporin genes (especially *PIP2;1*)	Mahakham et al. (2017)
CuO NP 500 μg/ml	Watermelon	Pathogen suppression and yield enhancement	PPO, pathogenicity-related (PR1), and polyamine oxidase (PAO)	Elmer et al. (2018)

diffuse in or localizes in plant tissues (endophytes; Pandey et al., 2022; Rai et al., 2023) and contribution to beneficial functional traits in favor of plants (Gosal et al., 2017). These beneficial traits include enhancement in plant growth and productivity (Gavelienė et al., 2021), amelioration of abiotic and biotic stresses in plants (Santoyo et al., 2021), lowering the challenges of climate changes effects (Fiodor et al., 2021), and biofortification benefits *via* improving micronutrients levels in crop edibles (Upadhayay et al., 2018, 2021, 2022a,b,c). Plant probiotics must contain some PGP traits such as the solubilization of elements (P, K, and Zn; Singh et al., 2022), nitrogen fixation (Pandey et al., 2022), production of phytohormones (Kurniawan and Chuang, 2022) aminocyclopropane-1-carboxylate (ACC) deaminase (Santos et al., 2022; Singh et al., 2022), siderophore (Upadhayay et al., 2022a,b), and ammonia (Santos et al., 2022). Production of compounds showing importance in killing pathogens such antibiotics, secretion of enzymes (chitinase, protease/elastase, cellulase, catalase, and β-(1,3)-glucanas; Duhan et al., 2022), volatile compounds (HCN; Vaghela and Gohel, 2022), and also induce systematic resistant in plants against pathogen is the important contribution of plant probiotics (Yin et al., 2022; Chaudhary et al., 2022a). In addition, the ability of plant probiotics to produce exopolysaccharides and biofilms has multiple benefits, including protection from abiotic stress (Banerjee et al., 2019) and desiccation (Mandal et al., 2022), effective root colonization (Naseem et al., 2018), and improved soil aggregation and stabilization (Jhuma et al., 2021). Numerous microbial strains have been identified to possess plant probiotic properties that stimulate plants' growth and improve crop yield (Das et al., 2022; Pantigoso et al., 2022; Khan et al., 2023). Therefore, such microorganisms can be utilized effectively as bioinoculants for eco-friendly agriculture (Daniel et al., 2022). Plant probiotics are effective "bioelicitors" or "biofertilizers" (Chen et al., 2022) because they improve crop yield-related traits, such as length of shoot and root, biomass of plants, photosynthetic pigments, grain yield, and biological output (Khan et al., 2022; Upadhayay et al., 2022a,b). A remarkable increase in yield-attributed traits was determined for rice, wheat, and maize in response to plant probiotics such as *Bacillus* (Abd El-Mageed et al., 2022), *Azospirillum brasilense* (Zaheer et al., 2019), and *Pseudomonas stutzeri* (Jiang S. et al., 2022), respectively. Plant probiotics such as *Burkholderia cepacia* and *Pantoea rodasii* having zinc solubilizing potential improved the overall growth of rice plants and provided biofortification benefits by increasing considerable Zn concentration in grains (Upadhayay et al., 2022b). Plant probiotics also ameliorate abiotic stress effects in plants *via* enhancing stress tolerance of plants which can be glimpsed by osmolyte accumulation (Tahiri et al., 2022), activation of antioxidant enzymes (Shultana et al., 2022), reduction in MDA content, reduction in electrolyte leakage, and improving in the activity of photosynthetic pigments (Zarei, 2022). Figure 1 shows schematic and beneficial outcomes that can result from using PPs as a green approach. Considering the productive effects of plant probiotics on crop wellbeing, systematic research is needed to identify and characterize a novel microbial strain or microbial consortium having multifarious plant growth-promoting effects. Deeper studies are required to reveal the interaction between plants and microbes at the molecular level and the microbial effects on plants in terms of enhancing physiological

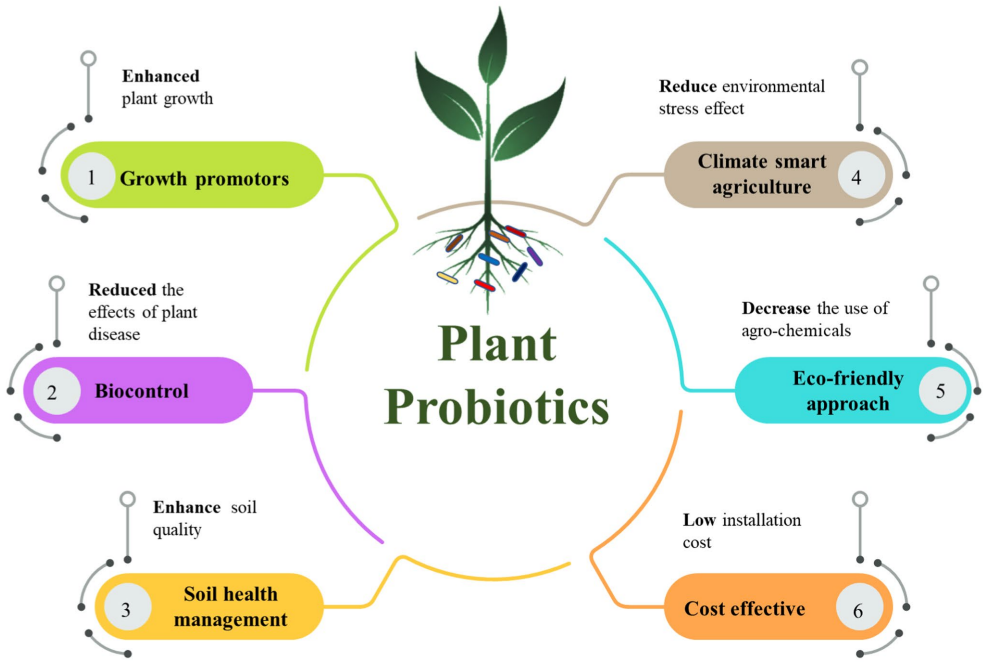


FIGURE 1
Schematic flow chart representing the prolific attributes of using plant probiotics (PPs).

phenomena. In addition, a comprehensive analysis is required to illustrate how the inoculation of plant probiotics has a significant impact on the local soil microbiota in addition to their soil-healing properties.

6. The synergy of nanomaterials and plant probiotics: A green solution for sustainable agriculture

The harmful effects of agrochemicals are well known and occur as a result of the indiscriminate use of various agrochemicals. In addition, the application of PPs as bioinoculant faces several challenges, including a decline in number, a slow rate of action, a lack of suitable carrier materials, susceptibility to certain stress conditions, such as desiccation and salinity, and a loss of effectiveness in field conditions (Nagpal et al., 2021; Walia et al., 2021). Therefore, to overcome these problems, the potential alternative is a cocktail of suitable nanomaterial and PP strain. Using a combination of PPs and NMs can provide the benefits of both biofertilizers and nanofertilizers (Chaudhary et al., 2021a,b,c). Application of the cocktail of NMs and PPs to agricultural crops is viewed as an alternative eco-friendly method to reduce the use of chemical or synthetic fertilizers in crop management (Kumari and Singh, 2020; Akhtar et al., 2022), due to the risk posed by the excessive use of chemical-based fertilizer and pesticides (Chitara et al., 2022). The slow-release ability of nanobiofertilizers makes them highly efficient, resulting in the accessibility of the nutrients for a longer period of time and increased nutrient use efficiency or vice versa, which reduces nutrient losses and supports agricultural development through increased crop growth and yield (Fazelian and Yousefzadi, 2022).

The microbial components of nanobiofertilizers include nitrogen-fixing microorganisms such as free-living *Azotobacter*, symbiotic *Rhizobium*, and associative *Azospirillium*, phosphorous solubilizing microorganisms such as *Pseudomonas striata*, *Penicillium* spp., *Bacillus* sp., and *Aspergillus* sp., and phosphorous mobilizers microorganism. On the contrary, nanomaterials such as nanosilicon dioxide (Kukreti et al., 2020), AgNPs (Nawaz and Bano, 2020), nano-iron oxide (Babaei et al., 2017), ZnO-NPs (Azmat et al., 2022), nanozeolite (Khati et al., 2019a,b), nanochitosan (Kumari et al., 2020), and nanogypsum (Kumar et al., 2019) have been employed as nano-constituents of "NMS-PPs cocktail." This association of microorganisms and nanoparticles exhibits a synergistic effect in soil by improving soil nutrient status through nitrogen fixation, iron chelation through siderophore production, phosphorus solubilization, phytohormone production, induces systemic resistance (ISR), systemically acquired resistance (SAR), and gives plants vigor against pests (Chitara et al., 2021; Chaudhary et al., 2021a,b,c,d,e, 2022b; Mahawer et al., 2022).

However, before using a combination of NMs and PPs, the impact of NMs on PPs should be assessed. The NMs should not be detrimental to the microbial component; rather, they must support microbial growth and activity. In previous studies, NM such as nanozeolite and nanogypsum showed positive impacts on the growth of plant growth-promoting bacteria isolated from NM-infested soil (Chaudhary and Sharma, 2019; Khati et al., 2019a). The synergistic effect of the NMs and PPs could be visualized in the form of enhanced physiological and morphological development through an increased rate of photosynthetic translocation in the aerial plant parts, resulting in improved grain quality and increased yield (Khati et al., 2018; Kukreti et al., 2020; Vedamurthy et al., 2021). Application of the

chitosan–iron nanobiofertilizer against bacterial leaf blight of rice caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo) under *in vitro* and *in vivo*. Under *in vitro* assay against bacteria, nanobiofertilizer significantly inhibit the biological function such as growth, mobility, and biofilm formation of the bacteria and under *in vivo* condition foliar spray of the nanobiofertilizer reduced the disease incidence as well as modulate the enzyme system of the plants and improved the photosynthesis by increasing chlorophyll content and carotenoid (Ahmed et al., 2022). Under drought, the application of the nano-Zn chelate and nano-biofertilizer effectively alleviate the impact of the drought stress and significantly augmented the plant biomass and grain yield (Farnia et al., 2015). In maize crops, under water scarcity, the application of the nanobiofertilzer improved water use efficiency and enhanced crop productivity (Janmohammadi et al., 2016). Similarly, the NMs influence the dynamics of PPs as the report of Fetsiukh et al. (2021) showed that silica NPs triggered *P. polymyxa* A26 for producing EPS and increased water-holding capacity and osmotic pressure of biofilm and such reprogrammed bacterium enhanced plant biomass under drought stress. The application of a combo of nanogypsum and *P. taiwanensis* improved plant growth and soil health, and the metagenomic study revealed the dominance of beneficial microbial groups such as *Acidobacteria*, *Bacteriodetes*, *Nitrospirae*, *Proteobacteria*, and *Planctomycetes* in soil (Chaudhary et al., 2021c). The optimized concentration of TiO_2 NPs with bacterial treatment increased maize plant growth, germination percentage, leaf area, and chlorophyll content (Kumari et al., 2021). Moreover, algal-based biofertilizers with mineral nanofertilizers can also be a game changer in agricultural productivity (Mahapatra et al., 2022).

Recent studies to determine the combined effect of NMs and PPs on plant growth and development are presented in Table 4. In addition, Figure 2 shows the advantageousness of using a cocktail of NMs and PPs to reap the benefits of agricultural production.

7. Combo of nanomaterials and plant probiotics in the mitigation of environmental stress

The agriculture sector shows its essentiality in food security as a human population relies on particular crop-based foods for basic diets. However, in the current climate change scenario, crop productivity is experiencing environmental stresses in form of either abiotic or biotic stresses (Xiong et al., 2022). The common instances of abiotic stresses include drought, salinity, heat stress, flood, cold stress, and heavy metal stress (Shikari et al., 2022). On the contrary, pathogens such as bacteria, fungi, and viruses that attack plants are categorized as biotic stressors (Barna, 2022). These categories of stress drastically affect crops in terms of reduction in yield (Anzano et al., 2022). In the coming decades, if the issue of global warming is not solved, the measured portion of arable land might be affected due to various types of abiotic stresses (Shahzad et al., 2021). Therefore, a concept of climate-smart agriculture is in fashion to adopt the strategy to ameliorate the effect of various stresses on crops. The use of agrochemicals to combat the drastic effects of environmental stresses is a leading factor in the contaminating environment and posing a big threat to human health (Omran and Baek, 2022). From the microbial perspective view, the use of plant probiotics can provide an alternative solution for redressing the effects of abiotic and biotic stresses in plants (Mishra et al., 2022). Pant probiotics are a smart player that not only protects the plant from abiotic stress but also reduce the risk of biotic stress by modulating their natural defense (Bhat et al., 2022). Logically, plant probiotics must already be tolerant to various stresses, after which they may only mitigate the effect of various stresses. These special characteristics of tolerance to different types of stress are in fact conferred by the production of exopolysaccharides, the accumulation of osmoprotectants and the production of ACC deaminase, and the activation of different stress-responsive genes (Fadiji et al., 2022). Moreover, when plant probiotics are used as a bioinoculant in plants, they improve the stress-tolerant behavior of host plants by enhancing photosynthetic pigments, accumulating osmolytes, accumulating high phenols, activating antioxidant enzymes, activating stress-responsive genes, and reducting in levels of malondialdehyde and electrolyte leakage (Gamalero and Glick, 2022). Furthermore, plant probiotics mitigate the biotic stress *via* several mechanisms such as the production of antimicrobial compounds (antibiotics, antifungal, etc.), synthesis of siderophore, volatile compounds (HCN), secretion of enzymes having the capacity to disintegrate pathogen cell wall, and induction of systematic resistance in plants (Boro et al., 2022). Second, the nonfertilizer application is another admirable approach for the fertilizer industry, as they are highly efficient in the context of controlled release of nutrients (Jakhar et al., 2022). However, to combat the negative impact of environmental stresses a systematic application of various nanomaterials such as nanochitosan (Hassan et al., 2021), ZnO NPs (Chanu Thounaojam et al., 2021), nano-selenium (Shalaby et al., 2021), AgNPs (Alabdallah and Hasan, 2021), and carbon nanotubes (CNTs; Faizan et al., 2021) have shown appreciable contribution in improving crop endurance under abiotic stress conditions. Recently, Adil et al. (2022) demonstrated that the application of nano-ZnO (0.12 g/pot) significantly increased photosynthetic pigments (chlorophyll a and b) contents plant height, shoot and spike lengths, root fresh and dry weights, and wheat grain yield under salt stress. Under drought stress conditions, nano-vermicompost application resulted in enhancement in growth, mineral uptake, and activation of antioxidant enzymes in tomatoes (Ahanger et al., 2021). The foliar spray of nanosilicon restored the growth and yield of essential oils of the medicinally important plant feverfew (*Tanacetum parthenium*) under drought conditions (Esmaili et al., 2022). Nanoparticles exhibit distinctive qualities in plants due to their charge-to-size ratio, such as an improvement in total antioxidant status, which lowers levels of harmful chemicals such as reactive oxygen species (Abdal Dayem et al., 2017). This, in turn, modulates different biochemical and molecular signal transducing pathways, resulting in improved signal perception and, as a result, increased growth and yield potential (Bhatt et al., 2020). However, recent evidence suggests that the coupling effect of plant probiotics (PPs) and NMs may play an excellent role in managing abiotic stress (Azmat et al., 2022; Muhammad et al., 2022; Alharbi et al., 2022a,b). The combo effect of NMs and PPs exhibits various stress ameliorating effects by improving levels of photosynthetic pigments, activities of antioxidant enzymes, total soluble sugars, and reducing stress markers such as MDA content and electrolytic leakage in plants under salt stress (Yasmin et al., 2021; Alharbi et al., 2022a) and drought stress (Akhtar et al., 2021; Azmat et al., 2022). Recently Etesami et al. (2022) deciphered how the combination of nanosilicon and arbuscular

TABLE 4 Role of combined effects of nanomaterials and plant probiotics in plant growth and development.

Combination of nanomaterials and plant probiotics	Plant	Growth related response on plants	References
PGPR (PS2 and PS10) + NMs (nanozeolite and nanochitosan; 50 mg/L)	Fenugreek (*Trigonella foenum-graecum*)	• Significant increase in plant height, leaf number, leaf area and fresh weight • Enhanced level of total chlorophyll, sugar, soluble leaf protein, catalase activity and improvement in soil health	Kumari et al. (2020)
Bacillus spp. + nanozeolite (50 mg/L)	Maize	• Increase in plant height, dry weight, photosynthetic pigments. • An increment (29.80%) in maize productivity • Enhanced level of antioxidant enzymes, and phenols	Chaudhary et al. (2021b)
Pseudomonas taiwanensis (PC1) and *Pantoea agglomerans* (PC2) + nano-chitosan	*Zea mays*	• Enhancement in seed germination • Improvement in plant height and photosynthetic pigments	Agri et al. (2021)
Nanochitosan (40 mg/L) + *Pseudomonas taiwanensis* and *Pantoea agglomerans*	*Zea mays*	• Enhancement in plant height, number of leaves, and photosynthetic pigments • Prominent soil enzymatic activity and improvement in nutrient assimilation	Agri et al. (2022)
PGPR + nanosilicon dioxide (10 mg/L)	*Zea mays*	• Enhancement in average plant height and number of leaves, total chlorophyll, carotenoid, sugar, soluble protein, phenol and flavonoid content • An increase in the activities of fluorescein diacetate, dehydrogenase and alkaline phosphatase in soil	Kukreti et al. (2020)
Pseudomonas putida (KX574857) and *Pseudomonas stutzeri* + Ag NPs (5 ppm)	Cucumber	• Enhance in flavonoids level, phenolics, protein, proline, total chlorophyll, sugar and PAL activity	Nawaz and Bano (2020)
Nano-Zinc oxide (1 g/L) + *Azosprillium*	*Triticale*	• Improvement in seed quality, increasing of grain filling period, zinc and protein content,	Kamari and Sharifi (2017)
CNPs (5 mg/ml) and AuNPs (100 µg/ml) + *Pseudomonas aeruginosa*	*Vigna unguiculata*	• enhancement effect on the shoot length and fresh weight of plants	Panichikkal and Krishnankutty (2022)
Nanocarbon material + Biofertilizer	*Hordeum vulgare*	• Increment in growth parameters of plants after adding zinc ferrites ($ZnFe_2O_4$) nanoparticles to the nanomaterials-biofertilisers combination	Hadj Alouane et al. (2021)
Pseudomonas monteilii + biogenic gold nanoparticles (AuNPs; 50 µg/ml)	*Vigna unguiculata*	• Enhancement in the production of IAA by *P. monteilii* in presence of NPs and increase in seedling growth	Panichikkal et al. (2019)

mycorrhiza can be a prolific tactic to mitigate environmental stresses in crops and achieve sustainable plant productivity. Table 5 illustrates the combined effect of NMs and PPs in alleviating environmental stresses (salinity, drought, and heavy metal pollution) in plants by demonstrating different mechanisms.

Combined integration of NPs and PPs to help plants deal with heavy metals and their basic mechanisms involved in the process of phytoremediation and soil remediation. Collective use of *Staphylococcus aureus* and ZnO NPs detoxifies the effects of chromium on wheat plants and increases its growth, showing a positive impact on plant physiological activities and defense system (Ahmad et al., 2022). Similarly, the joint effect of TiO_2 NPs and plant probiotics increased *T. repens* growth in cadmium-contaminated soil and also improved the accumulation and uptake of this metal by plant (Daryabeigi Zand et al., 2020a). Furthermore, the simultaneous application of nanoscale zero-valent iron (nZVI) and PPs contributed to promoting the phytoremediation of Sb (antimony)-contaminated soils and significantly increased the accumulation capacity of *Trifolium repens* for Sb (Daryabeigi Zand et al., 2020b). *B. subtilis* in combination with NMs (ZnO and TiO_2) controlled powdery mildew disease in cucumber plants (Hafez et al., 2020). Moreover, nanoencapsulated *B. subtilis* (Vru1) ameliorated biotic stress by controlling the pathogenic fungus *R. solani* and decreased the severity of the disease by 75% (Saberi-Rise and Moradi-Pour, 2020). The nanocomposite biofertilizer, which consisted of inclusion complexes of acylated homoserine lactone (AHL)-coated Fe–carbon nanofibers and endospores of *P. polymyxa* adsorbed in activated carbon beads, demonstrated a good ability to ameliorating effect of biotic stress by

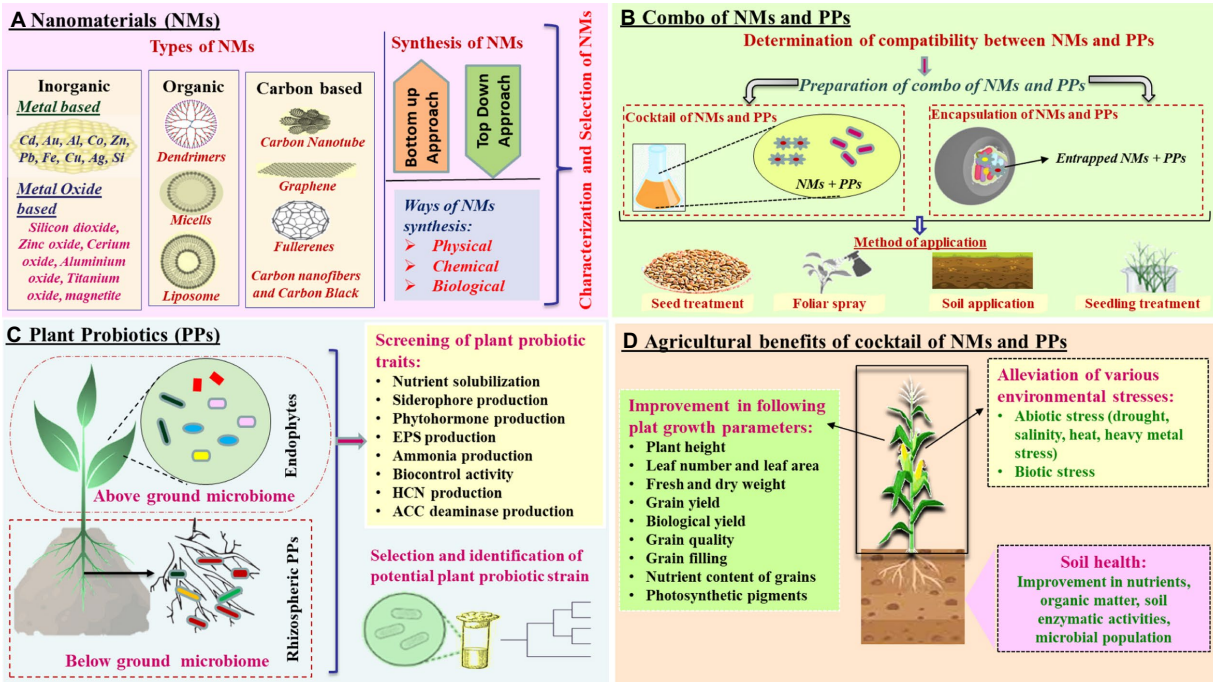


FIGURE 2
(A) Representation of NMs categorized into the following: inorganic-based (metal-based and metal oxide-based), organic NMs (dendrimers, micells, and liposomes), carbon-based NMs (carbon nanotubes, graphene, fullerenes, carbon nanofibers, and carbon black), and their approaches of synthesis (bottom-up and top-down) with their three physical, chemical, and biological ways of synthesis. **(B)** The schematization of PPs, especially endophytes and rhizospheric PPs, and their screening on various traits such as nutrient solubilization, production of siderophore, phytohormone, EPS, ammonia, HCN, ACC deaminase, and biocontrol activity. **(C)** Determination of compatibility between NMs and PPs, and preparation of their combo, either a cocktail of NMs and PPs or the encapsulation of NMs and PPs. Such a combo can be applied by following suitable methods such as seed treatment, foliar spraying, soil application, and seedling treatment. **(D)** Illustration of the agricultural benefits resulting from the application of a cocktail of NMs and PPs in terms of improvement in plant growth parameters, alleviation of environmental stresses, and prolific effects on soil health.

preventing *Fusarium* wilt of chickpea and root rot of wheat (Gahoi et al., 2021).

8. Soil health management through the cocktail of nanomaterials and plant probiotics

Soil is an absolute medium that supports the life of a range of flora and fauna, and provides a better milieu for various microbial activities. The belowground region of soil especially contains rhizospheric and non-rhizospheric environments (Orozco-Mosqueda et al., 2022). Rhizosphere, on the other hand, can be described as a particularly vibrant region due to plant-microbial activities that take part in nutrient cycling (Kumawat et al., 2022). Rhizospheric soil harbors to a variety of beneficial microbiomes that support plants by displaying a range of traits including the solubilization of mineral elements, N_2 fixation, siderophore production, and phytohormone synthesis (Mahmud et al., 2021). In addition to this, microbes keep the soil's nutrient levels balanced through processes such as nitrogen fixation, solubilization of complex inorganic compounds, and mineralization of organic materials (Kaviya et al., 2019). As a result, the soil has a sufficient amount of NPK to support both microbial and plant life. The synthesis of extracellular enzymes by soil microorganisms, such as dehydrogenase, fluorescein diacetate, alkaline phosphatase, and β-glucosidase, contributes to the smooth functioning of the soil environment. These enzymes also serve as a reflection of the microbial activity that takes place in the soil (Kleinert et al., 2018). In addition, the generation of EPS by microorganisms is advantageous in terms of improving soil structure and soil stability (Costa et al., 2018). Due to their extensive roles in soil formation, soil health management, and the remediation of contaminated soil, microorganisms are referred to as "soil probiotics." In the current scenario, the application of NMs and PPs deciphered a positive impact on soil. Kumari et al. (2020) observed that the application of a combination of NMs (nanozeolite and nanochitosan) and PPs increased soil enzymatic activities such as FDA, dehydrogenase, and alkaline phosphatase and, therefore, showed a growth-stimulating effect on the fenugreek plant. Khati et al. (2017) reported that combining two strains of *Bacillus* sp. with nanochitosan enhanced the organic carbon content, potassium content, and ammoniacal nitrogen in maize-grown soil. Enzymes that indicate the health of the soil, such as dehydrogenase and alkaline phosphatase, showed a 2- to 3-fold increase after the application of this combination. The study by Kumari et al. (2021) showed that the combination of 10 ppm NPs (TiO_2) and bacterial inoculants improved the enzymatic activities (fluorescein diacetate hydrolysis, dehydrogenase, and alkaline phosphatase) of the soil under maize cultivation. In addition, the combination of nanosilicon dioxide and PPs (*Pseudomonas taiwanensis* and *Pantoea agglomerans*) improved the pattern in the organic carbon, phosphorus, and potassium content of the cultivated soil and indicated a 1.5- to 2-fold increase in the activities of soil enzymes (dehydrogenase, fuorescein diacetate, and alkaline

TABLE 5 Prolific effects of a cocktail of nanomaterials and plant probiotics in alleviating various abiotic stresses in plants.

Combination of Nanomaterial and Plant probiotic	Plant	Abiotic stress Condition	Plant responses	References
ZnO nanoparticles (NPs; 150 mg/L) + *Azospirillum brasilense*	Wheat	Drought	• Enhancement in growth-yield parameters and nutrient uptake • Increment in level of proline, total soluble sugar, photosynthetic pigments, and antioxidant enzymes	Muhammad et al. (2022)
ZnO-NPs (17 mg/L) + biofertilizer	Safflower	Salinity	• Improvement in the activities of antioxidant enzymes • Reduction in intracellular Na + accumulation	Yasmin et al. (2021)
SiO_2 NPs (150 mg/kg soil) + *Bacillus* sp. *Azospirillum lipoferum* and *Azospirillum brasilense*	Wheat	Drought	• Improvement in relative water content (RWC), gas exchange attributes, nutrients uptake, and production of osmolytes production • Upregulation of antioxidant enzymes such as super oxide dismutase, catalase and peroxidase	Akhtar et al. (2021)
SiNPs (500 mg/L) + *Azotobacter chroococcum* SARS 10 and *Pseudomonas koreensis* MG209738	Barley	Salinity	• Enhancement in the physiological properties such as relative chlorophyll content relative water content stomatal conductance, • Activation of enzymes related to antioxidative defence (SOD, CAT, POX). • Mitigation of soil ESP by reducing the content of Na^+ and oxidative stress	Alharbi et al. (2022a)
ZnO NPs (10 ppm) + *Providencia vermicola*	*Luffa acutangula*	Heavy metal (arsenic) stress	• Substantial reduction in the 'As' bioaccumulation in shoots and roots • Reduction in the lipid peroxidation and electrolyte leakage • Increase in photosynthetic pigments, proline content, relative water content, total sugars content	Tanveer et al. (2022)
Biofertilizers (*Azotobacter*, *Azosperilium*, *Pseudomonas*) + nano Fe oxide (1.5 g/L)	Wheat (*Triticum aestivum* L.)	Salinity	• Improvement in grain yield, chlorophyll content, antioxidant enzyme activity, proline and soluble sugars	Babaei et al. (2017)
ZnO-NPs (10 ppm) and *Pseudomonas* sp.	Wheat	Heat and drought	• Enhancement in biomass, photosynthetic pigments, nutrients, soluble sugars, protein and indole acetic acid content • Production of higher proline, antioxidant enzymes, and abscisic acid. • Marked reduction in electrolytic leakage and MDA content	Azmat et al. (2022)
Biogenic molybdenum nanoparticles (MoNPs; 100 mg/L) + *Bacillus* sp. strain ZH16	Wheat	Arsenic contamination	• Improvements in morphological features, ionic balance and nutrient content of plant • Reduction in arsenic accumulation in plant	Ahmed et al. (2022)
Si-NP (12.5 mg/L) + *Pseudomonas koreensis* MG209738 and *Bacillus coagulans* NCAIM B.01123	Sugar beet (*Beta vulgaris*)	Salinity	• Decrease in oxidative stress indicators (hydrogen peroxide and lipid peroxidation) and sodium ions • Increment in activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX) enzymes,	Alharbi et al. (2022b)
ZnO-NPs (20 mg/kg) + *B. fortis* IAGS-223	*Cucumis melo*	Heavy metal (cadmium) stress	• Modulation in the activity of antioxidant enzymes • Decrease in the amount of stress markers (such as H_2O_2, and MDA)	Shah et al. (2021)

TABLE 6 Negative impacts of metal and metal oxide-based NMs on soil microbes and soil activities.

S. No.	Types of Nanomaterial(s)	Associated negative impact(s)	References
1	CuO NPs	Decline in soil microbial biomass in flooded paddy soil	Xu et al. (2015)
2	ZnO NPs	Reduction in CO_2 emission, carbon (130%) and nitrogen mineralization (122%) efficiency from the from Phoenix dactylifera leaf litter in sandy soil.	Rashid et al. (2017)
3	CuO NPs	Inhibition of denitrification process and electron transport system activity	Zhao S. et al. (2020)
4	Pristine and sulfidized ZnO NPs	Drastic impacts on bacterial communities and metabolite profile in rhizo-compartment of soybean	Chen et al. (2023)
5	High dose of ZnO NPs	Decrease in number of bacteroids and nodules, and relative abundance and diversity of the soil microorganisms	Sun et al. (2022)
6	Cu and Zn NPs	Decrease in abundance of *Azotobacter* genus in soil	Kolesnikov et al. (2019)

phosphatase; Kukreti et al., 2020). As the extensive use of agrochemicals has led to a decline in soil quality, an alternative nanobiofertilizers-based strategy can restore soil quality and increase the population of beneficial microbiota. Recent research by Chaudhary et al. (2022b) demonstrated an increase in the microbial population in soil treated with NMs (nanozeolite and nanochitosan) and *Bacillus* sp. Application of NM should maintain adequate soil microbial population as microbial diversity maintains the elegance of soil fertility level. Through a high-throughput sequencing approach, Khati et al. (2019b) determined the positive impact of nanozeolite on the survival of bacterial populations associated with nutrient cycling and residue degradation.

Although microbial use is usually environmentally acceptable, the combined use of effective microorganisms and nanomaterials is beneficial for improving agricultural production. However, nanoconjugates have not yet been fully determined in the context of environmental concerns. Nanobioferilizers are comparatively less toxic than traditional fertilizers, and very few studies have been reported to decipher the risk associated with the nanomaterial portion of nanobiofertilizer disturbing soil structure and soil microbial activities. Following the nanobiofertilizer application, the nanocomponents are released into the environment and can reach or drain into the soil depending on the type of soil and its properties (Sambangi et al., 2022). NMs, in soil, may show toxic effects on plant growth-promoting microbes, especially nitrogen-fixing bacteria and mineral-solubilizing bacteria, and thus a consequent shift in the bacterial community can affect the functioning of the local soil ecosystem (Chavan et al., 2020). Most NPs based on metal and metal oxide can show the highest degradative effect against microorganisms due to their toxic effects by affecting cell membrane architecture, enzymatic and metabolic activities, and nutrient availability, which ultimately results in microbial death (Kumar et al., 2018; Upadhayay et al., 2019). Recent studies have illustrated the destructive effects of NMs on soil microorganisms involved in various important activities. Ma et al. (2023) showed that the application of elevated levels of CO_2 (590 µmol mol^{-1}) and titanium dioxide NPs disrupted soil bacterial activities involved in the nitrogen and carbon cycles. The beneficial contribution of NMs glimpses as their application allows slow and sustained release of nutrients, supporting plant growth while conserving the diversity of the beneficial microbiome. Their toxicity can be attributed to their physical properties, and the ambiguous dose and structure of the exposed microbial community (Chhipa, 2021). Table 6 depicts the negative consequences of using metal and metal oxide-based NMs. An increasing number of researchers are focusing on this problem. Acquired results show contradiction; some authors illustrated evidence of safer use of NMs, while some researchers reported significant risk (Kolesnikov et al., 2019). However, the following points can be considered for the safer use of NMs with lesser toxic effects on the environment, such as (a) an eco-nanotechnological study for massively producing NMs due to nanotechnological advancement; (b) a proper and adequate characterization of NMs on physical and chemical basis and evaluation of environmentally safe exposure doses of NMs before their widespread applications; (c) proper monitoring and risk assessment of NMs use; (d) a comprehensive assessment to decipher the impact of NM as soil pollutants and their potential destructive behavior on soil microbial diversity and their functions.

9. Nanoencapsulation of plant probiotics: How can it shape crop growth?

Nanoencapsulation research is being increased in the last few years in response to the rising need for PPs (Nayana et al., 2020; Saberi Riseh et al., 2022b). Such kind of formulation can address the issues of free-form formulations of PPs (Bala, 2022). Nanoencapsulation can improve the efficacy of PPs by extending their shelf life and providing a controlled release of bio-component (Pour et al., 2019). After inoculation, several factors affect the competency of PPs in the natural environment in terms of ineffective colonization of plant roots by applied microbial inoculant, lesser microbial activity in the rhizospheric milieu, and decline in microbial population (Ahmad et al., 2011; Khare and Arora, 2015). Since a minimum number of inoculant cells (10^6 and 10^7) is a critical factor in deciding the positive impact on plants (de Moraes et al., 2021). Thus, PPs need suitable physical protection for an extended period. As a novel approach, the nanoencapsulated PPs is providing a better platform for enhancing crop growth and amelioration of abiotic and biotic stresses (Ravichandran et al., 2022; Saberi Riseh et al., 2022a). The nanoencapsulation provides stability and reproducibility of entrapped PPs by enhancing their resistance to UV radiation, heat, and desiccation (Balla et al., 2022). Encapsulating nanoparticles with biofertilizer is a step in the production of nanobiofertilizer. The encapsulation of biofertilizers and biocontrol agents works well in biopolymer-based nanocomposites (Akhtar et al., 2022). In addition, nanoencapsulation prevents bacterial strains from mechanical stress and lowers nutrient release, which further increases the efficacy of this

product (Kumari et al., 2020). Biofertilizer cells are incorporated into the nanomaterial capsule by a process called encapsulation, and this involves the application of non-hazardous, biodegradable materials such as starch and calcium alginate (Vejan et al., 2019; Akhtar et al., 2022). Three crucial steps are involved in the production of nanobiofertilizers: (1) the growth of culture for biofertilizer, (2) the encapsulation of culture with nanoparticles, and (3) the assessment of its efficacy, quality, purity, and shelf life (Akhtar et al., 2022). Microcapsules can also be used to make nanobiofertilizer. Its production includes mixing PGPR suspension in a 2:1 ratio with a solution of 1.5% sodium alginate, 3% starch, and 4% bentonite (Akhtar et al., 2022; Pour et al., 2022). After washing the microcapsules in sterile distilled water, the mixture is covered with the crosslinking calcium chloride solution (Adjuik et al., 2022).

Salicylic acid and nanoparticles have also been combined to form a nanobiofertilizer (Gupta et al., 2019). This technique involves mixing the biofertilizer with sodium alginate (2%), ZnO NPs (1 g/ml), and salicylic acid (1.5 mM). Then, 1-mm beads are prepared, shaped, and air-dried in the solution before incubating at 4°C with calcium chloride (3% solution; Panichikkal et al., 2019; Akhtar et al., 2022).

Pseudomonas sp. (DN18) entrapped in the alginate beads along with the salicylic acid and the ZnO NPs demonstrated antifungal activity against *Sclerotium rolfsii* and showed superior plant growth-promoting activity on *Oryza sativa* seedlings compared to the free-living bacterial strain (Panichikkal et al., 2021). Nanoencapsulation of *P. fluorescens* (VUPF5) and *B. subtilis* (VRU1; using silica nanoparticles and carbon nanotubes) and their metabolites improved pistachio micropropagation *via* a significant enhancement in the root length and proliferation (Pour et al., 2019). Nanoencapsulated *Bacillus subtilis* (VRU1) prepared with sodium alginate, starch, and bentonite have shown effectiveness in controlling the proliferation of *Rhizoctonia solani* and increased the bean vegetative growth parameters (Saberi-Rise and Moradi-Pour, 2020). "Sodium alginate–gelatin microcapsules" containing nanomaterials (SiO_2 and carbon nanotubes) and PPs *Bacillus velezensis* demonstrated synergistic suppression of pathogens (*Phytophthora drechsleri*) in *Pistacia vera* L. (pistachio; Moradi Pour et al., 2022). The study by De Gregorio et al. (2017) exhibited the nanofiber-immobilized rhizobacteria (*P. agglomerans* and *B. caribensis*) prepared by electrospinning and observed its efficiency as seed bioinoculant in terms of improving the length of root, dry weight of root and shoot, leaf, and the number of soybeans. The bacteria (*Pseudomonas stutzeri*) encapsulated in the coating composed of N-hydroxysuccinimide (NHS)-modified poly γ-PGA and Ca ions exhibited remarkable resistance against harsh conditions and showed better plant growth potential (Yang et al., 2021).

10. Cocktail of nanomaterials and plant probiotics: Understanding in the context of the bioeconomy

The concept of the bioeconomy is well described in the context of biofuel production (Zilberman et al., 2018), but the role of agriculture is also justified in strengthening the bioeconomy (Upadhayay et al., 2022c). In the context of agriculture, the bioeconomy can be described as improving crop productivity through the use of various resources. Indeed, innovations in life sciences, agriculture, biotechnology, and the evolving wisdom in these sectors provide the ultimate ground for sustainable production and sustain a stable bioeconomy. The lack of essential nutrients in the soil poses significant problems for farmers due to several factors including intensive and poor farming practices (Elbasiouny et al., 2022). In addition to these factors, soil types and different agroclimatic conditions at different altitudes are common features that contribute to declines in crop growth and production, and adversely affect the socioeconomics of farmers (Sivakumar, 2021; Upadhayay et al., 2022c). Various ways of soil nutrient management are used, such as the use of chemical fertilizers, which reduces soil fertility, have a detrimental impact on local soil microbial ecology, and cause health problems for consumers. The production of agrochemicals by various manufacturers around the world is effective and beneficial in increasing crop productivity, but it is more expensive and not ideal for underprivileged farmers. However, a variety of techniques (agronomic, breeding, and genetic modifications) are used to improve the nutrient content and yield of plants (Ahmar et al., 2020). On the other hand, in areas with a predominantly rural population, these methods are seen as both lucrative and undesirable. In addition, these crop yield-increasing techniques are not consumable as they require more effort and technical skill. In addition, the quality of the harvested commodities must be high so that farmers may sell them for a reasonable price. However, the use of nanotechnology has advanced agriculture, and nano-based fertilizers, insecticides, and herbicides are being used to protect and produce crops in a prodigious manner (Chand Mali et al., 2020). An increase in gain yield has the potential to play a significant job in the improvement of the bioeconomy. Babaei et al. (2017) reported a 17.40% increment in the grain yield of wheat by the application of nano-Zn–Fe oxide in comparison to the control. The nano-urea treatment (3 g/kg) exhibited maximum biological yield (332.7 g/bag) and economic yields (283.1 g/bag) at the third flush (Naim et al., 2020). On the other hand, PPs as potential biostimulators showed the highest grain yield in various crops such as wheat (between 9.6 and 29.29%) by *Bacillus* sp., (Öksel et al., 2022), rice (3.35 t/ha) by *B. subtilis* and *B. megatherium* strain (Abd El-Mageed et al., 2022), and maize (5,880 kg/ha) by *P. putida* (Mubeen et al., 2021). However, in recent years, the combined application of NM and PP has led to a breakthrough in the agricultural sector, especially in terms of increasing crop yield (Akhtar et al., 2022). Combined application of plant probiotics (*Azotobacter*) and nano-Zn–Fe oxide showed an 88% increase in wheat grain yield compared to water-restricted conditions (Seyed Sharifi et al., 2020). Hafez et al. (2021) observed that the synergy of rhizobacteria and 500 mg SiNPs per liter showed an increase in maize yield (6325.4 kg/ha) and also improved nutrient uptake such as NPK in plants. This synergistic strategy of utilizing microbes and nanomaterials is described in this article as an ecologically sound solution to optimize plant growth and yield. The use of agrochemicals is reduced in this way, and the combined use of NM and PP will significantly increase crop yield. Thus, the detection, characterization, and competence of PPs as prospective bioinoculants and as a synergistic partner of suitable NMs for improving yield appears to be promising goals in order to (i) *in vitro* evaluation of PPs from rhizospheric soils of plants and selection of cultivable microorganisms on the basis of multifarious plant growth-promoting traits, (ii) determination of the compatibility of a prospective PPs strain with suitable nanocompounds, (iii) improvement in the overall productivity of crops under the application of a cocktail of PPs and NMs, (iv) evaluating uptake and density of nutrients in different plant parts to illustrate the quality of crop harvest, (v) analyzing the soil health and dynamics of the inoculated bacterial population from field plots and conserving proficient microbial pools for future use, and (vi) ultimately reducing reliance on agrochemicals showing harmful impacts.

11. Future prospects for nano-biofertilizers: A roadmap

Sustainable agricultural practice can be represented as the coordinated action of abiotic and biotic factors to maintain the stability of agricultural production and soil nutrient balance. Nonetheless, the benevolent effect of PPs supports plant growth in a very harmless way and, hence, it is included as a main choice for use in agricultural applications. The incorporation of nanotechnology is both modernizing agriculture and winning consumer acceptance as nano-based fertilizers (Xin et al., 2020). However, the coming decade is eagerly waiting to further design the technology of combined application of NMs and PPs in the agricultural sector. The encapsulation of both PPs and NMs has the unique property of showing productiveness in the context of a smart farming system to improve crop yield, plant-derived food quality, and nutritional value of plant-based products.

The core agricultural sector needs attention in the future and may require the following ways to effectively apply the combination of NMs and PPs.

- The properties of NMs such as size, surface chemistry, structure, dose, and toxicity should be carefully monitored.
- Novel analytical methods are needed to develop NMs with unique properties, their detection, validation, effects under field conditions, and associated toxicity.
- Establish guidelines for the responsible use of NM in agriculture and a roadmap to reduce the risk of using nano-based products.
- The compatibility of PPs with target NMs must be established when NMs are used as a synergistic component of PPs.
- As a variety of environmental factors affect the microbial population in the soil, a PPs strain with the ability to survive under diverse stress conditions should be selected for subsequent application.
- The combined application of NMs and PPs should preserve the local microbial community and must not be detrimental to the soil ecology. The technology for the development of nanobiofertilizers has a significant impact on agricultural yields; therefore, the knowledge related to the effective application of nanobiofertilizer should be communicated from researchers to authorities and industrial sectors.
- A new venue for discussion needs to be established, and it should be used to discuss the significant impact that nanobiofertilizers have on agriculture, the economy, and human life.
- The performance of novel nano-based materials or products should be compared to that of previously formulated products.
- Multiple field studies should be conducted at diverse sites to evaluate the performance of created nanobioformulations in terms of their efficacy and environmental impact.

12. Conclusion

Improving food-based crop production is the primary need for a rapidly growing world population. This goal can be achieved through strategies that use agriculturally important microbe and nanomaterial-based fertilizers without relying heavily on agrochemicals. The abundant scientific literature supports the effectiveness of using NMs and microorganisms as PPs in improving plant growth, ameliorating environmental stresses, and improving soil health. In recent years, however, scientists have been keenly interested in investigating the synergistic effects of NMs and PPs in agriculture to maximize crop yields and maintain soil health. In this cocktail of NMs and PPs, nanomaterials serve as effective sources of nutrients for plants, while PPs stimulate plant growth, therefore serving as natural crop vitalizers. According to the recent literature, the synergistic effect of NMs and PPs has played a promising role in achieving the following target: (a) maximization of crop productivity and crop quality, (b) assurance of food security for the rapidly escalating global population, (c) amelioration of the drastic effects of various environmental stresses such as drought, salinity, and cold, as well as biotic stresses, (d) maintenance of soil health, (e) reduction of the massive reliance on chemical-based fertilizers, and (f) strengthening of the bioeconomy by improving grain yield, grain quality, and biomass in a sustainable way without showing negative impact on the environment. The breakthroughs in nanotechnology have also facilitated the inclusion of plant probiotic strains within the ideal nanomaterials or the entrapment of both NMs and PPs within a suitable carrier. In addition to the controlled and consistent supply of both NMs and PPs, this strategy retains the effectiveness and longevity of the PPs and exhibits a positive impact on crop productivity. In addition, the safe dose of NMs must be determined from an environmental perspective, and a risk assessment must be conducted to ensure that NMs are not hazardous to local soil microbial populations. In conclusion, the application of NMs and PPs in a synergistic manner is demonstrated as an efficient way of improving the quality and production of food-based crops and strengthening the bioeconomy. Furthermore, detailed investigations are also required to develop a customized cocktail of NMs and PPs, understanding their controlled and targeted delivery as well as their molecular mechanisms in plants, to pave the way for sustainable agriculture.

Author contributions

VU and MC: writing of original draft of the manuscript. All authors contributed to the article and approved the submitted version.

Acknowledgments

The authors gratefully acknowledge the Department of Microbiology, College of Basic Sciences and Humanities, Dr. Rajendra Prasad Central Agricultural University, Pusa, Samastipur - 848 125, Bihar, India.

Conflict of interest

The authors declare that the study was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Abd El-Mageed, T. A., Abd El-Mageed, S. A., El-Saadony, M. T., Abdelaziz, S., and Abdou, N. M. (2022). Plant growth-promoting rhizobacteria improve growth, morph-physiological responses, water productivity, and yield of rice plants under full and deficit drip irrigation. *Rice* 15:16. doi: 10.1186/s12284-022-00564-6

Abdal Dayem, A., Hossain, M., Lee, S., Kim, K., Saha, S., Yang, G.-M., et al. (2017). The role of reactive oxygen species (ROS) in the biological activities of metallic nanoparticles. *Int. J. Mol. Sci.* 18:120. doi: 10.3390/ijms18010120

Abdelkhalek, A., El-Gendi, H., Al-Askar, A. A., Maresca, V., Moawad, H., Elsharkawy, M. M., et al. (2022). Enhancing systemic resistance in faba bean (*Vicia faba* L.) to bean yellow mosaic virus via soil application and foliar spray of nitrogen-fixing *Rhizobium leguminosarum* bv. viciae strain 33504-Alex1. *Front. Plant Sci.* 13:933498. doi: 10.3389/fpls.2022.933498

Abedi, S., Iranbakhsh, A., Oraghi Ardebili, Z., and Ebadi, M. (2021). Nitric oxide and selenium nanoparticles confer changes in growth, metabolism, antioxidant machinery, gene expression, and flowering in chicory (*Cichorium intybus* L.): potential benefits and risk assessment. *Environ. Sci. Pollut. Res. Int.* 28, 3136–3148. doi: 10.1007/s11356-020-10706-2

Abigail, E. A., and Chidambaram, R. (2017). "Nanotechnology in herbicide resistance" in *Nanostructured materials - fabrication to applications*, ed. M. S. Seehra (InTech), 207–212.

Abou-Sreea, A. I. B., Kamal, M., El Sowfy, D. M., Rady, M. M., Mohamed, G. F., Al-Dhumri, S. A., et al. (2022). Small-sized nanophosphorus has a positive impact on the performance of fenugreek plants under soil-water deficit stress: a case study under field conditions. *Biology* 11:115. doi: 10.3390/biology11010115

Adil, M., Bashir, S., Bashir, S., Aslam, Z., Ahmad, N., Younas, T., et al. (2022). Zinc oxide nanoparticles improved chlorophyll contents, physical parameters, and wheat yield under salt stress. *Front. Plant Sci.* 13:932861. doi: 10.3389/fpls.2022.932861

Adjuik, T. A., Nokes, S. E., and Montross, M. D. (2022). Evaluating the feasibility of using lignin–alginate beads with starch additive for entrapping and releasing *Rhizobium* spp. *J. Appl. Polym. Sci.* 139:e53181. doi: 10.1002/app.53181

Agri, U., Chaudhary, P., and Sharma, A. (2021). In vitro compatibility evaluation of agriusable nanochitosan on beneficial plant growth-promoting rhizobacteria and maize plant. *Natl. Acad. Sci. Lett.* 44, 555–559. doi: 10.1007/s40009-021-01047-w

Agri, U., Chaudhary, P., Sharma, A., and Kukreti, B. (2022). Physiological response of maize plants and its rhizospheric microbiome under the influence of potential bioinoculants and nanochitosan. *Plant Soil* 474, 451–468. doi: 10.1007/s11104-022-05351-2

Ahanger, M. A., Qi, M., Huang, Z., Xu, X., Begum, N., Qin, C., et al. (2021). Improving growth and photosynthetic performance of drought stressed tomato by application of nano-organic fertilizer involves up-regulation of nitrogen, antioxidant and osmolyte metabolism. *Ecotoxicol. Environ. Saf.* 216:112195. doi: 10.1016/j.ecoenv.2021.112195

Ahmad, F., Husain, F. M., and Ahmad, I. (2011). "Rhizosphere and root colonization by bacterial inoculants and their monitoring methods: a critical area in PGPR research" in *Microbes and microbial technology* eds. I. Ahmad, F. Ahmad, and J. Pichtel (Springer, New York), 363–391.

Ahmad, S., Mfarrej, M. F. B., El-Esawi, M. A., Waseem, M., Alatawi, A., Nafees, M., et al. (2022). Chromium-resistant *Staphylococcus aureus* alleviates chromium toxicity by developing synergistic relationships with zinc oxide nanoparticles in wheat. *Ecotoxicol. Environ. Saf.* 230:113142. doi: 10.1016/j.ecoenv.2021.113142

Ahmar, S., Gill, R. A., Jung, K.-H., Faheem, A., Qasim, M. U., Mubeen, M., et al. (2020). Conventional and molecular techniques from simple breeding to speed breeding in crop plants: recent advances and future outlook. *Int. J. Mol. Sci.* 21:2590. doi: 10.3390/ijms21072590

Ahmed, T., Noman, M., Luo, J., Muhammad, S., Shahid, M., Ali, M. A., et al. (2021). Bioengineered chitosan-magnesium nanocomposite: a novel agricultural antimicrobial agent against Acidovorax oryzae and Rhizoctonia solani for sustainable rice production. *Int. J. Biol. Macromol.* 168, 834–845. doi: 10.1016/j.ijbiomac.2020.11.148

Ahmed, T., Noman, M., Rizwan, M., Ali, S., Ijaz, U., Nazir, M. M., et al. (2022). Green molybdenum nanoparticles-mediated bio-stimulation of *Bacillus* sp. strain ZH16 improved the wheat growth by managing in planta nutrients supply, ionic homeostasis and arsenic accumulation. *J. Hazard. Mater.* 423:127024. doi: 10.1016/j.jhazmat.2021.127024

Akhtar, N., Ilyas, N., Mashwani, Z.-U.-R., Hayat, R., Yasmin, H., Noureldeen, A., et al. (2021). Synergistic effects of plant growth promoting rhizobacteria and silicon dioxide nano-particles for amelioration of drought stress in wheat. *Plant Physiol. Biochem.* 166, 160–176. doi: 10.1016/j.plaphy.2021.05.039

Akhtar, N., Ilyas, N., Meraj, T. A., Pour-Aboughadareh, A., Sayyed, R. Z., Mashwani, Z. U., et al. (2022). Improvement of plant responses by nanobiofertilizer: a step towards sustainable agriculture. *Nano* 12:965. doi: 10.3390/nano12060965

Alabdallah, N. M., and Hasan, M. M. (2021). Plant-based green synthesis of silver nanoparticles and its effective role in abiotic stress tolerance in crop plants. *Saudi J. Biol. Sci.* 28, 5631–5639. doi: 10.1016/j.sjbs.2021.05.081

Alharbi, K., Hafez, E., Omara, A. E.-D., Awadalla, A., and Nehela, Y. (2022b). Plant growth promoting rhizobacteria and silica nanoparticles stimulate sugar beet resilience to irrigation with saline water in salt-affected soils. *Plan. Theory* 11:3117. doi: 10.3390/plants11223117

Alharbi, K., Rashwan, E., Mohamed, H. H., Awadalla, A., Omara, A. E.-D., Hafez, E. M., et al. (2022a). Application of silica nanoparticles in combination with two bacterial strains improves the growth, antioxidant capacity and production of barley irrigated with saline water in salt-affected soil. *Plan. Theory* 11:2026. doi: 10.3390/plants11152026

Ali, E. F., El-Shehawi, A. M., Ibrahim, O. H. M., Abdul-Hafeez, E. Y., Moussa, M. M., and Hassan, F. A. S. (2021). A vital role of chitosan nanoparticles in improvisation the drought stress tolerance in *Catharanthus roseus* (L.) through biochemical and gene expression modulation. *Plant Physiol. Biochem.* 161, 166–175. doi: 10.1016/j.plaphy.2021.02.008

Ali, Z., Ullah, R., Tuzen, M., Ullah, S., Rahim, A., and Saleh, T. A. (2022). Colorimetric sensing of heavy metals on metal doped metal oxide nanocomposites: a review. *Tren. Environ. Anal. Chem.* 37:e00187. doi: 10.1016/j.teac.2022.e00187

Amirifar, A., Hemati, A., Asgari Lajayer, B., Pandey, J., and Astatkie, T. (2022). "Impact of various environmental factors on the biosynthesis of alkaloids in medicinal plants" in *Environmental challenges and solutions*, ed. T. Aftab (Springer Cham), 229–248.

Anzano, A., Bonanomi, G., Mazzoleni, S., and Lanzotti, V. (2022). Plant metabolomics in biotic and abiotic stress: a critical overview. *Phytochem. Rev.* 21, 503–524. doi: 10.1007/s11101-021-09786-w

Arif, I., Batool, M., and Schenk, P. M. (2020). Plant microbiome engineering: expected benefits for improved crop growth and resilience. *Trends Biotechnol.* 38, 1385–1396. doi: 10.1016/j.tibtech.2020.04.015

Armenia, I., Cuestas Ayllón, C., Torres Herrero, B., Bussolari, F., Alfranca, G., Grazú, V., et al. (2022). Photonic and magnetic materials for on-demand local drug delivery. *Adv. Drug Deliv. Rev.* 191:114584. doi: 10.1016/j.addr.2022.114584

Asghar, W., Akça, M. O., Akça, H., Tarf, O. J., Kataoka, R., and Turgay, O. C. (2022). "Alternative strategies to synthetic chemical fertilizers: revitalization of soil quality for sustainable agriculture using organic-based approaches" in *New and Future Developments in Microbial Biotechnology and Bioengineering*, eds. H. B. Singh, and A. Vaishnav (Elsevier), 1–30.

Avila-Quezada, G. D., Ingle, A. P., Golińska, P., and Rai, M. (2022). Strategic applications of nano-fertilizers for sustainable agriculture: benefits and bottlenecks. *Nanotechnol. Rev.* 11, 2123–2140. doi: 10.1515/ntrev-2022-0126

Azam, M., Bhatti, H. N., Khan, A., Zafar, L., and Iqbal, M. (2022). Zinc oxide nano-fertilizer application (foliar and soil) effect on the growth, photosynthetic pigments and antioxidant system of maize cultivar. *Biocatal. Agric. Biotechnol.* 42:102343. doi: 10.1016/j.bcab.2022.102343

Azmat, A., Tanveer, Y., Yasmin, H., Hassan, M. N., Shahzad, A., Reddy, M., et al. (2022). Coactive role of zinc oxide nanoparticles and plant growth promoting rhizobacteria for mitigation of synchronized effects of heat and drought stress in wheat plants. *Chemosphere* 297:133982. doi: 10.1016/j.chemosphere.2022.133982

Babaei, K., Seyed Sharifi, R., Pirzad, A., and Khalilzadeh, R. (2017). Effects of bio fertilizer and nano Zn-Fe oxide on physiological traits, antioxidant enzymes activity and yield of wheat (*Triticum aestivum* L.) under salinity stress. *J. Plant Interact.* 12, 381–389. doi: 10.1080/17429145.2017.1371798

Bala, K. (2022). "Microbial fertilizer as an alternative to chemical fertilizer in modern agriculture" in *Beneficial microorganisms in agriculture*, eds. R. Prasad and S. H. Zhang (Springer, Singapore), 111–130.

Balah, M. A., and Pudake, R. N. (2019). "Use nanotools for weed control and exploration of weed plants in nanotechnology" in *Nanoscience for Sustainable Agriculture*, eds. R. Pudake, N. Chauhan, and C. Kole (Springer, Cham), 207–231.

Balla, A., Silini, A., Cherif-Silini, H., Chenari Bouket, A., Alenezi, F. N., and Belbahri, L. (2022). Recent advances in encapsulation techniques of plant growth-promoting microorganisms and their prospects in the sustainable agriculture. *Appl. Sci.* 12:9020. doi: 10.3390/app12189020

Bana, R. C., Yadav, S. S., Shivran, A. C., Singh, P., and Kudi, V. K. (2020). Site-specific nutrient management for enhancing crop productivity. *Int. Res. J. Pure Appl. Chem.* 21, 17–25. doi: 10.9734/irjpac/2020/v21i1530249

Banerjee, A., Sarkar, S., Cuadros-Orellana, S., and Bandopadhyay, R. (2019). "Exopolysaccharides and biofilms in mitigating salinity stress: the biotechnological

potential of halophilic and soil-inhabiting PGPR microorganisms" in *Soil biology*, eds. B. Giri & A. Varma (Springer, Cham), 133–153.

Barna, B. (2022). Manipulation of senescence of plants to improve biotic stress resistance. *Life* 12:1496. doi: 10.3390/life12101496

Beig, B., Niazi, M. B. K., Sher, F., Jahan, Z., Malik, U. S., Khan, M. D., et al. (2022). Nanotechnology-based controlled release of sustainable fertilizers. A review. *Environ. Chem. Lett.* 20, 2709–2726. doi: 10.1007/s10311-022-01409-w

Bhat, B. A., Tariq, L., Nissar, S., Islam, S. T., Islam, S. U., Mangral, Z., et al. (2022). The role of plant-associated rhizobacteria in plant growth, biocontrol and abiotic stress management. *J. Appl. Microbiol.* 133, 2717–2741. doi: 10.1111/jam.15796

Bhatt, D., Bhatt, M. D., Nath, M., Dudhat, R., Sharma, M., and Bisht, D. S. (2020). "Application of nanoparticles in overcoming different environmental stresses" in *Protective chemical agents in the amelioration of plant abiotic stress*. eds. A. Roychoudhury and D. K. Tripathi (John Wiley & Sons Ltd) 635–654. doi: 10.1002/9781119552154.ch32

Boregowda, N., Jogigowda, S. C., Bhavya, G., Sunilkumar, C. R., Geetha, N., Udikeri, S. S., et al. (2022). Recent advances in nanoremediation: carving sustainable solution to clean-up polluted agriculture soils. *Environ. Pollut.* 297:118728. doi: 10.1016/j.envpol.2021.118728

Boro, M., Sannyasi, S., Chettri, D., and Verma, A. K. (2022). Microorganisms in biological control strategies to manage microbial plant pathogens: a review. *Arch. Microbiol.* 204:666. doi: 10.1007/s00203-022-03279-w

Cai, L., Cai, L., Jia, H., Liu, C., Wang, D., and Sun, X. (2020). Foliar exposure of Fe3O4 nanoparticles on Nicotiana benthamiana: evidence for nanoparticles uptake, plant growth promoter and defense response elicitor against plant virus. *J. Hazard. Mater.* 393:122415. doi: 10.1016/j.jhazmat.2020.122415

Carro, L., and Nouioui, I. (2017). Taxonomy and systematics of plant probiotic bacteria in the genomic era. *AIMS Microbiol.* 3, 383–412. doi: 10.3934/microbiol.2017.3.383

Chand Mali, S., Raj, S., and Trivedi, R. (2020). Nanotechnology a novel approach to enhance crop productivity. *Biochem. Biophys. Rep.* 24:100821. doi: 10.1016/j.bbrep.2020.100821

Chanu Thounaojam, T., Thounaojam, T. M., and Upadhyaya, H. (2021). "Role of zinc oxide nanoparticles in mediating abiotic stress responses in plant" in *Zinc-Based Nanostructures for Environmental and Agricultural Applications*, eds. A. Kamel, and Abd-Elsalam (Elsevier), 323–337.

Chaudhary, P., Agri, U., Chaudhary, A., Kumar, A., and Kumar, G. (2022a). Endophytes and their potential in biotic stress management and crop production. *Front. Microbiol.* 13:933017. doi: 10.3389/fmicb.2022.933017

Chaudhary, P., Chaudhary, A., Bhatt, P., Kumar, G., Khatoon, H., Rani, A., et al. (2022b). Assessment of soil health indicators under the influence of nanocompounds and *Bacillus* spp. in field condition. *Front. Environ. Sci.* 9:769871. doi: 10.3389/fenvs.2021.769871

Chaudhary, P., Chaudhary, A., Parveen, H., Rani, A., Kumar, G., Kumar, R., et al. (2021a). Impact of nanophos in agriculture to improve functional bacterial community and crop productivity. *BMC Plant Biol.* 21:519. doi: 10.1186/s12870-021-03298-7

Chaudhary, P., Khati, P., Chaudhary, A., Gangola, S., Kumar, R., and Sharma, A. (2021b). Bioinoculation using indigenous bacillus spp. improves growth and yield of Zea mays under the influence of nanozeolite. *Biotech* :11. doi: 10.1007/s13205-020-02561-2

Chaudhary, P., Khati, P., Chaudhary, A., Maithani, D., Kumar, G., and Sharma, A. (2021c). Cultivable and metagenomic approach to study the combined impact of nanogypsum and Pseudomonas taiwanensis on maize plant health and its rhizospheric microbiome. *PLoS One* 16:e0250574. doi: 10.1371/journal.pone.0250574

Chaudhary, P., Khati, P., Gangola, S., Kumar, A., Kumar, R., and Sharma, A. (2021d). Impact of nanochitosan and bacillus spp. on health, productivity and defence response in Zea mays under field condition. *Biotech* 11:237. doi: 10.1007/s13205-021-02790-z

Chaudhary, P., and Sharma, A. (2019). Response of nanogypsum on the performance of plant growth promotory bacteria recovered from nanocompound infested agriculture field. *Environ. Ecol.* 37, 363–372.

Chaudhary, P., Sharma, A., Chaudhary, A., Khati, P., Gangola, S., and Maithani, D. (2021e). Illumina based high throughput analysis of microbial diversity of maize rhizosphere treated with nanocompounds and bacillus sp. *Appl. Soil Ecol.* 159:103836. doi: 10.1016/j.apsoil.2020.103836

Chaudhary, P., Singh, S., Chaudhary, A., Sharma, A., and Kumar, G. (2022c). Overview of biofertilizers in crop production and stress management for sustainable agriculture. *Front. Plant Sci.* 13:930340. doi: 10.3389/fpls.2022.930340

Chavan, S., Sarangdhar, V., and Nadanathangam, V. (2020). Toxicological effects of TiO_2 nanoparticles on plant growth promoting soil bacteria. *Emerg. Contam.* 6, 87–92. doi: 10.1016/j.emcon.2020.01.003

Chen, H., Chen, J., Qi, Y., Chu, S., Ma, Y., Xu, L., et al. (2022). Endophytic fungus Cladosporium tenuissimum DF11, an efficient inducer of tanshinone biosynthesis in *Salvia miltiorrhiza* roots. *Phytochemistry* 194:113021. doi: 10.1016/j.phytochem.2021.113021

Chen, C., Guo, L., Chen, Y., Qin, P., and Wei, G. (2023). Pristine and sulfidized zinc oxide nanoparticles alter bacterial communities and metabolite profiles in soybean rhizocompartments. *Sci. Total Environ.* 855:158697. doi: 10.1016/j.scitotenv.2022.158697

Chhipa, H. (2021). "Nano-toxicity to microbes: potential implications of nanomaterials on microbial activity" in *Environmental chemistry for a sustainable world*, eds. V. Kumar, P. Guleria, S. Ranjan, N. Dasgupta, and E. Lichtfouse (Springer, Cham), 99–123.

Chitara, M. K., Chauhan, S., and Singh, R. P. (2021). "Bioremediation of polluted soil by using plant growth–promoting rhizobacteria" in *Microbial rejuvenation of polluted environment*, eds. Panpatte, D.G., Jhala, Y.K. (Springer, Singapore), 203–226.

Chitara, M. K., Keswani, C., Bisen, K., Singh, V., Singh, S. P., Sarma, B. K., et al. (2017). "Improving crop performance under heat stress using thermotolerant agriculturally important microorganisms" in *Advances in PGPR research*, eds. H. B. Singh, B. K. Sarma, C. Keswani (Wallingford UK: CABI), 296–305.

Chitara, M. K., Singh, R. P., Gupta, P. K., Mishra, D., Jatav, S. S., Sharma, S., et al. (2022). "The Risk Associated with Crop Ecosystem Management and Pesticides Pollution" in Ecosystem Services, ed. : H. S. Jatav (Nova Science Publishers, Inc.), 151–163.

Costa, O. Y. A., Raaijmakers, J. M., and Kuramae, E. E. (2018). Microbial extracellular polymeric substances: ecological function and impact on soil aggregation. *Front. Microbiol.* 9:1636. doi: 10.3389/fmicb.2018.01636

Dalir Abdolahinia, E., Barati, G., Ranjbar-Navazi, Z., Kadkhoda, J., Islami, M., Hashemzadeh, N., et al. (2022). Application of nanogels as drug delivery systems in multicellular spheroid tumor model. *J. Drug Deliv. Sci. Technol.* 68:103109. doi: 10.1016/j.jddst.2022.103109

Daniel, A. I., Fadaka, A. O., Gokul, A., Bakare, O. O., Aina, O., Fisher, S., et al. (2022). Biofertilizer: the future of food security and food safety. *Microorganisms* 10:1220. doi: 10.3390/microorganisms10061220

Daryabeigi Zand, A., Tabrizi, A. M., and Heir, A. V. (2020a). Application of titanium dioxide nanoparticles to promote phytoremediation of Cd-polluted soil: contribution of PGPR inoculation. *Biorem. J.* 24, 171–189. doi: 10.1080/10889868.2020.1799929

Daryabeigi Zand, A., Tabrizi, A. M., and Heir, A. V. (2020b). The influence of association of plant growth-promoting rhizobacteria and zero-valent iron nanoparticles on removal of antimony from soil by *Trifolium repens*. *Environ. Sci. Pollut. Res. Int.* 27, 42815–42829. doi: 10.1007/s11356-020-10252-x

Das, P. P., Singh, K. R., Nagpure, G., Mansoori, A., Singh, R. P., Ghazi, I. A., et al. (2022). Plant-soil-microbes: a tripartite interaction for nutrient acquisition and better plant growth for sustainable agricultural practices. *Environ. Res.* 214:113821. doi: 10.1016/j.envres.2022.113821

De Gregorio, P. R., Michavila, G., Ricciardi Muller, L., de Souza Borges, C., Pomares, M. F., Saccol de Sá, E. L., et al. (2017). Beneficial rhizobacteria immobilized in nanofibers for potential application as soybean seed bioinoculants. *PLoS One* 12:e0176930. doi: 10.1371/journal.pone.0176930

de Moraes, A. C. P., da Ribeiro, L. S., de Camargo, E. R., and Lacava, P. T. (2021). The potential of nanomaterials associated with plant growth-promoting bacteria in agriculture. *Biotech* 11:318. doi: 10.1007/s13205-021-02870-0

Duhan, L., Kumari, D., Verma, R., and Pasrija, R. (2022). "Fungal hydrolytic enzymes produced by plant growth-promoting rhizobacteria (PGPR)" in *Secondary metabolites and volatiles of PGPR in plant-growth promotion*, eds. R. Z. Sayyed and V. G. Uarrota (Springer, Cham), 313–333.

Elbasiouny, H., El-Ramady, H., Elbehiry, F., Rajput, V. D., Minkina, T., and Mandzhieva, S. (2022). Plant nutrition under climate change and soil carbon sequestration. *Sustainability* 14:914. doi: 10.3390/su14020914

Elemike, E., Uzoh, I., Onwudiwe, D., and Babalola, O. (2019). The role of nanotechnology in the fortification of plant nutrients and improvement of crop production. *Appl. Sci.* 9:499. doi: 10.3390/app9030499

Elmer, W., De La Torre-Roche, R., Pagano, L., Majumdar, S., Zuverza-Mena, N., Dimkpa, C., et al. (2018). Effect of metalloid and metal oxide nanoparticles on Fusarium wilt of watermelon. *Plant Dis.* 102, 1394–1401. doi: 10.1094/PDIS-10-17-1621-RE

Elnahal, A. S. M., El-Saadony, M. T., Saad, A. M., Desoky, E.-S. M., El-Tahan, A. M., Rady, M. M., et al. (2022). The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: a review. *Eur. J. Plant Pathol.* 162, 759–792. doi: 10.1007/s10658-021-02393-7

Eslami, P., Rossi, F., and Fedeli, S. (2019). Hybrid nanogels: stealth and biocompatible structures for drug delivery applications. *Pharmaceutics* 11:71. doi: 10.3390/pharmaceutics11020071

Esmaili, S., Tavallali, V., Amiri, B., Bazrafshan, F., and Sharafzadeh, S. (2022). Foliar application of nano-silicon complexes on growth, oxidative damage and bioactive compounds of feverfew under drought stress. *Silicon* 14, 10245–10256. doi: 10.1007/s12633-022-01754-z

Etesami, H., Shokri, E., and Jeong, B. R. (2022). "The combined use of silicon/nanosilicon and arbuscular mycorrhiza for effective management of stressed agriculture: action mechanisms and future prospects" in *Silicon and Nano-silicon in Environmental Stress Management and Crop Quality Improvement*, eds. H. Etesami, A. H. Al Saeedi, H. El-Ramady, M. Fujita, M. Pessarakli, and M. A. Hossain (Academic Press), 241–264.

Ezealigo, U. S., Ezealigo, B. N., Aisida, S. O., and Ezema, F. I. (2021). Iron oxide nanoparticles in biological systems: antibacterial and toxicology perspective. *JCIS Open* 4:100027. doi: 10.1016/j.jciso.2021.100027

Fadiji, A. E., Santoyo, G., Yadav, A. N., and Babalola, O. O. (2022). Efforts towards overcoming drought stress in crops: revisiting the mechanisms employed by plant growth-promoting bacteria. *Front. Microbiol.* 13:962427. doi: 10.3389/fmicb.2022.962427

Faizan, M., Hussain, A., Mir, A. R., Rajput, V. D., Minkina, T., and Hayat, S. (2021). "Effect of carbon nanotubes on abiotic stress response in plants: an overview" in *Sustainable agriculture reviews*, eds. M. Faizan, S. Hayat, and F. Yu (Springer, Cham), 217–229.

Farnia, A., Omidii, M. M., and Farnia, A. (2015). Effect of nano-zinc chelate and nano-biofertilizer on yield and yield components of maize (Zea mays L.), under water stress condition. *Indian J Nat Sci*, 5, 4614–4624.

Fazelian, N., and Yousefzadi, M. (2022). "Nano-biofertilizers for enhanced nutrient use efficiency" in *Nano-enabled Agrochemicals in Agriculture*, eds. M. Ghorbanpour, and M. A. Shahid (Academic Press), 145–158.

Fen, L. B., Rashid, A. H. A., Nordin, N. I., Hossain, M. A. M., Uddin, S. M. K., Johan, M. R., et al. (2022). "Applications of nanomaterials in agriculture and their safety aspect" in *Biogenic nanomaterials*, eds. D. Thangadurai, S. Islam, J. Sangeetha, & N. Cruz-Martins (Boca Raton: Apple Academic Press), 243–299.

Ferreira Soares, D. C., Domingues, S. C., Viana, D. B., and Tebaldi, M. L. (2020). Polymer-hybrid nanoparticles: current advances in biomedical applications. *Biomed. Pharmacother.* 131:110695. doi: 10.1016/j.biopha.2020.110695

Fetsiukh, A., Conrad, J., Bergquist, J., and Timmusk, S. (2021). Silica particles trigger the exopolysaccharide production of harsh environment isolates of growth-promoting rhizobacteria and increase their ability to enhance wheat biomass in drought-stressed soils. *Int. J. Mol. Sci.* 22:6201. doi: 10.3390/ijms22126201

Fiodor, A., Singh, S., and Pranaw, K. (2021). The contrivance of plant growth promoting microbes to mitigate climate change impact in agriculture. *Microorganisms* 9:1841. doi: 10.3390/microorganisms9091841

Fuskele, V., and Sarviya, R. M. (2017). Recent developments in nanoparticles synthesis, preparation and stability of nanofluids. *Mater. Today* 4, 4049–4060. doi: 10.1016/j.matpr.2017.02.307

Gahoi, P., Omar, R. A., Verma, N., and Gupta, G. S. (2021). Rhizobacteria and acylated homoserine lactone-based nanobiofertilizer to improve growth and pathogen defense in *Cicer arietinum* and *Triticum aestivum* plants. *ACS Agric. Sci. Technol.* 1, 240–252. doi: 10.1021/acsagscitech.1c00039

Gamalero, E., and Glick, B. R. (2022). Recent advances in bacterial amelioration of plant drought and salt stress. *Biology* 11:437. doi: 10.3390/biology11030437

Gavelienė, V., Šocik, B., Jankovska-Bortkevič, E., and Jurkonienė, S. (2021). Plant microbial biostimulants as a promising tool to enhance the productivity and quality of carrot root crops. *Microorganisms* 9:1850. doi: 10.3390/microorganisms9091850

Ghoghari, N., Bharwad, K., Champaneria, A., and Rajkumar, S. (2022). "Microbial consortia for augmentation of plant growth–revisiting the promising approach towards sustainable agriculture" in *New and Future Developments in Microbial Biotechnology and Bioengineering*, eds. H. Singh, and A. Vaishnav (Elsevier), 231–256.

González-García, Y., Cadenas-Pliego, G., Alpuche-Solís, Á. G., Cabrera, R. I., and Juárez-Maldonado, A. (2021). Carbon nanotubes decrease the negative impact of *Alternaria solani* in tomato crop. *Nano* 11, 1080. doi: 10.3390/nano11051080

Gosal, S. K., Kaur, J., and Kaur, J. (2017). "Plant growth-promoting rhizobacteria: a probiotic for plant health and productivity" in *Probiotics and plant health*, eds. V. Kumar, M. Kumar, S. Sharma and R. Prasad (Springer, Singapore), 589–600.

Guleria, G., Thakur, S., Shandilya, M., Sharma, S., Thakur, S., and Kalia, S. (2022). Nanotechnology for sustainable agro-food systems: the need and role of nanoparticles in protecting plants and improving crop productivity. *Plant Physiol. Biochem.* 194, 533–549. doi: 10.1016/j.plaphy.2022.12.004

Gupta, G. S., Kumar, A., and Verma, N. (2019). Bacterial homoserine lactones as a nanocomposite fertilizer and defense regulator for chickpeas. *Environ. Sci. Nano* 6, 1246–1258. doi: 10.1039/c9en00199a

Gutiérrez-Cruz, A., Ruiz-Hernández, A. R., Vega-Clemente, J. F., Luna-Gazcón, D. G., and Campos-Delgado, J. (2022). A review of top-down and bottom-up synthesis methods for the production of graphene, graphene oxide and reduced graphene oxide. *J. Mater. Sci.* 57, 14543–14578. doi: 10.1007/s10853-022-07514-z

Hadj Alouane, M. H., Ahmed, F., Hussein El Semary, N. A., Aldayel, M. F., Alhaweti, F. H., and Nasr, O. (2021). Application of optimised snanocarbon materials and biofertilisers as a potent superfertiliser: towards sustainable agriculture production. *Sci. Adv. Mater.* 13, 812–819. doi: 10.1166/sam.2021.3948

Hafez, Y. M., Attia, K. A., Kamel, S., Alamery, S. F., El-Gendy, S., Al-Doss, A. A., et al. (2020). Bacillus subtilis as a bio-agent combined with nano molecules can control powdery mildew disease through histochemical and physiobiochemical changes in cucumber plants. *Physiol. Mol. Plant Pathol.* 111:101489. doi: 10.1016/j.pmpp.2020.101489

Hafez, E. M., Osman, H. S., Gowayed, S. M., Okasha, S. A., Omara, A. E.-D., Sami, R., et al. (2021). Minimizing the adversely impacts of water deficit and soil salinity on maize growth and productivity in response to the application of plant growth-promoting rhizobacteria and silica nanoparticles. *Agronomy* 11:676. doi: 10.3390/agronomy11040676

Hajji-Hedfi, L., and Chhipa, H. (2021). Nano-based pesticides: challenges for pest and disease management. *Euro-Mediterr. J. Environ. Integr.* 6:69. doi: 10.1007/s41207-021-00279-y

Hassan, F. A. S., Ali, E., Gaber, A., Fetouh, M. I., and Mazrou, R. (2021). Chitosan nanoparticles effectively combat salinity stress by enhancing antioxidant activity and alkaloid biosynthesis in *Catharanthus roseus* (L.) G. *Don. Plant Physiol. Biochem.* 162, 291–300. doi: 10.1016/j.plaphy.2021.03.004

Hernández-Díaz, J. A., Garza-García, J. J., Zamudio-Ojeda, A., León-Morales, J. M., López-Velázquez, J. C., and García-Morales, S. (2021). Plant-mediated synthesis of nanoparticles and their antimicrobial activity against phytopathogens. *J. Sci. Food Agric.* 101, 1270–1287. doi: 10.1002/jsfa.10767

Hezaveh, T. A., Pourakbar, L., Rahmani, F., and Alipour, H. (2019). Interactive effects of salinity and ZnO nanoparticles on physiological and molecular parameters of rapeseed (*Brassica napus* L.). *Commun. Soil Sci. Plant Anal.* 50, 698–715. doi: 10.1080/00103624.2019.1589481

Hofmann, T., Lowry, G. V., Ghoshal, S., Tufenkji, N., Brambilla, D., Dutcher, J. R., et al. (2020). Technology readiness and overcoming barriers to sustainably implement nanotechnology-enabled plant agriculture. *Nat. Food.* 1, 416–425. doi: 10.1038/s43016-020-0110-1

Hong, J., Jia, S., Wang, C., Li, Y., He, F., and Gardea-Torresdey, J. L. (2023). Transcriptome reveals the exposure effects of CeO_2 nanoparticles on pakchoi (*Brassica chinensis* L.) photosynthesis. *J. Hazard. Mater.* 444:130427. doi: 10.1016/j.jhazmat.2022.130427

Hosseinpour, A., Ilhan, E., Özkan, G., Öztürk, H. İ., Haliloglu, K., and Cinisli, K. T. (2022). Plant growth-promoting bacteria (PGPBs) and copper (II) oxide (CuO) nanoparticle ameliorates DNA damage and DNA methylation in wheat (*Triticum aestivum* L.) exposed to NaCl stress. *J. Plant Biochem. Biotechnol.* 31, 751–764. doi: 10.1007/s13562-021-00713-w

Janmohammadi, M., Navid, A., Segherloo, A. E., andSabaghnia, N. (2016). Impact of nano-chelated micronutrients and biological fertilizers on growth performance and grain yield of maize under deficit irrigation condition. *Biologija (Vilnius)* 62:143–147. doi: 10.6001/biologija.v62i2.3339

Jakhar, A. M., Aziz, I., Kaleri, A. R., Hasnain, M., Haider, G., Ma, J., et al. (2022). Nano-fertilizers: a sustainable technology for improving crop nutrition and food security. *NanoImpact* 27:100411. doi: 10.1016/j.impact.2022.100411

Jhuma, T. A., Rafeya, J., Sultana, S., Rahman, M. T., and Karim, M. M. (2021). Isolation of endophytic salt-tolerant plant growth-promoting rhizobacteria from *Oryza sativa* and evaluation of their plant growth-promoting traits under salinity stress condition. *Front. Sustain. Food Syst.* 5:687531. doi: 10.3389/fsufs.2021.687531

Jiang, S., Li, J., Wang, Q., Yin, C., Zhan, Y., Yan, Y., et al. (2022). Maize growth promotion by inoculation with an engineered ammonium-excreting strain of nitrogen-fixing *Pseudomonas stutzeri*. *Microorganisms* 10:1986. doi: 10.3390/microorganisms10101986

Jiang, Q., Liu, Q., Shi, Y., Wang, Z.-G., Zhan, P., Liu, J., et al. (2017). Stimulus-responsive plasmonic chiral signals of gold nanorods organized on DNA origami. *Nano Lett.* 17, 7125–7130. doi: 10.1021/acs.nanolett.7b03946

Jiang, G., Zhang, Y., Gan, G., Li, W., Wan, W., Jiang, Y., et al. (2022). Exploring rhizo-microbiome transplants as a tool for protective plant-microbiome manipulation. *ISME Commun.* 2, 10. doi: 10.1038/s43705-022-00094-8

Kamaly, N., Yameen, B., Wu, J., and Farokhzad, O. C. (2016). Degradable controlled-release polymers and polymeric nanoparticles: mechanisms of controlling drug release. *Chem. Rev.* 116, 2602–2663. doi: 10.1021/acs.chemrev.5b00346

Kamari, H., and Sharifi, R. (2017). Effects of nano-zinc oxide and plant growth promoting rhizobacteria on zinc and protein content, phosphatase activity and related traits to grain growth of triticale. *Iran. J. Seed Sci. Technol.* 6, 151–163. doi: 10.22034/ijsst.2017.113549

Kashyap, A. S., Manzar, N., Rajawat, M. V. S., Kesharwani, A. K., Singh, R. P., Dubey, S. C., et al. (2021). Screening and biocontrol potential of rhizobacteria native to Gangetic plains and hilly regions to induce systemic resistance and promote plant growth in Chilli against bacterial wilt disease. *Plan. Theory* 10:2125. doi: 10.3390/plants10102125

Kasperson, J. X., Kasperson, R. E., Turner, B. L., Hsieh, W., and Schiller, A. (2022). "Vulnerability to global environmental change" in *The social contours of risk*, eds. R. E. Kasperson, and J. Kasperson (Routledge), 245–285.

Kaviya, N., Upadhayay, V. K., Singh, J., Khan, A., Panwar, M., and Singh, A. V. (2019). "Role of microorganisms in soil genesis and functions" in *Mycorrhizosphere and Pedogenesis*, eds. A. Varma, D. Choudhary (Singapore: Springer, Singapore), 25–52.

Kenawy, A., Abo-Zaid, G., El-Gendi, H., Hegazy, G., Ho, T., and El Enshasy, H. (2021). "Probiotics applications in agriculture" in *Probiotics, the natural microbiota in living organisms*, eds. H. A. El-Enshasy, S. Yang (Boca Raton: CRC Press), 251–291.

Khairy, A. M., Tohamy, M. R. A., Zayed, M. A., Mahmoud, S. F., El-Tahan, A. M., El-Saadony, M. T., et al. (2022). Eco-friendly application of nano-chitosan for controlling potato and tomato bacterial wilt. *Saudi J. Biol. Sci.* 29, 2199–2209. doi: 10.1016/j.sjbs.2021.11.041

Khalil, M. S., Abd El-Aziz, M. H., and Selim, R. E.-S. (2022). Physiological and morphological response of tomato plants to nano-chitosan used against bio-stress induced by root-knot nematode (*Meloidogyne incognita*) and tobacco mosaic tobamovirus (TMV). *Eur. J. Plant Pathol.* 163, 799–812. doi: 10.1007/s10658-022-02516-8

Khan, M., Khan, A. U., Bogdanchikova, N., and Garibo, D. (2021). Antibacterial and antifungal studies of biosynthesized silver nanoparticles against plant parasitic nematode

Meloidogyne incognita, plant pathogens *Ralstonia solanacearum* and *Fusarium oxysporum*. *Molecules* 26:2462. doi: 10.3390/molecules26092462

Khan, A., Panthari, D., Sharma, R. S., Punetha, A., Singh, A. V., and Upadhayay, V. K. (2023). "Biofertilizers: a microbial-assisted strategy to improve plant growth and soil health" in *Advanced microbial techniques in agriculture, environment, and health management*, eds. S. C. Pandey, V. Pande, D. Sati, andM. Samant (Academic Press), 97–118.

Khan, A., Singh, A. V., Upadhayay, V. K., Ballabh, A., and Prasad, B. (2022). Influence of PGPR on growth and yield of oat (*Avena sativa* L.) under field conditions. *Indian. J. Ecol.* 49, 1351–1356. doi: 10.55362/ije/2022/3670

Khan, A., Singh, J., Upadhayay, V. K., Singh, A. V., and Shah, S. (2019). "Microbial biofortification: a green technology through plant growth promoting microorganisms" in *Sustainable green Technologies for Environmental Management*, eds. S. Shah, V. Venkatramanan, and R. Prasad (Springer, Singapore), 255–269.

Khare, E., and Arora, N. K. (2015). "Effects of soil environment on field efficacy of microbial inoculants" in *Plant microbes symbiosis: Applied facets*, ed. N. Arora (Springer, New Delhi), 353–381.

Khati, P., Chaudhary, P., Gangola, S., Bhatt, P., and Sharma, A. (2017). Nanochitosan supports growth of *Zea mays* and also maintains soil health following growth. *Biotech* 7:81. doi: 10.1007/s13205-017-0668-y

Khati, P., Chaudhary, P., Gangola, S., Bhatt, P., and Sharma, A. (2019a). Influence of nanozeolite on plant growth promotory bacterial isolates recovered from nanocompound infested agriculture field. *Environ. Ecol.* 37, 521–527.

Khati, P., Parul Bhatt, P., Nisha Kumar, R., and Sharma, A. (2018). Effect of nanozeolite and plant growth promoting rhizobacteria on maize. *Biotech* 8. doi: 10.1007/s13205-018-1142-1

Khati, P., Sharma, A., Chaudhary, P., Singh, A. K., Gangola, S., and Kumar, R. (2019b). High-throughput sequencing approach to access the impact of nanozeolite treatment on species richness and evenness of soil metagenome. *Biocatal. Agric. Biotechnol.* 20:101249. doi: 10.1016/j.bcab.2019.101249

Kleinert, A., Benedito, V. A., Morcillo, R. J. L., Dames, J., Cornejo-Rivas, P., Zuniga-Feest, A., et al. (2018). "Morphological and symbiotic root modifications for mineral acquisition from nutrient-poor soils" in *Soil biology*, eds. B. Giri, R. Prasad, and A. Varma (Springer, Cham), 85–142.

Kolesnikov, S. I., Timoshenko, A. N., Kazeev, K. S., Akimenko, Y. V., and Myasnikova, M. A. (2019). Ecotoxicity of copper, nickel, and zinc nanoparticles assessment on the basis of biological indicators of chernozems. *Eurasian Soil Sci.* 52, 982–987. doi: 10.1134/s106422931908009x

Kukreti, B., Sharma, A., Chaudhary, P., Agri, U., and Maithani, D. (2020). Influence of nanosilicon dioxide along with bioinoculants on Zea mays and its rhizospheric soil. *Biotech* 10:345. doi: 10.1007/s13205-020-02329-8

Kumar, P., Burman, U., and Kaul, R. K. (2018). "Ecological risks of nanoparticles" in *Nanomaterials in plants, algae, and microorganisms*, eds. D. K. Tripathi, P. Ahmad, S. Sharma, D. K. Chauhan, and N. K. Dubey (Academic Press), 429–452.

Kumar, S., Nehra, M., Dilbaghi, N., Marrazza, G., Hassan, A. A., and Kim, K.-H. (2019). Nano-based smart pesticide formulations: emerging opportunities for agriculture. *J. Control. Release* 294, 131–153. doi: 10.1016/j.jconrel.2018.12.012

Kumari, H., Khati, P., Gangola, S., Chaudhary, P., and Sharma, A. (2021). Performance of plant growth promotory rhizobacteria on maize and soil characteristics under the influence of TiO_2 nanoparticles. *Pantnagar J. Res.* 19, 28–39.

Kumari, S., Sharma, A., Chaudhary, P., and Khati, P. (2020). Management of plant vigor and soil health using two agriusable nanocompounds and plant growth promotory rhizobacteria in Fenugreek. *Biotech* 10:461. doi: 10.1007/s13205-020-02448-2

Kumari, R., and Singh, D. P. (2020). Nano-biofertilizer: an emerging eco-friendly approach for sustainable agriculture. *Proc. Natl. Acad. Sci. India Sect. B Biol. Sci.* 90, 733–741. doi: 10.1007/s40011-019-01133-6

Kumawat, K. C., Razdan, N., and Saharan, K. (2022). Rhizospheric microbiome: bio-based emerging strategies for sustainable agriculture development and future perspectives. *Microbiol. Res.* 254:126901. doi: 10.1016/j.micres.2021.126901

Kurniawan, A., and Chuang, H.-W. (2022). Rhizobacterial *Bacillus mycoides* functions in stimulating the antioxidant defence system and multiple phytohormone signalling pathways to regulate plant growth and stress tolerance. *J. Appl. Microbiol.* 132, 1260–1274. doi: 10.1111/jam.15252

Latif, M., Bukhari, S. A. H., Alrajhi, A. A., Alotaibi, F. S., Ahmad, M., Shahzad, A. N., et al. (2022). Inducing drought tolerance in wheat through exopolysaccharide-producing rhizobacteria. *Agronomy* 12:1140. doi: 10.3390/agronomy12051140

Li, Y., Xi, K., Liu, X., Han, S., Han, X., Li, G., et al. (2023). Silica nanoparticles promote wheat growth by mediating hormones and sugar metabolism. *J. Nanobiotechnol.* 21:2. doi: 10.1186/s12951-022-01753-7

Liliane, T. N., and Charles, M. S. (2020). "Factors affecting yield of crops" in *Agronomy - climate change & food security*, ed. Amanullah (IntechOpen), 1–16.

Lin, W., Lin, M., Zhou, H., Wu, H., Li, Z., and Lin, W. (2019). The effects of chemical and organic fertilizer usage on rhizosphere soil in tea orchards. *PLoS One* 14:e0217018. doi: 10.1371/journal.pone.0217018

Lu, X., Sun, D., Zhang, X., Hu, H., Kong, L., Rookes, J. E., et al. (2020). Stimulation of photosynthesis and enhancement of growth and yield in *Arabidopsis thaliana* treated with amine-functionalized mesoporous silica nanoparticles. *Plant Physiol. Biochem.* 156, 566–577. doi: 10.1016/j.plaphy.2020.09.036

Ma, W., Du, W., Gu, K., Xu, M., Yin, Y., Sun, Y., et al. (2023). Elevated CO_2 exacerbates effects of TiO_2 nanoparticles on rice (*Oryza sativa* L.) leaf transcriptome and soil bacteria. *Sci. Total Environ.* 857:159689. doi: 10.1016/j.scitotenv.2022.159689

Mahakham, W., Sarmah, A. K., Maensiri, S., and Theerakulpisut, P. (2017). Nanopriming technology for enhancing germination and starch metabolism of aged rice seeds using phytosynthesized silver nanoparticles. *Sci. Rep.* 7:8263. doi: 10.1038/s41598-017-08669-5

Mahapatra, D. M., Satapathy, K. C., and Panda, B. (2022). Biofertilizers and nanofertilizers for sustainable agriculture: phycoprospects and challenges. *Sci. Total Environ.* 803:149990. doi: 10.1016/j.scitotenv.2021.149990

Mahawer, S. K., Arya, S., Kabdal, T., Kumar, R., Prakash, O., Chitara, M. K., and Koli, P. (2022). Plant defense systems: mechanism of self-protection by plants against pathogens. Plant Protection: From Chemicals to Biologicals, 115.

Mahmud, K., Missaoui, A., Lee, K., Ghimire, B., Presley, H. W., and Makaju, S. (2021). Rhizosphere microbiome manipulation for sustainable crop production. *Curr. Plant Biol.* 27:100210. doi: 10.1016/j.cpb.2021.100210

Mandal, M., Chatterjee, S., and Majumdar, S. (2022). "Outside the cell surface: encoding the role of exopolysaccharide producing rhizobacteria to boost the drought tolerance in plants" in *Plant stress: challenges and management in the New Decade*, eds. S. Roy, P. Mathur, A. P. Chakraborty, & S. P . Saha (Springer, Cham), 295–310.

Mandal, A., Sarkar, B., Mandal, S., Vithanage, M., Patra, A. K., and Manna, M. C. (2020). "Impact of agrochemicals on soil health" in *Agrochemicals detection, treatment and remediation*, ed. M. N. V. Prasad (Butterworth-Heinemann), 161–187.

Mardi, A., Mohajjel Shoja, H., and Mohajel Kazemi, E. (2022). Comparative study of growth responses, photosynthetic pigment content, and gene expression pattern in tobacco plants treated with ZnO nano and ZnO bulk particles. *J. Nanopart. Res.* 24:208. doi: 10.1007/s11051-022-05583-4

Massa, F., Defez, R., and Bianco, C. (2022). Exploitation of plant growth promoting bacteria for sustainable agriculture: hierarchical approach to link laboratory and field experiments. *Microorganisms* 10:865. doi: 10.3390/microorganisms10050865

Mathur, A., Koul, A., and Hattewar, J. (2019). "Plant growth-promoting rhizobacteria (PGPRs): significant revolutionary tools for achieving long-term sustainability and combating the biotic stress caused by the attack of pathogens affecting crops in agriculture" in *Plant growth promoting Rhizobacteria for sustainable stress management*, ed. R. Sayyed (Springer, Singapore), 379–388.

Meena, R., Kumar, S., Datta, R., Lal, R., Vijayakumar, V., Brtnicky, M., et al. (2020). Impact of agrochemicals on soil microbiota and management: a review. *Land* 9:34. doi: 10.3390/land9020034

Mejias, J. H., Salazar, F., Pérez Amaro, L., Hube, S., Rodriguez, M., and Alfaro, M. (2021). Nanofertilizers: a cutting-edge approach to increase nitrogen use efficiency in grasslands. *Front. Environ. Sci.* 9:635114. doi: 10.3389/fenvs.2021.635114

Menéndez, E., and Paço, A. (2020). Is the application of plant probiotic bacterial consortia always beneficial for plants? Exploring synergies between rhizobial and non-rhizobial bacteria and their effects on agro-economically valuable crops. *Life* 10:24. doi: 10.3390/life10030024

Mishra, R. K., Rathore, U. S., Pandey, S., Mishra, M., Sharma, N., Kumar, S., et al. (2022). "Plant–rhizospheric microbe interactions: enhancing plant growth and improving soil biota" in *Re-visiting the Rhizosphere eco-system for agricultural sustainability*, eds. U. B. Singh, J. P. Rai, and A. K. Sharma (Springer, Singapore), 445–459.

Mitra, B., Chowdhury, A. R., Dey, P., Hazra, K. K., Sinha, A. K., Hossain, A., et al. (2021). "Use of agrochemicals in agriculture: alarming issues and solutions" in *Input use efficiency for food and environmental security*, eds. R. Bhatt, R. S. Meena, and A. Hossain (Springer, Singapore), 85–122.

Mohamed, N. G., and Abdel-Hakeem, M. A. (2023). Chitosan nanoparticles enhance drought tolerance in tomatoes (*Solanum lycopersicum* L) via gene expression modulation. *Plant Gene* 34:100406. doi: 10.1016/j.plgene.2023.100406

Moradi Pour, M., Saberi Riseh, R., and Skorik, Y. A. (2022). Sodium alginate-gelatin nanoformulations for encapsulation of *Bacillus velezensis* and their use for biological control of pistachio gummosis. *Materials* 15:2114. doi: 10.3390/ma15062114

Moradi, P., Vafaee, Y., Mozafari, A. A., and Tahir, N. A.-R. (2022). Silicon nanoparticles and methyl jasmonate improve physiological response and increase expression of stress-related genes in strawberry cv. Paros under salinity stress. *Silicon* 14, 10559–10569. doi: 10.1007/s12633-022-01791-8

Mubeen, M., Bano, A., Ali, B., Islam, Z. U., Ahmad, A., Hussain, S., et al. (2021). Effect of plant growth promoting bacteria and drought on spring maize (*Zea mays* L.). *Pak. J. Bot.* 53, 1–10. doi: 10.30848/pjb2021-2(38)

Muhammad, F., Raza, M. A. S., Iqbal, R., Zulfiqar, F., Aslam, M. U., Yong, J. W. H., et al. (2022). Ameliorating drought effects in wheat using an exclusive or co-applied rhizobacteria and ZnO nanoparticles. *Biology* 11:1564. doi: 10.3390/biology11111564

Mushtaq, Z., Nazir, A., Asghar, H. N., and Zahir, Z. A. (2022). Interactive effect of siderophore-producing bacteria and l-tryptophan on physiology, tuber characteristics,

yield, and iron concentration of potato. *Potato Res.* 65, 1015–1027. doi: 10.1007/s11540-022-09565-w

Muthukumaran, P., Suresh Babu, P., Shyamalagowri, S., Aravind, J., Kamaraj, M., and Govarthanan, M. (2022). Polymeric biomolecules based nanomaterials: production strategies and pollutant mitigation as an emerging tool for environmental application. *Chemosphere* 307:136008. doi: 10.1016/j.chemosphere.2022.136008

Nagpal, S., Sharma, P., and Kumawat, K. C. (2021). "Microbial bioformulations: revisiting role in sustainable agriculture" in *Biofertilizers*, eds. A. Rakshit, V. S. Meena, M. Parihar, H.B. Singh, and A.K. Singh (Woodhead Publishing), 329–346.

Naim, L., Alsanad, M. A., El Sebaaly, Z., Shaban, N., Fayssal, S. A., and Sassine, Y. N. (2020). Variation of *Pleurotus ostreatus* (Jacq. Ex Fr.) P. Kumm. (1871) performance subjected to different doses and timings of nano-urea. *Saudi J. Biol. Sci.* 27, 1573–1579. doi: 10.1016/j.sjbs.2020.03.019

Naseem, H., Ahsan, M., Shahid, M. A., and Khan, N. (2018). Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. *J. Basic Microbiol.* 58, 1009–1022. doi: 10.1002/jobm.201800309

Nawaz, S., and Bano, A. (2020). Effects of PGPR (*Pseudomonas* sp.) and ag-nanoparticles on enzymatic activity and physiology of cucumber. *Recent Pat. Food Nutr. Agric.* 11, 124–136. doi: 10.2174/2212798410666190716162340

Nayana, A. R., Joseph, B. J., Jose, A., and Radhakrishnan, E. K. (2020). "Nanotechnological advances with PGPR applications" in *Sustainable agriculture reviews 41*, eds. S. Hayat, J. Pichtel, M. Faizan, and Q. Fariduddin (Springer, Cham), 163–180.

Nazli, F., Mustafa, A., Ahmad, M., Hussain, A., Jamil, M., Wang, X., et al. (2020). A review on practical application and potentials of phytohormone-producing plant growth-promoting rhizobacteria for inducing heavy metal tolerance in crops. *Sustainability* 12:9056. doi: 10.3390/su12219056

Neme, K., Nafady, A., Uddin, S., and Tola, Y. B. (2021). Application of nanotechnology in agriculture, postharvest loss reduction and food processing: food security implication and challenges. *Heliyon* 7:e08539. doi: 10.1016/j.heliyon.2021.e08539

Nithya, N., Kiruthika, R., and Dhanaprakhash, S. (2022). Shift in the mindset: increasing preference towards organic food products in Indian context. *Org. Agric.* 12, 213–228. doi: 10.1007/s13165-021-00370-2

Okey-Onyesolu, C. F., Hassanisaadi, M., Bilal, M., Barani, M., Rahdar, A., Iqbal, J., et al. (2021). Nanomaterials as nanofertilizers and nanopesticides: an overview. *ChemistrySelect* 6, 8645–8663. doi: 10.1002/slct.202102379

Öksel, C., Balkan, A., and Bîlgîn, O., and Mîrîk, M., (2022). Investigation of the effect of pgpr on yield and some yield components in winter wheat. *Turk. J. Field Crop.* 27, 127–133. doi: 10.17557/tjfc.1019160

Omran, B. A., and Baek, K.-H. (2022). Control of phytopathogens using sustainable biogenic nanomaterials: recent perspectives, ecological safety, and challenging gaps. *J. Clean. Prod.* 372:133729. doi: 10.1016/j.jclepro.2022.133729

Orozco-Mosqueda, M. D. C., Fadiji, A. E., Babalola, O. O., Glick, B. R., and Santoyo, G. (2022). Rhizobiome engineering: unveiling complex rhizosphere interactions to enhance plant growth and health. *Microbiol. Res.* 263:127137. doi: 10.1016/j.micres.2022.127137

Pandey, S. S., Jain, R., Bhardwaj, P., Thakur, A., Kumari, M., Bhushan, S., et al. (2022). Plant probiotics - Endophytes pivotal to plant health. *Microbiol. Res.* 263:127148. doi: 10.1016/j.micres.2022.127148

Panichikkal, J., and Krishnankutty, R. E. (2022). Chitosan and gold nanoparticles supplementation for augmentation of indole-3-acetic acid production by rhizospheric Pseudomonas aeruginosa and plant growth enhancement. *Curr. Microbiol.* 79:185. doi: 10.1007/s00284-022-02850-4

Panichikkal, J., Prathap, G., Nair, R. A., and Krishnankutty, R. E. (2021). Evaluation of plant probiotic performance of *Pseudomonas* sp. encapsulated in alginate supplemented with salicylic acid and zinc oxide nanoparticles. *Int. J. Biol. Macromol.* 166, 138–143. doi: 10.1016/j.ijbiomac.2020.10.110

Panichikkal, J., Thomas, R., John, J. C., and Radhakrishnan, E. K. (2019). Biogenic gold nanoparticle supplementation to plant beneficial *Pseudomonas monteilii* was found to enhance its plant probiotic effect. *Curr. Microbiol.* 76, 503–509. doi: 10.1007/s00284-019-01649-0

Pantigoso, H. A., Newberger, D., and Vivanco, J. M. (2022). The rhizosphere microbiome: plant–microbial interactions for resource acquisition. *J. Appl. Microbiol.* 133, 2864–2876. doi: 10.1111/jam.15686

Pinelli, F., Saadati, M., Zare, E. N., Makvandi, P., Masi, M., Sacchetti, A., et al. (2022). A perspective on the applications of functionalized nanogels: promises and challenges. *Int. Mater. Rev.*, 68, 1–25. doi: 10.1080/09506608.2022.2026864

Pirzadah, B., Pirzadah, T. B., Jan, A., and Hakeem, K. R. (2020). "Nanofertilizers: a way forward for green economy" in *Nanotechnology in the life sciences*, eds. K. Hakeem, & T. Pirzadah, 99–112.

Pour, M. M., Riseh, R. S., Ranjbar-Karimi, R., Hassanisaadi, M., Rahdar, A., and Baino, F. (2022). Microencapsulation of *Bacillus velezensis* using alginate-gum polymers enriched with TiO_2 and SiO_2 nanoparticles. *Micromachines* 13:1423. doi: 10.3390/mi13091423

Pour, M. M., Saberi-Riseh, R., Mohammadinejad, R., and Hosseini, A. (2019). Nano-encapsulation of plant growth-promoting rhizobacteria and their metabolites using alginate-silica nanoparticles and carbon nanotube improves UCB1 pistachio micropropagation. *J. Microbiol. Biotechnol.* 29, 1096–1103. doi: 10.4014/jmb.1903.03022

Qazi, G., and Dar, F. A. (2020). "Nano-agrochemicals: economic potential and future trends" in *Nanotechnology in the life sciences*, eds. K. Hakeem, and T. Pirzadah (Springer, Cham), 185–193.

Qin, Y., Abatzoglou, J. T., Siebert, S., Huning, L. S., AghaKouchak, A., Mankin, J. S., et al. (2020). Agricultural risks from changing snowmelt. *Nat. Clim. Chang.* 10, 459–465. doi: 10.1038/s41558-020-0746-8

Raeisi Sadati, S. Y., Jahanbakhsh Godehkahriz, S., Ebadi, A., and Sedghi, M. (2022). Zinc oxide nanoparticles enhance drought tolerance in wheat via physio-biochemical changes and stress genes expression. *Iran. J. Biotechnol.* 20:e3027. doi: 10.30498/ijb.2021.280711.3027

Rahmatizadeh, R., Jamei, R., Arvin, M. J., and Rezanejad, F. (2021). Upregulation of LeNRAMP3 and LeFER genes in Solanum lycopersicum confers its cadmium tolerance. *Russ. J. Plant Physiol.* 68, S92–S102. doi: 10.1134/s1021443721070104

Rai, S., Solanki, M. K., Solanki, A. C., and Samal, S. (2023). "Microbial endophytes as probiotics for the plant health: an overview" in *Microbial endophytes and plant growth*, eds. M. K. Solanki, M. K. Yadav, B. P. Singh, and V. K. Gupta (Academic Press), 269–281.

Ramar, V., and Balraj, A. (2022). Critical review on carbon-based nanomaterial for carbon capture: technical challenges, opportunities, and future perspectives. *Energy Fuel* 36, 13479–13505. doi: 10.1021/acs.energyfuels.2c02585

Rashid, M. I., Shahzad, T., Shahid, M., Ismail, I. M. I., Shah, G. M., and Almeelbi, T. (2017). Zinc oxide nanoparticles affect carbon and nitrogen mineralization of Phoenix dactylifera leaf litter in a sandy soil. *J. Hazard. Mater.* 324, 298–305. doi: 10.1016/j.jhazmat.2016.10.063

Ravichandran, M., Samiappan, S. C., Rangaraj, S., Murugan, K., Al-Dhabi, N. A., and Karuppiah, P. (2022). "Nanoemulsion formulations with plant growth promoting rhizobacteria (PGPR) for sustainable agriculture" in *Bio-based nanoemulsions for agri-food applications*, eds. K. A. Abd-Elsalam, and K. Murugan (Elsevier), 207–223.

Reddy, E. C., Reddy, G. S., Goudar, V., Sriramula, A., Swarnalatha, G. V., Al Tawaha, A. R. M., et al. (2022). "Hydrolytic enzyme producing plant growth-promoting rhizobacteria (PGPR) in plant growth promotion and biocontrol" in *Secondary metabolites and volatiles of PGPR in plant-growth promotion*, eds. R. Z. Sayyed, and V. G. Uarrota (Springer, Cham), 303–312.

Rehman, N., and Pandey, A. (2022). "Introduction to nanotherapeutics: a synthetic preview" in *Nanotherapeutics in cancer*, ed. H. S. Tuli (New York: Jenny Stanford Publishing), 1–22.

Saberi Riseh, R., Hassanisaadi, M., Vatankhah, M., Soroush, F., and Varma, R. S. (2022a). Nano/microencapsulation of plant biocontrol agents by chitosan, alginate, and other important biopolymers as a novel strategy for alleviating plant biotic stresses. *Int. J. Biol. Macromol.* 222, 1589–1604. doi: 10.1016/j.ijbiomac.2022.09.278

Saberi Riseh, R., Tamanadar, E., Hajabdollahi, N., Vatankhah, M., Thakur, V. K., and Skorik, Y. A. (2022b). Chitosan microencapsulation of rhizobacteria for biological control of plant pests and diseases: recent advances and applications. *Rhizosphere* 23:100565. doi: 10.1016/j.rhisph.2022.100565

Saberi-Rise, R., and Moradi-Pour, M. (2020). The effect of *Bacillus subtilis* Vru1 encapsulated in alginate - bentonite coating enriched with titanium nanoparticles against Rhizoctonia solani on bean. *Int. J. Biol. Macromol.* 152, 1089–1097. doi: 10.1016/j.ijbiomac.2019.10.197

Saffan, M. M., Koriem, M. A., El-Henawy, A., El-Mahdy, S., El-Ramady, H., Elbehiry, F., et al. (2022). Sustainable production of tomato plants (*Solanum lycopersicum* L.) under low-quality irrigation water as affected by bio-nanofertilizers of selenium and copper. *Sustainability* 14:3236. doi: 10.3390/su14063236

Sahil, K., Sahil Keshan, R., Patra, A., Mehta, S., Abdelmotelb, K. F., Lavale, S. A., et al. (2021). "Expression and regulation of stress-responsive genes in plants under harsh environmental conditions" in *Harsh environment and plant resilience*, ed. A. Husen (Springer, Cham), 25–44.

Salama, A. M., Abd El-Halim, A. E.-H. A., Ibrahim, M. M., Aiad, M. A., and El-Shal, R. M. (2022). Amendment with nanoparticulate gypsum enhances spinach growth in saline-sodic soil. *J. Soil Sci. Plant Nutr.* 22, 3377–3385. doi: 10.1007/s42729-022-00893-x

Sambangi, P., Gopalakrishnan, S., Pebam, M., andRengan, A.K. (2022). Nano-biofertilizers on soil health, chemistry, and microbial community: benefits and risks. *Proc.Indian Natl. Sci. Acad.* 88, 357–368. doi: 10.1007/s43538-022-00094-1

Santos, A. P., Belfiore, C., Úrbez, C., Ferrando, A., Blázquez, M. A., and Farías, M. E. (2022). Extremophiles as plant probiotics to promote germination and alleviate salt stress in soybean. *J. Plant Growth Regul.* 42, 946–959. doi: 10.1007/s00344-022-10605-5

Santoyo, G., Gamalero, E., and Glick, B. R. (2021). Mycorrhizal-bacterial amelioration of plant abiotic and biotic stress. *Front. Sustain. Food Syst.* 5:672881. doi: 10.3389/fsufs.2021.672881

Sanzari, I., Leone, A., and Ambrosone, A. (2019). Nanotechnology in plant science: to make a long story short. *Front. Bioeng. Biotechnol.* 7:120. doi: 10.3389/fbioe.2019.00120

Sarbani, N. M. M., and Yahaya, N. (2022). Advanced development of bio-fertilizer formulations using microorganisms as inoculant for sustainable agriculture and environment – a review. *MJoSHT* 8, 92–101. doi: 10.33102/mjosht.v8i1.228

Seyed Sharifi, R., Khalilzadeh, R., Pirzad, A., and Anwar, S. (2020). Effects of biofertilizers and nano zinc-iron oxide on yield and physicochemical properties of wheat

under water deficit conditions. *Commun. Soil Sci. Plant Anal.* 51, 2511–2524. doi: 10.1080/00103624.2020.1845350

Shah, A. A., Aslam, S., Akbar, M., Ahmad, A., Khan, W. U., Yasin, N. A., et al. (2021). Combined effect of Bacillus fortis IAGS 223 and zinc oxide nanoparticles to alleviate cadmium phytotoxicity in *Cucumis melo*. *Plant Physiol. Biochem.* 158, 1–12. doi: 10.1016/j.plaphy.2020.11.011

Shahzad, A., Ullah, S., Dar, A. A., Sardar, M. F., Mehmood, T., Tufail, M. A., et al. (2021). Nexus on climate change: agriculture and possible solution to cope future climate change stresses. *Environ. Sci. Pollut. Res. Int.* 28, 14211–14232. doi: 10.1007/s11356-021-12649-8

Shalaby, T. A., Abd-Alkarim, E., El-Aidy, F., Hamed, E.-S., Sharaf-Eldin, M., Taha, N., et al. (2021). Nano-selenium, silicon and H_2O_2 boost growth and productivity of cucumber under combined salinity and heat stress. *Ecotoxicol. Environ. Saf.* 212:111962. doi: 10.1016/j.ecoenv.2021.111962

Shalaby, T. A., El-Bialy, S. M., El-Mahrouk, M. E., Omara, A. E.-D., El-Beltagi, H. S., and El-Ramady, H. (2022). Acclimatization of in vitro banana seedlings using root-applied bio-nanofertilizer of copper and selenium. *Agronomy* 12:539. doi: 10.3390/agronomy12020539

Sharifianjazi, F., Irani, M., Esmaeilkhanian, A., Bazli, L., Asl, M. S., Jang, H. W., et al. (2021). Polymer incorporated magnetic nanoparticles: applications for magnetoresponsive targeted drug delivery. *Mater. Sci. Eng. B Solid State Mater. Adv. Technol.* 272:115358. doi: 10.1016/j.mseb.2021.115358

Sharma, B., Afonso, L. O. B., Singh, M. P., Soni, U., and Cahill, D. M. (2022). Zinc- and magnesium-doped hydroxyapatite-urea nanohybrids enhance wheat growth and nitrogen uptake. *Sci. Rep.* 12:19506. doi: 10.1038/s41598-022-20772-w

Sharma, A., Kumar, S., and Singh, R. (2022). Synthesis and characterization of a novel slow-release nanourea/chitosan nanocomposite and its effect on *Vigna radiata* L. *Environ. Sci. Nano* 9, 4177–4189. doi: 10.1039/d2en00297c

Sharma, S. K., Sharma, P. K., Mandeewal, R. L., Sharma, V., Chaudhary, R., Pandey, R., et al. (2022). Effect of foliar application of nano-urea under different nitrogen levels on growth and nutrient content of pearl millet (*Pennisetum glaucum* L.). *Int. J. Plant Soil Sci.* 34, 149–155. doi: 10.9734/IJPSS/2022/v34i2031138

Shikari, A. B., Dikilitas, M., Simsek, E., Guldur, M. E., Simsek, U., Karakas, S., et al. (2022). "Nanotechnology and its role in cereal crops under abiotic stress" in *Sustainable remedies for abiotic stress in cereals*, ed. A. A. S. Abdel Latef (Springer, Singapore), 675–687.

Shultana, R., Zuan, A. T. K., Naher, U. A., Islam, A. K. M. M., Rana, M. M., Rashid, M. H., et al. (2022). The PGPR mechanisms of salt stress adaptation and plant growth promotion. *Agronomy* 12:2266. doi: 10.3390/agronomy12102266

Singh, D., Singh, S. K., Modi, A., Singh, P. K., Yeka Zhimo, V., and Kumar, A. (2020). "Impacts of agrochemicals on soil microbiology and food quality" in *Agrochemicals detection, treatment and remediation*, ed. M. N. V. Prasad (Butterworth-Heinemann), 101–116.

Singh, J., Singh, A. V., Upadhayay, V. K., Khan, A., and Chandra, R. (2022). Prolific contribution of *Pseudomonas* protegens in Zn biofortification of wheat by modulating multifaceted physiological response under saline and non-saline conditions. *World J. Microbiol. Biotechnol.* 38:227. doi: 10.1007/s11274-022-03411-4

Sivakumar, M. (2021). "Climate change, agriculture adaptation, and sustainability" in *Climate resilience and environmental sustainability approaches*, eds. A. Kaushik, C. P. Kaushik, and S. D. Attri (Springer, Singapore), 87–109.

Subotić, A., Jevremović, S., Milošević, S., Trifunović-Momčilov, M., Đurić, M., and Koruga, Đ. (2022). Physiological response, oxidative stress assessment and aquaporin genes expression of cherry tomato (*Solanum lycopersicum* L.) exposed to hyper-harmonized fullerene water complex. *Plan. Theory* 11:2810. doi: 10.3390/plants11212810

Sun, H., Peng, Q., Guo, J., Zhang, H., Bai, J., and Mao, H. (2022). Effects of short-term soil exposure of different doses of ZnO nanoparticles on the soil environment and the growth and nitrogen fixation of alfalfa. *Environ. Pollut.* 309:119817. doi: 10.1016/j.envpol.2022.119817

Tahiri, A.-I., Meddich, A., Raklami, A., Alahmad, A., Bechtaoui, N., Anli, M., et al. (2022). Assessing the potential role of compost, PGPR, and AMF in improving tomato plant growth, yield, fruit quality, and water stress tolerance. *J. Soil Sci. Plant Nutr.* 22, 743–764. doi: 10.1007/s42729-021-00684-w

Tanveer, Y., Yasmin, H., Nosheen, A., Ali, S., and Ahmad, A. (2022). Ameliorative effects of plant growth promoting bacteria, zinc oxide nanoparticles and oxalic acid on Luffa acutangula grown on arsenic enriched soil. *Environ. Pollut.* 300:118889. doi: 10.1016/j.envpol.2022.118889

Tariq, M., Mohammad, K. N., Ahmed, B., Siddiqui, M. A., and Lee, J. (2022). Biological synthesis of silver nanoparticles and prospects in plant disease management. *Molecules* 27:4754. doi: 10.3390/molecules27154754

Tazunoki, Y., Tokuda, M., Sakuma, A., Nishimuta, K., Oba, Y., Kadokami, K., et al. (2022). Comprehensive analyses of agrochemicals affecting aquatic ecosystems: a case study of Odonata communities and macrophytes in Saga Plain, northern Kyushu. *Japan. Environ. Pollut.* 292:118334. doi: 10.1016/j.envpol.2021.118334

Tripathi, S., Srivastava, P., Devi, R. S., and Bhadouria, R. (2020). "Influence of synthetic fertilizers and pesticides on soil health and soil microbiology" in *Agrochemicals detection, treatment and remediation*, ed. M. N. V. Prasad (Butterworth-Heinemann), 25–54.

Ul Haq, I., and Ijaz, S. (2019). "Use of metallic nanoparticles and nanoformulations as nanofungicides for sustainable disease management in plants" in *Nanobiotechnology in bioformulations*, eds. R. Prasad, V. Kumar, M. Kumar, & D. Choudhary (Springer, Cham), 289–316.

Upadhayay, V. K., Khan, A., Singh, J., and Singh, A. V. (2019). "Splendid role of nanoparticles as antimicrobial agents in wastewater treatment" in *Microorganisms for sustainability*, ed. R. Bharagava (Springer, Singapore), 119–136.

Upadhayay, V. K., Maithani, D., Dasila, H., Taj, G., and Singh, A. V. (2023). "Microbial services for mitigation of biotic and abiotic stresses in plants" in *Advanced microbial techniques in agriculture, environment, and health management*, eds. S. C. Pandey, V. Pande, D. Sati, & M. Samant (Academic Press), 67–81.

Upadhayay, V. K., Singh, A. V., and Khan, A. (2022a). Cross talk between zinc-solubilizing bacteria and plants: a short tale of bacterial-assisted zinc biofortification. *Front. Soil Sci.* 1:788170. doi: 10.3389/fsoil.2021.788170

Upadhayay, V. K., Singh, A. V., Khan, A., and Pareek, N. (2021). Influence of zinc solubilizing bacterial co-inoculation with zinc oxide supplement on rice plant growth and Zn uptake. *Pharm. Innov.* 10, 113–116.

Upadhayay, V. K., Singh, A. V., Khan, A., and Sharma, A. (2022c). Contemplating the role of zinc-solubilizing bacteria in crop biofortification: an approach for sustainable bioeconomy. *Front. Agron.* 4:903321. doi: 10.3389/fagro.2022.903321

Upadhayay, V. K., Singh, A. V., Khan, A., Singh, J., Pareek, N., and Raghav, A. (2022b). FE-SEM/EDX based zinc mobilization analysis of Burkholderia cepacia and Pantoea rodasii and their functional annotation in crop productivity, soil quality, and zinc biofortification of paddy. *Front. Microbiol.* 13:852192. doi: 10.3389/fmicb.2022.852192

Upadhayay, V. K., Singh, A. V., and Pareek, N. (2018). An insight in decoding the multifarious and splendid role of microorganisms in crop biofortification. *Int. J. Curr. Microbiol. App. Sci.* 7, 2407–2418. doi: 10.20546/ijcmas.2018.706.286

Vaghela, N., and Gohel, S. (2022). Medicinal plant-associated rhizobacteria enhance the production of pharmaceutically important bioactive compounds under abiotic stress conditions. *J. Basic Microbiol.* 63, 308–325. doi: 10.1002/jobm.202200361

Van Nguyen, D., Nguyen, H. M., Le, N. T., Nguyen, K. H., Nguyen, H. T., Le, H. M., et al. (2022). Copper nanoparticle application enhances plant growth and grain yield in maize under drought stress conditions. *J. Plant Growth Regul.* 41, 364–375. doi: 10.1007/s00344-021-10301-w

Vedamurthy, A. B., Bhattacharya, S., Das, A., and Shruthi, S. D. (2021). "Exploring nanomaterials with rhizobacteria in current agricultural scenario" in *Advances in nano-fertilizers and nano-pesticides in agriculture*, eds. S. Jogaiah, H. B. Singh, L. F. Fraceto, & R. de Lima (Woodhead Publishing), 487–503.

Vejan, P., Khadiran, T., Abdullah, R., Ismail, S., and Dadrasnia, A. (2019). Encapsulation of plant growth promoting rhizobacteria—prospects and potential in agricultural sector: a review. *J. Plant Nutr.* 42, 2600–2623. doi: 10.1080/01904167.2019.1659330

Vignardi, C. P., Muller, E. B., Tran, K., Couture, J. L., Means, J. C., Murray, J. L. S., et al. (2020). Conventional and nano-copper pesticides are equally toxic to the estuarine amphipod *Leptocheirus plumulosus*. *Aquat. Toxicol.* 224:105481. doi: 10.1016/j.aquatox.2020.105481

Walia, A., Putatunda, C., Bhatia, R. K., Solanki, P., and Pathania, S. (2021). "Techniques for improving microbial inoculants as a tool for sustainable development" in *Microbiological activity for soil and plant health management*, eds. R. Soni, D. C. Suyal, P. Bhargava, and R. Goel (Springer, Singapore), 599–627.

Xin, X., Judy, J. D., Sumerlin, B. B., and He, Z. (2020). Nano-enabled agriculture: from nanoparticles to smart nanodelivery systems. *Environ. Chem.* 17:413. doi: 10.1071/en19254

Xiong, W., Reynolds, M., and Xu, Y. (2022). Climate change challenges plant breeding. *Curr. Opin. Plant Biol.* 70:102308. doi: 10.1016/j.pbi.2022.102308

Xu, C., Peng, C., Sun, L., Zhang, S., Huang, H., Chen, Y., et al. (2015). Distinctive effects of TiO_2 and CuO nanoparticles on soil microbes and their community structures in flooded paddy soil. *Soil Biol. Biochem.* 86, 24–33. doi: 10.1016/j.soilbio.2015.03.011

Yadav, A. S., and Srivastava, D. S. (2015). Application of nano-technology in weed management: a review. *Res. Rev. J Crop Sci. Technol.* 4, 21–23.

Yang, R. X., McCandler, C. A., Andriuc, O., Siron, M., Woods-Robinson, R., Horton, M. K., et al. (2022). Big data in a nano world: a review on computational, data-driven design of nanomaterials structures, properties, and synthesis. *ACS Nano*, 16, 19873–19871. doi: 10.1021/acsnano.2c08411

Yang, K., Wang, Q., Wang, Y., Li, S., Gu, Y., Gao, N., et al. (2021). Poly (γ-glutamic acid) nanocoating to enhance the viability of *Pseudomonas stutzeri* NRCB010 through cell surface engineering. *ACS Appl. Mater. Interfaces* 13, 39957–39966. doi: 10.1021/acsami.1c12538

Yasmin, H., Mazher, J., Azmat, A., Nosheen, A., Naz, R., Hassan, M. N., et al. (2021). Combined application of zinc oxide nanoparticles and biofertilizer to induce salt resistance in safflower by regulating ion homeostasis and antioxidant defence responses. *Ecotoxicol. Environ. Saf.* 218:112262. doi: 10.1016/j.ecoenv.2021.112262

Yin, S., Duvigneau, J., and Vancso, G. J. (2021). Fluorescent polyethylene by in situ facile synthesis of carbon quantum dots facilitated by silica nanoparticle agglomerates. *ACS Appl. Polym. Mater.* 3, 5517–5526. doi: 10.1021/acsapm.1c00821

Yin, J., Zhang, Z., Guo, Y., Chen, Y., Xu, Y., Chen, W., et al. (2022). Precision probiotics in agroecosystems: multiple strategies of native soil microbiotas for conquering the competitor Ralstonia solanacearum. *mSystems* 7:e0115921. doi: 10.1128/msystems.01159-21

Yue, L., Feng, Y., Ma, C., Wang, C., Chen, F., Cao, X., et al. (2022). Molecular mechanisms of early flowering in tomatoes induced by manganese ferrite ($MnFe_2O_4$) nanomaterials. *ACS Nano* 16, 5636–5646. doi: 10.1021/acsnano.1c10602

Zaheer, M. S., Raza, M. A. S., Saleem, M. F., Khan, I. H., Ahmad, S., Iqbal, R., et al. (2019). Investigating the effect of *Azospirillum brasilense* and *Rhizobium pisi* on agronomic traits of wheat (*Triticum aestivum* L.). *Arch. Acker Pflanzenbau Bodenkd.* 65, 1554–1564. doi: 10.1080/03650340.2019.1566954

Zain, M., Yasmeen, H., Yadav, S. S., Amir, S., Bilal, M., Shahid, A., et al. (2022). "Applications of nanotechnology in biological systems and medicine" in *Nanotechnology for hematology, blood transfusion, and artificial blood*, eds. A. Denizli, T. A. Nguyen, M. Rajan, M. F. Alam, & K. Rahman (Elsevier), 215–235.

Zarei, T. (2022). Balancing water deficit stress with plant growth-promoting rhizobacteria: a case study in maize. *Rhizosphere* 24:100621. doi: 10.1016/j.rhisph.2022.100621

Zhang, Y., Qian, C., Shi, R., Li, S., Shi, F., Hu, J., et al. (2022). In-situ synthesis of metal-organic framework embedded in ordered mesoporous silica functionalized with carboxyl groups for 4-nitrophenol to 4-aminophenol. *Appl. Surf. Sci.* 597:153720. doi: 10.1016/j.apsusc.2022.153720

Zhao, S., Su, X., Wang, Y., Yang, X., Bi, M., He, Q., et al. (2020). Copper oxide nanoparticles inhibited denitrifying enzymes and electron transport system activities to influence soil denitrification and N_2O emission. *Chemosphere* 245:125394. doi: 10.1016/j.chemosphere.2019.125394

Zilberman, D., Gordon, B., Hochman, G., and Wesseler, J. (2018). Economics of sustainable development and the bioeconomy. *Appl. Econ. Perspect. Policy* 40, 22–37. doi: 10.1093/aepp/ppx051

Zu, M., Ma, Y., Cannup, B., Xie, D., Jung, Y., Zhang, J., et al. (2021). Oral delivery of natural active small molecules by polymeric nanoparticles for the treatment of inflammatory bowel diseases. *Adv. Drug Deliv. Rev.* 176:113887. doi: 10.1016/j.addr.2021.113887

frontiers | Frontiers in Plant Science

TYPE Original Research
PUBLISHED 15 May 2023
DOI 10.3389/fpls.2023.1137002

OPEN ACCESS

EDITED BY
Alvaro Sanz-Saez,
Auburn University, United States

REVIEWED BY
Mohamed Sheteiwy,
Mansoura University, Egypt
Sanjay Singh Rathore,
(ICAR), India

*CORRESPONDENCE
Dhruv Mishra
shivads594@gmail.com
Manoj Kumar Chitara
manojchitara01@gmail.com
Preeti Chaturvedi
an_priti@yahoo.co.in

RECEIVED 09 January 2023
ACCEPTED 12 April 2023
PUBLISHED 15 May 2023

CITATION
Mishra D, Chitara MK, Upadhayay VK, Singh JP and Chaturvedi P (2023) Plant growth promoting potential of urea doped calcium phosphate nanoparticles in finger millet (*Eleusine coracana* (L.) Gaertn.) under drought stress.
Front. Plant Sci. 14:1137002.
doi: 10.3389/fpls.2023.1137002

Plant growth promoting potential of urea doped calcium phosphate nanoparticles in finger millet (*Eleusine coracana* (L.) Gaertn.) under drought stress

Dhruv Mishra[1]*, Manoj Kumar Chitara[2]*, Viabhav Kumar Upadhayay[3], Jagat Pal Singh[4] and Preeti Chaturvedi[1]*

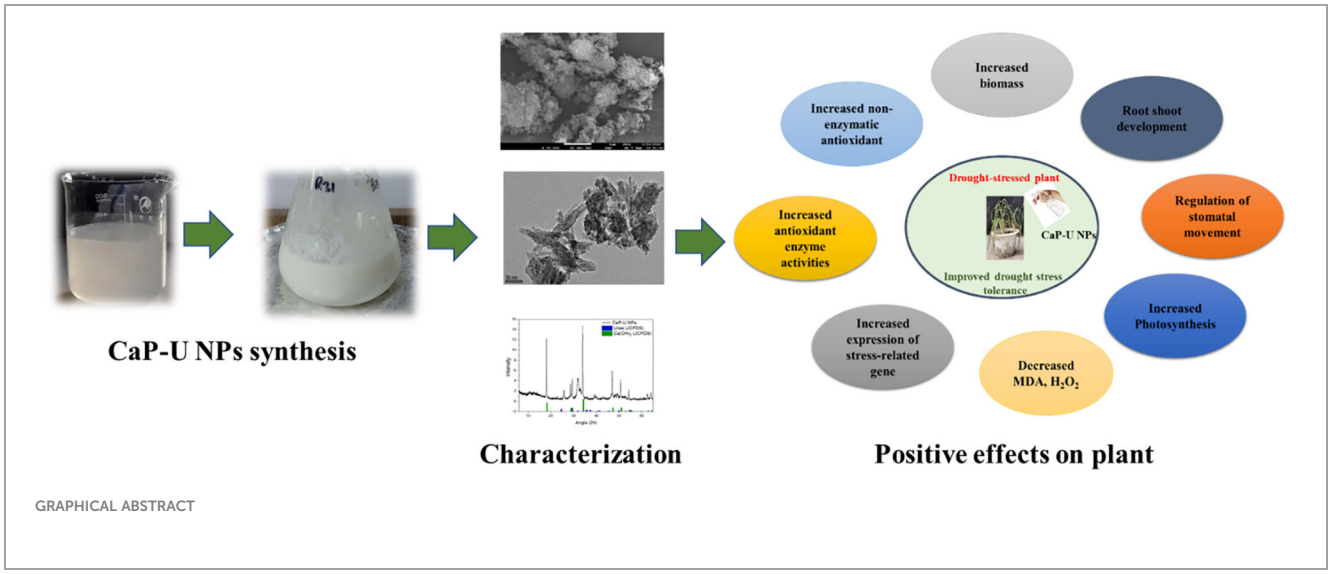
[1]Department of Biological Sciences, College of Basic Sciences and Humanities, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand (U.K.), India, [2]Department of Plant Pathology, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India, [3]Department of Microbiology, College of Basic Sciences & Humanities, Dr. Rajendra Prasad Central Agricultural University, Samastipur, Bihar, India, [4]Department of Physics, College of Basic Sciences and Humanities, G. B. Pant University of Agriculture and Technology, Pantnagar, India

Drought is a leading threat that impinges on plant growth and productivity. Nanotechnology is considered an adequate tool for resolving various environmental issues by offering avant-garde and pragmatic solutions. Using nutrients in the nano-scale including CaP-U NPs is a novel fertilization strategy for crops. The present study was conducted to develop and utilize environment-friendly urea nanoparticles (NPs) based nano-fertilizers as a crop nutrient. The high solubility of urea molecules was controlled by integrating them with a matrix of calcium phosphate nanoparticles (CaP NPs). CaP NPs contain high phosphorous and outstanding biocompatibility. Scanning electron microscopy (FE-SEM), transmission electron microscopy (TEM) and X-ray diffraction analysis (XRD) were used to characterize the fabricated NPs. FE-SEM determined no areas of phase separation in urea and calcium phosphate, indicating the successful formation of an encapsulated nanocomposite between the two nano matrices. TEM examination confirmed a fiber-like structure of CaP-U NPs with 15 to 50 nm diameter and 100 to 200 nm length. The synthesized CaP-U NPs and bulk urea (0.0, 0.1% and 0.5%) were applied by foliar sprays at an interval of 15 days on pre-sowed VL-379 variety of finger millet (*Eleusine coracana* (L.) Gaertn.), under irrigated and drought conditions. The application of the CaP-U NPs significantly enhanced different plant growth attributes such as shoot length (29.4 & 41%), root length (46.4 & 51%), shoot fresh (33.6 & 55.8%) and dry weight (63 & 59.1%), and root fresh (57 & 61%) and dry weight (78 & 80.7%), improved pigment system (chlorophyll) and activated plant defense enzymes such as proline (35.4%), superoxide dismutase (47.7%), guaiacol peroxidase (30.2%), ascorbate peroxidase (70%) under both irrigated and drought conditions. Superimposition of five treatment combinations on drought suggested that CaP-U NPs at 0.5 followed by 0.1% provided the highest growth indices and defense-related enzymes, which were significantly different. Overall, our findings suggested that synthesized CaP-U NPs treatment of finger millet seeds improved plant growth and enzymatic regulation, particularly more in drought conditions providing insight

into the strategy for not only finger millet but probably for other commercial cereals crops which suffer from fluctuating environmental conditions.

KEYWORDS

urea, finger millet, drought, plant growth promotion, calcium phosphate (Ca-P), nanoparticles



GRAPHICAL ABSTRACT

1 Introduction

Drought is one of the important abiotic stresses, where plants constantly do not receive sufficient rainfall required to complete their metabolic activities (Zhang et al., 2022). The unavailability of water reduces 9-10% of the total crop productivity worldwide (Lesk et al., 2016). Monsoon rainfall has decreased by roughly 6% from 1951 to 2015 as per the climate change assessment report by the Ministry of Earth and Science (Krishnan et al., 2020). Low rainfall makes the dry land areas more vulnerable to runoff losses leading to drought proneness. A study from South Africa during 2017-2021 revealed that 25000 agricultural sector-based workers lost their jobs due to the adverse impact of drought on the economy (Orimoloye et al., 2022).

Drought impacts seed germination, the number of tillers, spikes, grain per plant, grain weight, plant stand and grain yield (Oumarou Abdoulaye et al., 2019; Ning et al., 2020; Gui et al., 2021a; Gui et al., 2021b; Sheteiwy et al., 2021a; Sheteiwy et al., 2021b; Ben-Jabeur et al., 2022; Sial et al., 2022; Sheteiwy et al., 2022). The drought also impairs the nutrient absorption ability of plants from the upper soil horizon (Abdelaal et al., 2021). It also modulates the physiological processes of the plants such as photosynthesis, respiration, leaf water potential, mineral absorption, circadian rhythm and hormone regulation etc. (Seleiman et al., 2021; Wang et al., 2021; Ghani et al., 2022; Hemati et al., 2022). Drought stress increases the production of reactive oxygen species (ROS) such as superoxide (O_2^-), singlet oxygen (O_2), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-) to levels that are frequently greater than the plant's scavenging capability (Chitara et al., 2017; Kumari et al., 2021; Sachdev et al., 2021). ROS damages cells and cellular components, impair physiological and biochemical processes and can even cause plant death (Xie et al., 2019). Owing to ROS-induced oxidative stress increased electrolyte leakage followed by lipid peroxidation and plasmalemma damage. Lipid peroxidation causes the breakdown of polyunsaturated lipids in ketones and malondialdehyde (MDA) (Ju et al., 2018). Excessive ROS generation causes site-specific amino acid modification, peptide chain fragmentation, changed electric charge and enhanced protein proteolysis. ROS causes deoxyribose oxidation, strand breaks, nucleotide loss, a variety of changes to the bases of the nucleotides, and DNA-protein crosslinks (Sharma et al., 2019; Ahmed and Lingner, 2020).

Finger millet (*Eleusine coracana* (L.) Gaertn) is a millet crop widely produced in tropical and subtropical areas of Asia and Africa. It contains a very high amount of calcium (344 mg/100 g). The millet seed coat is an edible component of the kernel and has a high concentration of dietary fiber, phytochemicals such as polyphenols (0.2–3.0%) and high gallic acid (Hadimani and Malleshi, 1993; Chethan and Malleshi, 2007). Finger millet is important for pregnant and breastfeeding women and children's nutrition. It plays a significant role in the economies of marginal farmers. Furthermore, finger millet straw is an excellent animal

feed, containing up to 60% digestible elements. The seed coat also has anti-cancer and anti-diabetic properties owing to its high polyphenol content.

Nutrients play a significant role in plant growth and development. The scarcity of nutrients in the plants caused an irreversible change. Presently used fertilizers especially nitrogenous fertilizers in crops are less efficient due to their losses in the form of volatilization, surface runoff, leaching and gaseous form. The scarcity of nutrients are more severe when plants are suffering from water deficiency because most of the mineral uptake from the soil to plant cell take the same pathway as a water flow. The application of nanomaterials to crops would revolutionize farming practices by reducing the adverse environmental effects of modern agricultural activities and improving nutrient use efficiency (NUE), grain quality and crop yield (Liu and Lal, 2015; Mahil and Kumar, 2019). Nanotechnology can provide a workable solution to control the difficulties associated with increasing N-based fertilizer usage efficiency (Zulfiqar et al., 2019). It is anticipated to cause a paradigm shift in NUE, resulting in increased agricultural productivity (Ladha et al., 2005). In this context, sequential research was undertaken by synthesizing CaP-U NPs. In comparison to bulk counterparts, CaP-U NPs exhibit greater reactivity and surface area. Considering the above facts, the current study was conducted to reveal the Plant growth promoting potential of urea-doped calcium phosphate nanoparticles (CaP-U NPs) in finger millet (*Eleusine coracana* (L.) Gaertn.) under irrigated and drought stress conditions: an emerging fertilization technique under climate change scenario.

Nanofertilizer such as U-ACP nanoparticles were used as a nitrogen source for *Vitis vinifera* L. (Gaiotti et al., 2021). N-doped ACP NPs with half the absolute N-content than in conventional urea treatment promote the formation of an equivalent amount of root and shoot biomass, without nitrogen depletion (Carmona et al., 2021). The high nitrogen use efficiency (up to 69%) and a cost-effective preparation method support the sustainable real usage of N-doped ACP as a nano fertilizer. In a field experiment, the use of calcium phosphate NPs doped with urea (U-ACP) for the fertilization of *Triticum durum* plants, indicated that yields and quality of the crops treated with the nanoparticles at reduced nitrogen dosages (by 40%) were unaltered in comparison to positive control plants, which were given the minimum N dosages to obtain the highest values of yield and quality in fields. In light of these reports here bring to light the possibility of using engineered nanoparticles to deliver nitrogen to plants more safely and efficiently. However, further research is still needed to secure the most suitable application protocols for real agricultural practices (Ramírez-Rodríguez et al., 2020b). Nano-Urea applied to *Pennisetum glaucum* L. at 30 and 45 DAS, significantly increased plant height, dry matter accumulation, chlorophyll content and nitrogen content (Sharma et al., 2022).

Indeed, drought continues to ravage different regions of the globe, with devastating consequences on soil nutrient bioavailability and crop productivity. Nano NPK improved photosynthetic rate, stomatal conductance, CO_2 concentration, water use efficiency and relative water content. The chemical composition (plant pigments, total carbohydrates, total phenolic, tannin, total flavonoids, oil constituents, macro and micro-elements) with indigenous hormones (gibberellic acid GA3 and abscisic acid ABA) and antioxidant enzymes (peroxidase and superoxide dismutase) were also positively affected (Mahmoud and Swaefy, 2020). Furthermore, Ca2+ improved maize photosynthesis (45%), stomatal conductance (47%), and accumulation of total soluble sugars (20%) along with the decline in H_2O_2 content (23%) (Naeem et al., 2018). hydroxyapatite nanoparticles foliar application in *Adansonia digitata* provide a significant increase in plant growth characteristics (Soliman et al., 2016).

Mechanistically, Research has shown that increased nitrogen (N) improves crop drought tolerance and significant impact on photosynthesis. The nitrogen in plants influenced the water conductivity increasing the accumulation of osmoprotectants and antioxidants (Chang et al., 2016; Zhong et al., 2017; Song et al., 2019). But the majority of supplied N is lost through leaching, volatilization and denitrification leading to a reduction in crop N usage efficiency (Hussain et al., 2019; Pan et al., 2021). The objectives of the present study are to: i) synthesize and characterize urea-doped calcium phosphate nanoparticles (CaP-U NPs); ii) determine whether CaP-U NPs can mitigate the impact of drought stress on the performance of finger millet; and iii) evaluate whether using a lower dose of CaP-U NPs. Collectively, all effects were compared with those of bulk urea to determine the significance of nanoscale size.

2 Material and methods

2.1 Preparation and characterization of CaP-U NPs

To synthesize CaP-U NPs, urea (70%) was dissolved in a beaker containing distilled water (DW) and kept on a magnetic stirrer until proper mixing. Subsequently, calcium hydroxide [$Ca(OH)_2$] was added to the beaker. Afterward, orthophosphoric acid (H_3PO_4) was added drop by drop into the beaker containing suspension. Field Emission Scanning Electron Microscope (JEOL FE-SEM) was used to characterize the external morphology of the nanoparticles. The shape and size of the NPs were determined using Transmission Electron Microscopy (TALOS HR-TEM) facility at AIIMS, Delhi. Furthermore, the size and shape of NPs were determined using X-Ray Diffractometer (Bruker). Sonics VCX 750 ultrasonicator (750-watt power and 20kHz frequency) was used to prepare a homogenous solution of CaP-U NPs.

2.2 Pot experimental setup

Seeds of finger millet (*var.*VL-379) were procured from Vivekanand Parvartiya Krishi Anusandhan Sansthan (VPKAS), Almora, Uttarakhand, India. For the experiment, finger millet seeds were surface-disinfected by immersion, first in 3 per cent sodium hypochlorite and then in 70 per cent ethanol for 3 and 1 min, respectively. The seeds were then washed thoroughly three times with sterile distilled water. For germination, the seeds were kept on

sterilized Petri dishes containing one sheet of sterilized paper moistened with sterilized distilled water and placed in an incubator at 30°C for 2 days. All steps were carried out aseptically. Before seed sowing, the pots were filled with sandy loam soil: FYM (3:1). After proper seedling establishment in the pots, 6 seedlings were maintained in each pot till the experiment. CaP-U NPs were tested in the glasshouse to see their ability to increase finger millet growth under irrigated and drought conditions. After seed sowing, in both conditions, 3 treatments were divided into 3 sets; in the first set, pots were untreated, in the second set, pots were treated with foliar spray of bulk urea (0.1 and 0.5%) and in the third set, pots were treated with foliar spray of CaP-U NPs (0.1 and 0.5%) at 15 and 30 days after sowing (DAS). Each treatment was maintained in three replications.

2.3 Determination of plant parameters

2.3.1 Plants' vegetative development parameters

The observation concerning the length of shoot and root, fresh weight of shoot root, dry weight of shoot-root ratio and leaf ratio was recorded at 45 days after sowing. For dry weight, plant samples were kept in an oven at 75°C until constant weight. Shoot and root length was measured from the collar region to the tip of the flag leaf and from the coleoptile region to the tip of the root using a meter scale and expressed in centimeters (cmLeaf area was calculated by measuring the length and width of the leaves per replication. It is multiplied by the total number of small and medium leaves separately. The total leaf area per plant was calculated by the formula given below:

Total leaf area per plant (cm^2) = Leaf area of small leaf (cm^2) + Leaf area of medium leaf (cm^2).

2.3.2 Physiological parameters

2.3.2.1 Estimation of chlorophyll content

Chlorophyll a (Chl a) and chlorophyll b (Chl b) content was estimated by Arnon (1949) method. Fresh leaf of the plant (0.1 g) was collected and placed in a test tube, then added to 10 ml of 80% acetone, sealed with parafilm to prevent evaporation, and kept in the dark for 24 hours. The amounts of Chl a and Chl b were determined by a UV-Visible spectrophotometer at wavelengths 663 nm and 645 nm. The concentrations of chlorophyll a and chlorophyll b (mg g^{-1} FW) in leaf tissues were determined using the following equations:

$$\text{Chl a} = \frac{(12.7XA663) - (2.69XA645)XV}{WX1000}$$

$$\text{Chl b} = \frac{(22.9XA645) - (4.68XA663)XV}{WX1000}$$

A = Absorbance at specific wavelength, V = Final volume of chlorophyll extract in 80 percent acetone, W = Fresh weight of tissue extracted (g).

2.3.2.2 Estimation of proline content

Proline content was estimated by Bates et al. (1973) method. First, the plant sample's fresh leaf (0.2 g) was homogenized in 2.0 ml of 3 percent sulphosalicylic acid (w/v) and centrifuged to remove the residue. After this, 2 ml of leaf extract was treated with 2 ml glacial acetic acid and 2 ml acid ninhydrin for 60 minutes at 100°C. Finally, an ice bath terminated the reaction, and the proline was extracted with 4 ml of toluene. Sample absorbance was measured at 520 nm, and the quantity of proline was calculated using a standard curve. The results were represented in µg free proline per Gram fresh weight (FW).

2.3.2.3 Measurement of malondialdehyde concentration

The MDA content was estimated using Heath and Packer (1968) method. First, the fresh leaf sample (0.3 g) was homogenized in 4 ml of tricholoroacetic acid (0.1 percent). The homogenized sample was centrifuged at 10000 rpm for 15 min. at 4° C, the supernatant was used to estimate MDA. Next, the 0.3 ml of extract was mixed with 1.2 ml of 0.5percent (w/v) 2-thiobarbiturie acid (TBA) prepared in trichloroacetic acid (TAC) (20 percent). The mixture was incubated at 95°C for 30 min. The reaction was terminated by putting the test tubes in an ice bath **quickly** and then cool samples were centrifuged at 10000 rpm for 10 min. The absorbance of the clear supernatant was recorded at 532 nm and 600 nm. Absorbance at 600 nm is subtracted from the absorbance at 532 nm for non-specific absorbance. The MDA concentration was calculated by an extinction coefficient of 155 mM^{-1} cm^{-1}.

2.3.2.4 Estimation of hydrogen peroxide

The H_2O_2 content was determined by Alexieva et al. (2001) method. Hydrogen peroxide was detected spectrophotometrically after interaction with potassium iodide (KI). Leaf samples (0.1g) were homogenized in 2.0 ml of 0.1 percent trichloroacetic acid (TCA). The reaction mixture included 0.5 ml of supernatant, 0.5 ml of potassium phosphate buffer (0.1 M), and 2 ml of KI solution (1 M). The reaction was carried out in complete darkness for 1 hour and the absorbance was measured at 390 nm. The amount of H_2O_2 was determined using a standard curve generated with various dilutions of a working standard of 100 µM of H_2O_2.

2.3.2.5 Estimation of total phenol

The total phenol content was estimated by Zieslin and Ben Zaken (1993) method. Fresh leaf sample (0.2 g) were homogenized in 4 ml of 80 percent methanol, heated at 80°C for 20 min, and centrifugated at 10,000 rpm. Next, 1 mL of methanolic extract containing phenol was mixed with 5 mL of distilled water and 250 µl of Folin-Ciocalteau reagent (1 N) in a 5 mL vial. Finally, 1 mL saturated sodium carbonate (20 percent) was added immediately, and the mixture was incubated at 25°C for 30 min. A Genesys 10S UV–Vis Spectrophotometer was used to measure the absorbance of the generated blue color at 725 nm. Phenolic content is represented as µg GAE g^{-1} fresh weight.

2.4 Estimation of antioxidant enzymes of plants

2.4.1 Preparation of enzyme extracts

For determination of antioxidant enzyme activities, 0.5 g fresh leaf sample was homogenized with a pestle in an ice-cold mortar in

5 ml cold buffer containing: 50 mM potassium phosphate buffer (pH 7.0), 2 mM ethylene diamine tetra acetic acid (EDTA) and 1% polyvinyl-pyrrolidone (PVP). The whole extraction procedure was carried out at 4°C. The homogenate was centrifuged at 10,000 rpm for 30 min at 4°C and the supernatant collected was used to assay enzyme activity.

2.4.2 Estimation of superoxide dismutase activity

SOD activity was assay based on the ability of superoxide dismutase to inhibit the reduction of nitro-blue tetrazolium (NBT) (Beauchamp and Fridovich, 1971). The reaction mixture (3 ml) for the SOD assay contained 50 mM Na-phosphate buffer (pH 7.8), 13 mM L-methionine, 75 uM NBT, 10 µM EDTA, 2.0 µM riboflavin, and 0.1 ml enzyme extract. The reaction mixture was incubated in test tubes for 10 minutes at 35°C in 4000 lux. After illumination, the tubes were covered with black cloth, and absorbance was measured at 560 nm. The activity is represented as a unit per mg protein (unit mg^{-1} protein).

2.4.3 Estimation of guaiacol peroxidase activity

Peroxidase activity was determined by a pyrogallol method developed by Kar and Mishra (1975). H_2O_2 oxidized a colorless pyrogallol compound into a colored purpurogallin compound. 100 mM potassium phosphate buffer (pH 7.2), 0.1 mM EDTA, 5 mM guaiacol, 15 mM H_2O_2, and 100 µl enzyme extract were used in the reaction. At 470 nm, an increase in absorbance was recorded every 10 seconds. The amount of enzyme activity is determined by the formation of tetra-guaiacol. The activity is represented as µmol tetra-guaiacol formed per min. per mg protein.

2.4.4 Estimation of ascorbate peroxidase activity

Ascorbate peroxidase (APX) activity was determined by Nakano and Asada (1981) method. The enzyme was extracted in 50 mM phosphate buffer for APX activity. The APX reaction mixture contained 50 mM phosphate buffer, 0.5 mM ascorbic acid, 0.2 mM EDTA, and enzyme extract. The reaction began after the addition of 0.1 mM H_2O_2. Absorbance was measured spectrophotometrically at 290 nm and the reduction in absorbance was recorded for up to 90 seconds after the reaction began. Therefore, the activity is represented as nmol per minute per mg protein.

3 Statistical analysis

Data and results were represented in means, which were statistically examined by SPSS (Statistical package for the social science) software comparing variance (ANOVA) function. Duncan's multiple range test was used to compare the treatment mean values at the $P \leq 0.05$ significant level. Principal component analysis (PCA) and Pearsion correlation were done using Origin and R-square (version 4.1.2) to demonstrate the correlation between the various plant growth parameters and defense enzyme and their relationship with the different treatments.

4 Results

4.1 Synthesis and characterization of CaP-U NPs by FE-SEM, TEM and XRD analysis

In the visual examination of the CaP-U NPs urea solution, the color changed from transparent to white, indicating the formation of CaP-U NPs (Figure 1). The morphology of CaP-U NPs was determined by FE-SEM (magnification 20000 x) (Figure 2A). There are no areas of phase separation in urea and calcium phosphate, indicating the successful formation of an encapsulated nanocomposite between the two nano matrices. HR-TEM further confirmed this formation. TEM analysis depicted rod-like, irregularly shaped smaller particles of CaP-U NPs with diameters in the range from 15 to 50 nm and lengths ranging from 100 to 200 nm (Figure 2B). According to TEM analysis, the rods are covered with urea at the nanoscale. High-resolution images showed the partial porous structure of CaP-NPs, which was then executed to load urea onto it. X-ray diffraction (XRD) patterns of the powder samples were recorded using Cu K_α radiation (= 1.54178 Å). Spectra were recorded in the 2θ range from 10° to 60° with a step size (2θ) of 0.02 and a counting time of 0.5 s. The graph with the sharpest peaks, like the (101) plane, corresponds to the pure hexagonal structure of $Ca(OH)_2$ (JCPDS No. 84-1276), as indicated by the green bar diagram. The graph displays the diffraction peaks of urea, with the maximum intensity peak (111) corresponding to a pure tetragonal structure that matches JCPDS No. 99-101-0067 and is displayed as a blue bar diagram. Further evidence that there isn't any characteristic peak of the crystalline impurity is provided by the crystal phases of the mixture of $Ca(OH)_2$ and urea displayed in the graph (Figure 2C).

4.2 Pot experiment

In the pot experiment, the observation concerning plant growth parameters and biochemical analysis was recorded at 45 days after sowing (DAS) under both irrigated and drought conditions.

4.2.1 Shoot length

In this experiment, at 45 DAS, the maximum shoot length was recorded at 0.5% conc.of CaP-U NPs, with 29.4 and 41% increase

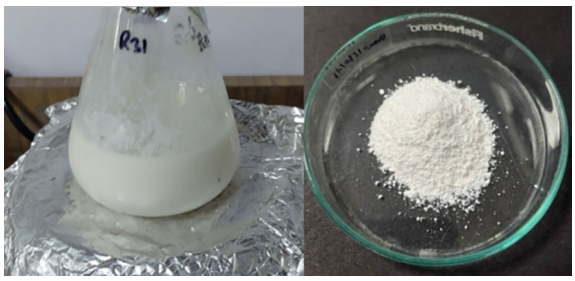


FIGURE 1
Visual examination of generated CaP-U NPs.

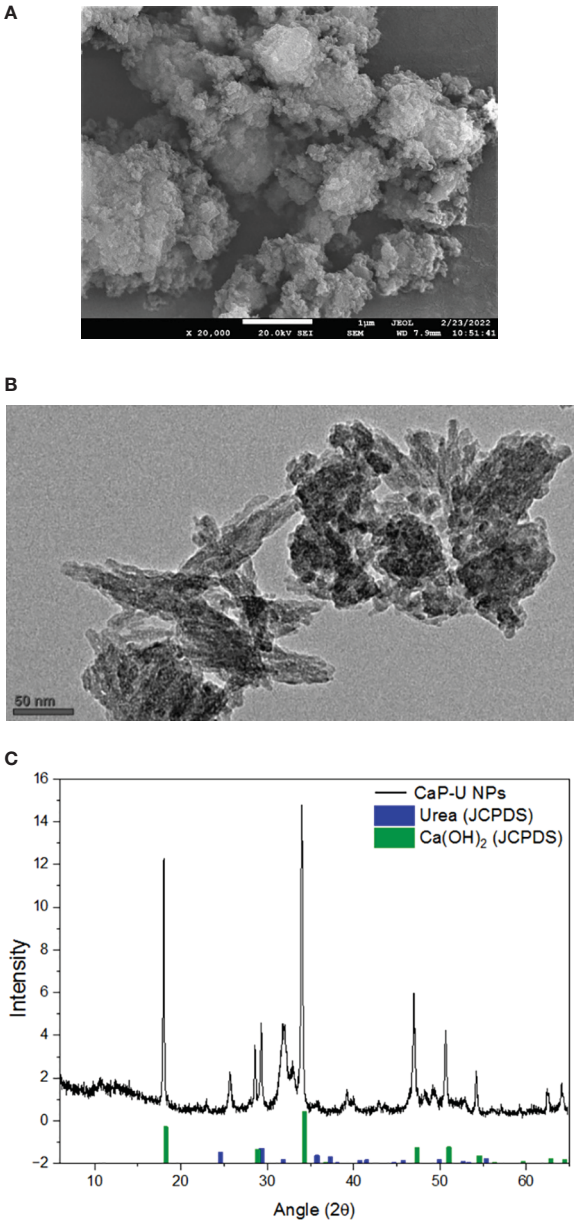


FIGURE 2
(A) CaP-U NPs under FE-SEM microscope **(B)** TEM-image showing CaP-U NPs with irregular morphology (scale bar 50 nm) (Tiny rods with diameters in the range from 15 to 50 nm and lengths ranging from 100 to 200 nm) **(C)** XRD analysis of CaP-U NPs.

followed by 0.1% conc. of CaP-U NPs, with 26.2 and 37.5% increase under irrigated and drought conditions respectively. In contrast, in case of urea, the maximum shoot length was recorded at 0.5% conc., with 11.1 and 18.7% increase followed by urea 0.1% conc., with 7.8 and 15% increase compared to control under irrigated and drought conditions respectively (Figure 3A).

4.2.2 Root length

Water deficiency first affects the roots (Hsiao and Xu, 2000); deep-rooted plants are better adapted to drought conditions (Ho et al., 2005). In this experiment, at 45 DAS, the maximum root length was recorded at 0.5% conc. of, with 46.4 and 51% increase followed by 0.1% conc. of CaP-U NPs treatment, with 41.4 and 47.4% increase. In case of urea, the maximum root length was recorded at 0.5% conc., with 20.7 and 29.3% increase followed by 0.1% conc. urea, with 12.6 and 21% increase compared to control, under irrigated and drought conditions respectively (Figure 3B).

4.2.3 Leaf area

Under drought conditions, the leaf area of the plants was significantly impacted. Prolonged drought stress caused a significant reduction in the leaf area due to decreased cell division and cell expansion (Koch et al., 2019). In this experiment, at 45 DAS, in the case of CaP-U NPs treatment, the maximum leaf area was recorded at 0.5% conc., with 34.1 and 58.6% increase followed by 0.1% conc. of CaP-U NPs, with 27.2 and 54.5% increase under irrigated and drought conditions respectively, compared to control. In the case of urea, the maximum leaf area was recorded at 0.5% conc., with 9.3 and 29.1% increase followed by 0.1% conc.of urea, with 6.4 and 20.2% increase compared to control, under irrigated and drought conditions respectively (Figure 3C).

4.2.4 Shoot fresh weight

Plants with lesser biomass reduction under drought stress are drought-tolerant (Passioura, 2002). In this experiment, at 45 DAS, in the case of foliar spray of CaP-U NPs, the maximum shoot fresh weight was recorded at 0.5% conc., with 33.6 and 55.8% increase followed by 0.1% conc. of CaP-U NPs with 25.3 and 49.7% increase under irrigated and drought conditions respectively. While in the case of urea the maximum shoot fresh weight was recorded at 0.5% conc., with 6 and 25.3% increase followed by 0.1% conc. of urea, with 3 and 17.3% increase compared to control, under irrigated and drought conditions respectively (Figure 4A).

4.2.5 Shoot dry weight

Dry weight loss in drought conditions has been more associated with shoot than root (Mohammadian et al., 2005). In this experiment, at 45 DAS, in CaP-U NPs treatment, the maximum shoot dry weight was recorded at 0.5% conc., with 63 and 59.1%i increase followed by 0.1% conc. of CaP-U NPs, with 58 and 51.8%i increase; while in the case of urea, the maximum shoot dry weight was recorded at 0.5% conc., with 32.6 and 28.8% increase followed by treatment with 0.1% conc. urea, with 23 and 23.3% increase compared to control under irrigated and drought conditions respectively (Figure 4C).

4.2.6 Root fresh weight

Drought stress has been reported to reduce roots' fresh and dry weight (Mohammadkhani and Heidari, 2008). In this experiment, at 45 DAS, in case of CaP-U NPs treatment, the maximum root fresh weight was recorded at 0.5% conc., with 57 and 61% increase followed by 0.1% conc. of CaP-U NPs, with 52 and 54.1% increase; while in urea treatment, the maximum root fresh weight was recorded at 0.5% conc., with 19.6 and 24.6% increase followed by 0.1% conc. of urea, with 16.9 and 18.2% increase compared to control, under irrigated and drought conditions respectively (Figure 4B).

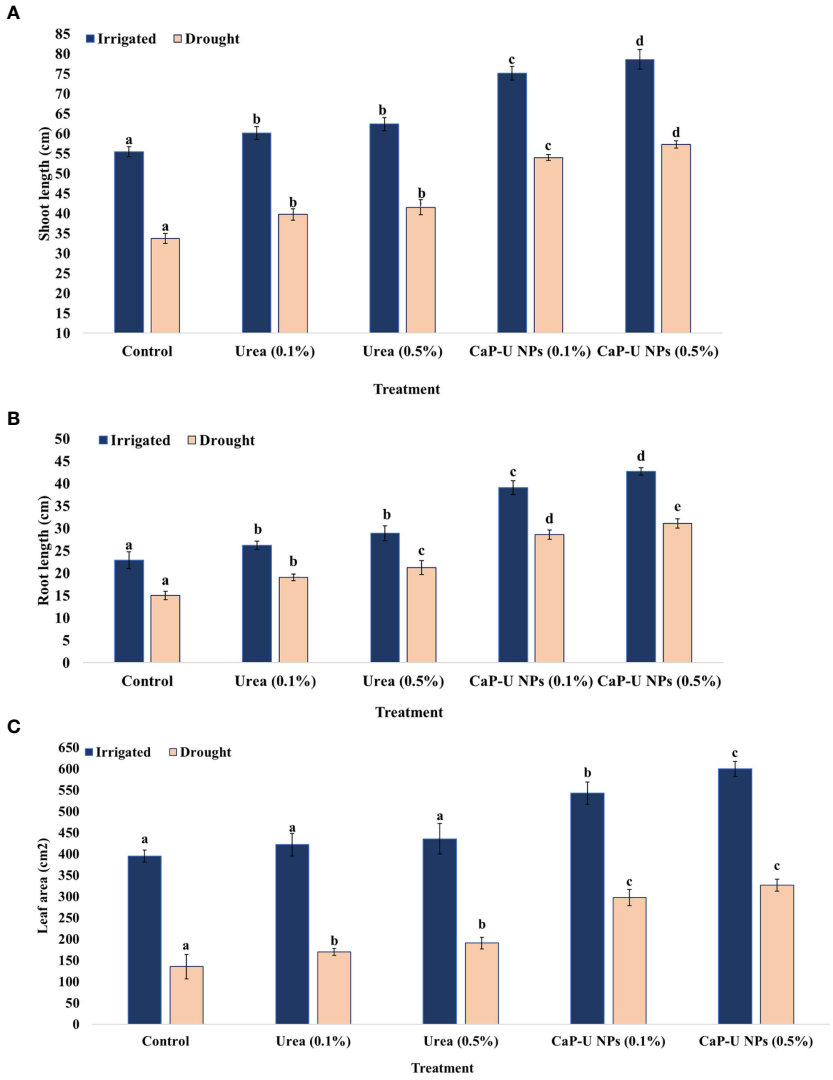


FIGURE 3
Effect of different concentrations of CaP-U NPs on **(A)** shoot length, **(B)** root length, and **(C)** leaf area of *Eleusine coracana* under irrigated and drought conditions. Results are indicated as means of three replications and vertical bars express the standard deviation (SD) of the means. Different letters denote significant differences among treatment outcomes taken at the same time interval according to Duncan's multiple range test at P≤ 0.05.

4.2.7 Root dry weight

In the case of CaP-U NPs, at 45 DAS, the maximum root dry weight was recorded at 0.5% conc., with 78 and 80.7% increase followed by 0.1% conc. of CaP-U NPs, with 73 and 74.6% increase; while in the case of urea, the maximum root dry weight was recorded at 0.5% conc. with 27 and 37.5% increase followed by 0.1% conc. of urea, with 22 and 25% increase compared to control, under irrigated and drought conditions respectively (Figure 4D).

4.2.8 Chlorophyll content

Under drought conditions, producing excessive reactive oxygen species might cause a decreased chlorophyll content. Therefore, retaining green leaves under drought conditions is considered an important parameter for drought tolerance (Deblonde and Ledent, 2001).

At 45 DAS, the maximum Chl a was recorded at 0.5% conc. of CaP-U NPs, with 56.4 and 62.3% increase followed by 0.1% conc of CaP-U NPs, with 48.6 and 58% increase. In contrast, with application of urea, the maximum Chl a was recorded at 0.5% conc., with 15.5 and 21.9% increase followed by 0.1% conc. urea, with a 9.4 and 15.1% increase compared to control, under irrigated and drought conditions respectively. Similarly, maximum Chl b was recorded at 0.5% conc. of CaP-U NPs, with 55.6 and 79.4% increase followed by 0.1% conc. resulting in a 49.2 and 72.9% increase. In the case of urea, the maximum Chl b was recorded at 0.5% conc., with 19.3 and 31.6% increase followed by treatment with 0.1% conc. of urea resulting in a 15.2 and 23.5% increase compared to control, under irrigated and drought conditions, respectively (Figures 5A, B).

4.2.9 Total proline content

During drought stress, plants accumulate more proline than in normal (no drought) conditions (Shakeel et al., 2011). In drought stress, a high level of leaf proline plays a crucial role in maintaining the osmotic potential of the tissues, which prevents severe dehydration. At

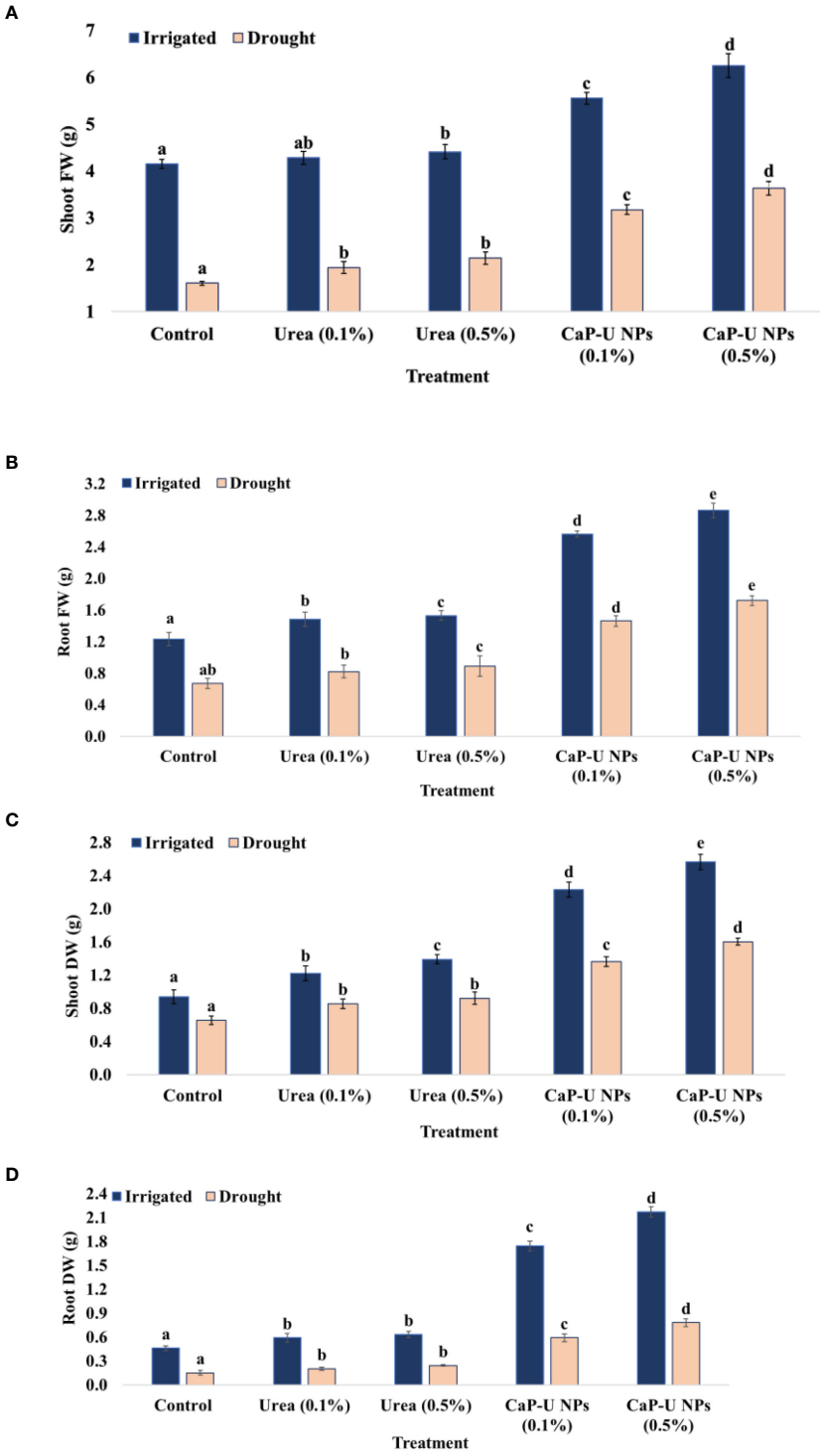


FIGURE 4
Effect of different concentrations of CaP-U NPs on **(A)** shoot fresh weight, **(B)** root fresh weight, **(C)** shoot dry weight and **(D)** root dry weight of *Eleusine coracana* under irrigated and drought conditions. Results are indicated as means of three replications and vertical bars express the standard deviation (SD) of the means. Different letters denote significant differences among treatment outcomes taken at the same time interval according to Duncan's multiple range test at $P \leq 0.05$.

45 DAS, in the case of CaP-U NPs, the maximum total proline content was recorded at 0.5% conc., with a 35.4% increase followed by 0.1% conc. of CaP-U NPs, with a 29.8% increase; while in the case of urea, the maximum total proline content was recorded at 0.5% conc., with a 17.9% increase followed by 0.1% conc. of urea, with a 13.4% increase compared to control under drought conditions. There were no significant differences between control and treated plants under irrigated conditions (Figure 5C).

10.3389/fpls.2023.1137002

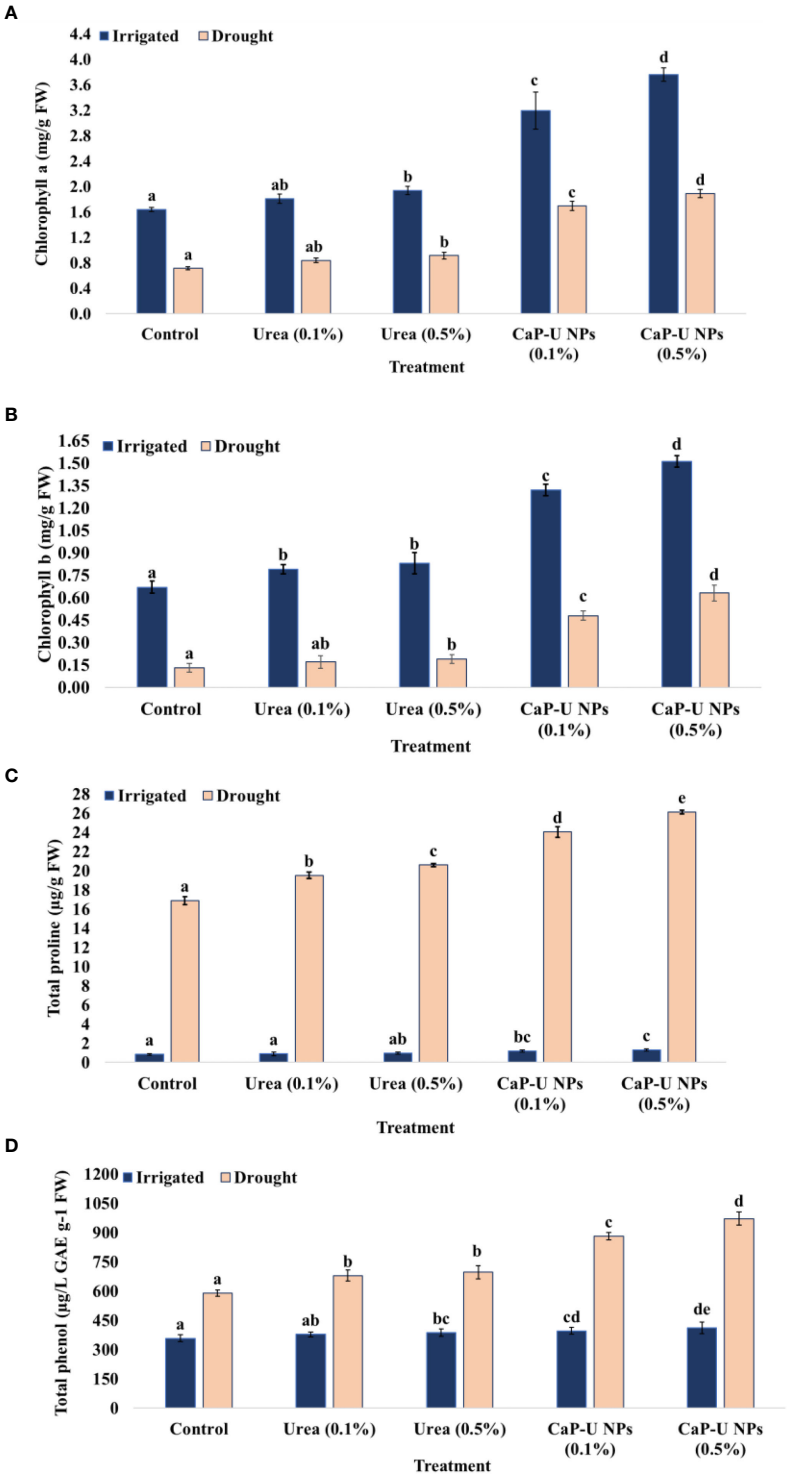


FIGURE 5
Effect of different concentrations of CaP-U NPs on **(A)** chlorophyll a, **(B)** chlorophyll b, **(C)** total proline content, and **(D)** total phenol content of *Eleusine coracana* under irrigated and drought conditions. Results are indicated as means of three replication and vertical bars express the standard deviation (SD) of the means. Different letters denote significant differences among treatment outcomes taken at the same time interval according to Duncan's multiple range test at $P \leq 0.05$.

4.2.10 Total phenol content

Drought induces oxidative stress in plants, which results in ROS production. Phenols and Flavonoids are examples of adaptive natural compounds that enable plants to scavenge ROS (Yadav et al., 2021). Increased synthesis of phenols promotes drought tolerance in plants (Verma and Deepti, 2016). n this experiment, at 45 DAS, in the case of CaP-U NPs, the maximum total phenol content was recorded at 0.5% conc., with a 39.3% increase followed by CaP-U NPs at 0.1%

conc., with a 33.1% increase. In case of urea, the maximum total phenol content was recorded at 0.5% conc., with a 15.3% increase followed by urea at 0.1% conc., with a 13.2% increase compared to control, under drought conditions. Thus, in the present study, TPC levels did not differ significantly under irrigated conditions, whereas TPC levels increased under drought-stressed conditions (Figure 5D).

4.3 Enzymatic antioxidant analysis

Under irrigated conditions, antioxidant enzyme activity did not differ significantly between the control and treatments. However, the activity of SOD, POD and APX was significantly increased in finger millet plants treated with foliar spray in response to drought stress compared to untreated control (Figures 6A–C). Correlation coefficient analysis of genes/proteins with NPs further revealed that the higher binding potential of the NPs on the proteins/genes would result in more transcriptional modulation and more expression of genes (Kumar et al., 2015; Chandra et al., 2021).

4.3.1 Super oxide dismutase

Abiotic stresses have been associated with a progressive rise in the activity of SOD, APX and CAT (Caverzan et al., 2016).

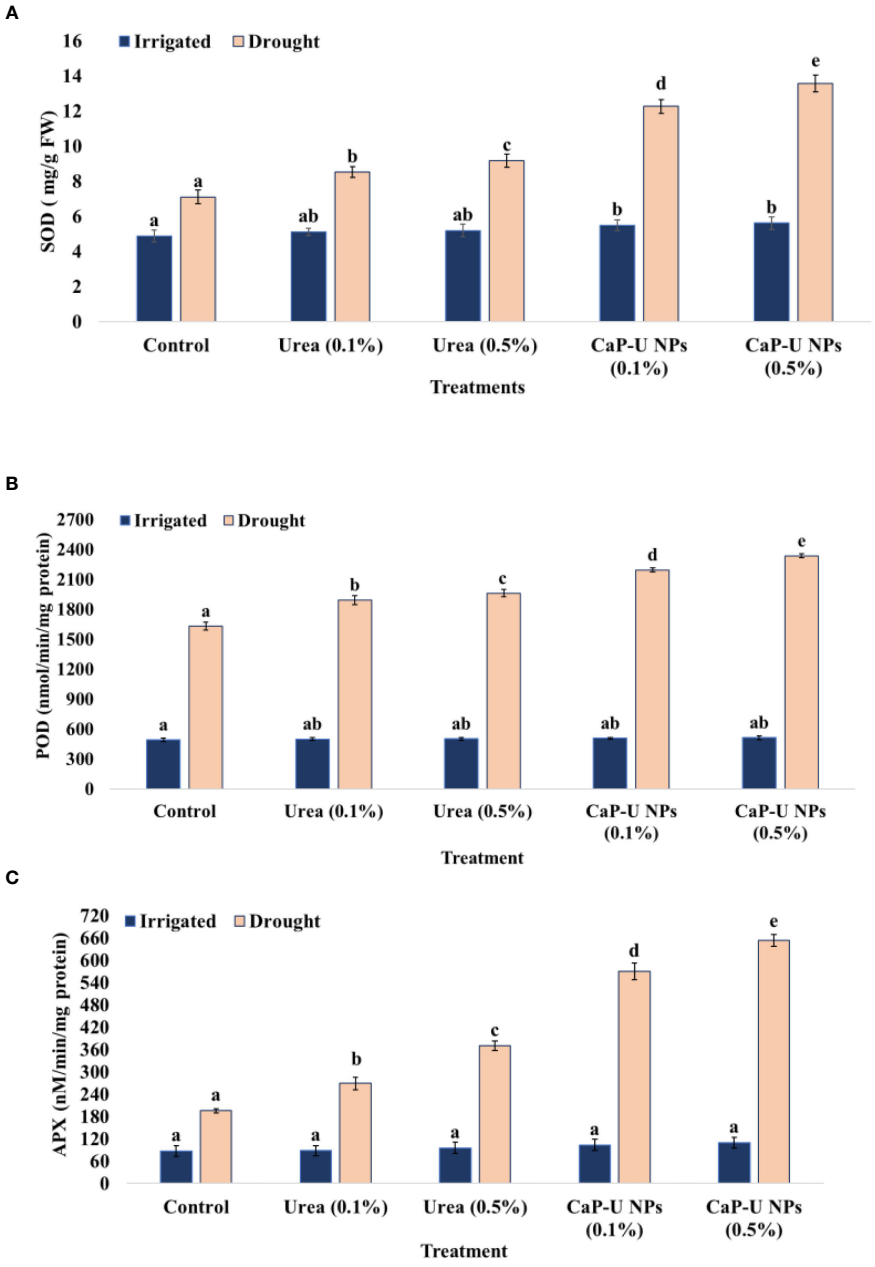


FIGURE 6
Effect of different concentrations of CaP-U NPs on **(A)** superoxide dismutase, **(B)** peroxidase (POD), and **(C)** ascorbate peroxidase (APX), of *Eleusinecoracana* (L.) Gaertn under irrigated and drought conditions. Results are indicated as means of three replication and vertical bars express the standard deviation (SD) of the means. Different letters denote significant differences among treatment outcomes taken at the same time interval according to Duncan's multiple range test at $P \leq 0.05$.

Increased antioxidant enzymes showed plant adaptation to counteract increased oxidant production (Bagheri et al., 2015). SOD is the primary scavenger of superoxide and plays a vital role in defense against cellular damage caused by environmental stress (Ren et al., 2016). SOD levels did not differ significantly under irrigated conditions, whereas SOD levels increased under drought-stressed conditions. In this experiment, at 45 DAS, the maximum SOD was recorded at 0.5% conc. of CaP-U NPs, with a 47.7% increase followed by 0.1% conc. of CaP-U NPs, with a 42.1% increase; while with urea treatment, maximum SOD was recorded at 0.5% conc., with a 22.6% increase followed by 0.1% conc. of urea, with a 16% increase compared to control under drought conditions (Figure 6A).

4.3.2 Peroxidase

POD levels did not differ significantly under irrigated conditions, whereas POD levels increased under drought conditions. In this experiment, at 45 DAS, in the case of CaP-U NPs treatment, the maximum POD activity was recorded at 0.5% conc., with a 30.2% increase followed by 0.1% conc. of CaP-U NPs, with a 25.7% increase, while in the case of urea, maximum POD was recorded at 0.5% conc., with a 16.9% increase followed by 0.1% conc. of urea, with a 13.9% increase compared to control, under drought conditions (Figure 6B).

4.3.3 Ascorbate peroxidase

APX levels did not differ significantly under irrigated conditions, whereas APX levels increased under drought conditions. In this experiment, at 45 DAS, in the case of CaP-U NPs, the maximum APX was recorded at 0.5% conc., with a 70% increase followed by 0.1% conc. of CaP-U NPs, with a 65.6% increase, while with urea treatment, the maximum APX was recorded at 0.5% conc., with a 47.1% increase followed by 0.1% conc. urea, with a 27.1% increase compared to control, under drought conditions (Figure 6C).

4.3.4 Malondialdehyde content

MDA levels did not differ significantly under irrigated conditions, whereas MDA levels increased under drought stress conditions. In this experiment, at 45 DAS, in the case of N-CaP U NPs, the minimum MDA was recorded at 0.5% conc., with a 112.5% decrease followed by 0.1% conc. of CaP-U NPs, with a 93.7% decrease, while in the case of urea, the minimum MDA was recorded at 0.5% conc., with a 46.1% decrease followed by 0.1% conc. of urea, with a 31.8% decrease compared to control, under drought conditions (Figure 7A).

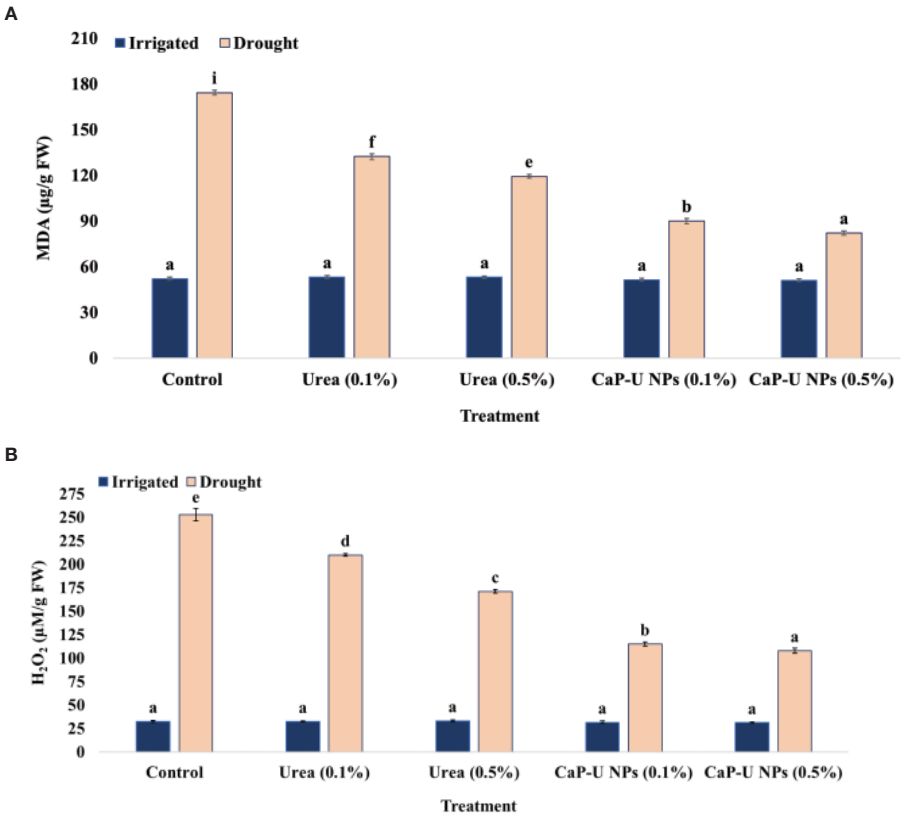


FIGURE 7
Effect of different concentrations of CaP-U NPs on **(A)** Malondialdehyde (MDA), and **(B)** Hydrogen peroxide (H_2O_2) of *Eleusinecoracana* (L.) Gaertn under irrigated and drought conditions. Results are indicated as means of three replication and vertical bars express the standard deviation (SD) of the means. Different letters denote significant differences among treatment outcomes taken at the same time interval according to Duncan's multiple range test at $P \leq 0.05$.

4.3.5 Hydrogen peroxide

Dismutation of superoxide radicals results in hydrogen peroxide accumulation under stress conditionsH_2O_2 levels did not differ significantly under irrigated conditions, whereas H_2O_2 levels increased under drought stress conditions. In this experiment, at 45 DAS, in the case of CaP-U NPs, the minimum H_2O_2 was recorded at 0.5% conc. with a 134.5% decrease followed by 0.1% conc. of CaP-U NPs, with a 119.9% decrease; while in the case of urea, the minimum H_2O_2 was recorded at 0.5% conc., with a 47.7% decrease followed by 0.1% conc. of urea, with a 20.4% decrease compared to control under drought conditions (Figure 7B).

4.4 Principal component analysis of plant growth and biochemical data under NP and urea treatment

PCA analysis was done to establish a relationship between plant growth and biochemical parameters in relation to CaPU NPs and urea applications under both irrigated and drought conditions. The distribution of growth and biochemical parameters in space defined by the first and second PCA dimensions is shown in Figure 8B. The PCA comprising two principal components (PC1 and PC2) explained 98.77 and 99.67% of the total variation in irrigated and drought conditions, respectively. Under irrigated conditions, PC1 explained 93.74% and PC2 explained 5.03% of the total variation while in drought conditions PC1, explained 97.88% and PC2 explained 1.79% of the total variation (Figure 8A). A strong correlation was observed between various growth and biochemical attributes. Superimposition of five treatments combinations on drought suggested that CaP-U NPs at 0.5 followed by 0.1% provided the highest growth indices and defense-related enzymes, which were significantly different. Further, in the control group, all the growth parameters and enzymatic activity were the least and did not show any correlation with growth and biochemical attributes. Under the irrigated conditions, the normal trend was observed, in which CaP-U NPs at 0.5 followed by 0.1% provided the highest growth indices and defense-related enzymes.

4.5 Pearson correlation explains the strength of the growth and biochemical attributes under irrigated and drought conditions influenced by the NP and urea treatment

The leaf area of a plant is considered one of the important components of the growth attributes due to its excellent role in photosynthesis accumulation. High leaf areas intercept more light compared to low ones resulting in more food accumulation in the plants which directly influenced plant growth and enzymatic regulations. Under irrigated conditions, leaf area had a significant strong positive correlation with the shoot (0.99) and root (0.99) length, shoot (1.0) and root (1.0) fresh weight, shoot (1.0) and root (1.0) dry weight and also a strong positive correlation with defense enzymes such

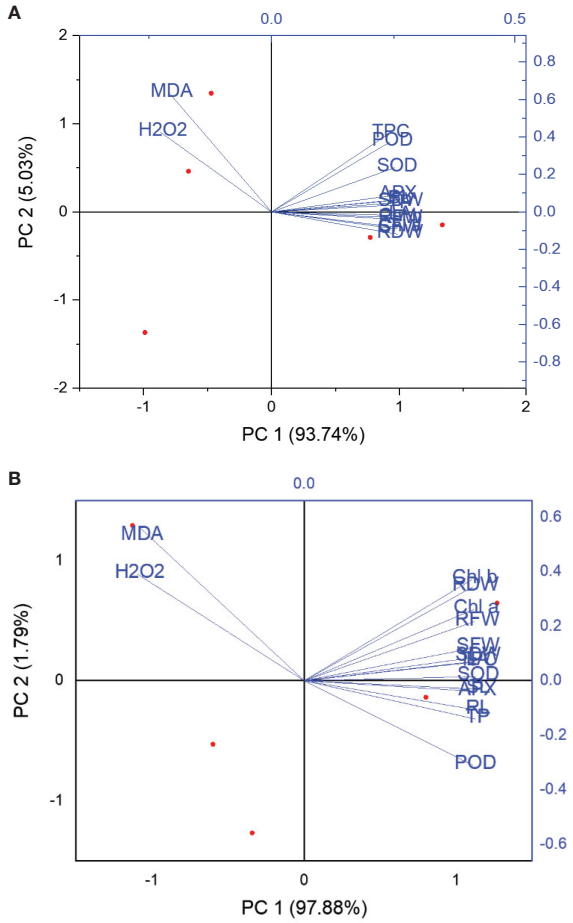


FIGURE 8
Principal component analysis of plant growth parameters upon application of CaP-U NPsa and urea under **(A)** Irrigated and **(B)** Drought conditions.

as Chl a (1.0), Chl b (1.0), SOD (0.97), TPC (0.92), total proline (1.0), APX (0.98) and POD (0.93) while negatively correlated with H_2O_2 (-0.88) and MDA (-0.82). However, other growth parameters such as root and shoot length also showed a significant strong positive correlation with leaf area, root fresh weight (0.99 & 0.99), shoot fresh weight, root dry weight (0.98 & 0.98), shoot dry weight (1.0 & 1.0), respectively. It also showed a strong positive correlation with enzymes such as Chl a & b, SOD (0.99 & 0.99), Total proline (1.0 & 0.99), TPC (0.94 & 0.94), APX (0.98 & 0.98) and POD (0.95 & 0.95) but negatively correlated with H_2O_2 (-0.84 & -0.85) and MDA (-0.78 & -0.77), respectively (Figure 9A).

Under drought conditions, leaf area has a significant strong positive correlation with the shoot (1.0) and root (0.99) length, shoot (1.0) and root (0.99) fresh weight, shoot (0.99) and root (0.99) dry weight as well as showed a strong positive correlation with biochemical parameters such as Chl a (0.99), Chl b (0.98) and defense enzymes such as SOD (1.0), TPC (1.0), total proline (0.99), APX (0.99) and POD (0.97) while negatively correlated with H_2O_2 (-0.97) and MDA (-0.94). However, other growth parameters such as root and shoot length also showed a significant strong positive correlation with leaf area (0.99 & 1.0), root fresh weight (0.98 &

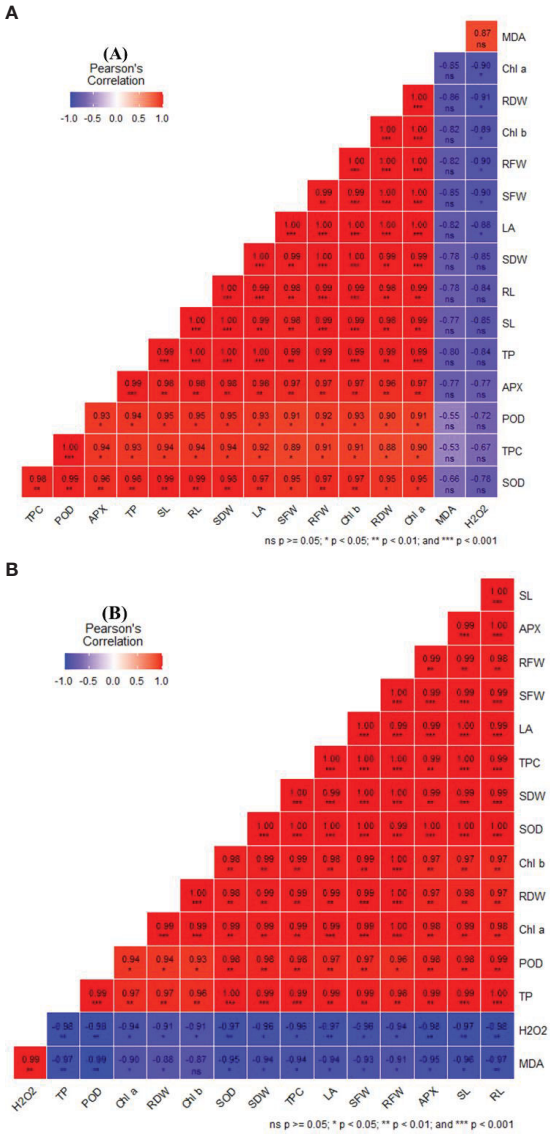


FIGURE 9
Correlation of different growth and defense parameters upon CaP-U NPs and urea application in finger millet under Irrigated **(A)** and drought **(B)** conditions.

0.99), shoot fresh weight (0.99 & 0.99), root dry weight (0.97 & 0.98), shoot dry weight (0.99 & 0.99), respectively. It also showed a strong positive correlation with enzymes such as Chl a (0.98 & 0.99) & Chl b (0.97 & 0.97), SOD (1.0 & 1.0), Total proline (1.0 & 0.99), TPC (0.99 & 1.0), APX (1.0 & 0.99) and POD (0.99 & 0.98) but negatively correlated with H_2O_2 (-0.98 & -0.97) and MDA (-0.97 & -0.96), respectively (Figure 9B).

5 Discussion

Water scarcity significantly influences plant performance by reducing growth, development and other physiological processes by higher accumulation of ROS levels, which causes cell dysfunction in the plants. However, in the present study, applying CaP-U NPs increased the growth, photosynthetic pigments as well as antioxidant enzyme activity by reducing the ROS level under drought-stress conditions. N accumulation in the foliar parts of the plants has a positive correlation with root water conductivity (Figure 10). The nitrogen in plants influenced the water conductivity, which is regulated by the expression of the aquaporin gene mainly nodulin 26-like protein (NIPs) and tonoplast intrinsic proteins (TIPs). However, over-expression of the aquaporin genes could enhance plant drought tolerance (Ren et al., 2015; Li et al., 2016). Generally, NIPs were observed to facilitate the transport of water and the efflux of N, as well as the entry of N into cells *via* the plasma membrane, followed by vacuolar loading through TIPs. Vacuolar loading is beneficial for the storage of excess N, and vacuolar unloading can remobilize the N under N starvation conditions (Ding et al., 2018).

Nano-fertilizers application significantly improved uptake through pores or uptake could be facilitated by complexation with molecular transporters, through the creation of new pores, or by exploitation of endocytosis or ion channels (Rico et al., 2011). Nano-fertilizers are nutrient carriers capable of holding bountiful nutrients due to their high surface area and releasing it slowly (Abdel-Aziz et al., 2016). Nano fertilizers control the release of nutrients from the fertilizer granules to improve nutrient utilization efficiency (NUE) while preventing the nutrient ions from getting fixed or lost in the environment (Subramanian et al., 2015; Chhipa, 2017). Nanoscale fertilizers could lead to the more effective delivery of nutrients as their small size may allow them access to various plant surfaces and transport channels. Leaf surfaces are nano- and microstructured surfaces containing cuticular pores and stomata. A study on the penetration of two different sizes particles (43 nm or 1.1 µm diameter) into leaves of *Vicia faba* L. indicated that the nano-sized particles could penetrate the leaf interior through the stomatal pores (Eichert et al., 2008). The stomatous leaf surfaces of *V. faba* and *Prunus cerasus* had an average pore radius ranging from 25 to 100 nm. Once within the plant, cell-to-cell transport within a plant could be facilitated by the plasmodesmata (Zambryski, 2004). Plasmodesmata are nanoscale channels, 50-60 nm in diameter, enabling cell-to-cell communication and transport (Gunning and Steer, 1996). Chitosan-NPK (10%) fertilizer application gives a significant increase in crop index and harvest index as compared to conventional fertilizer used in wheat crops (Abdel-Aziz et al., 2016). Although in *Abelmoschus esculentus*, the application of commercial fertilizer needed more quantity (5 g/week) compared to manufactured nano urea (50 mg/week) (Tarafder et al., 2020). Zeolite Based Nitrogen Nano-fertilizers increase yield and nitrogen content in Maize plants (Manikandan and Subramanian, 2016). Urea nano fertilizers can reduce a minimum of 25% of the recommended dose of conventional urea fertilizer, which may be introduced as a more sustainable and economical agricultural practice (Singh et al., 2023). A study was conducted in the Haryana state of India with a total area of 1225 acres and found that an average yield was recorded 5.35% higher in wheat, 24.24% in sesame and 8.4% in mustard by applying nano fertilizers of nitrogen and zinc along with the organic farming practice (Kumar et al., 2022). If N nano fertilizer was applied at the rate of 60 kg ha^{-1} on Sunflowers would produce the highest seed yield (17.6%) and oil yield (28.7%) as compared to conventional N fertilizer (Handayati

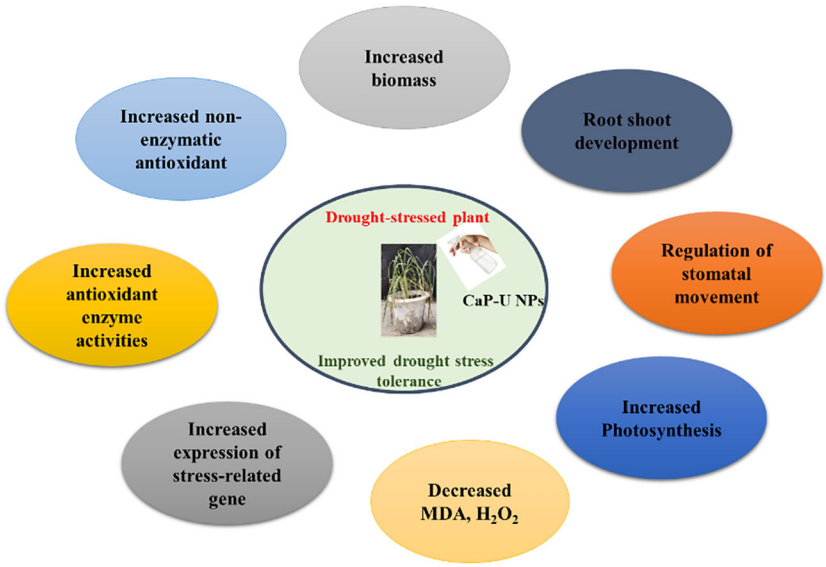


FIGURE 10
General mechanism of CaP-U NPs induced drought stress tolerance in plants.

and Sihombing, 2019). Half doze of HA-N nano fertilizer shows a similar effect of urea in rice (Bhavani et al., 2020).

CaP-U NPs are primarily used as a regulator rather than a nutrient source because they have the ability to control the release of urea and other nutrients. This controlled release feature allows for more efficient use of the nutrients by the plants. Furthermore, the calcium phosphate component of CaP-U NPs can also increase the availability of essential nutrients such as phosphorus and calcium. This can enhance plant growth and improve crop yields. In the present study, the formation of the CaP-U NPs was confirmed by the color change of the solution. FE-SEM determined the morphology of CaP-U NPs. In FE-SEM Neither urea nor calcium phosphate exhibit any areas of phase separation, indicating that the nanocomposite is successfully encapsulated between the two nano matrices. According to FE-SEM analysis, nano urea particles were of different sizes and possessed a fiberlike structure. These findings are similar to Tarafder et al. (2020) and Kottegoda et al. (2017). According to TEM analysis, the rods are covered with urea at the nanoscale. Carmona et al. (2021) found the existence of irregularly shaped Nano-U-ACP in TEM imaging. Nano NPK TEM analysis confirmed the precipitation of amorphous round-shaped nanoparticles with sizes in the 10-25 nm range (Ramírez-Rodríguez et al., 2020a). The shape of luminous europium-calcium phosphate nanoparticles was round, with sizes far below 100 nm under TEM analysis (Ortiz-Gómez et al., 2020). CaP NPs had a diameter of 26 nm as measured by TEM photomicrographs (Morgan et al., 2008).

Rajonee et al. (2016) designed a nitrogen delivery system wherein hexadecyl trimethyl ammonium bromide (HDTMABr) was used as a surfactant for modifying zeolite, which was then loaded with nitrogen. A pot experiment with *Ipomoea aquatica* was carried out to evaluate the efficiency of this synthesized nanocomposite and the results showed that nitrogen uptake by the plants treated with nanocomposite was higher than those treated with conventional urea. CaP-Urea NPs have a larger specific surface area and reactivity than their crystalline counterparts (bulk) material. In lettuce, foliar spray of the urea and dry yeast extract significantly improved vegetative growth characteristics, pigment content, chemical content as well as head yield compared to untreated control (Abd El Galil et al., 2021).

In the present study, urea is loaded onto the CaP surface and hence released more slowly than highly soluble traditional fertilizers; this helped in plants' gradual nitrogen absorption. CaP also shows high solubility in neutral or slightly acidic environments and hence can transfer more of these essential ions to the plant, allowing them to be used as multi-nutrient nano fertilizer (Giroto et al., 2017; Kopittke et al., 2019). Calcium plays a significant role in the development of the structural part and in the biochemical process, i.e., signaling of the plants (Sharma et al., 2017). Calcium also gives resistance to plants against fungal infection since it plays a crucial role in stabilizing and strengthening the cell wall (Cesco et al., 2020). In soybean (*Glycine max*), the application of the hydroxyapatite nanoparticles as a rich source of phosphorus was reported to be remarkably efficient in increasing growth rate and seed yield by 32.6 and 20.4%. In the current research, the well-characterized CaP-U NPs were used for foliar treatment of the finger millet under irrigated and drought conditions. Experimental results revealed that CaP-U NPs significantly improved all the growth-related parameters *viz*., shoot and root length, shoot and root dry weight, shoot and root fresh weight and leaf area of finger millet at both 0.1 and 0.5% concentrations under irrigated and drought conditions. Biochemical parameters such as chlorophyll a, chlorophyll b, total proline content, total phenol content, superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX) etc. Also significantly improved by the foliar treatment of CaP-U NPs under irrigated and drought conditions.

The maximum content of chlorophyll a (2.2 and 2.6-fold increase) (Figure 5A) and b (2.2 and 4.8-fold increase)

(Figure 5B) was recorded in CaP-U NPs treated plants, both under irrigated and drought conditions. Previous research has found that by controlling the biosynthesis of PSI, PSII, and LHCs, Cyt b6f, ATP synthase, and photosynthetic enzymes, N supply and allocation within the leaf have a significant impact on photosynthesis. Out of the total nitrogen (N) in leaf cells, 75% is present in the chloroplast (Onoda et al., 2017). About 24% of the N in leaves goes to thylakoids, and 75% of that nitrogen goes to light-harvesting proteins (Zhong et al., 2019). N is a part of the chlorophyll molecule. One molecule of Chl contains 4 molecules of N (Evans and Clarke, 2019), which helps in photosynthesis to absorb sunlight energy, promoting plant growth and grain yield (Li et al., 2008). Drought stress reduced plant photosynthesis by destroying the pigment system. Therefore, retaining green leaves during drought in plants is a significant indicator of drought tolerance.

N has a close relationship with stomatal conductance and/or movement. As the main N source for plants, nitrate could regulate stomatal movements (De Angeli et al., 2006). The leaf analysis from nano fertilizer-treated plots found 17.04% more nitrogen, 16.31% phosphorus, and 67.50% potassium compared to the control; the total chlorophyll content rose to 30.68%, and the net rate of photosynthesis increased to 71.7% (Ha et al., 2019). The number of leaves, plant height, and leaf area of the coffee seedlings under greenhouse conditions were also improved by the use of Chitosan-based NPK nano fertilizer (Ha et al., 2019). In *Sesame indicum* L., the combined application of potassium nano fertilizer and urea could relieve water stress and adverse effects (Mahdavi Khorami et al., 2020). The maximum shoot length was recorded in CaP-U NP at 0.5% with 1.4- and 1.7-fold increase (Figure 3A), while maximum root length was also recorded in CaP-U NP at 0.5% with 1.9 and 2-fold increase (Figure 3B), respectively. Nitrogen differentially regulates cell elongation and division (Luo et al., 2021). Generally, nitrogen-efficient plants developed a strong root system, which has large root biomass, root volume, root absorption surface area, root active absorption area and a high root oxidation capacity (Xiong et al., 2021). The deposition of lignin and suberin in the roots is controlled by N (Gao et al., 2017). In a study on *C. sativus*, foliar application of CaP-U NPs provided approximately a three-fold increase in the shoot length, as compared to the control, as well as increased nitrogen (N), calcium (Ca) and phosphorus (P) accumulation in both root and shoot (Feil et al., 2021). In wheat crops, foliar application of the chitosan nanoparticles loaded with nitrogen, phosphorus and potassium (NPK) increased shoot length and grain yield substantially (Abdel-Aziz et al., 2016). The leaf area of the plants was significantly impacted under drought conditions. The maximum leaf area was recorded in CaP-U NP at 0.5% with 1.4 and 2.3-fold increases respectively (Figure 3C). The maximum plant fresh weight was recorded in CaP-U NP at 0.5% with 1.6 and 2.3-fold increases (Figures 4A, B), while the dry biomass of plants decreased due to severe water stress. The maximum plant dry weight was recorded in CaP-U NP at 0.5% with 3.3 and 2.8-fold increases (Figures 4C, D) respectively, as compared to control, under irrigated and drought conditions. Pradhan et al. (2021) synthesized Urea Hydroxyapitide (UH) NPs and tested them only for the germination of rice seed (IR-36) and observed that UH NPs substantially increase seedling growth, fresh weight and dry weight of treatments compared to control. Applying CaP-U NPs to *Triticum durum* Desf., significantly increased the fresh and dry weight of the shoot (Ramírez-Rodríguez et al., 2020b). Rice plants fertilized with exogenous urea–chitosan nanohybrid (i.e., 500 mg/L) + 60% classical urea, significantly enhanced the growth and yield-related traits (Elshayb et al., 2022). In *Sorghum bicolor* (L.) Moench, application of the calcium nitrate-gelatin (CNG) coated urea showed maximum dry matter accumulation, high average plant chlorophyll content and apparent nitrogen recovery (ANR) of 71.14% in shoot and 4.5% in roots, respectively (Khan et al., 2021). In *Solanum tuberosum* L., application of the nano-tri combination (N+Mo+B) increased chlorophyll content, the yield of the dry vegetative part, starch content, total protein and ascorbic acid (Al-juthery and Al-Maamouri, 2020). In hydroponics also, *Cucumis sativus* L. supplemented with urea provides a maximum growth of root-shoot length and biomass of the plant (Carmona et al., 2021). In addition, *Pisum sativum* L. treated with SiO_2 NPs significantly increased their relative water content by 29% and specific leaf area by 17% compared to the non-treated control (Sutulienė et al., 2021). Applying the Chitosan nanoparticles in *Zea mays* significantly enhanced the plant height, leaf area, number of leaves and concentration of organic acids regulators of stress tolerance mechanisms (Khati et al., 2017).

During water scarcity in plants, the activity of the osmoprotectants is increased, which regulates the osmotic potential and increases the stability of membranes and metabolic enzymes of the cells by ROS scavenging (Ahanger et al., 2014). Many researchers suggested a positive correlation between proline accumulation and plant stress. Proline, an amino acid, plays a significant role in alleviating various stress conditions in plants. Besides acting as an excellent osmolyte, proline plays three major roles during stress, i.e., as a metal chelator, an antioxidative defense molecule, and a signaling molecule (Ghosh et al., 2022). Research suggested that proline is 300 times more soluble in water than other amino acids and thus acts as a comparatively non-toxic osmolyte. Nitrogen deficiency in *Phaseolus vulgaris* has declined the proline level by stimulating proline dehydrogenase. However, the proline level was raised under adequate nitrogen due to the activation of ornithine δ-aminotransferase (Sánchez et al., 2002). Proline helps to maintain the structural integrity of the plant cell, as well as the scavenging of reactive oxygen species (ROS) under drought stress. The maximum total proline content was recorded in CaP-U NP at 0.5% with 1.5-fold increase (Figure 5C) and total phenol with a 1.6-fold rise (Figure 5D) compared to control under drought conditions. No significant changes were observed between control and treated plants under irrigated conditions. The regulation of antioxidant enzymatic activity is a natural response of plants to oxidative stress caused by various external biotic and abiotic stress factors (Mohammadi et al., 2021). To deal with oxidative damage, plants have evolved an excellent defensive strategy of antioxidant enzyme activities such as SOD, POD, CAT, and APX (Xie et al., 2019). SOD catalyzes superoxide (O^-) elimination by dismutation into oxygen (O_2) and hydrogen peroxide (H_2O_2). The plant's ability to cope with drought stress is associated with low MDA and H_2O_2. Therefore, under drought conditions, the minimum MDA and H_2O_2 content were recorded (Figures 7A, B) in CaP-U NP-

treated plants at 0.5% as well as significantly improved SOD (1.9-fold) (Figure 6A), POD (1.4-fold) (Figure 6B) and APX (3.3-fold) (Figure 6C) activity under drought conditions compared to the control. Here, finger millet plants treated with CaP-U NPs showed a good resistance system to alleviate the damage caused by oxidative stress. The enhanced antioxidant enzymatic activities such as SOD, POD and CAT and reduction in MDA and H_2O_2 content indicated an increased redox defense system in response to drought stress. N fertilizer significantly increases leaf superoxide dismutase (SOD) and peroxidase (POD) activities of rice (Jalloh et al., 2009) growing under Cd stress and maize under water stress conditions (Zhang et al., 2007; Ahmad et al., 2022). Foliar application of Chitosan NPs under greenhouse conditions enhanced enzyme activity such as chitosanase, peroxidase and polyphenol oxidase (Sathiyabama and Manikandan, 2021). Chitosan (CHNPs) nanoparticles enhanced phenylalanine ammonia-lyase (PAL), peroxidase (POX), polyphenol oxidase (PPO), catalase (CAT) and β-1, 3 glucanase (GLU) activity in tomato during bacterial wilt infection (Narasimhamurthy et al., 2022). The foliar application of Fullerenol Nanoparticles reduced drought impact by increasing APX in sugarbeets (*Beta vulgaris* L.) (Borisev et al., 2016). During stress conditions, ascorbic acid (AA) acts as a reducing agent, which reduces H_2O_2 to H_2O and dehydroascorbate (DHA) in chloroplasts and cytosols, respectively (Sharma and Dubey, 2004). The cytosolic APX plays a crucial role in protecting plants from drought and heat stress (Koussevitzky et al., 2008). A heme-containing enzyme, GPX removes excess H_2O_2 in cytosol and vacuole (Sreenivasulu et al., 2004). The foliar application of chitosan nanoparticles (Cs NPs) on *L. iberica*. during water stress conditions provided the increased activity of superoxide dismutase (SOD), ascorbate peroxidase (APX) and peroxidase (POD) (Javanmard et al., 2022). Foliar and soil treatment of Chitosan NPs (30, 60, and 90 ppm)increased the proline level, catalase (CAT), and superoxide dismutase (SOD) activity during drought stress conditions in *Hordeum vulgare* L. (Behboudi et al., 2018). Si NPs alleviate the stress in finger millet by up-regulating the activity of antioxidant enzymes like APX, CAT, SOD and GPX (Mundada et al., 2021). The foliar application of Fullerene nanoparticles reduced drought impact by decreasing MDA in sugar beets (Borisev et al., 2016). Application of CaP-U NPs significantly improved morphological and physiological traits more compared to similar or higher doses of bulk urea. This improvement in the plants could be linked to the higher N availability from the CaP-U NPs treatment, as compared to the control. Foliar application of CaP-U NPs on finger millet showed positive effects in terms of improved leaf relative water content (LRWC), stomatal conductance, chlorophyll contents, photosynthetic rate, nitrogen assimilation, increased carbohydrate production and N metabolism under drought stress.

6 Conclusion

The present study aimed to synthesize and characterize CaP-Urea NPs to assess their potential role in plant growth promotion and defense activation in finger millet under drought conditions. Color changes in visual observation and morphology of NPs by FE-SEM, HR-TEM, and XRD analysis confirmed the synthesized nanoparticles as CaP-U NPs. A broader and valuable outcome of the present work is that a lower dose of CaP-U NPs seems superior in enhancing crop growth, relative to a higher bulk urea dose. Foliar application of the CaP-U NPs increased plant growth indices and activated plant defense under adverse climatic conditions compared to urea as bulk application. Furthermore, CaP-U NPs at 0.5 and 0.1% were found to be slightly more effective in growth indices and defense activation. This investigation demonstrates the roles of nanotechnology in agriculture, one of which is to minimize the input of chemicals into the environment while sustaining crop growth. In future, further studies on yield and nutritional quality improvement using these novel nano-particles under field studies challenged with environmental stresses would provide a deeper understanding of the overall field performance of CaP-U NPs and their potential for commercialization as nano-fertilizer.

Data availability statement

The original contributions presented in the study are included in the article/supplementary materials. Further inquiries can be directed to the corresponding author.

Author contributions

DM: conceptualization, methodology, and writing and original draft preparation. PC: supervised the research work and reviewed and edited the manuscript and provided inputs for framing of the manuscript. MC: provided technical assistance and editing of the manuscript. VU: reviewing of the manuscript. JS: provided technical assistance in XRD analysis. All authors contributed to the article and approved the submitted version.

Acknowledgments

The authors are thankful to the Dean, College of Basic Sciences & Humanities and Director, Experiment Station, G. B. Pant University of Agriculture and Technology, Pantnagar, India, for all the necessary support. First and last authors are also thankful to National Mission on Himalayan Studies under the Ministry of Environment, Forest and Climate Change, GOI for the supply of lab equipment.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Abdelaal, K., AlKahtani, M., Attia, K., Hafez, Y., Király, L., and Künstler, A. (2021). The role of plant growth-promoting bacteria in alleviating the adverse effects of drought on plants. *Biology* 10 (6), 1–23. doi: 10.3390/biology10060520

Abdel-Aziz, H. M., Hasaneen, M. N., and Omer, A. M. (2016). Nano chitosan-NPK fertilizer enhances the growth and productivity of wheat plants grown in sandy soil. *Span. J. Agric. Res.* 14 (1), 1–9. doi: 10.5424/sjar/2016141-8205

Abd El Galil, A., El-Salehein, A., and El Hamady, M. (2021). Effect of foliar spray with urea and dry yeast extract on head lettuce production. *J. Product. Dev.* 26 (4), 1071–1086. doi: 10.21608/jpd.2021.211864

Ahanger, M. A., Tyagi, S. R., Wani, M. R., and Ahmad, P. (2014). "Drought tolerance: role of organic osmolytes, growth regulators, and mineral nutrients," in *Physiological mechanisms and adaptation strategies in plants under changing environment* (New York, NY: Springer), 25–55. doi: 10.1007/978-1-4614-8591-9_2

Ahmad, S., Wang, G. Y., Muhammad, I., Chi, Y. X., Zeeshan, M., Nasar, J., et al. (2022). Interactive effects of melatonin and nitrogen improve drought tolerance of maize seedlings by regulating growth and physiochemical attributes. *Antioxidants* 11 (2), 1–17. doi: 10.3390/antiox11020359

Ahmed, W., and Lingner, J. (2020). PRDX1 counteracts catastrophic telomeric cleavage events that are triggered by DNA repair activities post oxidative damage. *Cell Rep.* 33 (5), 1–13. doi: 10.1016/j.celrep.2020.108347

Alexieva, V., Sergiev, I., Mapelli, S., and Karanov, E. (2001). The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant Cell Environ.* 24 (12), 1337–1344. doi: 10.1046/j.1365-3040.2001.00778.x

Al-juthery, H. W. A., and Al-Maamouri, E.H. O. (2020). Effect of urea and nano-nitrogen fertigation and foliar application of nano-boron and molybdenum on some growth and yield parameters of potato. *Al-Qadisiyah J. Agric. Sci.* 10 (1), 253–263. doi: 10.33794/qjas.2020.167074

Arnon, D. I. (1949). Copper enzymes in isolated chloroplasts. polyphenoloxidase in *Beta vulgaris*. *Plant Physiol.* 24 (1), 1–15. doi: 10.1104/pp.24.1.1

Bagheri, R., Bashir, H., Ahmad, J., Iqbal, M., and Qureshi, M. I. (2015). Spinach *(Spinacia oleracea* l.) modulates its proteome differentially in response to salinity, cadmium and their combination stress. *Plant Physiol. Biochem.* 97, 235–245. doi: 10.1016/j.plaphy.2015.10.012

Bates, L. S., Waldren, R. P., and Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant Soil.* 39 (1), 205–207. doi: 10.1007/BF00018060

Beauchamp, C., and Fridovich, I. (1971). Superoxide dismutase: improved assays and an assay applicable to acrylamide gels. *Anal. Biochem.* 44 (1), 276–287. doi: 10.1016/0003-2697(71)90370-8

Behboudi, F., TahmasebiSarvestani, Z., Kassaee, M. Z., ModaresSanavi, S. A. M., Sorooshzadeh, A., and Ahmadi, S. B. (2018). Evaluation of chitosan nanoparticles effects on yield and yield components of barley *(Hordeum vulgare* l.) under late season drought stress. *J. Water Environ. Nanotechnol.* 3 (1), 22–39. doi: 10.22090/jwent.2018.01.003

Ben-Jabeur, M., Chamekh, Z., Jallouli, S., Ayadi, S., Serret, M. D., Araus, J. L., et al. (2022). Comparative effect of seed treatment with thyme essential oil and paraburkholderiaphytofirmans on growth, photosynthetic capacity, grain yield, δ15N and δ13C of durum wheat under drought and heat stress. *Ann. Appl. Biol.* 181 (1), 58–69. doi: 10.1111/aab.12754

Bhavani, P., Prakash, S. S., Harinikumar, K. M., Thimmegowda, M. N., Benherlal, P. S., and Yoganand, S. B. (2020). Performance of slow release hydroxyapatite coated urea nanofertilizer on aerobic paddy. *Int. J. Curr. Microbiol. App. Sci.* 9 (11), 1320–1330. doi: 10.20546/ijcmas.2020.911.155

Borisev, M., Borisev, I., Zupunski, M., Arsenov, D., Pajević, S., Curcic, Z., et al. (2016). Drought impact is alleviated in sugar beets *(Beta vulgaris* l.) by foliar application of fullerenol nanoparticles. *PLoS One* 11 (11), 1–20. doi: 10.1371/journal.pone.0166248

Carmona, F. J., Dal Sasso, G., Ramírez-Rodríguez, G. B., Pii, Y., Delgado-López, J. M., Guagliardi, A., et al. (2021). Urea-functionalized amorphous calcium phosphate nanofertilizers: optimizing the synthetic strategy towards environmental sustainability and manufacturing costs. *Sci. Rep.* 11 (1), 1–14. doi: 10.1038/s41598-021-83048-9

Caverzan, A., Casassola, A., and Brammer, S. P. (2016). Antioxidant responses of wheat plants under stress. *Genet. Mol. Biol.* 39, 1–6. doi: 10.1590/1678-4685-GMB-2015-0109

Cesco, S., Tolotti, A., Nadalini, S., Rizzi, S., Valentinuzzi, F., Mimmo, T., et al. (2020). *Plasmoparaviticola* Infection affects mineral elements allocation and distribution in *Vitis vinifera* leaves. *Sci. Rep.* 10 (1), 1–18. doi: 10.1038/s41598-020-75990-x

Chandra, A. K., Pandey, D., Tiwari, A., Gururani, K., Agarwal, A., Dhasmana, A., et al. (2021). Metal based nanoparticles trigger the differential expression of key regulatory genes which regulate iron and zinc homeostasis mechanism in finger millet. *J. Cereal Sci.* 100, 1–14. doi: 10.1016/j.jcs.2021.103235

Chang, Z., Liu, Y., Dong, H., Teng, K., Han, L., and Zhang, X. (2016). Effects of cytokinin and nitrogen on drought tolerance of creeping bentgrass. *PLoS One* 11 (4), 1–19. doi: 10.1371/journal.pone.0154005

Chethan, S., and Malleshi, N. G. (2007). Finger millet polyphenols: optimization of extraction and the effect of pH on their stability. *Food Chem.* 105 (2), 862–870. doi: 10.1016/j.foodchem.2007.02.012

Chhipa, H. (2017). Nanofertilizers and nanopesticides for agriculture. *Environ. Chem. Lett.* 15 (1), 15–22. doi: 10.1007/s10311-016-0600-4

Chitara, M. K., Chetan Keswani, C. K., Kartikay Bisen, K. B., Vivek Singh, V. S., Singh, S. P., Sarma, B. K., et al. (2017). "Improving crop performance under heat stress using thermotolerant agriculturally important microorganisms," in *Advances in PGPR research* (Wallingford UK: CABI), 296–305. doi: 10.1079/9781786390325.0296

De Angeli, A., Monachello, D., Ephritikhine, G., Frachisse, J. M., Thomine, S., Gambale, F., et al. (2006). The nitrate/proton antiporter AtCLCa mediates nitrate accumulation in plant vacuoles. *Nature* 442 (7105), 939–942. doi: 10.1038/nature05013

Deblonde, P. M. K., and Ledent, J. F. (2001). Effects of moderate drought conditions on green leaf number, stem height, leaf length and tuber yield of potato cultivars. *Eur. J. Agron.* 14 (1), 31–41. doi: 10.1016/S1161-0301(00)00081-2

Ding, L., Lu, Z., Gao, L., Guo, S., and Shen, Q. (2018). Is nitrogen a key determinant of water transport and photosynthesis in higher plants upon drought stress? *Front. Plant Sci.* 9. doi: 10.3389/fpls.2018.01143

Eichert, T., Kurtz, A., Steiner, U., and Goldbach, H. E. (2008). Size exclusion limits and lateral heterogeneity of the stomatal foliar uptake pathway for aqueous solutes and water-suspended nanoparticles. *Physiol. Plant* 134 (1), 151–160. doi: 10.1111/j.1399-3054.2008.01135.x

Elshayb, O. M., Nada, A. M., Farroh, K. Y., AL-Huqail, A. A., Aljabri, M., Binothman, N., et al. (2022). Utilizing urea–chitosan nanohybrid for minimizing synthetic urea application and maximizing *Oryza sativa* l. productivity and n uptake. *Agriculture* 12 (7), 1–15. doi: 10.3390/agriculture12070944

Evans, J. R., and Clarke, V. C. (2019). The nitrogen cost of photosynthesis. *J. Exp. Bot.* 70 (1), 7–15. doi: 10.1093/jxb/ery366

Feil, S. B., Rodegher, G., Gaiotti, F., Zuluaga, M. Y. A., Carmona, F. J., Masciocchi, N., et al. (2021). Physiological and molecular investigation of urea uptake dynamics in *Cucumis sativus* l. plants fertilized with urea-doped amorphous calcium phosphate nanoparticles. *Front. Plant Sci.* 12. doi: 10.3389/fpls.2021.745581

Gaiotti, F., Lucchetta, M., Rodegher, G., Lorenzoni, D., Longo, E., Boselli, E., et al. (2021). Urea-doped calcium phosphate nanoparticles as sustainable nitrogen nanofertilizers for viticulture: implications on yield and quality of pinot gris grapevines. *Agronomy* 11 (6), 1–16. doi: 10.3390/agronomy11061026

Gao, C., Ding, L., Li, Y., Chen, Y., Zhu, J., Gu, M., et al. (2017). Nitrate increases ethylene production and aerenchyma formation in roots of lowland rice plants under water stress. *Funct. Plant Biol.* 44 (4), 430–442. doi: 10.1071/FP16258

Ghani, M. I., Saleem, S., Rather, S. A., Rehmani, M. S., Alamri, S., Rajput, V. D., et al. (2022). Foliar application of zinc oxide nanoparticles: an effective strategy to mitigate drought stress in cucumber seedling by modulating antioxidant defense system and osmolytes accumulation. *Chemosphere* 289, 133202. doi: 10.1016/j.chemosphere.2021.133202

Ghosh, U. K., Islam, M. N., Siddiqui, M. N., Cao, X., and Khan, M. A. R. (2022). Proline, a multifaceted signalling molecule in plant responses to abiotic stress: understanding the physiological mechanisms. *Plant Biol.* 24 (2), 227–239. doi: 10.1111/plb.13363

Giroto, A. S., Guimarães, G. G., Foschini, M., and Ribeiro, C. (2017). Role of slow-release nanocomposite fertilizers on nitrogen and phosphate availability in soil. *Sci. Rep.* 7 (1), 1–11. doi: 10.1038/srep46032

Gui, Y. W., Sheteiwy, M. S., Zhu, S. G., Batool, A., and Xiong, Y. C. (2021a). Differentiate effects of non-hydraulic and hydraulic root signaling on yield and water use efficiency in diploid and tetraploid wheat under drought stress. *Environ. Exp. Bot.* 181, 1–18. doi: 10.1016/j.envexpbot.2020.104287

Gui, Y., Sheteiwy, M. S., Zhu, S., Zhu, L., Batool, A., Jia, T., et al. (2021b). Differentiate responses of tetraploid and hexaploid wheat (Triticum aestivum l.) to

moderate and severe drought stress: a cue of wheat domestication. *Plant Signal. Behav.* 16 (1), 1–13. doi: 10.1080/15592324.2020.1839710

Gunning, B. E., and Steer, M. W. (1996). Plant cell biology: structure and function. *Jones Bartlett Learn.*, 1–5.

Ha, N. M. C., Nguyen, T. H., Wang, S. L., and Nguyen, A. D. (2019). Preparation of NPK nanofertilizer based on chitosan nanoparticles and its effect on biophysical characteristics and growth of coffee in green house. *Res. Chem. Intermed.* 45, 51–63. doi: 10.1007/s11164-018-3630-7

Hadimani, N. A., and Malleshi, N. G. (1993). Studies on milling, physico-chemical properties, nutrient composition and dietary fibre content of millets. *J. Food Sci. Technol.* 30 (1), 17–20.

Handayati, W., and Sihombing, D. (2019). "Study of NPK fertilizer effect on sunflower growth and yield," in *AIP conference proceedings*, vol. 2120. (AIP Publishing LLC), 030031. doi: 10.1063/1.5115635

Heath, R. L., and Packer, L. (1968). Photoperoxidation in isolated chloroplasts: i. kinetics and stoichiometry of fatty acid peroxidation. *Arch. Biochem. Biophys.* 125 (1), 189–198. doi: 10.1016/0003-9861(68)90654-1

Hemati, A., Moghiseh, E., Amirifar, A., Mofidi-Chelan, M., and AsgariLajayer, B. (2022). "Physiological effects of drought stress in plants," in *Plant stress mitigators* (Singapore: Springer), 113–124. doi: 10.1007/978-981-16-7759-5_6

Ho, M. D., Rosas, J. C., Brown, K. M., and Lynch, J. P. (2005). Root architectural tradeoffs for water and phosphorus acquisition. *Funct. Plant Biol.* 32 (8), 737–748. doi: 10.1071/FP05043

Hsiao, T. C., and Xu, L. K. (2000). Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *J. Exp. Bot.* 51 (350), 1595–1616. doi: 10.1093/jexbot/51.350.1595

Hussain, M. Z., Bhardwaj, A. K., Basso, B., Robertson, G. P., and Hamilton, S. K. (2019). Nitrate leaching from continuous corn, perennial grasses, and poplar in the US Midwest. *J. Environ. Qual.* 48 (6), 1849–1855. doi: 10.2134/jeq2019.04.0156

Jalloh, M. A., Chen, J., Zhen, F., and Zhang, G. (2009). Effect of different n fertilizer forms on antioxidant capacity and grain yield of rice growing under cd stress. *J. Hazard. Mater.* 162 (2-3), 1081–1085. doi: 10.1016/j.jhazmat.2008.05.146

Javanmard, A., Ashrafi, M., Morshedloo, M. R., Machiani, M. A., Rasouli, F., and Maggi, F. (2022). Optimizing phytochemical and physiological characteristics of balangu *(Lallemantiaiberica)* by foliar application of chitosan nanoparticles and myco-root inoculation under water supply restrictions. *Horticulturae* 8 (8), 1–17. doi: 10.3390/horticulturae8080695

Ju, Y. L., Yue, X. F., Zhao, X. F., Zhao, H., and Fang, Y. L. (2018). Physiological, micro-morphological and metabolomic analysis of grapevine (Vitis vinifera l.) leaf of plants under water stress. *Plant Physiol. Biochem.* 130, 501–510. doi: 10.1016/j.plaphy.2018.07.036

Kar, M., and Mishra, D. (1975). Inorganic pyrophosphatase activity during rice leaf senescence. *Canad. J. Bot.* 53 (5), 503–511. doi: 10.1139/b75-061

Khan, O., Niazi, M. B. K., Shah, G. A., Hazafa, A., Jahan, Z., Sadiq, M., et al. (2021). Green synthesis and evaluation of calcium-based nanocomposites fertilizers: a way forward to sustainable agricultural. *J. Saudi Soc Agric. Sci.* 20 (8), 519–529. doi: 10.1016/j.jssas.2021.06.005

Khati, P., Chaudhary, P., Gangola, S., Bhatt, P., and Sharma, A. (2017). Nanochitosan supports growth of zea mays and also maintains soil health following growth. *3 Biotech.* 7 (1), 1–9. doi: 10.1007/s13205-017-0668-y

Koch, G., Rolland, G., Dauzat, M., Bédiée, A., Baldazzi, V., Bertin, N., et al. (2019). Leaf production and expansion: a generalized response to drought stresses from cells to whole leaf biomass–a case study in the tomato compound leaf. *Plants* 8 (10), 1–17. doi: 10.3390/plants8100409

Kopittke, P. M., Lombi, E., Wang, P., Schjoerring, J. K., and Husted, S. (2019). Nanomaterials as fertilizers for improving plant mineral nutrition and environmental outcomes. *Environ. Sci. Nano* 6 (12), 3513–3524. doi: 10.1039/C9EN00971J

Kottegoda, N., Sandaruwan, C., Priyadarshana, G., Siriwardhana, A., Rathnayake, U. A., Berugoda Arachchige, D. M., et al. (2017). Urea-hydroxyapatite nanohybrids for slow release of nitrogen. *ACS nano* 11 (2), 1214–1221. doi: 10.1021/acsnano.6b07781

Koussevitzky, S., Suzuki, N., Huntington, S., Armijo, L., Sha, W., Cortes, D., et al. (2008). Ascorbate peroxidase 1 plays a key role in the response of *Arabidopsis thaliana* to stress combination. *J. Biol. Chem.* 283 (49), 34197–34203. doi: 10.1074/jbc.M806337200

Krishnan, R., Gnanaseelan, C., Sanjay, J., Swapna, P., Dhara, C., Sabin, T. P., et al. (2020). "Introduction to climate change over the Indian region," in *Assessment of climate change over the Indian region* (Singapore: Springer), 1–20. doi: 10.1007/978-981-15-4327-2_13

Kumar, A., Gaur, V. S., Goel, A., and Gupta, A. K. (2015). *De novo* Assembly and characterization of developing spikes transcriptome of finger millet *(Eleusine coracana)*: a minor crop having nutraceutical properties. *Plant Mol. Biol. Rep.* 33 (4), 905–922. doi: 10.1007/s11105-014-0802-5

Kumar, A., Singh, K., Verma, P., Singh, O., Panwar, A., Singh, T., et al. (2022). Effect of nitrogen and zinc nanofertilizer with the organic farming practices on cereal and oil seed crops. *Sci. Rep.* 12 (1), 1–7. doi: 10.1038/s41598-022-10843-3

Kumari, A., Bhinda, M. S., Sharma, S., Chitara, M. K., Debnath, A., Maharana, C, et al. (2021). ROS regulation mechanism for mitigation of abiotic stress in plants. *Reactive Oxygen Species* 28, 197–238. doi: 10.5772/intechopen.99845

Ladha, J. K., Pathak, H., Krupnik, T. J., Six, J., and van Kessel, C. (2005). Efficiency of fertilizer nitrogen in cereal production: retrospects and prospects. *Adv. Agron.* 87, 85–156. doi: 10.1016/S0065-2113(05)87003-8

Lesk, C., Rowhani, P., and Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature* 529 (7584), 84–99. doi: 10.1038/nature16467

Li, Y., Horsman, M., Wang, B., Wu, N., and Lan, C. Q. (2008). Effects of nitrogen sources on cell growth and lipid accumulation of green alga neochlorisoleoabundans. *Appl. Microbiol. Biotechnol.* 81 (4), 629–636. doi: 10.1007/s00253-008-1681-1

Li, G., Tillard, P., Gojon, A., and Maurel, C. (2016). Dual regulation of root hydraulic conductivity and plasma membrane aquaporins by plant nitrate accumulation and high-affinity nitrate transporter NRT2. 1. *Plant Cell Physiol.* 57 (4), 733–742. doi: 10.1093/pcp/pcw022

Liu, R., and Lal, R. (2015). Potentials of engineered nanoparticles as fertilizers for increasing agronomic productions. *Sci. Total Environ.* 514, 131–139. doi: 10.1016/j.scitotenv.2015.01.104

Luo, Y., Peng, Q., Li, K., Gong, Y., Liu, Y., and Han, W. (2021). Patterns of nitrogen and phosphorus stoichiometry among leaf, stem and root of desert plants and responses to climate and soil factors in xinjiang, China. *Catena* 199, 1–25. doi: 10.1016/j.catena.2020.105100

Mahdavi Khorami, A., Masoud Sinaki, J., Amini Dehaghi, M., Rezvan, S., and Damavandi, A. (2020). Sesame *(Sesame indicum* l.) biochemical and physiological responses as affected by applying chemical, biological, and nano-fertilizers in field water stress conditions. *J. Plant Nutr.* 43 (3), 456–475. doi: 10.1080/01904167.2019.1683189

Mahil, E. I. T., and Kumar, B. A. (2019). Foliar application of nanofertilizers in agricultural crops–a review. *J. Farm Sci.* 32 (3), 239–249.

Mahmoud, A. W. M., and Swaefy, H. M. (2020). Comparison between commercial and nano NPK in presence of nano zeolite on sage plant yield and its components under water stress. *Agriculture* 66 (1), 24–39. doi: 10.2478/agri-2020-0003

Manikandan, A., and Subramanian, K. S. (2016). Evaluation of zeolite based nitrogen nano-fertilizers on maize growth, yield and quality on inceptisols and alfisols. *Int. J. Plant Soil Sci.* 9 (4), 1–9. doi: 10.9734/IJPSS/2016/22103

Mohammadi, M. A., Cheng, Y., Aslam, M., Jakada, B. H., Wai, M. H., Ye, K., et al. (2021). ROS and oxidative response systems in plants under biotic and abiotic stresses: revisiting the crucial role of phosphite triggered plants defense response. *Front. Microbiol.* 12. doi: 10.3389/fmicb.2021.631318

Mohammadian, R., Moghaddam, M., Rahimian, H., and Sadeghian, S. Y. (2005). Effect of early season drought stress on growth characteristics of sugar beet genotypes. *Turk. J. Agric. For.* 29 (5), 357–368.

Mohammadkhani, N., and Heidari, R. (2008). Effects of drought stress on soluble proteins in two maize varieties. *Turk. J. Biol.* 32 (1), 23–30.

Morgan, T. T., Muddana, H. S., Altinoglu, E. I., Rouse, S. M., Tabakovic, A., Tabouillot, T., et al. (2008). Encapsulation of organic molecules in calcium phosphate nanocomposite particles for intracellular imaging and drug delivery. *Nano Lett.* 8 (12), 4108–4115. doi: 10.1021/nl8019888

Mundada, P. S., Ahire, M. L., Umdale, S. D., Barmukh, R. B., Nikam, T. D., Pable, A. A., et al. (2021). Characterization of influx and efflux silicon transporters and understanding their role in the osmotic stress tolerance in finger millet *(Eleusinecoracana* (L.) gaertn.). *Plant Physiol. Biochem.* 162, 677–689. doi: 10.1016/j.plaphy.2021.03.033

Naeem, M., Naeem, M. S., Ahmad, R., Ihsan, M. Z., Ashraf, M. Y., Hussain, Y., et al. (2018). Foliar calcium spray confers drought stress tolerance in maize *via* modulation of plant growth, water relations, proline content and hydrogen peroxide activity. *Arch. Agron. Soil Sci.* 64 (1), 116–131. doi: 10.1080/03650340.2017.1327713

Nakano, Y., and Asada, K. (1981). Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. *Plant Cell Physiol.* 22 (5), 867–880. doi: 10.1093/oxfordjournals.pcp.a076232

Narasimhamurthy, K., Udayashankar, A. C., De Britto, S., Lavanya, S. N., Abdelrahman, M., Soumya, K., et al. (2022). Chitosan and chitosan-derived nanoparticles modulate enhanced immune response in tomato against bacterial wilt disease. *Int. J. Biol. Macromol.* 220, 223–237. doi: 10.1016/j.ijbiomac.2022.08.054

Ning, D., Qin, A., Liu, Z., Duan, A., Xiao, J., Zhang, J., et al. (2020). Silicon-mediated physiological and agronomic responses of maize to drought stress imposed at the vegetative and reproductive stages. *Agronomy* 10 (8), 1–19. doi: 10.3390/agronomy10081136

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., et al. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytol.* 214 (4), 1447–1463. doi: 10.1111/nph.14496

Orimoloye, I. R., Belle, J. A., Orimoloye, Y. M., Olusola, A. O., and Ololade, O. O. (2022). Drought: a common environmental disaster. *Atmosphere* 13 (1), 1–21. doi: 10.3390/atmos13010111

Ortiz-Gómez, I., Ramírez-Rodríguez, G. B., Capitán-Vallvey, L. F., Salinas-Castillo, A., and Delgado-López, J. M. (2020). Highly stable luminescent europium-doped calcium phosphate nanoparticles for creatinine quantification. *Colloids Surf. B: Biointerfaces.* 196, 1–8. doi: 10.1016/j.colsurfb.2020.111337

Oumarou Abdoulaye, A., Lu, H., Zhu, Y., Alhaj Hamoud, Y., and Sheteiwy, M. (2019). The global trend of the net irrigation water requirement of maize from 1960 to 2050. *Climate* 7 (10), 1–19. doi: 10.3390/cli7100124

Pan, Y., She, D., Chen, X., Xia, Y., and Timm, L. C. (2021). Elevation of biochar application as regulator on denitrification/NH3 volatilization in saline soils. *Environ. Sci. pollut. Res.* 28 (31), 41712–41725. doi: 10.1007/s11356-021-13562-w

Passioura, J. B. (2002). Soil conditions and plant growth. *Plant Cell Environ.* 25 (2), 311–318. doi: 10.1046/j.0016-8025.2001.00802.x

Pradhan, S., Durgam, M., and Mailapalli, D. R. (2021). Urea loaded hydroxyapatite nanocarrier for efficient delivery of plant nutrients in rice. *Arch. Agron. Soil Sci.* 67 (3), 371–382. doi: 10.1080/03650340.2020.1732940

Rajonee, A. A., Nigar, F., Ahmed, S., and Imamul Huq, S. M. (2016). Synthesis of nitrogen nano fertilizer and its efficacy. *Can. J. Pur. Appl. Sci.* 10, 3913–3919.

Ramírez-Rodríguez, G. B., Dal Sasso, G., Carmona, F. J., Miguel-Rojas, C., Pérez-de-Luque, A., Masciocchi, N., et al. (2020a). Engineering biomimetic calcium phosphate nanoparticles: a green synthesis of slow-release multinutrient (NPK) nanofertilizers. *ACS Appl. Bio Mater.* 3 (3), 1344–1353. doi: 10.1021/acsabm.9b00937

Ramírez-Rodríguez, G. B., Miguel-Rojas, C., Montanha, G. S., Carmona, F. J., Dal Sasso, G., Sillero, J. C., et al. (2020b). Reducing nitrogen dosage in triticum durum plants with urea-doped nanofertilizers. *J. Nanomater.* 10 (6), 1–16. doi: 10.3390/nano10061043

Ren, J., Sun, L. N., Zhang, Q. Y., and Song, X. S. (2016). Drought tolerance is correlated with the activity of antioxidant enzymes in cerasus humilis seedlings. *BioMed. Res. Int.* 7, 1–9. doi: 10.1155/2016/9851095

Ren, B., Wang, M., Chen, Y., Sun, G., Li, Y., Shen, Q., et al. (2015). Water absorption is affected by the nitrogen supply to rice plants. *Plant Soil* 396 (1), 397–410. doi: 10.1007/s11104-015-2603-5

Rico, C. M., Majumdar, S., Duarte-Gardea, M., Peralta-Videa, J. R., and Gardea-Torresdey, J. L. (2011). Interaction of nanoparticles with edible plants and their possible implications in the food chain. *J. Agric. Food Chem.* 59 (8), 3485–3498. doi: 10.1021/jf104517j

Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., and Hasanuzzaman, M. (2021). Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. *Antioxidants* 10 (2), 1–37. doi: 10.3390/antiox10020277

Sánchez, E., Garcia, P. C., López-Lefebre, L. R., Rivero, R. M., Ruiz, J. M., and Romero, L. (2002). Proline metabolism in response to nitrogen deficiency in French bean plants (Phaseolus vulgaris l. cv strike). *Plant Growth Regul.* 36 (3), 261–265. doi: 10.1023/A:1016583430792

Sathiyabama, M., and Manikandan, A. (2021). Foliar application of chitosan nanoparticle improves yield, mineral content and boosts innate immunity in finger millet plants. *Carbohydr. Polym.* 258, 1–8. doi: 10.1016/j.carbpol.2021.117691

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., et al. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* 10 (2), 1–25. doi: 10.3390/plants10020259

Shakeel, A. A., Xiao-yu, X., Long-chang, W., Muhammad, F. S., Chen, M., and Wang, L. (2011). Morphological, physiological and biochemical responses of plants to drought stress. *Afr. J. Agric. Res.* 6 (9), 2026–2032. doi: 10.5897/AJAR10.027

Sharma, P., and Dubey, R. S. (2004). Ascorbate peroxidase from rice seedlings: properties of enzyme isoforms, effects of stresses and protective roles of osmolytes. *Plant Sci.* 167 (3), 541–550. doi: 10.1016/j.plantsci.2004.04.028

Sharma, A., Gupta, P., and Prabhakar, P. K. (2019). Endogenous repair system of oxidative damage of DNA. *Curr. Chem. Biol.* 13 (2), 110–119. doi: 10.2174/2212796813666190221152908

Sharma, D., Jamra, G., Singh, U. M., Sood, S., and Kumar, A. (2017). Calcium biofortification: three pronged molecular approaches for dissecting complex trait of calcium nutrition in finger millet *(Eleusinecoracana*) for devising strategies of enrichment of food crops. *Front. Plant Sci.* 7. doi: 10.3389/fpls.2016.02028

Sharma, S. K., Sharma, P. K., Mandeewal, R. L., Sharma, V., Chaudhary, R., Pandey, R., et al. (2022). Effect of foliar application of nano-urea under different nitrogen levels on growth and nutrient content of pearl millet (Pennisetum glaucum l.). *Int. J. Plant Sci.* 34 (20), 149–155. doi: 10.9734/ijpss/2022/v34i2031138

Sheteiwy, M. S., Abd Elgawad, H., Xiong, Y. C., Macovei, A., Brestic, M., Skalicky, M., et al. (2021a). Inoculation with bacillus amyloliquefaciens and mycorrhiza confers tolerance to drought stress and improve seed yield and quality of soybean plant. *Physiol. Plant* 172 (4), 2153–2169. doi: 10.1111/ppl.13454

Sheteiwy, M. S., Ali, D. F. I., Xiong, Y. C., Brestic, M., Skalicky, M., Hamoud, Y. A., et al. (2021b). Physiological and biochemical responses of soybean plants inoculated with arbuscular mycorrhizal fungi and bradyrhizobium under drought stress. *BMC Plant Biol.* 21 (1), 1–21. doi: 10.1186/s12870-021-02949-z

Sheteiwy, M., Ulhassan, Z., Qi, W., Lu, H., AbdElgawad, H., Minkina, T., et al. (2022). Association of jasmonic acid priming with multiple defense mechanisms in wheat plants under high salt stress. *Front. Plant Sci.* 2614. doi: 10.3389/fpls.2022.886862

Sial, N. Y., Faheem, M., Sial, M. A., Roonjho, A. R., Muhammad, F., Keerio, A. A., et al. (2022). Exotic wheat genotypes response to water-stress conditions. *J. Breed. Genet.* 54 (2), 297–304. doi: 10.54910/sabrao2022.54.2.8

Singh, P. P., Priyam, A., Singh, J., and Gupta, N. (2023). Biologically synthesised urea-based nanomaterial shows enhanced agronomic benefits in maize and rice crops during kharif season. *Sci. Hortic.* 315, 1–21. doi: 10.1016/j.scienta.2023.111988

Soliman, A. S., Hassan, M., Abou-Elella, F., Ahmed, A. H., and El-Feky, S. A. (2016). Effect of nano and molecular phosphorus fertilizers on growth and chemical composition of baobab (Adansonia digitata l.). *J. Plant Sci.* 11 (4), 52–60. doi: 10.3923/jps.2016.52.60

Song, Y., Li, J., Liu, M., Meng, Z., Liu, K., and Sui, N. (2019). Nitrogen increases drought tolerance in maize seedlings. *Funct. Plant Biol.* 46 (4), 350–359. doi: 10.1071/FP18186

Sreenivasulu, N., Miranda, M., Prakash, H. S., Wobus, U., and Weschke, W. (2004). Transcriptome changes in foxtail millet genotypes at high salinity: identification and characterization of a PHGPX gene specifically up-regulated by NaCl in a salt-tolerant line. *J. Plant Physiol.* 161 (4), 467–477. doi: 10.1078/0176-1617-01112

Subramanian, K. S., Manikandan, A., Thirunavukkarasu, M., and Rahale, C. S. (2015). "Nano-fertilizers for balanced crop nutrition," in *Nanotechnologies in food and agriculture* (Cham: Springer), 69–80. doi: 10.1007/978-3-319-14024-7_3

Sutulienė, R., Ragelienė, L., Samuolienė, G., Brazaitytė, A., Urbutis, M., and Miliauskienė, J. (2021). The response of antioxidant system of drought-stressed green pea *(Pisum sativum* l.) affected by watering and foliar spray with silica nanoparticles. *Horticulturae* 8 (1), 1–15. doi: 10.3390/horticulturae8010035

Tarafder, C., Daizy, M., Alam, M. M., Ali, M. R., Islam, M. J., Islam, R., et al. (2020). Formulation of a hybrid nanofertilizer for slow and sustainable release of micronutrients. *ACS omega* 5 (37), 23960–23966. doi: 10.1021/acsomega.0c03233

Verma, A. K., and Deepti, S. (2016). Abiotic stress and crop improvement: current scenario. *Adv. Plants Agric. Res.* 4 (4), 345–346. doi: 10.15406/apar.2016.04.00149

Wang, K., Bu, T., Cheng, Q., Dong, L., Su, T., Chen, Z., et al. (2021). Two homologous LHY pairs negatively control soybean drought tolerance by repressing the abscisic acid responses. *New Phytol.* 229 (5), 2660–2675. doi: 10.1111/nph.17019

Xie, X., He, Z., Chen, N., Tang, Z., Wang, Q., and Cai, Y. (2019). The roles of environmental factors in regulation of oxidative stress in plant. *BioMed. Res. Int.* 2019, 1–11. doi: 10.1155/2019/9732325

Xiong, Q., Hu, J., Wei, H., Zhang, H., and Zhu, J. (2021). Relationship between plant roots, rhizosphere microorganisms, and nitrogen and its special focus on rice. *Agriculture* 11 (3), 1–18. doi: 10.3390/agriculture11030234

Yadav, B., Jogawat, A., Rahman, M. S., and Narayan, O. P. (2021). Secondary metabolites in the drought stress tolerance of crop plants: a review. *Gene Rep.* 23, 1–14. doi: 10.1016/j.genrep.2021.101040

Zambryski, P. (2004). Cell-to-cell transport of proteins and fluorescent tracers *via* plasmodesmata during plant development. *Int. J. Cell Biol.* 164 (2), 165–168. doi: 10.1083/jcb.200310048

Zhang, L. X., Li, S. X., Zhang, H., and Liang, Z. S. (2007). Nitrogen rates and water stress effects on production, lipid peroxidation and antioxidative enzyme activities in two maize (Zea mays l.) genotypes. *J. Agron. Crop Sci.* 193 (6), 387–397. doi: 10.1111/j.1439-037X.2007.00276.x

Zhang, G., St. Clair, A. L., Dolezal, A. G., Toth, A. L., and O'Neal, M. E. (2022). Can native plants mitigate climate-related forage dearth for honey bees (Hymenoptera: apidae)? *J. Econ. Entomol.* 115 (1), 1–9. doi: 10.1093/jee/toab202

Zhong, C., Cao, X., Hu, J., Zhu, L., Zhang, J., Huang, J., et al. (2017). Nitrogen metabolism in adaptation of photosynthesis to water stress in rice grown under different nitrogen levels. *Front. Plant Sci.* 8. doi: 10.3389/fpls.2017.01079

Zhong, C., Jian, S. F., Huang, J., Jin, Q. Y., and Cao, X. C. (2019). Trade-off of within-leaf nitrogen allocation between photosynthetic nitrogen-use efficiency and water deficit stress acclimation in rice (Oryza sativa l.). *Plant Physiol. Biochem.* 135, .41–.50. doi: 10.1016/j.plaphy.2018.11.021

Zieslin, N., and Ben Zaken, R. (1993). Peroxidase activity and presence of phenolic substances in peduncles of rose flowers. *Plant Physiol. Biochem.* 31, 3, 333–339.

Zulfiqar, F., Navarro, M., Ashraf, M., Akram, N. A., and Munné-Bosch, S. (2019). Nanofertilizer use for sustainable agriculture: advantages and limitations. *Plant Sci.* 289, 1–7. doi: 10.1016/j.plantsci.2019.110270

frontiers | Frontiers in Agronomy

TYPE Review
PUBLISHED 30 May 2023
DOI 10.3389/fagro.2023.1183691

OPEN ACCESS

EDITED BY
Parul Chaudhary,
Graphic Era Hill University, India

REVIEWED BY
Viabhav Kumar Upadhayay,
Dr. Rajendra Prasad Central Agricultural University, India
Sami Abou Fayssal,
University of Forestry, Sofia, Bulgaria

*CORRESPONDENCE
Olubukola O. Babalola
olubukola.babalola@nwu.ac.za

RECEIVED 10 March 2023
ACCEPTED 18 May 2023
PUBLISHED 30 May 2023

CITATION
Ayilara MS and Babalola OO (2023) Bioremediation of environmental wastes: the role of microorganisms.
Front. Agron. 5:1183691.
doi: 10.3389/fagro.2023.1183691

Bioremediation of environmental wastes: the role of microorganisms

Modupe S. Ayilara[1,2,3] and Olubukola O. Babalola[1*]

[1]Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa, [2]Department of Biological Sciences, Kings University, Ode-Omu, Nigeria, [3]Environmental Pollution Science and Technology, (ENPOST), Ido-Ijesha, Ilesha, Nigeria

The growing rate of urbanization and industrialization has led to an increase in several types of pollution caused by the release of toxic chemicals to the environment. This is usually perpetuated by the manufacturing industry (e.g. detergent and dye), agricultural sectors (e.g. fertilizers and pesticides), mining industry (e.g. cyanide and sulphuric acid) and construction companies (e.g. cement and metals). These pollutants have adverse effects on the health of plants, animals, and humans. They also lead to the destruction of the microbial population in both aquatic and the terrestrial regions, and hence, have necessitated the need for remediation. Although different remediation methods, such as the physical and chemical methods, have been adopted for years, however, the drawbacks and challenges associated with them have promoted the use of an alternative which is bioremediation. Bioremediation involves using biological agents such as plants and microbes to remove or lessen the effects of environmental pollutants. Of the two, microbes are more utilized primarily because of their rapid growth and ability to be easily manipulated, thus enhancing their function as agents of bioremediation. Different groups of bacteria, fungi and algae have been employed to clean up various environmental pollutants. This review discusses the types, mechanisms, and factors affecting microbial bioremediation. It also recommends possible steps that could be taken to promote the use of microbes as bioremediation agents.

KEYWORDS

microbial bioremediation, bioaugmentation, biostimulation, siderophores, biosorption

1 Introduction

The rise of urbanization and industrialization, has left the environment exposed to numerous pollutants which are toxic to living things. Pollutants arising from different industrial processes are major sources of pollution to the soil and aquatic environment. Different types and quantities of heavy metals are released during the industrial production process and as effluents after further industrial production. For instance, the wastewater from dye-producing companies are associated with antimony, chromium and mercury

(Methneni et al., 2021). The application of fertilizers, pesticides and herbicides in the agricultural sector generates pollutants that include aluminium, copper, zinc, nickel, lead and arsenic to the environment (Ayilara et al., 2020; Prabagar et al., 2021). Similarly, untreated pollutants from wastewaters of the agri-food industries disposed into river canals and other waterbodies have harmful effects on the environment (Siric et al., 2022a; AL-Huqail et al., 2022). Crude oil also serves as a major environmental pollutant particularly through pipeline vandalization, transportation leakage, and/or accidental spillage (Ogunlaja et al., 2019). During mining, some chemicals such as lead, arsenic, cadmium, and copper which are toxic to the immediate environment are released (Liu et al., 2020). Some other environmentally toxic chemicals including but not limited to cyanide and sulphuric acid are used during the mining process. (Ayangbenro et al., 2018; Orlovic-Leko et al., 2022). Equally, other industrial wastes such as those produced in cement-making industries release zinc, copper and cadmium and can be found in the top soils (Jafari et al., 2019). Chromium and lead from pharmaceutical effluents (Kumari and Tripathi, 2020), plastics containing lead, manganese, iron, copper, chromium, silver, cadmium, antimony and mercury all pollute water (Zhou et al., 2019). In addition, copper, arsenic, mercury, chromium, lead, nickel, cadmium and zinc from the coal industry serve as environmental pollutant (Sun et al., 2019). These heavy metals are very toxic to aquatic and terrestrial habitats and their inhabitants. In humans, mercury, cadmium and lead alters the central nervous system, especially in infants, while lead results in liver and kidney dysfunction, cardiovascular diseases, malfunctioning of the reproductive and immune system (Zwolak et al., 2019; Fashola et al., 2020a; Fashola et al., 2020b; Ayangbenro and Babalola, 2020). Cadmium causes cancers, skeletal disorders, neurotoxic and nefrotoxic complexities, and dysfunction of the reproductive system (Zwolak et al., 2019; Fashola et al., 2020a; Fashola et al., 2020b; Ayangbenro and Babalola, 2020). Wastes containing heavy metals are often improperly disposed into soil and water environments. When disposed into water bodies, they can lead to the death of fishes, and other aquatic inhabitants, otherwise, they are biomagnified and cause chronic diseases in humans and animals. Therefore, there is need for the remediation of these pollutants using physical, chemical, or biological methods. The physical and chemical methods have been used for years but they come with their drawbacks which include the need for an expert and special equipment for the chemical bioremediation procedure while the physical bioremediation procedure is expensive (Mahmood et al., 2021). This has called for the need for a better alternative which is the biological remediation (Bioremediation). Bioremediation is a most efficient, eco-friendly and cost effective technology for the transformation of contaminants (Sonune, 2021). Biological remediation can be carried out using both plants and microorganism, nonetheless, plants take a longer time to grow and cannot be easily manipulated like the microbes which makes the microbes more preferable (Hussain et al., 2022). In addition, microbes mitigates heavy metals and improve soil fertility and plant development (Chaudhary et al., 2023b). Hence, this review discusses the types, mechanism, challenges as well as the factors affecting microbial bioremediation, with recommendation on how to enhance the use of microbes in aquatic and terrestrial bioremediation.

2 Different pollutants and their toxicity on living things

Exposure of humans to air pollutants can cause developmental disorders, respiratory problems, cancers, cardiovascular diseases, and other health issues (Table 1). For instance, it has been reported that exposure to particulate matter in the air was associated with an increased risk of premature death in humans (Pope et al., 2019). Nitrogen oxides produced by combustion processes, are significant air pollutants. They irritate the respiratory system, cause cough, shortness of breath, and exacerbate asthma (Zhao et al., 2020). Equally, Sulfur dioxide, produced by burning fossil fuels, can cause respiratory and cardiovascular diseases, including bronchoconstriction, shortness of breath, and coughing. A recent study found that exposure to sulfur dioxide was associated with increased mortality from respiratory diseases in China (Luo et al., 2015). Volatile organic compounds (VOCs), emitted by various sources, including paints, cleaning products, and vehicle emissions, can cause eye, nose, and throat irritation, headaches, nausea, and dizziness. Some VOCs (such as benzene) are also carcinogenic, and are associated with an increased risk of leukemia (Bala et al., 2021). Water pollutants which include pesticides, heavy metals, and organic compounds are sometimes ingested by humans either directly or indirectly (through the consumption of aquatic animals). These pollutants can cause various health problems, including cancer, neurological disorders, and reproductive issues. It has been reported that exposure to heavy metals result in a higher risk of hypertension and kidney damage in humans (Wu et al., 2018; Rai et al., 2019).

Similarly, different animal diseases are caused by pollutants. Exposure to particulate matter (PM) can cause inflammation and damage to the respiratory system of animals, leading to respiratory diseases such as chronic obstructive pulmonary disease (COPD) and asthma (Manisalidis et al., 2020). When animals consume water contaminated with heavy metals, pesticides, and pharmaceuticals, it leads to reproductive disorders, liver damage, and cancer (Hitt et al., 2023). Nitrogen dioxide when present in the environment, reduces the growth of plants and the yield of crops while sulfur dioxide causes acid rain and acidification (Manisalidis et al., 2020). An impairment in the photosynthetic rhythm and metabolism is observed in plants exposed to ozone (Zuhara and Isaifan, 2018). In the aquatic environment, eutrophication occurs when there is a high concentration of nitrogen availability. This leads to algal bloom and cause death and disequilibration in the diversity of fish (Zuhara and Isaifan, 2018).

2.1 Types of remediation

There are different types of remediation, namely the physical, chemical and biological techniques. The physical remediation involves the use of skimmers, sorbent materials and booms.

TABLE 1 Effect of pollutants on living things.

Pollutants	Sources	Organism affected	Effect on the organism	References
Mercury	Mining and industrial production	Humans	Central Nervous System injury, hepatotoxicity and renal dysfunction	(Zhang et al., 2020)
Aluminium	Weathering, mining and industrial activities	Plants	Retardation of cell division, loosening of cell wall, destruction of plasma membrane, and the alteration of calcium homeostasis	(Rehman et al., 2021)
Pesticides (containing deltamethrin, fenthion, spinosyn, etc.) and heavy metals such as aluminum, copper and zinc	Agricultural and mining activities	Animals (bats)	DNA damage and morphology hepatocytes	(de Souza et al., 2020)
Cadmium	Agricultural amendments	Plants	Chlorosis, retarded growth, and alteration in water balance	(Rehman et al., 2021)
Chromium and lead	Industry and mining	Plants	Declined growth, reduced photosynthesis and root growth	(Zeng et al., 2012)
Lead	Industrial activities	Humans	Lung dysfunction, liver damage, central nervous system injury and cardiovascular dysfunction	(Balali-Mood et al., 2021)
Chromium	Industrial activities	Humans	Kidney disease, skin diseases and cancers	(Deng et al., 2019; Pavesi and Moreira, 2020)
Cadmium	Smoking and industrial activities	Humans	Liver damage, lung diseases, cancer and bone degeneration	(Fay et al., 2018; Wang Y. et al., 2018)
Arsenic	Industrial activity	Humans	CNS injury, skin and hair infection, cardiovascular dysfunction and liver damage	(Balali-Mood et al., 2021)
Chloride	Industrial activities	Animals (rats)	Kidney destruction and central nervous system injury	(Aragao et al., 2018)

Boom is a physical barrier made of materials that absorbs oil pollutants and prevents it from spreading before a further remediation procedure is carried out (Vocciante et al., 2019) (Figure 1). Skimmers and sorbents are methods that are further used to absorb and adsorb pollutants after booms (Kumari et al., 2019). The major challenge associated with the use of bloom remediation technique is that it is dependent on the buoyancy and roll response. When the boom is buoyant, it floats and remains longer on the water surface. The roll response refers to the torque required to rotate the bloom from its vertical position. That is, an

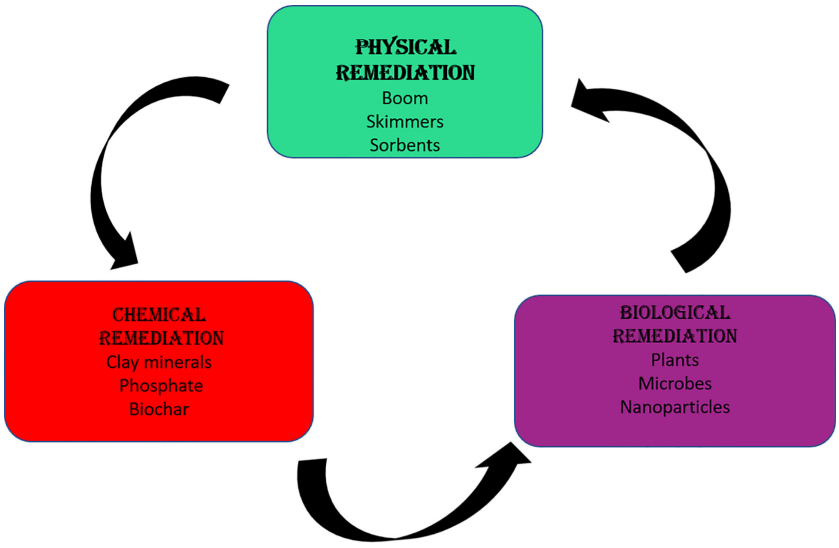


FIGURE 1
Types of bioremediations.

increased roll response results in a higher remediation process (Dhaka and Chattopadhyay, 2021).

Chemical remediation is the process of adding chemicals such as clay minerals, phosphate, biochar, aluminum salts, silicocalcium materials, and sulfide to stabilize and remove heavy metals from the environment. The mechanism behind the use of these chemicals include adsorption, reduction, oxidation, complexation, precipitation and ion exchange (Xu et al., 2022). Chemical remediation technique is an easy, simple, and rapid technique; however, the chemical used can also serve as a source of environmental pollution (Xu et al., 2022) (Figure 1).

Bioremediation is another method of pollution treatment, it is a sustainable, affordable and safe remediation technique (Kumar A. et al., 2021; Kumar G. et al., 2021; Patel A. K. et al., 2022). The technology involves the use of organics such as plants and microbes. The viability of this method depends on the nature, location and level of pollution (Patel A. K. et al., 2022). Microbes on the other hand have proved to be efficient in the remediation of environmental pollutants. They are preferred to plants in remediation, this is due to their ease of growth, rapid growth period and easy manipulation. It is therefore necessary to improve the use of microbes as agent of bioremediation to promote a sustainable environment.

3 Different microbes used as bioremediation agents

Microorganisms can convert toxic elements into water, carbon dioxide, and other less toxic compounds, which are further degraded by other microbes in a process referred to as mineralization (Mahmoud, 2021; Kumar G. et al., 2022). Bioremediation can be carried out using bacteria, fungi, algae, etc. (Table 2). Microbes are ubiquitous in nature, and they utilize a wide range of substrates as carbon source; hence, they are found in unusual environments where they can absorb a wide range of pollutants (Kour et al., 2022). Also, their ability to survive in odd environments promote their efficiency. For example the acidophiles survive in acidic environments, the psychrophiles thrive in cold climates and the halophiles survive in saline region (Perera and Hemamali, 2022).

4 Mechanisms of microbial bioremediation

Microbes can remove pollutants from the environment using different mechanisms. These mechanisms can be placed into two broad categories namely immobilization and mobilization (Ndeddy Aka and Babalola, 2016; Verma and Kuila, 2019). Mobilization process involves, enzymatic oxidation, bioleaching, biostimulation, bioaugmentation and enzymatic reduction procedure. On the other hand, immobilization includes bioaccumulation, complexation, biosorption, and precipitation (solidification) (Tak et al., 2012; Ayangbenro et al., 2019). During mineralization, microbes help transform pollutants into end products such as carbon dioxide and water or other intermediate metabolic substances. Similarly, immobilization is the conversion of compounds into a form where it will be unavailable in the environment. For instance, the conversion of nitrate nitrogen into organic nitrogen (Pratush et al., 2018). The method is usually utilized for the bioremediation of heavy metals, especially in highly contaminated environments.

Immobilization can be carried out using the *in-situ* and the ex-situ methods (Pratush et al., 2018). The ex-situ process involves the removal of polluted soils from the site of pollution to another location where it would undergo a microbial process to immobilize the metal ions responsible for the contamination (Ayangbenro and Babalola, 2017). On the other hand, in the *in-situ* procedure, the pollution is treated on site (Cao et al., 2020). Microbes such as *E. asburiae* and *B. cereus* have been reported to be involved in immobilization of heavy metals which pollute the environment (Fashola et al., 2020a). During microbial bioremediation, microbes protect themselves from toxic compounds by forming hydrophobic or solvent efflux pump that protects the outer membrane of the cell (Verma and Kuila, 2019).

4.1 Enzymatic oxidation

Enzymatic oxidation is the process of oxidizing pollutant compounds from a higher oxidation state to a lower one, during which heavy metals lose an electron and become less toxic. This process utilizes an enzyme (oxidoreductase) released by the microbes involved. This method is highly effective in the remediation of dyes, phenols, and other pollutants which are not easily degraded by bacteria (Unuofin et al., 2019). The oxidative enzymes form radicals which can be broken down into different fractions, eventually forming compounds with high molecular weight (Unuofin et al., 2019). An example of an oxidoreductase enzyme is laccase, which catalyzes the oxidation of aromatic amines (Gangola et al., 2018). Other examples are phenols and polyphenols, which cause the reduction of molecular oxygen to water (Kushwaha et al., 2018; Sahay, 2021). Laccase production has been reported in *Pycnoporus* sp. and *Leptosphaerulina* sp. where it was outlined to degrade heavy metals (Copete-Pertuz et al., 2018; Tian et al., 2020).

4.2 Enzymatic reduction

This process is the opposite of enzymatic oxidation, here, the pollutants are converted to a reduced oxidized state where they become insoluble. Obligate and facultative anaerobes carry out the process; this method is effective in the bioremediation of compounds such as polychlorinated dibenzo-p-dioxins and dibenzofurans (Zacharia, 2019). Equally, chrome reductase catalyzes the reduction of hexavalent chromium to trivalent chromium, and azoreductase reduces the azo compounds by cleaving to azo bonds (Saxena et al., 2020). Much more research is needed to unravel other organisms which are capable of bioremediating pollutants in the environment.

TABLE 2 Different microbes used in bioremediation.

Type of organism	Species	Pollutant remediated	References
Bacteria			
	Bacillus licheniformis JUG GS2 (MK106145) and *Bacillus sonorensis*	Naphthalene	(Rabani et al., 2022)
	Bacillus sp., *Rhodopirellula* sp., *Rhodovibrio* sp. and *Formosa* sp.	Hydrocarbon	(Machado et al., 2019)
	P. cepacia, *B. coagulans*, *B. cereus*, and *Serratia ficaria*	Diesel oil	(Miri et al., 2022)
	Pseudoalteromonas sp. and *Agarivorans* sp.	Hydrocarbons	(Dell'Anno et al., 2021)
	P. aeruginosa and *Aeromonas* sp.	Chromium, uranium, nickel and copper	(Gaur et al., 2022)
	E.coli	Hexavalent chromium	(Mohamed et al., 2020)
	Oscillatoria laete-virens, *Arthrospira platensis*, *Pseudochlorococcum typicum* and *Spirogyra insignis*	Lead	(Song et al., 2019)
	Microbacterium sp., *Micrococcus* sp., *Bacillus* sp., and *Shigella* sp.	Uranium and Arsenic	(Bhakat et al., 2019)
	Lysinibacillus sphaericus CBAM5	Lead, cobalt, copper crude oil and chromium	(Kharangate-Lad and D'Souza, 2021)
	Pseudomonas aeruginosa	Crude oil	(Mukjang et al., 2022)
	Cyclotella cryptica, *Pseudochlorococcum typicum*, *Spirogyra hyaline* and *Chlamydomonas reinhardtii*	Mercury	(Shah and Jain, 2020)
	Dehalococcoides sp.	Chloroethenes	(Dutta et al., 2022)
	Burkholderia sp. and *Myceliophthora thermophila*	N, N-dimethylpphenylenediamine and polycyclic aromatic hydrocarbons	(Mohapatra and Phale, 2021)
	Bacillus sp. and *Staphylococcus* sp.and	Endosulfans	(Liu et al., 2018)
	A. versicolor, *Cladosporium* sp., *Paecilomyces* sp., *A. fumigatus*, *Paecilomyces* sp., *Terichoderma* sp. and *Cladosporium* sp.	Cadmium	(Unuofin et al., 2021)
	Fusarium sp., *Corynebacterium propinquum*, *P. aeruginosa* and *Alcaligenes odorans*	Oils	(Pande et al., 2020)
	C. reinhardtii, *Ulothrix tenuissima* and *Spirulina* sp.	Chromium	(Aregbesola et al., 2020)
	Ralstonia sp., *Microbacterium* sp., *Pseudomonas* sp. and *Acinetobacter* sp.,	Aromatic hydrocarbons	(Basu et al., 2018)
	Aerococcus sp., and *Rhodopseudomonas palustris*	Cadmium, lead and chromium	(Sravya and Sangeetha, 2022)
	P. aeruginosa, *Corynebacterium propinquum*, *Alcaligenes odorans* and *B. subtilis*	Phenol	(Gaur et al., 2018)
	K. oxytoca, *B. firmus*, *B. macerans*, and *Staphylococcus aureus*	Vat dyes	(Sangkharak et al., 2020)
	Chlorella sp. and *Spirulina* sp.	Lead, nickel and dichromate	(Geetha et al., 2021)
	Saccharomyces cerevisiae and *Cunninghamella elegans*	Heavy metals and mercury	(Duc et al., 2021)
	Bacillus licheniformis	Dyes	(Mousavi et al., 2021)
	Bacillus subtilis and *Pseudomonas fluorescence*	Iron and zinc	(Siric et al., 2022b)
	Pseudomonas sp., *Bacillus* sp., *Escherichia* sp., *Shewanella* sp., *Enterobacter* sp. and *Thermus* sp.	Chromium	(Mousavi et al., 2021)
Fungi			
	Phanerochaete chrysosporium	N-heterocyclic explosives, benzene, xylene, ethylbenzene, toluene and organochlorines	(Singh et al., 2020)

(Continued)

TABLE 2 Continued

Type of organism	Species	Pollutant remediated	References
	Phanerochaete chrysosporium	4,4 dibromodiphenyl ether	(Sen et al., 2019)
	Saccharomyces cerevisiae	Arsenic	(Verma et al., 2019)
	Aspergillus sp.	Arsenic	(Mohd et al., 2019)
	Coprinus comatus	4-Hydroxy-3,5- dichlorobiphenyl	(Li et al., 2018)
	Aspergillus sp. and *Penicillium* sp.	Aliphatic hydrocarbons, polycyclic aromatic hydrocarbons and chlorophenols	(Li et al., 2020)
	Aspergillus sp.	N-hexadecane	(Al-Hawash et al., 2018)
	Phomopsis liquidambari	Phenanthrene	(Fu et al., 2018)
	Ganoderma lucidum	Pyrene	(Agrawal et al., 2018)
	Trichoderma sp., *Penicillium* sp. and *Aspergillus* sp.	Cobalt and copper	(Dusengemungu et al., 2020)
Algae			
	Microcystis aeruginosa	Arsenic	(Wang Z. et al., 2018)
	Chlamydomonas reinhardtii and *S. almeriensis*	Arsenic	(Saavedra et al., 2018)
	Fucus vesiculosus	Zinc	(Brinza et al., 2020)
	Chlorococcum humicola	Iron	(Chugh et al., 2022)
	Chlorella sp., *Isochrysis galbana* and *Phaeodactylum tricornutum*	Phenol	(Wu et al., 2022)
	F. vesiculosus	Chromium, nickel, cadmium and lead	(Moreira et al., 2019)
	Cystoseria indicant	Nickel and cadmium	(Moreira et al., 2019)
	Chlamydomonas reinhardtii	Chromium and cadmium	(Nowicka et al., 2020)
	Microcystis aeruginosa	Cadmium	(Deng et al., 2020)
	Scenedesmus accuminatus, Scenedesmus protuberans and *Cyclotella* sp.	Cadmium	(Vo et al., 2020)
	Chlorococcum humicola	Cobalt	(Chugh et al., 2022)

4.3 Bioaugmentation

Microorganisms are specially added to polluted sites to feed on toxic pollutants in a process referred to as bioaugmentation. It is a very effective, rapid and cost-effective method of bioremediation (Mahmoud, 2021). External microbes are added to polluted sites to augment the resident microbes. In other cases, it could also involve the isolation and genetic modification of microbes from the site of pollution before returning them to the same site for remediation. Genetic manipulation of resident microbes of polluted sites is carried out because the organisms may naturally not be capable of degrading the pollutant present at a site, and hence are modified to enhance their ability. In some other cases, non-resident microbes are added to polluted areas to promote the degradation of pollutants. The effectiveness of these new strains depends on some factors, which include the ability to compete with the resident microbes and the ability to adapt to the new environment (Fashola et al., 2016; Ayangbenro and Babalola, 2017; Goswami et al., 2018; Babalola et al., 2019). *Burkholderia* sp. FDS-1 which was added to a polluted site, has been reported to degrade nitrophenolic compound present in pesticides polluted soil to a less toxic form at a slightly acidic pH and a temperature of about 30° C (Goswami et al., 2018; Ojuederie et al., 2021) (Table 3).

4.4 Biostimulation

Biostimulation is the addition of nutrients (such as nitrogen, potassium, phosphorus), metabolites, electron donors, enzymes, electron acceptors, biosurfactants, etc., which are limiting to the soil to enhance the activity of the resident microbes and increase the remediation process (Ojuederie and Babalola, 2017; Ayangbenro and Babalola, 2018). It is an affordable, environmentally friendly and efficient process (Goswami et al., 2018). Compared to the bioaugmentation method, the biostimulation method is preferable because indigenous microbes are more competitive than the introduced ones (Sayed et al., 2021), and this method helps to maintain the natural microbial diversity balance of the environment. Nivetha et al. (2022) reported the effectiveness of *Bacillus* sp., *Rhodococcus* sp., *Staphylococcus* sp., *Klebsiella* sp.,

TABLE 3 Mechanism of Bioremediation.

Microorganism	Pollutant remediated	Mechanism of remediation	References
Bacillus sp.	Nickel	Biosorption	(Taran et al., 2019)
Lysinibacillus sphaericus	Azo dyes	Enzymatic reductase	(Lu et al., 2020)
Oudemansiella canarii	Congo red dye	Enzymatic reduction	(Iark et al., 2019)
Pseudomonas aeruginosa and *Bacillus cereus*	Lead and Cadmium	Bioaugmentation	(Nath et al., 2018)
Bacillus sp., *Lysinibacillus* sp. and *Rhodococcus* sp.	Aluminium, lead, cadmium, and copper	Bioaugmentation	(Nanda et al., 2019)
Cupriavidus sp.	Cadmium	Bioprecipitation	(Li et al., 2019)
Pseudomonas sp.	Copper and lead	Bioattenuation	(Nanda et al., 2019)
Bacillus subtilis	Lead	Bioimmobilization	(Qiao et al., 2019)
Desulfovibrio desulfuricans	Copper, zinc and cadmium	Extracellular sequestration	(Thakare et al., 2021)
Pseudomonas aeruginosa	Cadmium	Biosorption	(Chellaiah, 2018)
Sulfolobus solfataricus	Copper	Intracellular sequestration	(Thakare et al., 2021)

Pseudomonas sp., and *Citrobacter* sp. in bioremediation of heavy metals through the biostimulation technique. Unfortunately, as effective as this method of bioremediation may be, it could lead to some other environmental complications, including eutrophication due to the excess nutrient present in the environment. Also, if the sources of the nutrients are chemicals (synthetic), they can serve as a source of pollution to the environment defeating the initial purpose of bioremediation (Table 3).

4.5 Bioleaching

Bioleaching is the process of utilizing acidophilic microbes to promote the solubilization of heavy metals which are in a solid state from the sediment matrix. The process is particularly useful for iron or sulfur pollutants (Sun et al., 2021; Bhandari et al., 2023). Therefore, iron- or sulfur-oxidizing bacteria are majorly recruited for this process; examples of such organisms are *A. thiooxidans*, *Aspergillus* sp., *Mucor* sp., *Penicillium* sp., *Cladosporium* sp. and *Rhizopus* sp. (Medfu Tarekegn et al., 2020). These microbes create an acid environment and solubilize heavy metals in an immobilized state, into an aqueous solution (Medfu Tarekegn et al., 2020).

4.6 Biosorption

This is the adsorption of heavy metals from pollutants through proton and ion displacement, complexation, chelation and physical interaction with electrostatic forces (Mahmoud, 2021). It involves the removal of contaminants from solutions as a result of the outer cell shield of bacteria, fungi and algae which are bioremediation agents. Generally, metals are linked through the active groups of the compounds which exist at the cells surface layer. This results in the transfer of ion between metal cations and the negatively charged active group potentials present at the outer part of the microorganism structure. *Rhodococcus erythropolis*, *Streptomyces* sp. K11, and *Bacillus anthracis* have been reported to be capable of bioremediation through the biosorption process (Mathew and Krishnamurthy, 2018; Baltazar et al., 2019; Sedlakova-Kadukova et al., 2019). Oftentimes, heavy metal pollutants (e.g., gold, zinc and copper) have some economic importance and are very useful in industrial processes. Hence, the ability of the compounds to be recovered through a process called desorption (using the solution of weak mineral solution or chelating compounds), which is a reversible step in biosorption makes it a good process (Medfu Tarekegn et al., 2020).

Complexation involves using ligand to form a complex with inorganic metals, which are pollutants in the environment, especially solid wastes (Ayangbenro and Babalola, 2017). Complexation is carried out mainly through different agents, namely the high molecular weight ligands, siderophores and toxic metal-binding compounds as well as the low-molecular weight organic acids (alcohols, tricarboxylic acids and citric acids) (Pratush et al., 2018). Complexation occurs when extracellular polymeric substances, found on the surfaces of microbes interact with heavy metals which pollute the environment (Xie et al., 2020). Xiao et al. (2019) reported the removal of copper (II) oxide and hexavalent chromium from wastewater using biochar in a mechanism which includes complexation. The organisms that have been reported to be involved in complexation include *Rhodobacter blasticus* (Bai et al., 2019) and *B.lichenformisis* (Wang et al., 2019).

When microbes are exposed to a polluted environment where there is iron-deficiency, they produce siderophores which are iron chelators. The siderophores have binding groups such as hydroxamate, catecholate and phenolates that form complexes with heavy metals and increase their solubility (Khan et al., 2018). Siderophores are capable of producing reactive oxygen species, which also enhance their function as bioremediation agents for organic contaminants (Albelda-Berenguer et al., 2019). Cyanobacteria have been reported to be effective as bioremediation agents due to the production of siderophores; for example, they are capable of bioremediating complex compounds like polythene and are capable of producing different types of

siderophores, which include the anachelin, synechobactin and schizokinen (Arstol and Hohmann-Marriott, 2019; Sarmah and Rout, 2020) (Table 3).

4.7 Bioaccumulation

Bioaccumulation refers to the process where the rate of absorption of a compound is more than the rate at which the compound is lost. This process leads to the (toxic) build-up of compounds in the intracellular portion of the microbes. (Sharma et al., 2022a). Heavy metals move across the membrane of microbes using different mechanisms such as carrier-mediated transport, protein channel and ion pumps (Mir-Tutusaus et al., 2018). Many organisms have been reported to be very active in bioaccumulation of heavy metals. For example, *Rhizopus arrhizus*, bioremediates mercury, *Pseudomonas putida*, bioremediates cadmium and *Aspergillus niger* bioremediates thorium (Sharma et al., 2022a).

4.8 Precipitation

This is the conversion of heavy metals or pollutants into precipitates or crystals, resulting in a reduced toxicity level; this process can occur during the biogeochemical cycling to form deposing of metals (iron and manganese), mineralized manganese and silver as well as microfossils, due to the activity of enzymes and galactosis of secondary metabolites (Sharma et al., 2022a). For instance, sulfate-reducing bacteria are capable of converting organo-phosphate to ortho-phosphate when the pH is alkaline (i.e. above 7) (Pratush et al., 2018). Similarly, *Bacillus subtilis* and *Oceanobacillus indicireducens* have also been reported to be associated with the precipitation of heavy metals in the environment (Maity et al., 2019).

5 Factors affecting microbial bioremediation

The ability of microbes to bioremediate heavy metals is determined by different factors, which include the total metal ion concentration, redox potential, chemical forms of the metals, competition among microbes, pH, temperature, soil structure, presence of oxygen, moisture content, nature of the soil and the solubility of the heavy metal in water (Medfu Tarekegn et al., 2020). At acidic pH, free ionic species are formed by heavy metals, leading to the availability of more protons which would saturate the binding site of the metals. The pH of an environment affects the structure of the pollutant and also determines the ability of the microbe to survive in such an environment; the optimum pH that enhances bioremediation falls between 6.5 and 8.5 (Kharangate-Lad and D'Souza, 2021).

Microbes compete for carbon which is a limited resource and serve as an energy source for microbes. Therefore, the inherent ability of the microbes, which compete better to degrade heavy metal pollutant, would affect the biodegradation rate. In addition to carbon, microbes responsible for biodegradation also require nitrogen (N) and phosphorus (P), thus it is important to balance the C:N:P ratio to enhance the rate of biodegradation, in environment when these essential nutrients are limited. They can be added to increase microbial activities (Bala et al., 2022). The type and population of microbes determine the rate and success of a bioremediation process, for instance in the laboratory, a strain of organism might successfully bioremediate a particular heavy metal, which becomes problematic in a field situation where a consortium of microbes would be needed (Patel A. B. et al., 2022). The molecular nature, gene and enzyme induction, metabolite production, growth efficiency and survival rate affect the ability of individual microbes as bioremediation agents (Kebede et al., 2021). In addition, the ionization of the cell wall's chemical moieties, the configuration of the microbial cell wall and sorption site also affect the rate of microbial biodegradation (Mahmoud, 2021).

The amount of moisture present in an environment affects the solubility of the heavy metals in water, as well as their availability, pH and osmotic pressure (Medfu Tarekegn et al., 2020). At a high moisture content, the microbial biodegradation rate is very low. This might be a result of an anaerobic condition that is created, which prevents the survival of aerobic microbes. Also, at a low moisture content, microbes might not be able to survive; hence an optimum moisture content is required for a successful microbial biodegradation process. In the cold regions where only psychrophiles can survive, the rate of microbial degradation of heavy metals is slow. This is because metabolic activities are reduced as the microbial transport channels is freezed by the sub-zero water; the degradation of each compound also occurs at different temperature even though most bioremediation processes are favored by high temperature (Ren et al., 2018; Bala et al., 2022; Sharma et al., 2022c). At an increased temperature, the rate of heavy metal solubility is increased, which consequently increases their rate of availability as well as the rate of microbial biodegradation (Mahmoud, 2021).

Similarly, the chemical structure, bioavailability, concentration, toxicity and stability of the metal or pollutant determines the rate at which microbial biodegradation takes place (Kebede et al., 2021). For instance, heavy metals with a simple chemical structure and low concentration would be easier to be remediated by microbes compared to those with a complex chemical structure and high temperature. Cycloalkane compounds that are highly condensed as well as high molecular weight polymatic hydrocarbons (those containing four rings and above) are more difficult to degrade compared to the lighter polyhydrocarbons (anthracene, naphthalene and phenanthrene) and unbranched alkanes (alkanes with intermediate length of about C_{10}–C_{25}) (Kebede et al., 2021). Hence, in order of ascending degradation, the n-alkanes are more easily degraded compared to the branched alkanes, low molecular weight aromatics, high molecular weight hydrocarbons and the asphaltenes (Imam et al., 2019). Biodegradation is carried out aerobically and anaerobically. The ability of an organism which degrades a particular nutrient to survive in such an environment depends on the nature of the organism (Jacob et al., 2018). For example, oxygenase associated with organisms that are active in aerobic regions is only produced in the presence of oxygen.

Different soil parameters, including the soil region, moisture-holding capacity texture and particle size, affect the rate of microbial biodegradation (Alvarez et al., 2020). There is a higher population and diversity of microbes at the top layer of the soil (0-10cm). This is due to the increased availability of oxygen and organic matter, which is the opposite of what happens in sediment soils (Ndeddy Aka and Babalola, 2017). In soils with fine particles, such as clayey soils, hydrocarbon retention takes place more at the surface, which renders the nutrient of the soil and oxygen unavailable. Therefore the best soil texture that promotes increased microbial biodegradation is the well-drained soil which supports oxygen availability and inhabits more soil microbes (Huang et al., 2019). The presence of salinity has an effect on the hydrocarbonoclastic activity of the halotolerant and halophilic microbes, and it also exposes the soil microbes to stress conditions. The osmotic pressure of microorganisms increases as the saline concentration of an environment increases. This has a direct negative impact on the metabolic activities, of the microbes as well as the transportation system and solubility of the heavy metals (Imron et al., 2020; Kebede et al., 2021).

6 Microbial enzymes used in bioremediation

Different microbial enzymes have been reported to be helpful in the removal of pollutants (especially heavy metals) in the environment (Verma and Kuila, 2019; Bhatt et al., 2021a; Chaudhary et al., 2023a) (Table 4). Mechanisms such as elimination, oxidation, ring-opening and reduction are used by enzymes in bioremediation (Bhandari et al., 2021). Different factors which include temperature, contact time, concentration and pH affect the potency of microbial enzymes (Bhandari et al., 2021). Enzyme bioremediation is expensive and time-consuming and therefore cannot be used when there is an urgent need for bioremediation (Narayanan et al., 2023). Equally, the stability and activity of the pollutants, affects the potency of the bioremediation process. It is difficult to determine and discover multiple sources of a particular type of enzyme which might make the procedure unsustainable (Narayanan et al., 2023).

7 Molecular approaches for validating microbial remediation

Molecular mechanisms help to unravel the microbial metabolism, genes, nature, diversity and dynamics of microbes involved in microbial remediation. Diverse molecular mechanisms are utilized in the study of microbes used in bioremediation. Metabolic and protein profiling, sequencing as well as the use of advanced bioinformatics resources are particularly used to unravel the different groups of microbes and the factors affecting them in bioremediation process (Sharma et al., 2022b). On the other hand, conventional and culture-dependent molecular methods are also used in the monitoring of microbial communities during bioremediation. These methods include the use of terminal-restriction fragment (T-RF) length polymorphism, amplified ribosomal DNA restriction analysis, temperature gradient gel electrophoresis, randomly amplified polymorphic DNA analysis, length heterogeneity polymerase chain reaction, amplified fragment length polymorphisms, denaturing gradient gel electrophoresis, length heterogeneity polymerase chain reaction, automated ribosomal intergenic spacer analysis and single strand conformation polymorphism (Bharagava et al., 2019).

TABLE 4 Enzymes used in Microbial Bioremediation.

Enzyme	Microbial sources	Pollutant remediated	References
Hydrolases	*T. fusca* *Pseudomonas* sp., *Burkholderia* sp., *Ralstonia* sp., *Achromobacter* sp., *Sphingomonas* sp. *and Comamonas* sp.	Polyester plastics Hydrocarbons	(Gricajeva et al., 2022) (Dave and Das, 2021)
Oxidoreductase	*Bacillus safenis*	Xenobiotics	(Malakar et al., 2020)
Phosphotriesterase	*Brevundimonas diminuta*	Pesticides	(Thakur et al., 2019)
Lipase	*Bacillus pumilus*	Oil containing industrial wastewater	(Saranya et al., 2019)
Laccase	*Pseudomonas putida*	Synthetic dyes	(Bhandari et al., 2021)
Lignin peroxidase	*Escherichia coli* and *Bacillus* sp. F31	Synthetic dyes	(Dave and Das, 2021)
Dehydrogenase	*E. coli* *S. rhizophila*	Steroids Polyvinyl alcohol	(Ye et al., 2019) (Wei et al., 2018)
Protease	*Bacillus subtilis*	Casein and feather	(Bhandari et al., 2021)
Amylase	*Bacillus cereus*	Waste water pollutants	(Sonune and Garode, 2018)
Oxygenase	*Pseudomonas* sp.	Pesticides	(Malakar et al., 2020)
Lipase	*Bacillus pumilus*	Palm oil	(Saranya et al., 2019)

Moreover, omics approaches such as transcriptomics, proteomics and metagenomics have greatly contributed in this field. Metagenomics involve the extraction of genomic DNA from all forms of life residing in a sample. Thereafter, the DNA will be fragmented, cloned, transformed and screened in the metagenome library (Bharagava et al., 2019). The approaches to metagenomics include metabolomics, metatranscriptomics, fluxomics and metabolomics. Metatranscriptomics involve the use of metagenomic mRNA which unravel the function and expression of microbes present in a sample (Mukherjee and Reddy, 2020). Metaproteomics involved the assessment of all the protein samples that comes from environmental samples (Bargiela et al., 2015). Metabolomics is the identification and quantification of all the metabolites released into an environment (Liu et al., 2022). Fluxomics refers to the different approaches used to study the rate of metabolic activities in a biological sample (Kumar V. et al., 2022). More recently, the use of Next-Generation sequencing which is viewed as the most powerful technology for gene sequencing has become more popular (Eisenhofer et al., 2019).

8 Other bioremediation metabolites produced by microbes

Microbes produce metabolites such as organic acids, biosurfactants and polymeric substances which are also used in bioremediation. Organic acids improve the bioavailability, mobility and solubility of metals; examples of organic acids include citric acids, malate and acetic acids (Saha et al., 2021). Polymeric substances are beneficial in bioremediation by enhancing the phytostabilization of metals (through mobility), examples of polymeric substances include polyesters, polysaccharides and polyphosphates. Equally, biosurfactants which include viscosin, polymixin, glycoprotein and gramicidin help to solubilise, mobilise and increase the bioavailability of hydrophobic substrates (Ojuederie and Babalola, 2017; Saha et al., 2021).

9 Recent advancements in microbial bioremediate

Lately, many improvements have been observed with the use of microbes as agents of bioremediation. Microbial glycoconjugates help to reduce the surface tension, increase the bioavailability, and create a solvent interface of organic pollutants. This helps to enhance the removal of the pollutants in the environment (Bhatt et al., 2021b). Atakpa et al. (2022) reported the use of microbial glycoconjugates from *Scedosporium* sp. and *Acinetobacter* sp. in the biodegradation of petroleum hydocarbons.

Microbial biofilms which consist of polysaccharides, extracellular DNAs and proteins are also lately used in the bioremediation of organic pollutants (Sonawane et al., 2022). They are particularly used in the remediation of recalcitrant pollutants. The technology is presently being made better by improving on the quorum sensing, environmental factors and surface of adhesion (Sonawane et al., 2022). In a research carried out by Andreasen et al. (2018), it was revealed that *Exiguobacterium profundum* was able to significantly reduce the concentration of arsenic in synthetic wastewater after 48 hours of incubation.

Bioelectrochemical system is another emerging technology which combines the use of biological and electrochemical methods in the control of pollutants (Ambaye et al., 2023). This technology helps to majorly remediate petroleum hydrocarbon pollutants and its efficiency depends mainly on the syntrophic and cooperative interactions between the members of the microbial groups involved (Ambaye et al., 2023). Sharma et al. (2020) stated that *Pseudomonas* sp., *Ralstonia* sp., *Rhodococcus* sp., and *Thauera* sp. are capable of remediating phenanthrene from petroleum hydrocarbon polluted soils.

Nanotechnology is a thriving method of pollution control globally. Nanomaterials can be sourced from different sources which include the physical and chemical sources (Shanmuganathan et al., 2019). The efficiency of nanoparticles as bioremediation agents is dependent on different factors such as the size, chemical nature, surface coating and shape of the nanoparticles (Tan et al., 2018). Other factors such as the nature of the pollutants, type of media, temperature and the environmental pH affect the potency of nanoparticles in the bioremediation process (Tan et al., 2018). For instance, carbon dots nanoparticles have recently gained attention in the remediation of environmental pollutants owing to their abundance, low toxicity and unique optical properties (Long et al., 2021). It is therefore necessary to carry out further research to unravel technologies and mechanisms to improve the efficiency of the bioremediation process.

10 Future perspectives and conclusions

A number of research endeavours have been carried out on the use of microbial enzymes for bioremediation of waste materials; however, it is very important to improve the process to ensure a safer and more sustainable environment. It is imperative to intensify research to unravel novel microbes that can effectively and rapidly bioremediate different pollutants, especially from industrial sources. Perhaps the novel microbes and their enzymes may have the inherent ability to bioremediate pollutants better than the presently used ones. It is also very important to carry out more studies to innovate rapid detection methods to reveal the progress or help to confirm total biodegradation of pollutants in the environment. Similarly, microbes presently used in bioremediation can be genetically modified to produce more enzymes which will enhance their biodegrading ability. A combination of different microbial consortium other than a single microbial consortium would be a better approach to bioremediation, as this would bring about the presence of different organisms which utilizes different substrate, consequently increasing the rate of microbial biodegradation.

Often, microbes are majorly used to degrade organic substrates, leaving out the persistent inorganic pollutants. Hence, research

should be intensified to discover microbes that are capable of degrading inorganic (synthetic) pollutants. In recent years, nuclear wastes generated from the research sectors, hospitals, fuel processing plants and nuclear reactors have remained a global source of pollution. Therefore, the use of microbes and microbial enzymes in the bioremediation of nuclear wastes should be seriously taken into consideration. Occasionally, microbes themselves serve as a source of pollution instead of remediating pollutants. An example of such can be found when microbial biostimulation which results in algal bloom is carried out Consequently, methods to prevent this should be devised to ensure a sustainable environment.

Furthermore, in nature (outside the laboratory), the degradation of different compounds occurs at a different temperature, while the survival of microbes in nature are also environment-specific (temperature). It is therefore essential to carry out more field research to determine the optimum temperature for the degradation of different compounds in nature. In addition, it is also essential to find a balance between the environmental temperature and the temperature for the survival of different microbes in the environment. This would help to prevent bioremediation failure when external microbes are to be recruited or introduced to an environment. As positive and effective microbes might be recruited in the bioremediation of pollutants, it is important to carry out follow-up research to understand their effects on the environment after bioremediation, as some organisms which are introduced to an environment might later constitute pollution to the environment through mutation and other means. Hence, there should be regulatory bodies which would monitor the potential risk associated with microbes in specific environments.

Finally, if enzymes or microbes are directly applied to the soil, they might die or lose their potency before the remediation process begins; therefore, their combination with other agents, such as the nanoparticle could enhance their activity. More awareness is needed on the adoption of microbial degradation, and this will help policymakers as well as the populace to utilize this method. Many people unaware of this procedure might use the available conventional method, which might not be as safe and effective as the microbial biodegradation.

Author contributions

MA and OB conceptualized, wrote, reviewed, and edited the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This research was funded by the National Research Foundation, South Africa, grant number UID: 123634; 132595.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Agrawal, N., Verma, P., and Shahi, S. K. (2018). Degradation of polycyclic aromatic hydrocarbons (phenanthrene and pyrene) by the ligninolytic fungi ganoderma lucidum isolated from the hardwood stump. *Bioresour. Bioprocess.* 5 (1), 1–9. doi: 10.1186/s40643-018-0197-5

Albelda-Berenguer, M., Monachon, M., and Joseph, E. (2019). Siderophores: from natural roles to potential applications. *Adv. Appl. Microbiol.* 106, 193–225. doi: 10.1016/bs.aambs.2018.12.001

Al-Hawash, A. B., Zhang, J., Li, S., Liu, J., Ghalib, H. B., Zhang, X., et al. (2018). Biodegradation of n-hexadecane by aspergillus sp. RFC-1 and its mechanism. *Ecotoxicol. Environ. Saf.* 164, 398–408. doi: 10.1016/j.ecoenv.2018.08.049

AL-Huqail, A. A., Kumar, P., Eid, E. M., Adelodun, B., Abou Fayssal, S., Singh, J., et al. (2022). Risk assessment of heavy metals contamination in soil and two rice (Oryza sativa l.) varieties irrigated with paper mill effluent. *Agriculture* 12 (11), 1864.

Alvarez, L. M., Ruberto, L. A. M., Gurevich, J., and Mac Cormack, W. P. (2020). Environmental factors affecting reproducibility of bioremediation field assays in Antarctica. *Cold Regions Sci. Technol.* 169, 102915. doi: 10.1016/j.coldregions.2019.102915

Ambaye, T. G., Vaccari, M., Franzetti, A., Prasad, S., Formicola, F., Rosatelli, A., et al. (2023). Microbial electrochemical bioremediation of petroleum hydrocarbons (PHCs) pollution: recent advances and outlook. *Chem. Eng. J.* 452, 139372. doi: 10.1016/j.cej.2022.139372

Andreasen, R., Li, Y., Rehman, Y., Ahmed, M., Meyer, R., and Sabri, A. (2018). Prospective role of indigenous *Exiguobacterium profundum* PT2 in arsenic biotransformation and biosorption by planktonic cultures and biofilms. *J. Appl. Microbiol.* 124 (2), 431–443.

Aragao, W. A. B., Teixeira, F. B., Fagundes, N. C. F., Fernandes, R. M., Fernandes, L. M. P., da Silva, M. C. F., et al. (2018). Hippocampal dysfunction provoked by mercury chloride exposure: evaluation of cognitive impairment, oxidative stress, tissue injury and nature of cell death. *Oxid. Med. Cell. Longevity* 2018 (1):1-11. doi: 10.1155/2018/7878050

Aregbesola, O. A., Kumar, A., Mokoena, M. P., and Olaniran, A. O. (2020). Cloning, overexpression, purification, characterization and structural modelling of a metabolically active Fe2+ dependent 2, 6-dichloro-p-hydroquinone 1, 2-dioxygenase (CpsA) from bacillus cereus strain AOA-CPS_1. *Int. J. Biol. Macromol.* 161, 247–257. doi: 10.1016/j.ijbiomac.2020.05.268

Arstol, E., and Hohmann-Marriott, M. F. (2019). Cyanobacterial siderophores–physiology, structure, biosynthesis, and applications. *Mar. Drugs* 17 (5), 281.

Atakpa, E. O., Zhou, H., Jiang, L., Ma, Y., Liang, Y., Li, Y., et al. (2022). Improved degradation of petroleum hydrocarbons by co-culture of fungi and biosurfactant-producing bacteria. *Chemosphere* 290, 133337. doi: 10.1016/j.chemosphere.2021.133337

Ayangbenro, A. S., and Babalola, O. O. (2017). A new strategy for heavy metal polluted environments: a review of microbial biosorbents. *Int. J. Environ. Res. Public Health* 14 (1), 94. doi: 10.3390/ijerph14010094

Ayangbenro, A. S., and Babalola, O. O. (2018). Metal(loid) bioremediation: strategies employed by microbial polymers. *Sustainability* 10 (9), 3028. doi: 10.3390/su10093028

Ayangbenro, A. S., and Babalola, O. O. (2020). Genomic analysis of *Bacillus cereus* NWUAB01 and its heavy metal removal from polluted soil. *Sci. Rep.* 10 (1), 1–12. doi: 10.1038/s41598-020-75170-x

Ayangbenro, A. S., Babalola, O. O., and Aremu, O. S. (2019). Bioflocculant production and heavy metal sorption by metal resistant bacterial isolates from gold mining soil. *Chemosphere* 231, 113–120. doi: 10.1016/j.chemosphere.2019.05.092

Ayangbenro, A. S., Olanrewaju, O. S., and Babalola, O. O. (2018). Sulfate-reducing bacteria as an effective tool for sustainable acid mine bioremediation. *Front. Microbiol.* 1, 1986. doi: 10.3389/fmicb.2018.01986

Ayilara, M. S., Olanrewaju, O. S., Babalola, O. O., and Odeyemi, O. (2020). Waste management through composting: challenges and potentials. *Sustainability* 12 (11), 4456. doi: 10.3390/su12114456

Babalola, O. O., Aremu, B. R., and Ayangbenro, A. S. (2019). Draft genome sequence of heavy metal-resistant bacillus cereus NWUAB01. *Microbiol. Resour. Announc.* 8 (7), e01706–e01718. doi: 10.1128/MRA.01706-18

Bai, L., Zhang, Q., Wang, C., Yao, X., Zhang, H., and Jiang, H. (2019). Effects of natural dissolved organic matter on the complexation and biodegradation of 17α-ethinylestradiol in freshwater lakes. *Environ. pollut.* 246, 782–789. doi: 10.1016/j.envpol.2018.12.098

Bala, S., Garg, D., Thirumalesh, B. V., Sharma, M., Sridhar, K., Inbaraj, B. S., et al. (2022). Recent strategies for bioremediation of emerging pollutants: a review for a green and sustainable environment. *Toxics* 10 (8), 484. doi: 10.3390/toxics10080484

Bala, G.-P., Rajnoveanu, R.-M., Tudorache, E., Motisan, R., and Oancea, C. (2021). Air pollution exposure–the (in) visible risk factor for respiratory diseases. *Environ. Sci. pollut. Res.* 28, 19615–19628. doi: 10.1007/s11356-021-13208-x

Balali-Mood, M., Naseri, K., Tahergorabi, Z., Khazdair, M. R., and Sadeghi, M. (2021). Toxic mechanisms of five heavy metals: mercury, lead, chromium, cadmium, and arsenic. *Front. Pharmacol.* 12, 227. doi: 10.3389/fphar.2021.643972

Baltazar, M., Gracioso, L. H., Avanzi, I. R., Karolski, B., Tenório, J. A. S., do Nascimento, C. A. O., et al. (2019). Copper biosorption by rhodococcus erythropolis isolated from the sossego mine–PA–Brazil. *J. Mater. Res. Technol.* 8 (1), 475–483. doi: 10.1016/j.jmrt.2018.04.006

Bargiela, R., Herbst, F. A., Martínez-Martínez, M., Seifert, J., Rojo, D., Cappello, S., et al. (2015). Metaproteomics and metabolomics analyses of chronically petroleum-polluted sites reveal the importance of general anaerobic processes uncoupled with degradation. *Proteomics* 15 (20), 3508–3520. doi: 10.1002/pmic.201400614

Basu, S., Rabara, R. C., Negi, S., and Shukla, P. (2018). Engineering PGPMOs through gene editing and systems biology: a solution for phytoremediation? *Trends Biotechnol.* 36 (5), 499–510.

Bhakat, K., Chakraborty, A., and Islam, E. (2019). Characterization of arsenic oxidation and uranium bioremediation potential of arsenic resistant bacteria isolated from uranium ore. *Environ. Sci. pollut. Res.* 26 (13), 12907–12919. doi: 10.1007/s11356-019-04827-6

Bhandari, G., Gupta, S., Chaudhary, P., Chaudhary, S., and Gangola, S. (2023). "Bioleaching: a sustainable resource recovery strategy for urban mining of e-waste," in *Microbial technology for sustainable e-waste management*. Eds. P. Debbarma, S. Kumar, D. C. Suyal and R. Soni (Cham: Springer), 157–175.

Bhandari, S., Poudel, D. K., Marahatha, R., Dawadi, S., Khadayat, K., Phuyal, S., et al. (2021). Microbial enzymes used in bioremediation. *J. Chem.* 2021, 1–17. doi: 10.1155/2021/8849512

Bharagava, R. N., Purchase, D., Saxena, G., and Mulla, S. I. (2019). "Applications of metagenomics in microbial bioremediation of pollutants: from genomics to environmental cleanup," in *Microbial diversity in the genomic era* (Amsterdam: Elsevier), 459–477.

Bhatt, P., Gangola, S., Joshi, C., Chaudhary, P., Kumar, G., Bhandari, G., et al. (2021a). Recent advancements and mechanism of microbial enzymes in sustainable agriculture. *Microb. Technol. Sustain. Environ.* 1, 247–259. doi: 10.1007/978-981-16-3840-4_15

Bhatt, P., Verma, A., Gangola, S., Bhandari, G., and Chen, S. (2021b). Microbial glycoconjugates in organic pollutant bioremediation: recent advances and applications. *Microb. Cell Factories* 20 (1), 1–18. doi: 10.1186/s12934-021-01556-9

Brinza, L., Geraki, K., Cojocaru, C., Holdt, S. L., and Neamtu, M. (2020). Baltic Fucus vesiculosus as potential bio-sorbent for zn removal: mechanism insight. *Chemosphere* 238, 124652. doi: 10.1016/j.chemosphere.2019.124652

Cao, H.-L., Liu, C., Cai, F.-Y., Qiao, X.-X., Dichiara, A. B., Tian, C., et al. (2020). *In situ* immobilization of ultra-fine Ag NPs onto magnetic Ag@RF@Fe3O4 core-satellite nanocomposites for the rapid catalytic reduction of nitrophenols. *Water Res.* 179, 115882. doi: 10.1016/j.watres.2020.115882

Chaudhary, P., Ahamad, L., Chaudhary, A., Kumar, G., Chen, W.-J., and Chen, S. (2023a). Nanoparticle-mediated bioremediation as a powerful weapon in the removal of environmental pollutants. *J. Environ. Chem. Eng.* 11, 109591. doi: 10.1016/j.jece.2023.109591

Chaudhary, P., Xu, M., Ahamad, L., Chaudhary, A., Kumar, G., Adeleke, B. S., et al. (2023b). Application of synthetic consortia for improvement of soil fertility, pollution remediation, and agricultural productivity: a review. *Agronomy* 13 (3), 643. doi: 10.3390/agronomy13030643

Chellaiah, E. (2018). Cadmium (heavy metals) bioremediation by *Pseudomonas aeruginosa*: a minireview. *Appl. Water Sci.* 8, 1–10. doi: 10.1007/s13201-018-0796-5

Chugh, M., Kumar, L., Shah, M. P., and Bharadvaja, N. (2022). Algal bioremediation of heavy metals: an insight into removal mechanisms, recovery of by-products, challenges, and future opportunities. *Energy Nexus* 7, 100129. doi: 10.1016/j.nexus.2022.100129

Copete-Pertuz, L. S., Plácido, J., Serna-Galvis, E. A., Torres-Palma, R. A., and Mora, A. (2018). Elimination of isoxazolyl-penicillins antibiotics in waters by the ligninolytic native Colombian strain leptosphaerulina sp. considerations on biodegradation process and antimicrobial activity removal. *Sci. Total Environ.* 630, 1195–1204. doi: 10.1016/j.scitotenv.2018.02.244

Dave, S., and Das, J. (2021). Role of microbial enzymes for biodegradation and bioremediation of environmental pollutants: challenges and future prospects. *Bioremediat. Environ. Sustainability*, 325–346. doi: 10.1016/B978-0-12-820524-2.00013-4

Dell'Anno, F., Rastelli, E., Tangherlini, M., Corinaldesi, C., Sansone, C., Brunet, C., et al. (2021). Highly contaminated marine sediments can host rare bacterial taxa potentially useful for bioremediation. *Front. Microbiol.* 12, 584850. doi: 10.3389/fmicb.2021.584850

Deng, J., Fu, D., Hu, W., Lu, X., Wu, Y., and Bryan, H. (2020). Physiological responses and accumulation ability of microcystis aeruginosa to zinc and cadmium: implications for bioremediation of heavy metal pollution. *Bioresour. Technol.* 303, 122963. doi: 10.1016/j.biortech.2020.122963

Deng, Y., Wang, M., Tian, T., Lin, S., Xu, P., Zhou, L., et al. (2019). The effect of hexavalent chromium on the incidence and mortality of human cancers: a meta-analysis based on published epidemiological cohort studies. *Front. Oncol.* 9, 24. doi: 10.3389/fonc.2019.00024

de Souza, M. B., de Souza Santos, L. R., Borges, R. E., Nunes, H. F., Vieira, T. B., Pacheco, S. M., et al. (2020). Current status of ecotoxicological studies of bats in Brazil. *Bull. Environ. Contam. Toxicol.* 104, 393–399. doi: 10.1007/s00128-020-02794-0

Dhaka, A., and Chattopadhyay, P. (2021). A review on physical remediation techniques for treatment of marine oil spills. *J. Environ. Manage.* 288, 112428. doi: 10.1016/j.jenvman.2021.112428

Duc, H., Hung, N., and Oanh, N. (2021). Anaerobic degradation of endosulfans by a mixed culture of pseudomonas sp. and staphylococcus sp. *Appl. Biochem. Microbiol.* 57 (3), 327–334. doi: 10.1134/S0003683821030030

Dusengemungu, L., Kasali, G., Gwanama, C., and Ouma, K. O. (2020). Recent advances in biosorption of copper and cobalt by filamentous fungi. *Front. Microbiol.* 11, 3285. doi: 10.3389/fmicb.2020.582016

Dutta, N., Usman, M., Ashraf, M. A., Luo, G., and Zhang, S. (2022). Efficacy of emerging technologies in addressing reductive dechlorination for environmental bioremediation: a review. *J. Hazard. Mater. Lett.* 3, 100065. doi: 10.1016/j.hazl.2022.100065

Eisenhofer, R., Minich, J. J., Marotz, C., Cooper, A., Knight, R., and Weyrich, L. S. (2019). Contamination in low microbial biomass microbiome studies: issues and recommendations. *Trends Microbiol.* 27 (2), 105–117. doi: 10.1016/j.tim.2018.11.003

Fashola, M. O., Ngole-Jeme, V. M., and Babalola, O. O. (2016). Heavy metal pollution from gold mines: environmental effects and bacterial strategies for resistance. *Int. J. Environ. Res. Public Health* 13 (11), 1047. doi: 10.3390/ijerph13111047

Fashola, M. O., Ngole-Jeme, V. M., and Babalola, O. O. (2020a). Heavy metal immobilization potential of indigenous bacteria isolated from gold mine tailings. *Int. J. Environ. Res.* 14 (1), 71–86. doi: 10.1007/s41742-019-00240-6

Fashola, M. O., Ngole-Jeme, V. M., and Babalola, O. O. (2020b). Physicochemical properties, heavy metals, and metal-tolerant bacteria profiles of abandoned gold mine tailings in krugersdorp, south Africa. *Can. J. Soil Sci.* 100 (3), 217–233. doi: 10.1139/cjss-2018-0161

Fay, M. J., Alt, L. A., Ryba, D., Salamah, R., Peach, R., Papaeliou, A., et al. (2018). Cadmium nephrotoxicity is associated with altered microRNA expression in the rat renal cortex. *Toxics* 6 (1), 16. doi: 10.3390/toxics6010016

Fu, W., Xu, M., Sun, K., Hu, L., Cao, W., Dai, C., et al. (2018). Biodegradation of phenanthrene by endophytic fungus phomopsis liquidambari in vitro and in vivo. *Chemosphere* 203, 160–169. doi: 10.1016/j.chemosphere.2018.03.164

Gangola, S., Sharma, A., Bhatt, P., Khati, P., and Chaudhary, P. (2018). Presence of esterase and laccase in bacillus subtilis facilitates biodegradation and detoxification of cypermethrin. *Sci. Rep.* 8 (1), 12755.

Gaur, N., Narasimhulu, K., and PydiSetty, Y. (2018). Recent advances in the bio-remediation of persistent organic pollutants and its effect on environment. *J. Clean. Prod.* 198, 1602–1631. doi: 10.1016/j.jclepro.2018.07.076

Gaur, V. K., Tripathi, V., and Manickam, N. (2022). "Bacterial-and fungal-mediated biodegradation of petroleum hydrocarbons in soil," in *Development in wastewater treatment research and processes* (Amsterdam: Elsevier), 407–427.

Geetha, N., Bhavya, G., Abhijith, P., Shekhar, R., Dayananda, K., and Jogaiah, S. (2021). Insights into nanomycoremediation: secretomics and mycogenic biopolymer nanocomposites for heavy metal detoxification. *J. Hazard. Mater.* 409, 124541. doi: 10.1016/j.jhazmat.2020.124541

Goswami, M., Chakraborty, P., Mukherjee, K., Mitra, G., Bhattacharyya, P., Dey, S., et al. (2018). Bioaugmentation and biostimulation: a potential strategy for environmental remediation. *J. Microbiol. Exp.* 6 (5), 223–231.

Gricajeva, A., Nadda, A. K., and Gudiukaite, R. (2022). Insights into polyester plastic biodegradation by carboxyl ester hydrolases. *J. Chem. Technol. Biotechnol.* 97 (2), 359–380. doi: 10.1002/jctb.6745

Hitt, L. G., Khalil, S., Blanchette, A., Finkelstein, M. E., Iverson, E. N., McClelland, S. C., et al. (2023). Lead exposure is correlated with reduced nesting success of an urban songbird. *Environ. Res.* 227 (1), 115711. doi: 10.1016/j.envres.2023.115711

Huang, Y., Pan, H., Wang, Q., Ge, Y., Liu, W., and Christie, P. (2019). Enrichment of the soil microbial community in the bioremediation of a petroleum-contaminated soil amended with rice straw or sawdust. *Chemosphere* 224, 265–271. doi: 10.1016/j.chemosphere.2019.02.148

Hussain, A., Rehman, F., Rafeeq, H., Waqas, M., Asghar, A., Afsheen, N., et al. (2022). In-situ, ex-situ, and nano-remediation strategies to treat polluted soil, water, and air–a review. *Chemosphere* 289, 133252. doi: 10.1016/j.chemosphere.2021.133252

Iark, D., dos Reis Buzzo, A. J., Garcia, J. A. A., Côrrea, V. G., Helm, C. V., Corrêa, R. C. G., et al. (2019). Enzymatic degradation and detoxification of azo dye Congo red by a new laccase from *Oudemansiella canarii*. *Bioresour. Technol.* 289, 121655. doi: 10.1016/j.biortech.2019.121655

Imam, A., Suman, S. K., Ghosh, D., and Kanaujia, P. K. (2019). Analytical approaches used in monitoring the bioremediation of hydrocarbons in petroleum-contaminated soil and sludge. *TrAC Trends Anal. Chem.* 118, 50–64. doi: 10.1016/j.trac.2019.05.023

Imron, M. F., Kurniawan, S. B., Ismail, N. I., and Abdullah, S. R. S. (2020). Future challenges in diesel biodegradation by bacteria isolates: a review. *J. Clean. Prod.* 251, 119716. doi: 10.1016/j.jclepro.2019.119716

Jacob, J. M., Karthik, C., Saratale, R. G., Kumar, S. S., Prabakar, D., Kadirvelu, K., et al. (2018). Biological approaches to tackle heavy metal pollution: a survey of literature. *J. Environ. Manage.* 217, 56–70. doi: 10.1016/j.jenvman.2018.03.077

Jafari, A., Ghaderpoori, M., Kamarehi, B., and Abdipour, H. (2019). Soil pollution evaluation and health risk assessment of heavy metals around douroud cement factory, Iran. *Environ. Earth Sci.* 78 (8), 1–9. doi: 10.1007/s12665-019-8220-5

Kebede, G., Tafese, T., Abda, E. M., Kamaraj, M., and Assefa, F. (2021). Factors influencing the bacterial bioremediation of hydrocarbon contaminants in the soil: mechanisms and impacts. *J. Chem.* 2021, 1-17. doi: 10.1155/2021/9823362

Khan, A., Singh, P., and Srivastava, A. (2018). Synthesis, nature and utility of universal iron chelator–siderophore: a review. *Microbiol. Res.* 212, 103–111. doi: 10.1016/j.micres.2017.10.012

Kharangate-Lad, A., and D'Souza, N. C. (2021). Current approaches in bioremediation of toxic contaminants by application of microbial cells; biosurfactants and bioemulsifiers of microbial origin. *Rhizobiont Bioremediat. Hazard. Waste*, 217–263. doi: 10.1007/978-981-16-0602-1_11

Kour, D., Khan, S. S., Kour, H., Kaur, T., Devi, R., Rai, P. K., et al. (2022). Microbe-mediated bioremediation: current research and future challenges. *J. Appl. Biol. Biotechnol.* 10 (2), 6–24. doi: 10.7324/JABB.2022.10s202

Kumar, V., Garg, V. K., Kumar, S., and Biswas, J. K. (2022). *Omics for environmental engineering and microbiology systems* (Florida: CRC Press).

Kumar, G., Lal, S., Maurya, S. K., Bhattacherjee, A., Chaudhary, P., Gangola, S., et al. (2021). Exploration of klebsiella pneumoniae M6 for paclobutrazol degradation, plant growth attributes, and biocontrol action under subtropical ecosystem. *PloS One* 16 (12), e0261338. doi: 10.1371/journal.pone.0261338

Kumar, G., Lal, S., Soni, S. K., Maurya, S. K., Shukla, P. K., Chaudhary, P., et al. (2022). Mechanism and kinetics of chlorpyrifos co-metabolism by using environment restoring microbes isolated from rhizosphere of horticultural crops under subtropics. *Front. Microbiol.* 13, 2796. doi: 10.3389/fmicb.2022.891870

Kumar, A., Sharma, A., Chaudhary, P., and Gangola, S. (2021). Chlorpyrifos degradation using binary fungal strains isolated from industrial waste soil. *Biologia* 76 (10), 3071–3080. doi: 10.1007/s11756-021-00816-8

Kumari, A., Kaur, R., and Kaur, R. (2019). A review on fate and remediation techniques of oil spills. *Int. J. Res. Pharm. Sci.* 10, 111.

Kumari, V., and Tripathi, A. (2020). Remediation of heavy metals in pharmaceutical effluent with the help of bacillus cereus-based green-synthesized silver nanoparticles supported on alumina. *Appl. Nanosci.* 10 (6), 1709–1719. doi: 10.1007/s13204-020-01351-9

Kushwaha, A., Maurya, S., Pathak, R. K., Agarwal, S., Chaurasia, P. K., and Singh, M. (2018). "Laccase from white rot fungi having significant role in food, pharma, and other industries," in *Research advancements in pharmaceutical, nutritional, and industrial enzymology* (Pennsylvania: IGI Global), 253–277.

Li, Q., Liu, J., and Gadd, G. M. (2020). Fungal bioremediation of soil co-contaminated with petroleum hydrocarbons and toxic metals. *Appl. Microbiol. Biotechnol.* 104 (21), 8999–9008. doi: 10.1007/s00253-020-10854-y

Li, N., Xia, Q., Niu, M., Ping, Q., and Xiao, H. (2018). Immobilizing laccase on different species wood biochar to remove the chlorinated biphenyl in wastewater. *Sci. Rep.* 8 (1), 1–9. doi: 10.1038/s41598-018-32013-0

Li, F., Zheng, Y., Tian, J., Ge, F., Liu, X., Tang, Y., et al. (2019). *Cupriavidus* sp. strain Cd02-mediated pH increase favoring bioprecipitation of Cd2+ in medium and reduction of cadmium bioavailability in paddy soil. *Ecotoxicol. Environ. Saf.* 184, 109655.

Liu, Z., Shao, B., Zeng, G., Chen, M., Li, Z., Liu, Y., et al. (2018). Effects of rhamnolipids on the removal of 2, 4, 2, 4-tetrabrominated biphenyl ether (BDE-47) by phanerochaete chrysosporium analyzed with a combined approach of experiments and molecular docking. *Chemosphere* 210, 922–930. doi: 10.1016/j.chemosphere.2018.07.114

Liu, X., Shi, H., Bai, Z., Zhou, W., Liu, K., Wang, M., et al. (2020). Heavy metal concentrations of soils near the large opencast coal mine pits in China. *Chemosphere* 244, 125360. doi: 10.1016/j.chemosphere.2019.125360

Liu, L., Wu, Q., Miao, X., Fan, T., Meng, Z., Chen, X., et al. (2022). Study on toxicity effects of environmental pollutants based on metabolomics: a review. *Chemosphere* 286, 131815. doi: 10.1016/j.chemosphere.2021.131815

Long, C., Jiang, Z., Shangguan, J., Qing, T., Zhang, P., and Feng, B. (2021). Applications of carbon dots in environmental pollution control: a review. *Chem. Eng. J.* 406, 126848. doi: 10.1016/j.cej.2020.126848

Lu, J., Zhang, C., Leong, H. Y., Show, P. L., Lu, F., and Lu, Z. (2020). Overproduction of lipoxygenase from pseudomonas aeruginosa in *Escherichia coli* by auto-induction expression and its application in triphenylmethane dyes degradation. *J. Biosci. Bioeng.* 129 (3), 327–332. doi: 10.1016/j.jbiosc.2019.09.006

Luo, H., Yuan, D. B., and Zhang, W. (2015). Association between cadmium exposure and renal cancer risk: a meta-analysis of observational studies. *Sci. Rep.* 5 (1), 1–8.

Machado, L. F., de Assis Leite, D. C., da Costa Rachid, C. T. C., Paes, J. E., Martins, E. F., Peixoto, R. S., et al. (2019). Tracking mangrove oil bioremediation approaches and bacterial diversity at different depths in an *in situ* mesocosms system. *Front. Microbiol.* 10, 2107. doi: 10.3389/fmicb.2019.02107

Mahmood, A., Bilal, B., Naeem, Z., and Iram, S. (2021). "Physical, chemical, and biological remediation techniques for textile effluents in context with developed and developing countries," in *Rhizobiont in bioremediation of hazardous waste* (Singapore: Springer), 409–441.

Mahmoud, G. A.-E. (2021). "Microbial scavenging of heavy metals using bioremediation strategies," in *Rhizobiont in bioremediation of hazardous waste*. Eds. K. Vivek, P. Ram and K. Manoj (Singapore: Springer), 265–289.

Maity, J. P., Chen, G.-S., Huang, Y.-H., Sun, A.-C., and Chen, C.-Y. (2019). Ecofriendly heavy metal stabilization: microbial induced mineral precipitation (MIMP) and biomineralization for heavy metals within the contaminated soil by indigenous bacteria. *Geomicrobiol. J.* 36 (7), 612–623. doi: 10.1080/01490451.2019.1597216

Malakar, N., Mitra, S., Toppo, P., and Mathur, P. (2020). Understanding the functional attributes of different microbial enzymes in bioremediation. *NBU J. Plant Sci.* 12 (1), 58–69. doi: 10.55734/NBUJPS.2020.v12i01.005

Manisalidis, I., Stavropoulou, E., Stavropoulos, A., and Bezirtzoglou, E. (2020). Environmental and health impacts of air pollution: a review. *Front. Public Health* 1), 14. doi: 10.3389/fpubh.2020.00014

Mathew, B. B., and Krishnamurthy, N. B. (2018). Screening and identification of bacteria isolated from industrial area groundwater to study lead sorption: kinetics and statistical optimization of biosorption parameters. *Groundwater Sustain. Dev.* 7, 313–327. doi: 10.1016/j.gsd.2018.07.007

Medfu Tarekegn, M., Zewdu Salilih, F., and Ishetu, A. I. (2020). Microbes used as a tool for bioremediation of heavy metal from the environment. *Cogent Food Agric.* 6 (1), 1783174. doi: 10.1080/23311932.2020.1783174

Methneni, N., Morales-Gonzalez, J. A., Jaziri, A., Mansour, H. B., and Fernandez-Serrano, M. (2021). Persistent organic and inorganic pollutants in the effluents from the textile dyeing industries: ecotoxicology appraisal via a battery of biotests. *Environ. Res.* 196, 110956. doi: 10.1016/j.envres.2021.110956

Miri, S., Rasooli, A., Brar, S. K., Rouissi, T., and Martel, R. (2022). Biodegradation of p-xylene–a comparison of three psychrophilic pseudomonas strains through the lens of gene expression. *Environ. Sci. pollut. Res.* 29 (15), 21465–21479. doi: 10.1007/s11356-021-17387-5

Mir-Tutusaus, J. A., Baccar, R., Caminal, G., and Sarrà, M. (2018). Can white-rot fungi be a real wastewater treatment alternative for organic micropollutants removal? a review. *Water Res.* 138, 137–151. doi: 10.1016/j.watres.2018.02.056

Mohamed, M. S., El-Arabi, N. I., El-Hussein, A., El-Maaty, S. A., and Abdelhadi, A. A. (2020). Reduction of chromium-VI by chromium-resistant escherichia coli FACU: a prospective bacterium for bioremediation. *Folia Microbiol.* 65 (4), 687–696. doi: 10.1007/s12223-020-00771-y

Mohapatra, B., and Phale, P. S. (2021). Microbial degradation of naphthalene and substituted naphthalenes: metabolic diversity and genomic insight for bioremediation. *Front. Bioeng. Biotechnol.* 9, 602445. doi: 10.3389/fbioe.2021.602445

Mohd, S., Kushwaha, A. S., Shukla, J., Mandrah, K., Shankar, J., Arjaria, N., et al. (2019). Fungal mediated biotransformation reduces toxicity of arsenic to soil dwelling microorganism and plant. *Ecotoxicol. Environ. Saf.* 176, 108–118. doi: 10.1016/j.ecoenv.2019.03.053

Moreira, V., Lebron, Y., Lange, L., and Santos, L. (2019). Simultaneous biosorption of cd (II), Ni (II) and Pb (II) onto a brown macroalgae fucus vesiculosus: mono-and multi-component isotherms, kinetics and thermodynamics. *J. Environ. Manage.* 251, 109587. doi: 10.1016/j.jenvman.2019.109587

Mousavi, S. M., Hashemi, S. A., Iman Moezzi, S. M., Ravan, N., Gholami, A., Lai, C. W., et al. (2021). Recent advances in enzymes for the bioremediation of pollutants. *Biochem. Res. Int.* 2021, 1-12.

Mukherjee, A., and Reddy, M. S. (2020). Metatranscriptomics: an approach for retrieving novel eukaryotic genes from polluted and related environments. *3 Biotech.* 10 (2), 71. doi: 10.1007/s13205-020-2057-1

Mukjang, N., Chitov, T., Mhuantong, W., Champreda, V., Pathom-Aree, W., Sattayawat, P., et al. (2022). Bacterial communities associated with crude oil bioremediation through composting approaches with indigenous bacterial isolate. *Life* 12 (11), 1712. doi: 10.3390/life12111712

Nanda, M., Kumar, V., and Sharma, D. (2019). Multimetal tolerance mechanisms in bacteria: the resistance strategies acquired by bacteria that can be exploited to 'clean-up'heavy metal contaminants from water. *Aquat. Toxicol.* 212, 1–10. doi: 10.1016/j.aquatox.2019.04.011

Narayanan, M., Ali, S. S., and El-Sheekh, M. (2023). A comprehensive review on the potential of microbial enzymes in multipollutant bioremediation: MechanAisms, challenges, and future prospects. *J. Environ. Manage.* 334, 117532. doi: 10.1016/j.jenvman.2023.117532

Nath, S., Deb, B., and Sharma, I. (2018). Isolation of toxic metal-tolerant bacteria from soil and examination of their bioaugmentation potentiality by pot studies in cadmium-and lead-contaminated soil. *Int. Microbiol.* 21, 35–45. doi: 10.1007/s10123-018-0003-4

Ndeddy Aka, R. J., and Babalola, O. O. (2016). Effect of bacterial inoculation of strains of pseudomonas aeruginosa, alcaligenes feacalis and bacillus subtilis on germination, growth and heavy metal (Cd, cr, and Ni) uptake of brassica juncea. *Int. J. Phytoremediation* 18 (2), 200–209.

Ndeddy Aka, R. J., and Babalola, O. O. (2017). Identification and characterization of cr-, cd-, and Ni-tolerant bacteria isolated from mine tailings. *Bioremediat. J.* 21 (1), 1–19.

Nivetha, N., Srivarshine, B., Sowmya, B., Rajendiran, M., Saravanan, P., Rajeshkannan, R., et al. (2022). A comprehensive review on bio-stimulation and bio-enhancement towards remediation of heavy metals degeneration. *Chemosphere* 3, 137099.

Nowicka, B., Fesenko, T., Walczak, J., and Kruk, J. (2020). The inhibitor-evoked shortage of tocopherol and plastoquinol is compensated by other antioxidant mechanisms in chlamydomonas reinhardtii exposed to toxic concentrations of cadmium and chromium ions. *Ecotoxicol. Environ. Saf.* 191, 110241. doi: 10.1016/j.ecoenv.2020.110241

Ogunlaja, A., Ogunlaja, O. O., Okewole, D. M., and Morenikeji, O. A. (2019). Risk assessment and source identification of heavy metal contamination by multivariate and hazard index analyses of a pipeline vandalised area in Lagos state, Nigeria. *Sci. Total Environ.* 651, 2943–2952. doi: 10.1016/j.scitotenv.2018.09.386

Ojuederie, O. B., and Babalola, O. O. (2017). Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. *Int. J. Environ. Res. Public Health* 14 (12), 1504. doi: 10.3390/ijerph14121504

Ojuederie, O. B., Chukwuneme, F., Olanrewaju, O., Ayilara, M., Adegboyega, T. T., and Babalola, O. O. (2021). Contribution of microbial inoculants in sustainable maintenance of human health, including test methods and evaluation of safety of microbial pesticide microorganisms. *Biopesticides: Botanicals Microorganisms Improving Agric. Hum. Health* 2021, 207–240.

Orlovic-Leko, P., Farkas, B., and Galic, I. (2022). A short review of environmental and health impacts of gold mining. *Reliability: Theory Appl.* 17(SI 4 (SI 4 (70), 242–248.

Pande, V., Pandey, S. C., Sati, D., Pande, V., and Samant, M. (2020). Bioremediation: an emerging effective approach towards environment restoration. *Environ. Sustainability* 3 (1), 91–103. doi: 10.1007/s42398-020-00099-w

Patel, A. B., Jain, K. R., Manvar, T., Desai, C., and Madamwar, D. (2022). Enriched bacterial community efficiently degrade polycyclic aromatic hydrocarbons in soil ecosystem: insights from a mesocosms study. *Biochem. Eng. J.* 185, 108516. doi: 10.1016/j.bej.2022.108516

Patel, A. K., Singhania, R. R., Albarico, F. P. J. B., Pandey, A., Chen, C.-W., and Dong, C.-D. (2022). Organic wastes bioremediation and its changing prospects. *Sci. Total Environ.* 824, 153889. doi: 10.1016/j.scitotenv.2022.153889

Pavesi, T., and Moreira, J. C. (2020). Mechanisms and individuality in chromium toxicity in humans. *J. Appl. Toxicol.* 40 (9), 1183–1197. doi: 10.1002/jat.3965

Perera, I. C., and Hemamali, E. H. (2022). Genetically modified organisms for bioremediation: current research and advancements. *Bioremediat. Environ. Pollut.: Emerg. Trends Strategies* 1, 163–186.

Pope, C. A., Lefler, J. S., Ezzati, M., Higbee, J. D., Marshall, J. D., Kim, S.-Y., et al. (2019). Mortality risk and fine particulate air pollution in a large, representative cohort of US adults. *Environ. Health Perspect.* 127 (7), 077007.

Prabagar, S., Dharmadasa, R. M., Lintha, A., Thuraisingam, S., and Prabagar, J. (2021). Accumulation of heavy metals in grape fruit, leaves, soil and water: a study of influential factors and evaluating ecological risks in jaffna, Sri Lanka. *Environ. Sustainability Indic.* 12, 100147. doi: 10.1016/j.indic.2021.100147

Pratush, A., Kumar, A., and Hu, Z. (2018). Adverse effect of heavy metals (As, Pb, Hg, and cr) on health and their bioremediation strategies: a review. *Int. Microbiol.* 21 (3), 97–106. doi: 10.1007/s10123-018-0012-3

Qiao, W., Zhang, Y., Xia, H., Luo, Y., Liu, S., Wang, S., et al. (2019). Bioimmobilization of lead by bacillus subtilis X3 biomass isolated from lead mine soil under promotion of multiple adsorption mechanisms. *R. Soc. Open Sci.* 6 (2), 181701. doi: 10.1098/rsos.181701

Rabani, M. S., Sharma, R., Singh, R., and Gupta, M. (2022). Characterization and identification of naphthalene degrading bacteria isolated from petroleum contaminated sites and their possible use in bioremediation. *Polycyclic Aromatic Compounds* 42 (3), 978–989. doi: 10.1080/10406638.2020.1759663

Rai, P. K., Lee, S. S., Zhang, M., Tsang, Y. F., and Kim, K.-H. (2019). Heavy metals in food crops: health risks, fate, mechanisms, and management. *Environ. Int.* 125 (1), 365–385. doi: 10.1016/j.envint.2019.01.067

Rehman, A. U., Nazir, S., Irshad, R., Tahir, K., ur Rehman, K., Islam, R. U., et al. (2021). Toxicity of heavy metals in plants and animals and their uptake by magnetic iron oxide nanoparticles. *J. Mol. Liquids* 321, 114455. doi: 10.1016/j.molliq.2020.114455

Ren, X., Zeng, G., Tang, L., Wang, J., Wan, J., Wang, J., et al. (2018). The potential impact on the biodegradation of organic pollutants from composting technology for soil remediation. *Waste Manage.* 72, 138–149. doi: 10.1016/j.wasman.2017.11.032

Saavedra, R., Muñoz, R., Taboada, M. E., Vega, M., and Bolado, S. (2018). Comparative uptake study of arsenic, boron, copper, manganese and zinc from water by different green microalgae. *Bioresour. Technol.* 263, 49–57. doi: 10.1016/j.biortech.2018.04.101

Saha, L., Tiwari, J., Bauddh, K., and Ma, Y. (2021). Recent developments in microbe–plant-based bioremediation for tackling heavy metal-polluted soils. *Front. Microbiol.* 12, 731723. doi: 10.3389/fmicb.2021.731723

Sahay, R. (2021). Synthetic applications of laccase and its catalytic potentials. *Inter J. Adv. Eng. Res. Sci.* 8 (6), 112–120. doi: 10.22161/ijaers.86.12

Sangkharak, K., Choonut, A., Rakkan, T., and Prasertsan, P. (2020). The degradation of phenanthrene, pyrene, and fluoranthene and its conversion into medium-chain-length polyhydroxyalkanoate by novel polycyclic aromatic hydrocarbon-degrading bacteria. *Curr. Microbiol.* 77 (6), 897–909. doi: 10.1007/s00284-020-01883-x

Saranya, P., Selvi, P., and Sekaran, G. (2019). Integrated thermophilic enzyme-immobilized reactor and high-rate biological reactors for treatment of palm oil-containing wastewater without sludge production. *Bioprocess Biosyst. Eng.* 42, 1053–1064. doi: 10.1007/s00449-019-02104-x

Sarmah, P., and Rout, J. (2020). "Role of algae and cyanobacteria in bioremediation: prospects in polyethylene biodegradation," in *Advances in cyanobacterial biology* (Amsterdam: Elsevier), 333–349.

Saxena, G., Kishor, R., and Bharagava, R. N. (2020). "Application of microbial enzymes in degradation and detoxification of organic and inorganic pollutants," in *Bioremediation of industrial waste for environmental safety* (New York: Springer), 41–51.

Sayed, K., Baloo, L., and Sharma, N. K. (2021). Bioremediation of total petroleum hydrocarbons (TPH) by bioaugmentation and biostimulation in water with floating oil spill containment booms as bioreactor basin. *Int. J. Environ. Res. Public Health* 18 (5), 2226. doi: 10.3390/ijerph18052226

Sedlakova-Kadukova, J., Kopcakova, A., Gresakova, L., Godany, A., and Pristas, P. (2019). Bioaccumulation and biosorption of zinc by a novel streptomyces K11 strain isolated from highly alkaline aluminium brown mud disposal site. *Ecotoxicol. Environ. Saf.* 167, 204–211. doi: 10.1016/j.ecoenv.2018.09.123

Sen, S. K., Patra, P., Das, C. R., Raut, S., and Raut, S. (2019). Pilot-scale evaluation of bio-decolorization and biodegradation of reactive textile wastewater: an impact on its use in irrigation of wheat crop. *Water Resour. Industry* 21, 100106. doi: 10.1016/j.wri.2019.100106

Shah, H., and Jain, S. (2020). "Bioremediation: an approach for environmental pollutants detoxification," in *Waste to energy: prospects and applications* (New York: Springer), 121–142.

Shanmuganathan, R., Karuppusamy, I., Saravanan, M., Muthukumar, H., Ponnuchamy, K., Ramkumar, V. S., et al. (2019). Synthesis of silver nanoparticles and their biomedical applications-a comprehensive review. *Curr. Pharm. Design* 25 (24), 2650–2660. doi: 10.2174/1381612825666190708185506

Sharma, P., Dutta, D., Udayan, A., Nadda, A. K., Lam, S. S., and Kumar, S. (2022a). Role of microbes in bioaccumulation of heavy metals in municipal solid waste: impacts on plant and human being. *Environ. pollut.* 305, 119248. doi: 10.1016/j.envpol.2022.119248

Sharma, M., Nandy, A., Taylor, N., Venkatesan, S. V., Kollath, V. O., Karan, K., et al. (2020). Bioelectrochemical remediation of phenanthrene in a microbial fuel cell using an anaerobic consortium enriched from a hydrocarbon-contaminated site. *J. Hazard. Mater.* 389, 121845. doi: 10.1016/j.jhazmat.2019.121845

Sharma, P., Singh, S. P., Iqbal, H. M., and Tong, Y. W. (2022b). Omics approaches in bioremediation of environmental contaminants: an integrated approach for environmental safety and sustainability. *Environ. Res.* 211, 113102. doi: 10.1016/j.envres.2022.113102

Sharma, P., Singh, S. P., Parakh, S. K., and Tong, Y. W. (2022c). Health hazards of hexavalent chromium (Cr (VI)) and its microbial reduction. *Bioengineered* 13 (3), 4923–4938. doi: 10.1080/21655979.2022.2037273

Singh, R. K., Tripathi, R., Ranjan, A., and Srivastava, A. K. (2020). "Fungi as potential candidates for bioremediation," in *Abatement of environmental pollutants* (Amsterdam: Elsevier), 177–191.

Siric, I., Eid, E. M., El-Morsy, M. H., Osman, H. E., Adelodun, B., Abou Fayssal, S., et al. (2022a). Health risk assessment of hazardous heavy metals in two varieties of mango fruit (Mangifera indica l. var. dasheri and langra). *Horticulturae* 8 (9), 832. doi: 10.3390/horticulturae8090832

Siric, I., Eid, E. M., Taher, M. A., El-Morsy, M. H., Osman, H. E., Kumar, P., et al. (2022b). Combined use of spent mushroom substrate biochar and PGPR improves growth, yield, and biochemical response of cauliflower (Brassica oleracea var. botrytis): a preliminary study on greenhouse cultivation. *Horticulturae* 8 (9), 830. doi: 10.3390/horticulturae8090830

Sonawane, J. M., Rai, A. K., Sharma, M., Tripathi, M., and Prasad, R. (2022). Microbial biofilms: recent advances and progress in environmental bioremediation. *Sci. Total Environ.* 824, 153843. doi: 10.1016/j.scitotenv.2022.153843

Song, J., Zhang, S., Xie, Y., and Li, Q. (2019). Purification and characteristics of an aflatoxin B1 degradation enzyme isolated from pseudomonas aeruginosa. *FEMS Microbiol. Lett.* 366 (5), fnz034. doi: 10.1093/femsle/fnz034

Sonune, N. (2021). "Microbes: a potential tool for bioremediation," in *Rhizobiont in bioremediation of hazardous waste*. Eds. K. Vivek, P. Ram and K. Manoj (Singapore: Springer), 391–407.

Sonune, N., and Garode, A. (2018). Isolation, characterization and identification of extracellular enzyme producer bacillus licheniformis from municipal wastewater and evaluation of their biodegradability. *Biotechnol. Res. Innovation* 2 (1), 37–44. doi: 10.1016/j.biori.2018.03.001

Sravya, K., and Sangeetha, S. (2022). Feasibility study on bioremediation techniques to contaminated soils. *Mater. Today: Proc.* 51, 2556–2560. doi: 10.1016/j.matpr.2021.12.364

Sun, W., Cheng, K., Sun, K. Y., and Ma, X. (2021). Microbially mediated remediation of contaminated sediments by heavy metals: a critical review. *Curr. pollut. Rep.* 7 (2), 201–212. doi: 10.1007/s40726-021-00175-7

Sun, L., Guo, D., Liu, K., Meng, H., Zheng, Y., Yuan, F., et al. (2019). Levels, sources, and spatial distribution of heavy metals in soils from a typical coal industrial city of tangshan, China. *Catena* 175, 101–109. doi: 10.1016/j.catena.2018.12.014

Tak, H. I., Ahmad, F., and Babalola, O. O. (2012). Advances in the application of plant growth-promoting rhizobacteria in phytoremediation of heavy metals. *Rev. Environ. Contam. Toxicol.* 223 (1), 33–52.

Tan, W., Peralta-Videa, J. R., and Gardea-Torresdey, J. L. (2018). Interaction of titanium dioxide nanoparticles with soil components and plants: current knowledge and future research needs–a critical review. *Environ. Sci.: Nano* 5 (2), 257–278. doi: 10.1039/C7EN00985B

Taran, M., Fateh, R., Rezaei, S., and Gholi, M. K. (2019). Isolation of arsenic accumulating bacteria from garbage leachates for possible application in bioremediation. *Iranian J. Microbiol.* 11 (1), 60. doi: 10.18502/ijm.v11i1.707

Thakare, M., Sarma, H., Datar, S., Roy, A., Pawar, P., Gupta, K., et al. (2021). Understanding the holistic approach to plant-microbe remediation technologies for removing heavy metals and radionuclides from soil. *Curr. Res. Biotechnol.* 3, 84–98. doi: 10.1016/j.crbiot.2021.02.004

Thakur, M., Medintz, I. L., and Walper, S. A. (2019). Enzymatic bioremediation of organophosphate compounds–progress and remaining challenges. *Front. Bioeng. Biotechnol.* 7, 289. doi: 10.3389/fbioe.2019.00289

Tian, Q., Dou, X., Huang, L., Wang, L., Meng, D., Zhai, L., et al. (2020). Characterization of a robust cold-adapted and thermostable laccase from pycnoporus sp. SYBC-L10 with a strong ability for the degradation of tetracycline and oxytetracycline by laccase-mediated oxidation. *J. Hazard. Mater.* 382, 121084.

Unuofin, J. O., Falade, A. O., and Aladekoyi, O. J. (2021). Applications of microbial laccases in bioremediation of environmental pollutants: potential issues, challenges, and prospects. *Bioremediat. Environ. Sustainability* 1, 519–540. doi: 10.1016/B978-0-12-820524-2.00021-3

Unuofin, J. O., Okoh, A. I., and Nwodo, U. U. (2019). Aptitude of oxidative enzymes for treatment of wastewater pollutants: a laccase perspective. *Molecules* 24 (11), 2064. doi: 10.3390/molecules24112064

Verma, S., and Kuila, A. (2019). Bioremediation of heavy metals by microbial process. *Environ. Technol. Innovation* 14, 100369. doi: 10.1016/j.eti.2019.100369

Verma, S., Verma, P. K., and Chakrabarty, D. (2019). Arsenic bio-volatilization by engineered yeast promotes rice growth and reduces arsenic accumulation in grains. *Int. J. Environ. Res.* 13 (3), 475–485. doi: 10.1007/s41742-019-00188-7

Vo, M.-T., Nguyen, V.-T., and Dao, T.-S. (2020). Responses of green algae and diatom upon exposure to chromium and cadmium. *Vietnam J. Sci. Technol. Eng.* 62 (1), 69–73. doi: 10.31276/VJSTE.62(1).69-73

Vocciante, M., Finocchi, A., De Folly D′ Auris, A., Conte, A., Tonziello, J., Pola, A., et al. (2019). Enhanced oil spill remediation by adsorption with interlinked multilayered graphene. *Materials* 12 (14), 2231. doi: 10.3390/ma12142231

Wang, L., Liu, Y., Shu, X., Lu, S., Xie, X., and Shi, Q. (2019). Complexation and conformation of lead ion with poly-γ-glutamic acid in soluble state. *PloS One* 14 (9), e0218742. doi: 10.1371/journal.pone.0218742

Wang, Z., Luo, Z., Yan, C., Rosenfeldt, R. R., Seitz, F., and Gui, H. (2018). Biokinetics of arsenate accumulation and release in microcystis aeruginosa regulated by common environmental factors: practical implications for enhanced bioremediation. *J. Clean. Prod.* 199, 112–120. doi: 10.1016/j.jclepro.2018.07.131

Wang, Y., Mandal, A. K., Son, Y.-O., Pratheeshkumar, P., Wise, J. T., Wang, L., et al. (2018). Roles of ROS, Nrf2, and autophagy in cadmium-carcinogenesis and its prevention by sulforaphane. *Toxicol. Appl. Pharmacol.* 353, 23–30. doi: 10.1016/j.taap.2018.06.003

Wei, Y., Fu, J., Wu, J., Jia, X., Zhou, Y., Li, C., et al. (2018). Bioinformatics analysis and characterization of highly efficient polyvinyl alcohol (PVA)-degrading enzymes from the novel PVA degrader stenotrophomonas rhizophila QL-P4. *Appl. Environ. Microbiol.* 84 (1), e01898–e01817. doi: 10.1128/AEM.01898-17

Wu, W., Jiang, S., Zhao, Q., Zhang, K., Wei, X., Zhou, T., et al. (2018). Environmental exposure to metals and the risk of hypertension: a cross-sectional study in China. *Environ. pollut.* 233, 670–678. doi: 10.1016/j.envpol.2017.10.111

Wu, P., Zhang, Z., Luo, Y., Bai, Y., and Fan, J. (2022). Bioremediation of phenolic pollutants by algae-current status and challenges. *Bioresour. Technol.* 350, 126930. doi: 10.1016/j.biortech.2022.126930

Xiao, F., Cheng, J., Cao, W., Yang, C., Chen, J., and Luo, Z. (2019). Removal of heavy metals from aqueous solution using chitosan-combined magnetic biochars. *J. Colloid Interface Sci.* 540, 579–584. doi: 10.1016/j.jcis.2019.01.068

Xie, Q., Liu, N., Lin, D., Qu, R., Zhou, Q., and Ge, F. (2020). The complexation with proteins in extracellular polymeric substances alleviates the toxicity of cd (II) to chlorella vulgaris. *Environ. pollut.* 263, 114102. doi: 10.1016/j.envpol.2020.114102

Xu, Q., Wu, B., and Chai, X. (2022). *In situ* remediation technology for heavy metal contaminated sediment: a review. *Int. J. Environ. Res. Public Health* 19 (24), 16767. doi: 10.3390/ijerph192416767

Ye, X., Peng, T., Feng, J., Yang, Q., Pratush, A., Xiong, G., et al. (2019). A novel dehydrogenase 17β-HSDx from rhodococcus sp. P14 with potential application in bioremediation of steroids contaminated environment. *J. Hazard. Mater.* 362, 170–177. doi: 10.1016/j.jhazmat.2018.09.023

Zacharia, J. T. (2019). Degradation pathways of persistent organic pollutants (POPs) in the environment. *Persistent Organic Pollutants*, 17–30. doi: 10.5772/intechopen.79645

Zeng, F., Qiu, B., Wu, X., Niu, S., Wu, F., and Zhang, G. (2012). Glutathione-mediated alleviation of chromium toxicity in rice plants. *Biol. Trace Elem. Res.* 148, 255–263. doi: 10.1007/s12011-012-9362-4

Zhang, C., Gan, C., Ding, L., Xiong, M., Zhang, A., and Li, P. (2020). Maternal inorganic mercury exposure and renal effects in the wanshan mercury mining area, southwest China. *Ecotoxicol. Environ. Saf.* 189, 109987. doi: 10.1016/j.ecoenv.2019.109987

Zhao, B., Johnston, F. H., Salimi, F., Kurabayashi, M., and Negishi, K. (2020). Short-term exposure to ambient fine particulate matter and out-of-hospital cardiac arrest: a nationwide case-crossover study in Japan. *Lancet Planet. Health* 4 (1), e15–e23. doi: 10.1016/S2542-5196(19)30262-1

Zhou, Y., Liu, X., and Wang, J. (2019). Characterization of microplastics and the association of heavy metals with microplastics in suburban soil of central China. *Sci. Total Environ.* 694, 133798. doi: 10.1016/j.scitotenv.2019.133798

Zuhara, S., and Isaifan, R. (2018). The impact of criteria air pollutants on soil and water: a review. *J. Environ. Sci. pollut. Res.* 4 (2), 278–284. doi: 10.30799/jespr.133.18040205

Zwolak, A., Sarzyńska, M., Szpyrka, E., and Stawarczyk, K. (2019). Sources of soil pollution by heavy metals and their accumulation in vegetables: a review. *Water Air Soil pollut.* 230 (7), 1–9. doi: 10.1007/s11270-019-4221-y

frontiers | Frontiers in Microbiology

TYPE Original Research
PUBLISHED 14 June 2023
DOI 10.3389/fmicb.2023.1206217

OPEN ACCESS

EDITED BY
Parul Chaudhary,
Graphic Era Hill University, India

REVIEWED BY
Razak Hussain,
University of Illinois at Urbana-Champaign, United States
Ahmad Faraz,
Glocal University, India

*CORRESPONDENCE
Aashaq Hussain Bhat
✉ aashiqhussainbhat10@gmail.com
Aasha Rana
✉ aasha.aasharana@ymail.com

RECEIVED 15 April 2023
ACCEPTED 11 May 2023
PUBLISHED 14 June 2023

CITATION
Ahamad L, Bhat AH, Kumar H, Rana A, Hasan MN, Ahmed I, Ahmed S, Machado RAR and Ameen F (2023) From soil to plant: strengthening carrot defenses against *Meloidogyne incognita* with vermicompost and arbuscular mycorrhizal fungi biofertilizers. *Front. Microbiol.* 14:1206217. doi: 10.3389/fmicb.2023.1206217

From soil to plant: strengthening carrot defenses against *Meloidogyne incognita* with vermicompost and arbuscular mycorrhizal fungi biofertilizers

Lukman Ahamad[1], Aashaq Hussain Bhat[2,3]*, Harendra Kumar[4], Aasha Rana[5]*, Md. Nurul Hasan[6], Ishtiaq Ahmed[6], Shakoor Ahmed[7], Ricardo A. R. Machado[3] and Fuad Ameen[8]

[1]Section of Plant Pathology and Nematology, Department of Botany, Aligarh Muslim University, Aligarh, India, [2]Department of Biosciences, University Center for Research and Development, Mohali, Punjab, India, [3]Experimental Biology Research Group, Faculty of Science, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland, [4]Department of Zoology, J.S. University, Shikohabad, Uttar Pradesh, India, [5]Department of Zoology, Faculty of Basic and Applied Sciences, Madhav University, Pindwara, Rajasthan, India, [6]Zoological Survey of India, F.P.S. Building, Kolkata, India, [7]Zoological Survey of India, New Alipore, Kolkata, India, [8]Department of Botany and Microbiology, College of Science, King Saud University, Riyadh, Saudi Arabia

Introduction: Sustainable agricultural practices for controlling crop pests are urgently needed to reduce the reliance on chemical pesticides, which have long-term detrimental effects on ecosystems. In this study, we assessed the effectiveness of arbuscular mycorrhizal fungi (AMF) and vermicompost (Vc) supplementation, alone and in combination, in mitigating the negative impacts of *Meloidogyne incognita* infestation on carrot (*Daucus carota* L.) growth, development, and physiology.

Methods: We measured different plant growth parameters such as plant height and biomass accumulation, several plant physiological parameters such as the levels of photosynthetic pigments, phenolics, and the activity of defense enzymes such as peroxidases and polyphenol oxidases, and evaluated the severity of *Meloidogyne incognita* nematode infestation on plants treated or not treated with vermicompost (Vc) and/or arbuscular mycorrhizal fungi (AMF).

Results: Our findings show that *M. incognita* significantly affects plant growth, biomass accumulation, and photosynthetic pigment and carotenoid content. The incorporation of Vc and AMF into the soil, either individually or in combination, significantly alleviates the negative effects of nematode infestation on carrot plants. This was accompanied by the induction of phenolic compounds and defense enzymes such as peroxidases (+15.65%) and polyphenol oxidases (29.78%), and by a reduction in the severity of nematode infestation on Vc and AMF-treated plants compared to nematode-infested plants. Principal component analysis (PCA) shows significant correlations between various of the studied parameters. In particular, we observed negative correlations between the application of AMF and Vc alone and in combination and disease severity, and positive correlations between plant growth, photosynthetic pigments phenol content, and activity of defense enzymes.

Discussion: Our study highlights the relevance of cultural practices and beneficial microorganisms for the sustainable and environmentally friendly management of agricultural pests.

KEYWORDS

arbuscular mycorrhizal fungi, sustainable agriculture, *Daucus carota*, disease management, *Meloidogyne incognita*, vermicompost

1. Introduction

Carrot (Apiaceae; *Daucus carota* L) is an economically important and nutrient-rich root vegetable crop cultivated in several countries worldwide. Its edible part, the taproot, is particularly rich in ß-carotene, vitamins, proteins and nutrients (Megueni et al., 2017; Fabiyi, 2021). One of the major threats to the production of carrots is root-knot nematodes (*Meloidogyne* spp., RKN). These minute worm-like animals create metabolic sinks in infested plants that limit photo-assimilates' availability for plant growth. In addition, RKN colonizes the taproot, the root hairs and the lateral roots, forming a syncytium that disrupts the uptake of nutrients and water, thus causing substantial damage to carrot plants (Hussain et al., 2016; Khan et al., 2018). Moreover, by inducing galling and forking in the carrot roots, these nematodes render the infested carrot taproots unmarketable, thereby causing substantial direct economic losses (Prasad et al., 2014; Hussain et al., 2016). Therefore, finding sustainable and effective control measures against this agricultural pest is compulsory.

The fields infested with plant parasitic nematodes can be controlled by agricultural practices such as the use of nematicides, the application of biocontrol agents (Vagelas and Gowen, 2012), soil amendments (Asif et al., 2016, 2017), and other cultural practices such as crop rotation and the use of antagonistic plants (Hussain et al., 2011; Kayania et al., 2012). The application of chemical nematicides is highly effective in controlling root-knot nematodes, but their use is not recommended due to the huge detrimental effects on human health, the environment, and non-target organisms (Damalas and Eleftherohorinos, 2011). Currently, there is a worldwide swing towards eco-friendly, cost-effective and biocontrol management practices to combat nematode infestation for sustainable agriculture (Collange et al., 2011). One of the promising methods to combat nematodes is the application of vermicomposting and arbuscular mycorrhizal fungi (AMF).

Vermicomposting (Vc) is an eco-friendly biotechnological process that involves the combined action of earthworms and microbes to transform organic matter or waste to Vc nutrient-enriched products (Yadav et al., 2022). The microbes present in the gut of earthworms and feed-stock are accountable for the biochemical degradation of the organic matter (OM), while the earthworms are responsible for substrate breakdown and expanding the surface area accessible to microorganisms (Xu and Mou, 2016). Vermicompost nourish plants because it is rich in various nutrients, including calcium (Ca), phosphorus (P) and soluble potassium (K), which are essential for plant growth (Kumar et al., 2021). In addition, Vc is rich in humic acid compounds, nematicidal compounds (hydrogen sulfate, ammonia and nitrite) and hormones (cytokinins, indole acetic acid and gibberellins) that prevent nematode infestation (Oka, 2010; Khorshidi et al., 2013).

AMF are beneficial soil microorganisms that forms a symbiotic relationship with plants (Smith and Read, 2010). They have the potential to stimulate plant growth by improving the uptake of nutrients in return for photo-synthetic carbon (Vos et al., 2012). AMF decrease the severity of phytopathogenic nematodes (Fellbaum et al., 2012; da Silva Campos, 2020). Various mechanisms are involved in AMF-mediated biocontrol, including direct effects on the pathogen, such as competition for space and nutrients, or indirect effects, including the induction of plant defenses (Schouteden et al., 2015).

The current investigation explores the interactive effects of Vc and AMF applications on the growth, photosynthetic pigments, phenol contents and defense enzymes (peroxidase and polyphenol oxidase) in carrot plants when challenged with *M. incognita* nematodes. Our results reveal the great potential of Vc and AMF applications to ameliorate the negative impact of nematode infestation on carrot plants. Hence, our study highlights the relevance and feasibility of cultural practices and the use of beneficial microorganisms to control agricultural pests in eco-friendly and sustainable practices.

2. Materials and methods

2.1. Experimental setup

The experiment was carried out in a completely randomized block design (CRD). Plants were maintained at 28°C, 96% relative humidity, and 16/8 h photoperiod under greenhouse conditions. The light source in greenhouse was the sun during the daytime and an electric bulb during the early evenings. The following treatments were included: 1) Control, 2) *Meloidogyne incognita*, 3) AMF (*Funneliformis mosseae*) + *M. incognita*, 4) Vermicompost (Vc) + *M. incognita*, 5) Vc + AMF + *M. incognita*. Five independent replicates per treatment were analyzed.

2.2. Planting conditions

Plants were grown on loam soil collected in agricultural farms of the Aligarh district (Uttar Pradesh, India). Soil was crushed and passed through a 10-mesh sieve to obtain fine soil particles. The fine soil was mixed with farmyard manure in a ratio of 3:1, then autoclaved at 137.9 kPa pressure for 20 min. After sterilization, 1 kg soil mixture was filled in clay pots (15 × 8.5 × 13.5 cm). Prior to sowing, *Daucus carota* L. seeds cv. Red Rose were surface sterilized with 0.1% $HgCl_2$ solution for 2 min followed by three times rinsing in autoclaved distilled water (DW). Seeds were purchased from the local market of Aligarh city, U.P., India. Five sterilized seeds were sown 2 cm deep in each pot. After emergence, the seedlings were thinned at the two-leaf stage to maintain one healthy plant in each pot. Plants were watered at regular intervals.

2.3. Collection of earthworms, leaf litter, and cow dung

The earthworms used in the experiments were purchased from a private vermiculture unit (Manglakanshi, Mahila Mandal F-1 Sai

Vatika, Devpuri Raipur, Chhattisgarh), and were reared on partially decomposed cow dung under greenhouse conditions. A total of 10 worms were narcotized in 70% alcohol and preserved in 5% formaldehyde for species identification. The earthworm species were identified as *Eisenia fetida* Savigny based on taxonomic characters. The identification was carried out in the Zoological Survey of India (ZSI) (Kolkata, India). Fresh cow dung was collected from nearby cattle shed and stored for 1 week before its use for vermicomposting. The leaf litter (mixture of *Ricinus communis* L. and *Parthenium hysterophorus* L.) was collected from the vicinity of the Aligarh Muslim University, and chopped and dried prior to its use for vermicompost (Vc).

2.4. Preparation of vermicompost

Seven-day-old cow dung was mixed with chopped leaf litter in a 3:1 ratio respectively, and left in a pit (size 90 × 30 × 15 cm) for 3 weeks. During initial decomposition, organic material (OM) was mixed and turned upside down several times. In addition, water was added regularly to maintain the compost with moisture of 30%. After this time, a plastic container (45 × 30 × 30 cm) was filled up to 20 cm with the mixture of partially decomposed cow dung and leaf litter. This mixture was watered to reach 65–70% moisture and was kept for 24 h at 25–30°C to stabilize. One hundred mature *Eisenia fetida* worms were then released in 4 kg of the resulting compost (i.e., 25 worms/kg of compost). Then the top surface of the compost was covered with gunny bags and sprinkled with water to maintain 60–65% moisture for 60 days till the compost was ready to use. After 60 days, watering was stopped, the earthworms were sieved out, and the Vc was let to partially dry before its use for the experiments. 50 g of this Vc was used as a soil amendment for the experiments.

2.5. Preparation of sample for scanning electron microscopy and energy dispersive X-ray analysis

A small amount of Vc was fixed with a few drops of glutaraldehyde (2.5%) for 24 h at 4°C. After this, the sample was washed with 0.1 M phosphate buffer and centrifuged at 5,000–7,000 × g for 15 min at 4°C. The supernatant was discarded and the pellet was rewashed with 0.1 M phosphate buffer. This procedure was repeated thrice. The resulting pellet was fixed with a 1% OsO_4 solution for 2 h at 4°C and washed thrice with 0.1 M phosphate buffer as described above. The pellet was then dried, mounted on SEM stubs and coated with gold. The mounts were examined for ultrastructural studies with a JEOL 6490LV low vacuum scanning electron microscope (Akishima, Tokyo, Japan). The Vc sample elemental composition was determined by Energy dispersive X-ray spectroscopy (EDX). After capturing the images of a particular sample, peaks of elements present in the sample were identified. After peak identification, the composition of elements present in the sample on a percentage basis was computed using an EDX spectroscope (INCA x-act, Oxford Instruments, Paris, France).

2.6. Sample preparation for Fourier transform infra-red spectroscopy

The vermicompost of cattle manure was processed for the FT-IR analysis. The raw Vc was dried at 40–50°C clean environments to avoid contamination for 4 to 5 h to remove the excessive moisture. The dried sample was crushed into a fine powder using a sterile mortar and pestle, and 1 mg of the sample was mixed with 100 mg of dry potassium bromide (KBr). The KBr-based pellets were compressed into thin disks using a hydraulic press (PCI Analytic, Mumbai, India) by establishing about 15-ton pressure. The disks were fixed into the sample holder of the FT-IR spectrometer (Thermo Nicolet 6700, Waltham, Massachusetts, United States), and the spectra were analyzed with a total of 32 scans against the KBr background. The FT-IR spectra were collected for the wave number 4,000–400 cm^{-1}. Peak heights of spectra were measured using OMNIC software.

2.7. Collection and isolation of AM fungi from the rhizosphere of *Daucus carota* root

Soil samples collected from the carrot fields were processed using wet sieving and decanting techniques (Gerdemann and Nicholson, 1963). 100 g soil sample was dissolved into 1 L water, thoroughly shaken and left for 1 min to let the heavier particles settle down. The soil solution was first passed through a coarse sieve and then decanted on a series of sieves, i.e., 80, 150 and 300 meshes. The spores obtained on sieves were collected with water in separate beakers. The suspension of the spores was repeatedly washed with Ringer's solution (NaCl 6 g/L, KCl 0.1 g/L and $CaCl_2$ 0.1 g/L in distilled water of pH 7.4) to remove adherent soil particles from the spores and surface sterilized (Mosse and Hayman, 1971). The spore suspensions were poured on the filter papers placed in the funnels. The spores of similar shape and size were picked with the help of a camel hair brush under the stereomicroscope and put on a glass slide. Some of the collected AM fungal spores were mounted permanently on a glass slide in polyvinyl-lacto-glycerin (PVLG) containing polyvinyl alcohol 8.33 g, glycerin 5 mL and distilled water 50 mL (Koske and Tessier, 1983). The PVLG solution was mixed 1:1 (v/v) with Melzer's reagent (Iodine 2.5 g; Potassium iodide 7.5 g; Chloral hydrate 100 g; Distilled water 100 mL) for the staining of fungal spores.

2.8. Morphological and molecular identification of arbuscular mycorrhizal fungi

The fungal species were identified morphologically under a 40X light microscope (Olympus SZ61). Spores ($n = 3–5$) of similar morphology were assembled on a strip in polyvinyl alcohol-lactic acid-glycerol (PVLG) mixture with Melzer's reagent. The AMF spores were identified based on morphological characters such as spore color, dimension, the thickness of walls, number of walls and width of subtending hypha using the synoptic keys of Trappe (1982) and Schenck and Pervez (1990).

For molecular characterization, genomic DNA (gDNA) of the fungal spores collected above was extracted using PureLink® Genomic Plant DNA Purification Kit (Thermo Fisher Scientific). Internal Transcribed Spacer (ITS) rRNA was amplified by PCR with the following components: 1 µL of gDNA, 0.5 µL of ITS1 (5′tccgtaggtgaacctgcgg-3′) and 0.5 µL of ITS4 (5′-tcctccgcttattgatatgc-3′) primers, 12.5 µL of Thermo Scientific DreamTaq Green PCR Master Mix and 10.5 µL nuclease-free dH2O (Bhat et al., 2023). The cycling conditions on the thermal cycler were set as follows: 1 cycle at 94°C for 5 min, followed by 37 cycles at 95°C for 60 s, 58°C for 45 s, 70°C for 60 s, and a final extension at 72°C for 10 min (Sebumpan et al., 2022). Sanger sequencing was performed in a bidirectional manner, and generated sequences were submitted to the National Centre for Biotechnology Information (NCBI) under the accession number OQ703041. The genomic sequences of fungi (*Funneliformis* sp.) closely related to the present sequence were searched using the Basic Local Alignment Search Tool (BLAST) of NCBI. The downloaded sequences were aligned with MUSCLE (v3.8.31) (Edgar, 2004), and evolutionary relationships were drawn by the Maximum Likelihood method based on the Tamura-Nei (T93 + G + 1) nucleotide substitution model in MEGA 11 (Tamura et al., 2021). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Graphical representation and edition of the phylogenetic tree were performed with Interactive Tree of Life (v3.5.1) (Chevenet et al., 2006; Letunic and Bork, 2016).

2.9. Inoculum preparation of AM fungi

Spores of AM fungi were transferred to sterile paper cones. A solution of 2% chloramines-T and 0.025% streptomycin sulphate was poured drop by drop into each cone for 20 min (Hepper and Mosse, 1980). The spores were then washed thoroughly with sterilized distilled water. A pure culture of AM fungus (*Funneliformis* sp.) was maintained separately into each pot on *Chloris gayana* Kunth (Rhodes grass) grown in sandy loam soil mixed with river sand and farmyard manure in the ratio of 3:1:1 (v/v) respectively. The populations of AM fungus in the inoculums were assessed by the most probable number method (Porter, 1979). 50 g inoculum with soil was added around the seedling to inoculate 100 infective propagules of AM fungus per pot. The crude inoculum consists of soil, extra matrical spores and sporocarps, hyphal fragments and infective Rhodes grass segments. 50 g of AMF soil inoculum with approximately 200 spores was used for the experiments (Bhardwaj and Sharma, 2006). The crude inoculum of AMF consisted of soil, extra metrical spores and sporocarps, hyphal fragments and infected grass fragments.

2.10. Molecular and morphological identification of *Meloidogyne incognita*

Nuclear DNA was extracted from single specimens of nematodes as described by Bhat et al. (2021). The D2-D3 expansion segment of 28S rRNA was amplified by polymerase chain reaction (PCR) using the primers D2F: 5′-CCTTAGTAACGGCGAGTGAAA-3′ (forward) and D3R 5′-CAGCTATCCTGAGGAAAC-3′ (reverse) (Nadler et al., 2006). PCR reactions and cycling profiles were set as described by Rana et al. (2019). PCR products were purified, sanger sequenced and submitted to the NCBI under the accession number ON514606. The closely related sequences of other *Meloidogyne* species were downloaded from NCBI using the Basic Local Alignment Search Tool (BLAST) (Altschul et al., 1990). Resulting sequences were aligned with MUSCLE (v3.8.31) (Edgar, 2004), and phylogenetic relationships were constructed by the Maximum Likelihood method based on the Kimura 3–parameter (T92 + G) nucleotide substitution model in MEGA 11 (Tamura et al., 2021). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Graphical representation and edition of the phylogenetic tree were performed with Interactive Tree of Life (v3.5.1) (Chevenet et al., 2006; Letunic and Bork, 2016). Perineal pattern arrangement was observed for the morphological characterization of nematodes in mature females.

2.11. Preparation of *Meloidogyne incognita* inoculum

Nematode inoculum was prepared by using the method described by Ahamad and Siddiqui (2021). Egg masses from severely infested roots of eggplants were picked for isolation of the infective juveniles (J2) using sterilized forceps. These egg masses were washed twice with dH2O and placed in sieves (9 cm diameter with 1 mm pore size) containing double-layered tissue paper and then placed in Petri dishes filled with distilled water deep enough to make a film with the egg masses. The whole setup was then incubated at 25 ± 1°C. The nematode J2s were collected in a culture flask daily, fresh distilled water was added as required in Petri dishes, and the process was repeated continuously to obtain the required number of nematode populations. The density of J2 nematodes in the suspension was assessed by direct counting under a light microscope. The volume of the suspension was adjusted to 100 nematodes per mL. 20 mL of this suspension were applied to each pot around the carrot seedlings (2000 freshly hatched J2s). Prior to inoculation, three holes were made gently around the roots so that J2 nematodes could reach the roots of seedlings and inoculum suspension was poured carefully into these holes.

2.12. Determination of plant growth characters

After inoculation, the plants were harvested after 90 days and cleaned with tap water to remove the adhered soil particles. Different growth traits such as plant length (cm), plant fresh weight (g), and shoot and root dry weight (g) were measured. The plant length was recorded by measuring the plant from the top of the shoot to the bottom of the root. To measure plant fresh weight, the roots were gently dried using blotting sheets before weighing them. Plant dry weight was evaluated in roots and shoots independently by cutting the plants at the root initiation zone with the help of a sharp knife to separate roots and shoots. Roots and shoots were kept in envelopes in an oven at 60°C for 7–10 days.

2.13. Determination of leaf photosynthetic pigment content

Chlorophyll and carotenoid content in fresh leaves were determined using the Mackinney method (MacKinney, 1941). Briefly, 1 g of freshly harvested leaves was mixed with 20 mL of 80% acetone and ground to a fine pulp using a mortar and pestle. The mixture was centrifuged at 5,000 × g for 5 min, and the supernatant was collected in 100 cm^3 volumetric flasks. The residue was washed thrice with 80% acetone. Each washing was collected in the same volumetric flask, and volume was made up to mark, using 80% acetone. The absorbance was read at 645 and 663 nm for chlorophyll and 480 and 510 nm for carotenoid against the blank (80% acetone) on a spectrophotometer (Shimadzu UV-1700, Tokyo, Japan).

2.14. Determination of phenol content

The estimation of total phenol content was determined by the Folin-Ciocalteau reagent (Singleton and Rossi, 1965). Fresh leaves (2.0 g) were homogenized in 80% aqueous ethanol at room temperature and then placed in a cooled centrifuge at 10,000 × g for 15 min. Supernatants were collected and the remaining leaf pellets were re-extracted twice with 80% ethanol. All supernatants were pooled, put into evaporating dishes, evaporated to dryness at room temperature, and reconstituted in 5 mL distilled water. 100 µL of the resulting extract were mixed with 3 mL of distilled water, and 0.5 mL of Folin-Ciocalteau reagent. After 3 min, 2 mL of sodium carbonate (20%) was added. Samples were then thoroughly mixed and incubated for 1h. Then, absorbance at 650 nm was measured in a spectrophotometer (Shimadzu UV-1700, Tokyo, Japan). The results were expressed as mg catechol/g of fresh weight.

2.15. Determination of activities of peroxidase and polyphenol oxidase

To determine peroxidase (POX) and polyphenol oxidase (PPO) activities, 500 mg of fresh leaf tissues were homogenized in 5 mL of 50 mM phosphate buffer (pH 6.5) containing EDTA.Na2 (1 mM) and 1% polyvinylpyrrolidone. The homogenate was centrifuged at 15,000 × g for 10 min at 5°C, and the supernatant was used as an enzyme extract. Peroxidase (POX, EC 1.11.1.7) activities were measured by the method described by Chance and Maehly (1955) in fresh leaf samples. Pyrogallol phosphate buffer (3 mL), enzyme extract (0.1 mL) and 1% H_2O_2 (0.5 mL) were mixed in glass cuvettes, and changes in absorbance at 420 nm were measured at intervals of 20 s for 3 min using a spectrophotometer (Shimadzu UV-1700, Tokyo, Japan). The control group was prepared in a similar manner, but no enzyme extract was used. The peroxidase activity was expressed as U mg^{-1} fresh weight.

Polyphenol oxidase (PPO, EC 1.14.18.1) activities were measured using the protocol of Mayer et al. (1965) with minor modifications. The reaction mixture consisted of 200 µL of the enzyme extract and 1.5 mL of 0.1 M sodium phosphate buffer (pH 6.5). The reaction was started after adding 200 µL of 0.01 M catechol, and absorbance was recorded at intervals of 30 s for 3 min at 495 nm on a spectrophotometer (Shimadzu UV-1700, Tokyo, Japan). The control group was prepared in a similar manner, but no enzyme extract was used. The activity of polyphenol oxidase (PPO) was expressed as U mg^{-1} fresh weight.

2.16. Determination of root colonization by arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) root colonization was determined by the grid line intersecting method (Giovannetti and Mosse, 1980). AMF-inoculated roots were collected and washed gently with dH2O to remove soil particles. Roots were then cut into small pieces (1 cm), placed in KOH solution (10%) in a beaker, and autoclaved for 10 min at 103.4 kPa to remove the cytoplasmic content. The KOH solution was poured off and the root segments were rinsed in distilled water until no brown color appeared in the water. These root segments were then transferred in another beaker containing alkaline H_2O_2 at room temperature for 20 min for bleaching. Then, the roots were thoroughly rinsed with distilled water. The root segments were placed into a beaker containing HCl (1%) for 3 to 4 min. The solution was poured off and root segments were placed in another beaker with trypan blue lactophenol solution (0.05%). The root segments were observed under the stereomicroscope (Olympus, Mumbai, India) for mycorrhizal colonization. The per cent root colonization was calculated using the following formula:

$$\text{Percent}\,(\%)\,\text{root colonization} = \frac{\text{Number of root segments colonized by AM fungi}}{\text{Total number of segments observed}} \times 100$$

2.17. Root galling and nematode density determination

The number of nematodes were determined by the Cobb's sieving and decanting technique followed by Baermann funnel extraction (Southey, 1986). A total of 250 g of well-mixed soil from each treatment was processed. Nematode suspension was collected after 24 h, and the number of nematodes was counted in five aliquots of 1 mL of suspension from each sample. The mean of five counts was used to calculate the population of nematodes per kg of soil. To estimate the number of juveniles (J2s), eggs and females inside the roots, 1 g of roots was macerated in a Waring blender, and counts were made from the suspension thus obtained. The number of nematodes present in roots was calculated by multiplying the number of nematodes present in 1 g of the root by the total weight of the root. The number of galls and egg masses per root system was also counted.

2.18. Instruments

The chemical analysis of vermicompost was performed using a energy dispersive X-ray instrument from France and Thermo Nicolet 6,700, FT-IR spectrometer from United States. Biochemical studies were conducted using a Shimadzu UV-1700, UV-Vis spectrophotometer from Japan, which had a wavelength range of 190–1,100 nm and an accuracy of ±0.3 nm. The scanning electron

microscope JEOL JSM-6490LV from Japan was utilized for ultrastructural studies.

2.19. Statistical analysis

At least five independent replicates were analysed for all the parameters measured. Data were analyzed using R software (2.14.0). Analysis of variance (ANOVA) was used to test the significance ($p \leq 0.05$) of applied treatments. Least significant differences (LSD) and Duncan's multiple range tests (DMRT) were employed to represent the significant differences between the treatments. Graphs were made by using SigmaPlot 14.0 software. Presentations of error bars in graphs showed the standard error (±SE). Principal component analysis (PCA) was done through OriginPro_2022 software.

3. Results

3.1. Occurrence and identification of AM fungi

From the soil samples, five genera of AMF were observed and identified morphologically: *Funneliformis* sp., *Gigaspora* sp., *Septoglomus* sp., *Claroideoglomus* sp. and *Acaulospora* sp. (Figures 1A–E). *Funneliformis* isolates possess visible septum, often cylindrical or funnel-shaped, and have subtending hypha. *Gigaspora* isolates bear irregular to rarely subglobose septum, spore wall consisting of two layers, stained dark red to red-brown in Melzer's reagent. *Septoglomus* isolates display dark black colored spores visible when stained with Melzer's reagent and having two- or three-layered walls, one subtending hypha. *Claroideoglomus* isolates show flexible, thin, colorless innermost layer; and bill-shaped, colorless subtending hyphae. *Acaulospora* sp. shows a wall structure with three layers, whitish-yellow in color, and possesses a granular germ layer with a beaded surface that reacts to Melzer's reagent.

The number of spores of AM fungi also varied across treatments. *Funneliformis* sp. was the most abundant genus (4.3 spores/g of soil), followed by *Gigaspora* (3.01 spores/g of soil), *Claroideoglomus* sp. (2.6 spores/g of soil), *Acaulospora* sp. (2.38 spores/g of soil) and *Septoglomus* sp. (1.88 spores/g of soil) (Table 1). Of these AMF genera, *Funneliformis* sp. was used in the present investigation and was subjected to detailed morphological and molecular characterization.

Based on morphological characters, the *Funneliformis* sp. strain isolated in this study was identified as *Funneliformis mosseae*. It has visible septum, often cylindrical or funnel-shaped, and spore showing subtending hyphae, germ tube, and a three-layered wall (Figure 1A). The *Funneliformis* AM fungi were further characterized by analyzing the sequences of the ITS rRNA (OQ703041). The nucleotide sequences of the ITS rRNA of the fungal isolate used in this study show 100% similarity with the sequences of *F. mosseae* from different

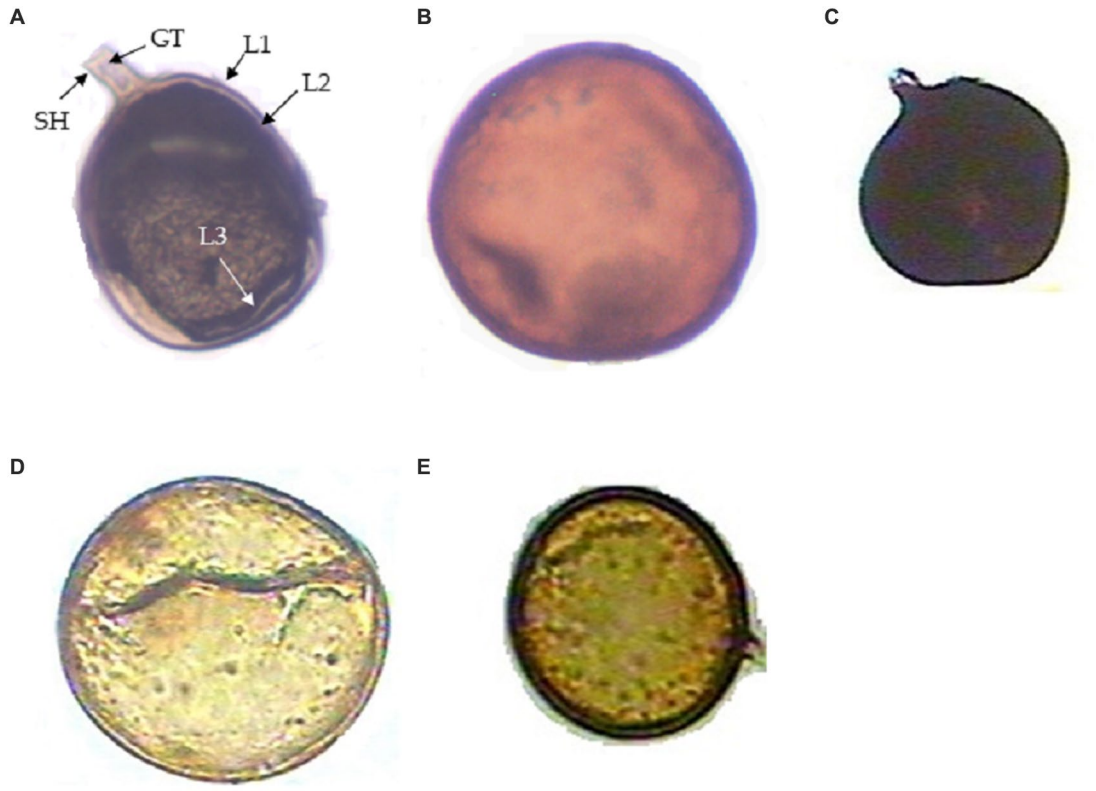


FIGURE 1
Different arbuscular mycorrhizal fungi (AMF) from the rhizosphere of *Daucus carota*. **(A)** *Funneliformis mossae* spore showing subtending hyphae (SH), germ tube (GH), wall structure-Layer 1, Layer 2, and Layer 3 designated as (L1), (L2), and (L3), respectively; **(B)** *Gigaspora* sp., **(C)** *Septoglomus* sp., **(D)** *Claroideoglomus* sp., and **(E)** *Acaulospora* sp.

geographical regions of the world deposited in the NCBI. Upon alignment, no nucleotide difference was observed between the sequences analyzed. Phylogenetic reconstructions based on these sequences show that the AM fungi used in this study form a clade with previously described *F. mosseae* species from Germany, Italy, and India, and form a clade with *Funneliformis coronatum*, and together form a sister clade with *Funneliformis geosporum* and *Funneliformis caledonium* (Figure 2). Thus, morphological, molecular and phylogenetic studies confirm that the fungal isolate used in this study is *F. mosseae*.

TABLE 1 Occurrence of different arbuscular mycorrhizal fungi isolated from the rhizosphere of carrot roots.

S. No.	Arbuscular mycorrhizal fungi	Spore per 100g soil
1	*Funneliformis mosseae*	430
2	*Gigaspora* sp.	301
3	*Septoglomus* sp.	188
4	*Claroideoglomus* sp.	260
5	*Acaulospora* sp.	238

3.2. Identification of root-knot nematodes

Morphologically, the perineal pattern of the adult females used in the present study showed an angular oval structure and an inverted V shape (Figure 3). This perineal pattern is similar to the previously described for *M. incognita* (Hunt and Handoo, 2009). These *Meloidogyne* nematodes were further characterized by analyzing the sequences of the D2-D3 region of the 28S rRNA gene (ON514606). The nucleotide sequences of the D2-D3 region of the nematodes used in this study show 100% similarity with the sequences of several other *M. incognita* nematodes from the United States, China, Brazil, Colombia, Myanmar, Vietnam and other regions of the world deposited in the NCBI. Upon alignment, no nucleotide difference was observed between the sequences analyzed. Phylogenetic reconstructions based on these sequences show that the nematodes used in this study form a clade with previously described *M. incognita* nematode species from China and USA, and together formed a group with other species (Figure 4). Thus, morphological, molecular and phylogenetic studies confirm that the nematode used in this study is *M. incognita*.

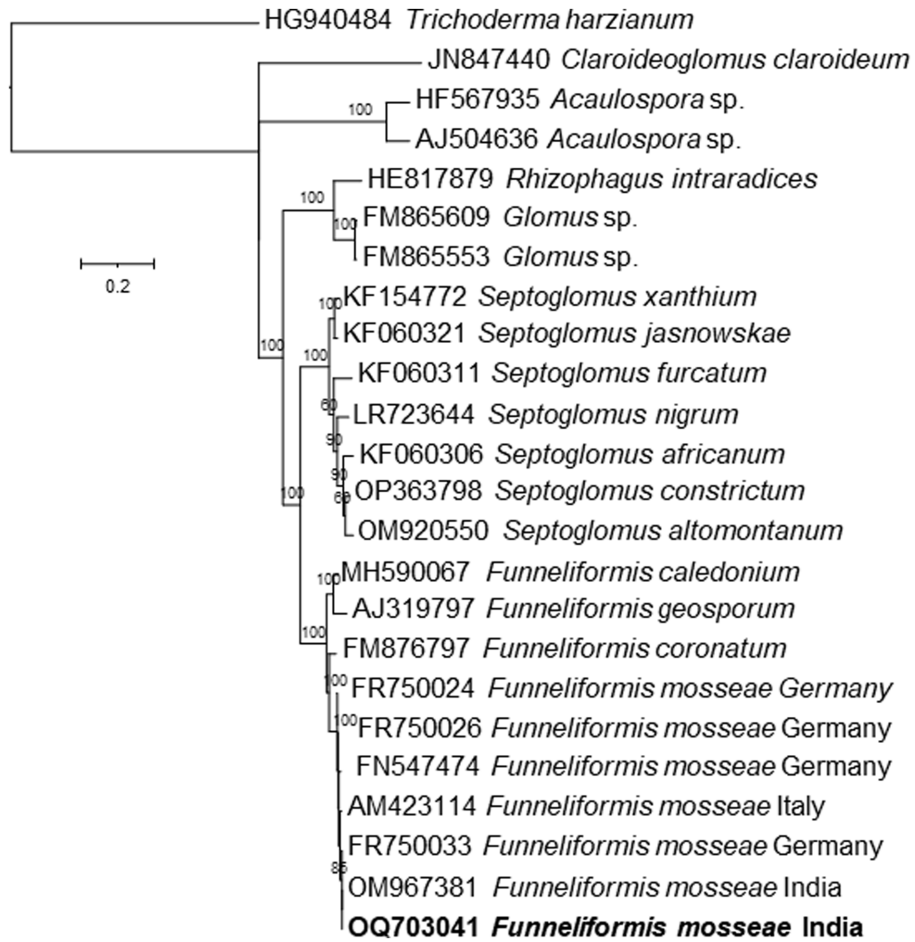


FIGURE 2
Phylogenetic tree based on ITS rRNA gene sequences of the *Funneliformis mosseae* isolated in this study and several related species inferred by using the Maximum Likelihood method based on the Timura-Nei Parameter Model. The percentage of trees in which the associated taxa clustered together is shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site.

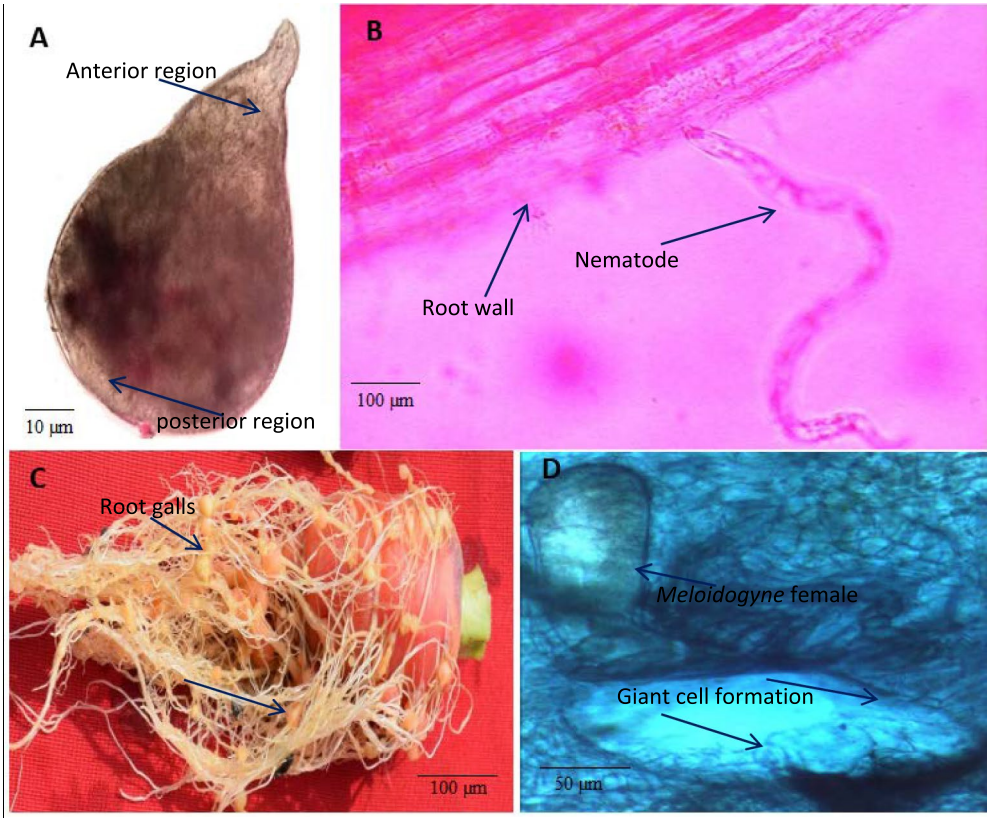


FIGURE 3
Light microscopy of *Meloidogyne incognita* nematodes on carrot plants. **(A)** *M. incognita* female, **(B)** A nematode juvenile (J2) invading root, **(C)** Root galling caused by *M. incognita* nematodes on carrot roots, **(D)** Transverse section (TS) of root gall showing the giant cell formation induced by the *M. incognita* female.

3.3. Energy-dispersive X-ray spectroscopy and scanning electron microscopy

The observations of EDX analysis showed that O, N, Na, Mg, Al, Si, P, Cl, K, Ca, and Fe elements were found in the cow manure Vc. Moreover, oxygen (O) was the most predominant atom (46.29%) and sodium (Na) the least (0.25%) in the Vc (Figure 5A). Other elements, such as Fe, Mg, Ca, and K were also present in the of Vc at medium concentrations (Figure 5A).

SEM analysis was used to study the ultrastructural morphology of the prepared Vc. The SEM micrograph of the Vc sample revealed that the surface area of the Vc sample was larger and had more porosity, fragmentation, and granular structures. The highest proportion of surface area and the smaller particle size were recorded in the Vc sample. The micrographs showed a greater surface area with single particles packed together to form aggregates. Such aggregation is responsible for the uncertainty about the real surface area of Vc because the internal area was not fully accessible (Figure 5B).

3.4. Fourier transform infra-red spectroscopy

The FT–IR spectra were used to determine the compounds' functional group(s) based on the peak values. The presence of primary amine was confirmed by the high absorption bands seen at 3,406 cm^{-1} as a result of the bonded N-H stretching (Figure 5C). The strong variable bands were observed at 2926.6 cm^{-1} to 2957.6 cm^{-1} due to asymmetric stretching of bonded C–H, which shows the presence of alkene (CH_2) and alkane (CH_3) groups. In addition, the bands observed at 2852.9 cm^{-1} to 2856.6 cm^{-1} due to the C–H symmetric stretch show the presence of alkene as a common biochemical constituent. The C–O bands were predominantly observed at 2363.7 cm^{-1} due to the carboxyl group, whereas the spectral band observed at 1743.2 cm^{-1} due to C=O stretch vibration corresponds to the presence of saturated aliphatic esters (Figure 5C).

The secondary structure of amine caused by N–H bending is observed at 1653.4 cm^{-1} to 1555.9 cm^{-1}. The bands observed at 1405.1 cm^{-1} are caused by alcohols and phenols' bonded C–O/O–H bending. The band observed at 1360.7 cm^{-1} due to C–H bending shows the presence of alkane. The IR spectrum seen at 1315.5 cm^{-1} as a result of S=O stretching shows the presence of sulphone. The bonded C–O absorbed IR spectrum at 1206.1 cm^{-1} shows the presence of ether functional groups. The strong bands observed at 1073.8 cm^{-1} to 1034.0 cm^{-1} due to C–O–C symmetric stretching shows the presence of polysaccharides. The presence of sulfide and disulfide compounds can be seen in the faint absorption bands at 575.5 cm^{-1}, which may be caused by S-S stretching (Figure 5C).

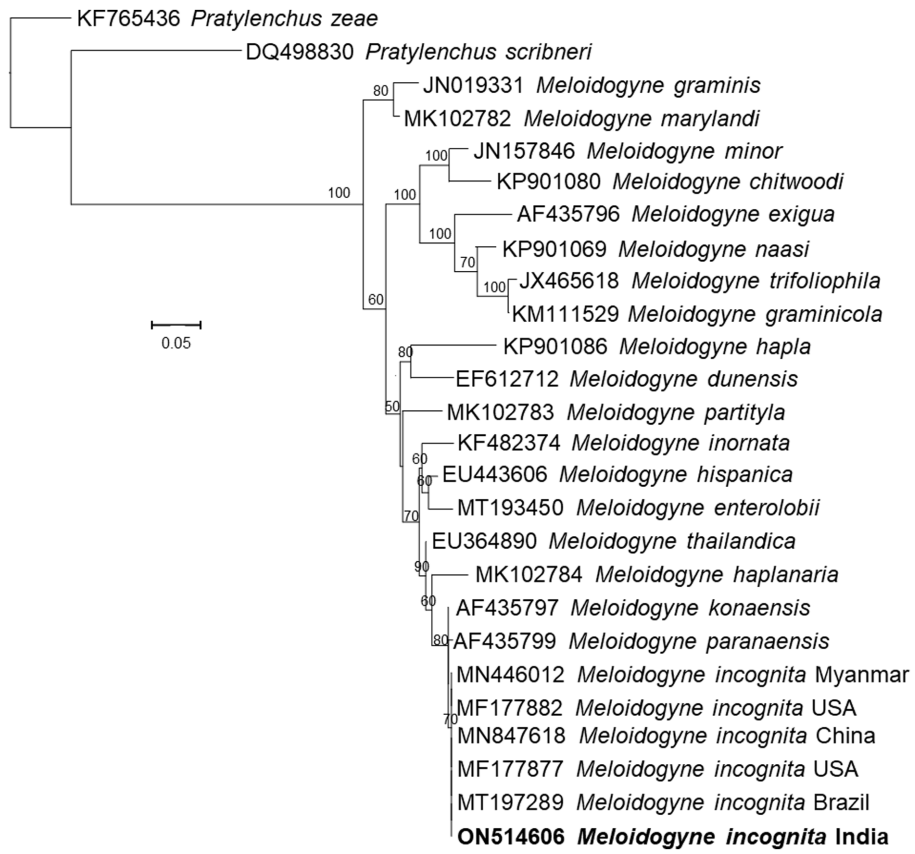


FIGURE 4
Phylogenetic tree based on D2D3 expansion segments of the 28S rRNA gene sequences of the *Meloidogyne incognita* isolated in this study and several related species inferred by using the Maximum Likelihood method based on the General Time Reversible model. The percentage of trees in which the associated taxa clustered together is shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site.

3.5. Effects on plant growth parameters

Meloidogyne incognita significantly reduced plant growth parameters such as plant height, fresh weight, and shoot and root dry weight. The application of Vc and AMF (*F. mosseae*), both individually and in combination, significantly increased several plant growth parameters (Figures 6A–D). Interestingly, a more substantial positive effect was observed when Vc was applied to nematode-infested plants than when *F. mosseae* fungi were applied. Moreover, the combined applications of *F. mosseae* and Vc to nematode-infested plants increased the plant length by 13.60%, fresh plant weight by 37.85%, shoot dry weight by 42.85%, and root dry weight by 59.17% (Figures 6A–D).

3.6. Effects on chlorophyll and carotenoid content

A significant reduction in chlorophyll and carotenoid content was observed in *M. incognita*-infested plants (Figures 6E,F). A significant chlorophyll and carotenoid increase content was observed when *M. incognita*-infested plants were treated with Vc but not with AMF (*F. mosseae*). In addition, synergistic effects of Vc and *F. mosseae* treatments were observed. More specifically, the combined applications of both *F. mosseae* and Vc to *M. incognita*-infested plants increase chlorophyll and carotenoid content by 21.51 and 14.10%, respectively (Figures 6E,F).

3.7. Effects on phenol content, peroxidase and polyphenol oxidase enzyme activity

A significant induction of phenol content, peroxidase (POX) and polyphenol oxidase (PPO) enzyme activity was observed in *M. incognita*-infested plant (Figures 7A–C). When *M. incognita*-infested plants were treated with AMF (*F. mosseae*) or with Vc, phenol content, peroxidase (POX) and polyphenol oxidase (PPO) enzyme activity were further increased, although these effects were stronger in Vc-treated plants than in AMF-treated plants. In addition, synergistic effects of Vc and *F. mosseae* treatments were observed. More specifically, the combined applications of both *F. mosseae* and Vc to *M. incognita*-infested plants increase phenol content, POX and PPO activities by 23.78, 15.65, and 29.78%, respectively (Figures 7A–C).

3.8. Effects on root galling and nematode population with arbuscular mycorrhizal fungi colonization

A significant reduction in root galls and nematode population was observed when *M. incognita*-infested plants were treated with AMF or with Vc, alone or in combination. However, these effects were stronger in Vc-treated plants than in AMF-treated plants. In addition, synergistic effects of Vc and AMF treatments were observed

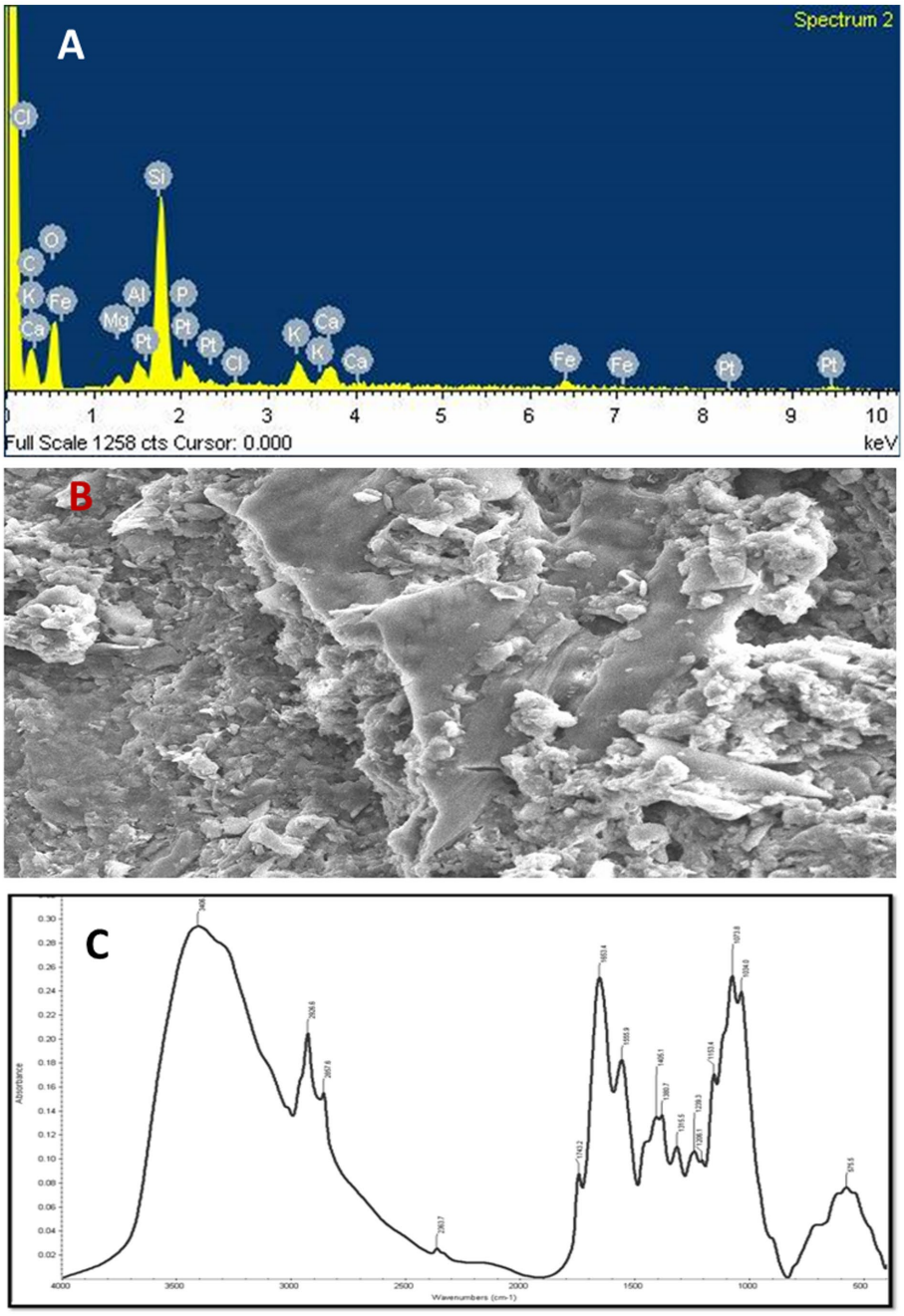


FIGURE 5
(A) Energy-dispersive X-ray (EDX) spectrum of vermicompost, **(B)** scanning electron microscope (SEM) analysis of vermicompost **(C)** absorbance spectrum and FT-IR dominant peaks of the vermicompost.

(Figure 7). More specifically, the combined applications of both AMF (*F. mosseae*) and Vc to *M. incognita*-infested plants reduce root galling and nematode populations by 42.04 and 55.51%, respectively (Figures 7D,E). The mycorrhizal response of carrots inoculated with *M. incognita*, showed that the addition of Vc considerably ($p = 0.05$) boosted root colonization by *F. mosseae* (Figures 7F, 8). The application of Vc treatments resulted in a notable increase in mycorrhiza colonization in carrot plants that were infested with *M. incognita*. Among the treatments, the combination of AMF (*F. mosseae*) and Vc showed the highest percentage of root colonization (63%) in the presence of *M. incognita*, followed by the inoculation of *F. mosseae* alone (57%) (Figures 7F, 8).

3.9. Principal component analysis

Principal component analysis was carried out to study the effect of AMF (*F. mosseae*) and Vc on plant growth parameters (plant length, plant fresh weight, shoot and root dry weight), plant biochemical profiles (chlorophyll, carotenoid and phenol content),

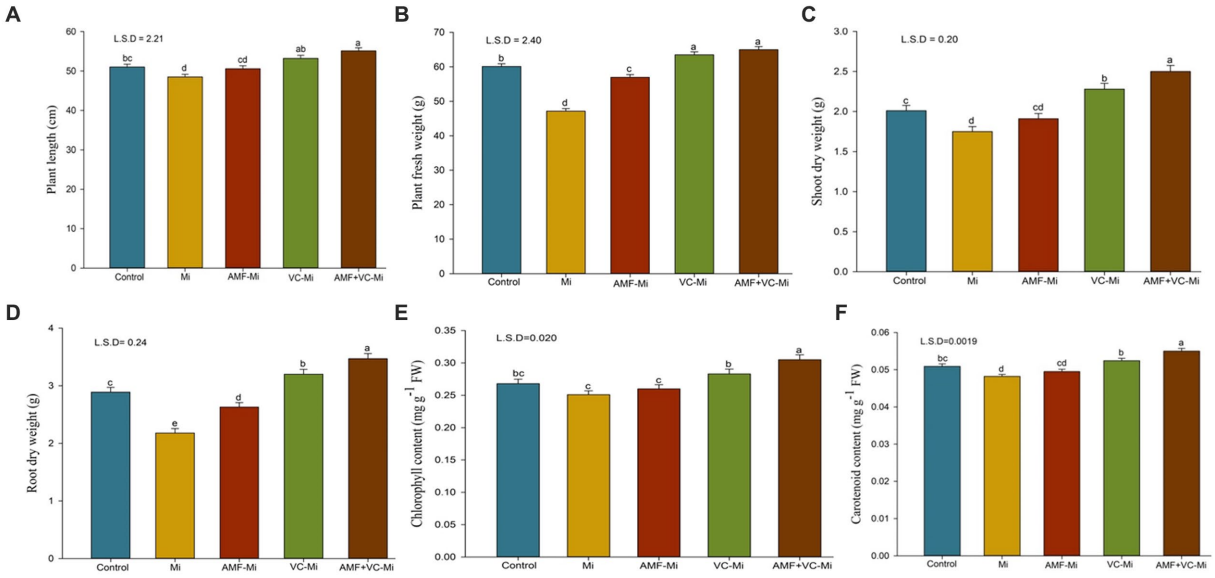


FIGURE 6
(A–F) Effects of arbuscular mycorrhizal fungi (*Funneliformis mosseae*) and vermicompost applications on different traits of plants infested or not by *M. incognita*. **(A)** Mean (±SEM) plant length. **(B)** Mean (±SEM) plant fresh weight. **(C)** Mean (±SEM) shoot dry weight. **(D)** Mean (±SEM) root dry weight. **(E)** Mean (±SEM) chlorophyll content. **(F)** Mean (±SEM) carotenoid content. AMF, Arbuscular-mycorrhizal fungi (*Funneliformis mosseae*); Vc, Vermicompost; Mi, *Meloidogyne incognita*; Error bars represent standard error (SE); Data present mean values of 5 replicates (n=5).

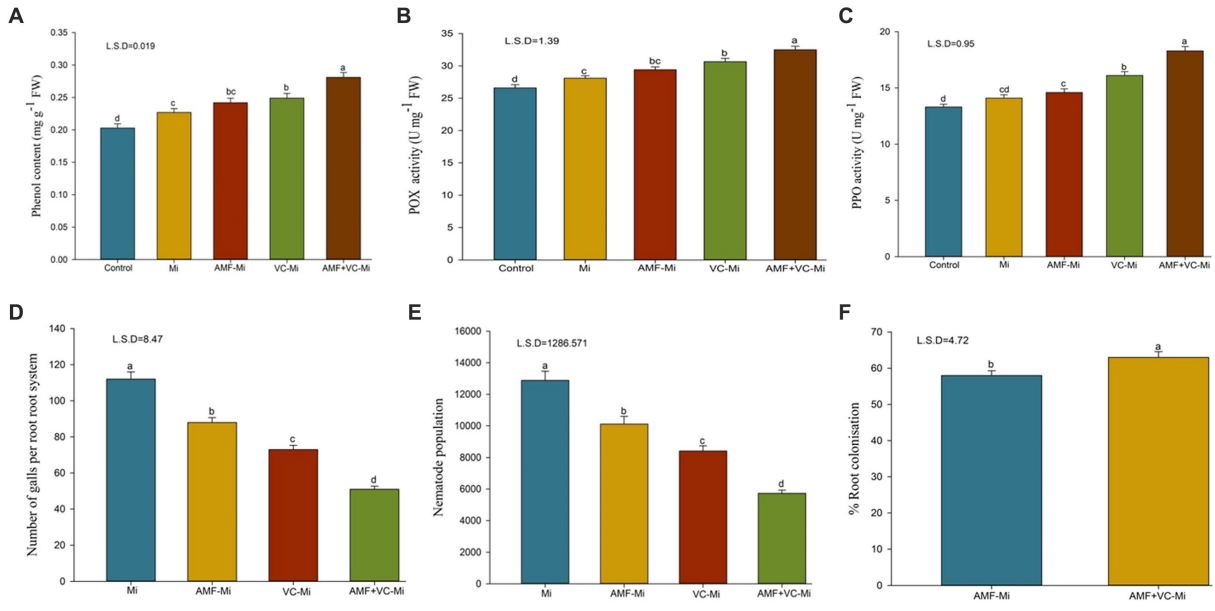


FIGURE 7
(A–F) Effects of arbuscular mycorrhizal fungi (*Funneliformis mosseae*) and vermicompost applications on different traits of plants infested or not by *M. incognita*. **(A)** Mean (±SEM) phenol content. **(B)** Mean (±SEM) peroxidase (POX) activity. **(C)** Mean (±SEM) polyphenol oxidase (PPO) activity. **(D)** Mean (±SEM) number of galls per plant. **(E)** Mean (±SEM) number of nematodes per plant. **(F)** Mean (±SEM) proportion of roots colonized by AMF (%). AMF, Arbuscular-mycorrhizal fungi (*Funneliformis mosseae*); Vc, Vermicompost; Mi, *Meloidogyne incognita*. Error bars represent standard error (SE); Data present mean values of 5 replicates (n=5).

plant defense enzyme activities (POX and PPO), nematode disease severity parameters (root galling and nematode population). The PCA data showed an accumulated variability of 93.19%. The PC1 and PC2 displayed 69.10 and 24.09% (total 93.19%) of the novel information, respectively (Figure 9). AMF and Vc treatments, individually and in combination, show significant positive correlations with plant growth, photosynthetic pigment content, phenol contents and defense enzyme activities. Moreover, these latest plant traits showed a negative correlation with number of galls and nematode densities (Figure 9).

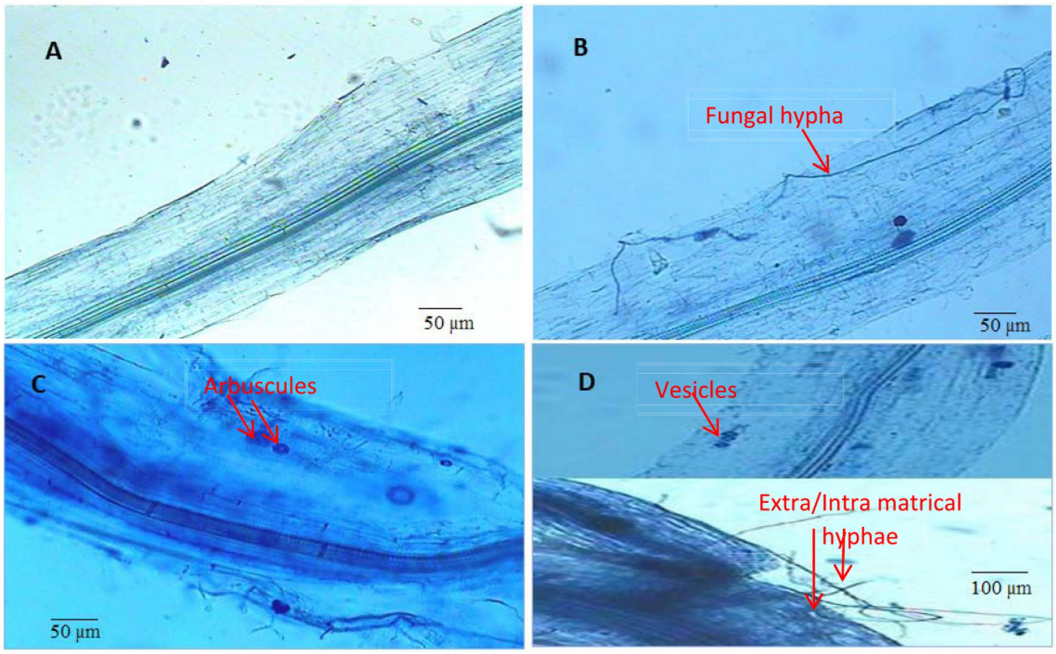


FIGURE 8
Root colonization by arbuscular mycorrhizal fungi (*Funneliformis mosseae*). **(A)** Control (without root colonization) **(B)** AMF treated plants (with root colonization) **(C,D)** AMF+Vermicompost treated plants (with root colonization).

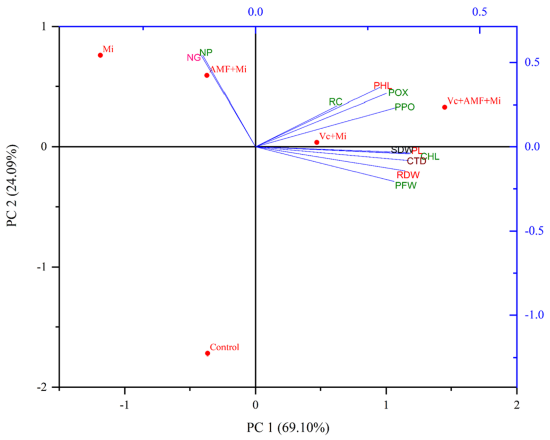


FIGURE 9
Biplots of principal component analysis (PCA) comparing the effects of arbuscular mycorrhizal fungi, vermicompost treatments and *M. incognita* infestation on different plant traits. PL, Plant length; PFW, Plant fresh weight; SDW, Shoot dry weight; RDW, Root dry weight; CHL, Chlorophyll content; CTD, Carotenoid content; PHL, Phenol content; POX, Peroxidase; PPO, Polyphenol oxidase; NG, Number of galls; NP, Nematode population; RC, Root colonization; Mi, *M. incognita*; AMF, Arbuscular mycorrhizal fungi (*Funneliformis mosseae*); Vc, Vermicompost.

4. Discussion

In this study we show that the application of vermicompost and AMF to *M. incognita* attacked plants significantly alleviates the negative impact of these nematodes on plant growth. These effects are accompanied by the suppression of galling and nematode populations and a greater induction of phenolic compounds and defensive enzymes in vermicompost- and AMF-treated plants.

The application of Vc and AMF as soil amendments is a fast-emerging and encouraging area of research. Our results showed that the application of Vc and AMF to the soil significantly improved several plant growth parameters and greatly alleviated the negative consequences of *M. incognita* attack. A potential explanation for this observation is the induction of defense compounds that suppress nematodes and/or the increase of several macro- and micronutrients required for plant growth. In support of this hypothesis, previous studies also showed that the application of Vc in susceptible tomato plants increases root defense against root-knot nematodes by increasing the levels of defense compounds and by changing soil properties, which translates into better plant growth (Xiao et al., 2016). Furthermore, AMF significantly increased the growth through the induction of resistance against *M. incognita* in cherry tomatoes (Wang et al., 2022). In addition, AMF and Vc treatments improve plant defenses against other pathogens (Meng et al., 2021). In addition, some other studies show that Vc and AMF treatment enhances N, K, Ca, Zn, S and P contents in the soil, improving plant growth (Balliu et al., 2015). The AMF can significantly boost plant and soil characteristics in both root and shoot systems (Al-Hmoud and Al-Momany, 2017). Only a few reports are available on Vc and AMF, which showed beneficial roles in the growth and development of crops (Khorshidi et al., 2013; Khan et al., 2014; Oliveira et al., 2015; Shamshiri and Fattahi, 2016; Naeeni et al., 2017). The present study showed the AMF application alone and with the combination of Vc significantly increases the productivity of carrots and decreases the nematode infestation.

We also observed that AMF and Vc applications alone and in combinations increased the contents of plant pigments (chlorophyll

and carotenoids). An increase in the pigments may be due to increase in nitrogen content of leaves of plants supplied with vermicompost (Yadav and Garg, 2015). Previous studies have shown that the Vc amendments in the soil increase the chlorophyll and carotenoid contents in plants, which in turn improves plant resistance against *M. incognita* (Xiao et al., 2016), and soil amendment with Rhizophagus irregularis (AMF) increases chlorophyll and carotenoid content of carrot plants infested with *M. incognita* (Ahamad and Siddiqui, 2021). Moreover, mycorrhizal inoculations enhance magnesium and phosphorus uptake in plants, which in turn increases chlorophyll content and overall performance of plants (Ait-El-Mokhtar et al., 2020). Vermicompost and AMF synergistically increase total chlorophyll content in plants when applied with *Rhizobium* (Rajasekaran and Nagarajan, 2004; Rajasekaran et al., 2006; Arumugam and Rajasekaran, 2010). Total chlorophyll content, fresh weight, and leaf area were higher in AMF-treated plants than in plants without AMF, but variations were notable under drought stress environments (Morte et al., 2000; Zhu et al., 2012; Sivakumar et al., 2020).

Our results also show that AMF and Vc applications alone and in combinations increased the phenolic contents and defense enzymes (POX and PPO). Several studies show that phenolics play an important role in plant resistance against biotic and abiotic stresses (Rehman et al., 2012; Tuominen, 2013). AMF effectively induces the accumulation of phenols and flavonoids, which are powerful antioxidants that act as free radical scavengers and reducing agents (Chen et al., 2013). The addition of AMF in the soil with or without *M. incognita* increases phenol contents in plants (Nagesh and Reddy, 2004). Soil amendments with Vc followed by inoculation of *M. incognita* increased the activities of defense enzymes (POX and PPO) in olive trees (Mohamed et al., 2019). Several studies report that the addition of compost increases plant defense against pathogens (Zhang et al., 1998). Similarly, AMF inoculations induces POX and PPO activities in cucumber plants infested with *M. incognita* (Choshali et al., 2019). AMF can improve plant tolerance to biotic and abiotic stressors and stimulate plant development under these conditions (Plassard and Dell, 2010; Alqarawi et al., 2014; Navarro et al., 2014). AMF immunization increases the nutritional value, physiology, quality and quantity of the plant products and pumps the biological activity, increasing the biochemical process (Yang et al., 2014; Canellas et al., 2015; Shi-Chua et al., 2019; Gao et al., 2020). In addition, the interaction between Vc and AMF may help speed up ^{15}N acquisition through mineralization induced by vermicompost amendment and transfer from the soil to the plant (Liu et al., 2020).

With reference to root galling and nematode multiplication, when Vc was applied to carrot plants, a decrease in *M. incognita* population and the formation of galls was observed. Similar results were shown in tomato plants infected with *M. javanica* (Hemmati and Saeedizadeh, 2019). Moreover, nematode hatching is reduced when Vc exudates are applied (Mondal et al., 2021). Arugula Vc also decreases the reproduction factor of the nematode by 54.4 to 70.5% in infected tomato plants. It affects the expression of resistance genes and induces systemic resistance against root-knot nematodes (Rostami et al., 2022). Moreover, soil application of AMF fungi also reduced plants' root galling and nematode population (Siddiqui and Akhtar, 2007). The mycorrhizal fungi could activate plant systemic resistance to resist possible nematode invasion (Nafady et al., 2022). Alternatively, mycorrhizal fungi may have a direct mechanism to suppress nematode root infection by competing for feeding and root space. The mechanisms by which this elicitation in the systemic defensive capacity of the roots occurs are related to the activation of genes that encode PR proteins, chitinases and enzymes that participate in reactive oxygen species (ROS) detoxification (whose accumulation occurs during hypertrophy and cell death by the nematodes) like glutathione S-transferase (GSTs)/superoxide dismutase (SOD), enzymes involved in the biosynthesis of lignin, and shikimate pathway which in turn, produces precursors of various aromatic secondary metabolites against nematodes (Schouteden et al., 2015; Sharma and Sharma, 2017; Balestrini et al., 2019). AMF colonization could reduce the density of *M. incognita* in soil (Wang et al., 2022). Soil amended with Vc increased the root colonization caused by AM fungi in the presence of *M. incognita* in carrot plants. Other studies also supported this statement that Vc application with AMF improves root colonization in tomato plants when infected with *M. incognita* compared to the individual application (Serfoji et al., 2010).

The surface area of the Vc was found to be larger, and it showed more porosity, fragmentation, and granular structures that are packed together to form aggregates as compared to pre-vermicompost. Complete internal area was not accessible due to these aggregates. The changes in surface morphology of pre- and post-vermicompost substrate mixtures and maturity were studied by SEM of Vc samples (Kumar et al., 2014; Unuofin and Mnkeni, 2014; Sharma and Garg, 2018; Srivastava et al., 2020). Irregular morphology in Vc samples with a high number of pores was observed by Kumar et al. (2014). Similar findings were observed in cation exchange capacity value in Vc samples (Pereira and Arruda, 2003; Ravindran et al., 2008). Disaggregation in the lignin matrix was followed by Hussain et al. (2016), it is because of the joint action of earthworms and microbes. Authors suggested that earthworms ingest and grind the substrate in their gizzard and pass it to the intestine, where enzymes and microbes carry out further degradation and disaggregation (Bhat et al., 2017). The EDX analysis in the present study showed the presence of various inorganic and organic elements in the cow manure vermicompost. The results of this study also corroborated with Zulhipri and Purwanto (2021), which showed that multiple elements of vermicompost were present in small and large proportions.

FT-IR analysis results indicate that this technique is suitable for the identification of the functional groups in Vc maturity and stability. Bhat et al. (2017) applied FT-IR spectra to analyze the mineralization of organic matter and degradation of complex aromatics (lignin, polyphenols) into simpler compounds (carbohydrates, lipids) by earthworms. The band height reduction was observed at 3,100–3,600 cm^{-1} in the Vc samples compared to the raw waste. Moreover, Sen and Chandra (2007) applied an estimate of humic acid derived from sugar industry wastes, which showed the broadband at 3,400–3,300 cm^{-1}. Ravindran et al. (2008) identify the chemical structural changes in the control and final Vc mixtures of solid waste (animal fleshing) produced from the leather industry by applying FT-IR spectroscopy technique. FT-IR spectra observed a reduction of aliphatic compounds in the final Vc mixture. Deka et al. (2011) confirmed that FT-IR spectra of final Vc mixtures increased nitrogen compounds and decreased aliphatic and aromatic compounds compared to the pre-Vc waste mixtures. This indicates the degradation of bio-waste during the vermicomposting process. Lv et al. (2013) applied FT-IR spectra on water extractable organic matter (WEOM) extracted from the vermicomposting process of cattle dung, and observed a decreasing

trend of aliphatic C–H stretching at 2936–2958 cm − 1 that confirms lipids and carbohydrate degradation. Similar findings were observed in FT-IR spectroscopy analysis of Parthenium mediated Vc (Rajiv et al., 2013). Ravindran et al. (2013) observed the appearance of COO groups and relative reduction in OH, CH_3 and CH_2 groups in Vc prepared from biodegradation of fermented animal fleshing mixed with leaf litter and cow dung using earthworm, *Eudrilus eugeniae*.

5. Conclusion

The root-knot nematode, *Meloidogyne incognita* causes significant damage to carrots under greenhouse and field conditions. Supplementation of Vc and AMF alone and in combination, enhanced plant growth, chlorophyll, carotenoid, and phenol contents, and increased in the defense enzyme activities. In addition, mycorrhizal root colonization was also increased when plants were amended with Vc in the presence of *M. incognita*. Vc and AMF soil amendments in carrot plants suppressed root galls and nematode populations. The results of the present study, therefore, strongly support the use of Vc and AMF against *M. incognita*. Hence, Vc along with AMF could be an efficient alternative to promote sustainable plant production under biotic stress conditions.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Author contributions

LA, AB, and AR: conceptualization, formal analysis, investigation, and writing—original draft. LA, AB, AR, and HK: data curation and methodology. RM and FA: funding acquisition. LA, AB, AR, RM, and FA: project administration. HK, MH, SA, RM, and FA: resources. LA, AB, AR, and RM: supervision and validation. LA, AB, AR, HK, MH, and SA: visualization. LA, AB, AR, HK, MH, SA, RM, and FA: writing—review and editing. All authors contributed to the article and approved the submitted version.

Funding

The work of RM is supported by the Swiss National Science Foundation (Grant 186094 to RM). The work of AB is supported by Swiss Government Excellence Scholarship (Grant Nr. 2021.0463 to AB). The authors also extend their appreciation to the Deputyship for Research and Innovation, Ministry of Education in Saudi Arabia for funding this research work through the project no. (IFKSUOR3-005-2).

Acknowledgments

The authors are thankful to the Chairperson of the Department of Botany and the University Sophisticated Instrument Facility (USIF) of the Aligarh Muslim University (India) for providing access to laboratory and instrument facilities. The authors also thank the Madhav University (India), Swiss National Science Foundation, the Institute of Biology of the University of Neuchâtel (Switzerland), King Saud University (Saudi Arabia), and Chandigarh University (India) for their support.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Ahamad, L., and Siddiqui, Z. A. (2021). Effects of *pseudomonas putida* and *Rhizophagus irregularis* alone and in combination on growth, chlorophyll, carotenoid content and disease complex of carrot. *Indian Phytopathol.* 74, 763–773. doi: 10.1007/s42360-021-00346-y

Ait-El-Mokhtar, M., Baslam, M., Ben-Laouane, R., Anli, M., Boutasknit, A., Mitsui, T., et al. (2020). Alleviation of detrimental effects of salt stress on date palm (*Phoenix dactylifera* L.) by the application of arbuscular mycorrhizal fungi and/or compost. *Front. Sustain. Food Syst.* 4:131. doi: 10.3389/fsufs.2020.00131

Al-Hmoud, G., and Al-Momany, A. (2017). Effect of four mycorrhizal products on squash plant growth and its effect on physiological plant elements. *Adv. Crop. Sci. Tech.* 05:260. doi: 10.4172/2329-8863.1000260

Alqarawi, A. A., Abd-Allah, E. F., and Hashem, A. (2014). Alleviation of salt-induced adverse impact via mycorrhizal fungi in *Ephedra aphylla* Forssk. *J. Plant Interact.* 9, 802–810. doi: 10.1080/17429145.2014.949886

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., and Lipman, D. J. (1990). Basic local alignment search tool. *J. Mol. Biol.* 215, 403–410. doi: 10.1016/S0022-2836(05)80360-2

Arumugam, R., and Rajasekaran, S. (2010). Nagarajan, S.M. response of arbuscular mycorrhizal fungi and *Rhizobium* inoculation on growth and chlorophyll content of *Vigna unguiculata* (L.) Walp. Var. Pusa 151. *J. Appl. Sci. Environ.* 14, 113–115. doi: 10.4314/jasem.v14i4.63282

Asif, M., Tariq, M., Khan, A., Rehman, B., Parihar, K., and Siddiqui, M. A. (2016). Potential role of aqueous extract of some weeds against egg hatching and juvenile mortality of root-knot nematode *Meloidogyne incognita*. *J. Agri. Crops.* 3, 17–24.

Asif, M., Tariq, M., Khan, A., and Siddiqui, M. A. (2017). Biocidal and antinemic properties of aqueous extracts of ageratum and coccinia against root-knot nematode, *Meloidogyne incognita in vitro*. *J. Agri. Crops.* 12:108. doi: 10.4038/jas.v12i2.8229

Balestrini, R., Rosso, L. C., Veronico, P., Melillo, M. T., De Luca, F., and Fanelli, E. (2019). Transcriptomic responses to water deficit and nematode infection in mycorrhizal tomato roots. *Front. Microbiol.* 10:1807. doi: 10.3389/fmicb.2019.01807

Balliu, A., Sallaku, G., and Rewald, B. (2015). AMF inoculation enhances growth and improves the nutrient uptake rates of transplanted, salt-stressed tomato seedlings. *Sustainability* 7, 15967–15981. doi: 10.3390/su71215799

Benaffari, W., Boutasknit, A., Anli, M., Ait-El-Mokhtar, M., Ait-Rahou, Y., and Ben-Laouane, R. (2022). The native arbuscular mycorrhizal fungi and vermicompost-based organic amendments enhance soil fertility, growth performance, and the drought stress tolerance of quinoa. *Plan. Theory* 11:393. doi: 10.3390/plants11030393

Bhardwaj, A., and Sharma, S. (2006). Biocontrol of *Meloidogyne incognita* in *Lycopersicon esculantum* with AM fungi and oil cakes. *J. Pl. Pathol.* 5, 166–172. doi: 10.3923/ppj.2006.166.172

Bhat, A. H., Ameni, L., Abolafia, J., Machado, R. A. R., and Kallel, S. (2023). Comparative morphological and molecular analyses of *Acrobeloides bodenheimeri* and *A. tricornis* cobb, 1924 (Rhabditida, Cephalobidae) from Tunisia. *Nematol.* 25, 207–226. doi: 10.1163/15685411-bja10215

Bhat, A. H., Gautam, S., Rana, A., Chaubey, A. K., Půža, V., and Abolafia, J. (2021). Morphological and molecular characterization of *Oscheius* sp. (Nematoda: Rhabditida) from India with its taxonomic consequences and revision of the Insectivorus-group of the genus *Oscheius*. *Biology* 10:1239. doi: 10.3390/biology10121239

Bhat, S. A., Singh, J., and Vig, A. P. (2017). Instrumental characterization of organic wastes for evaluation of vermicompost maturity. *J. Analytical Sci. Technol.* 8:2. doi: 10.1186/s40543-017-0112-2

Canellas, L. P., Olivares, F. L., Aguiar, N. O., Jones, D. L., Nebbioso, A., and Mazzei, P. (2015). Humic and fulvic acids as biostimulants in horticulture. *Sci. Horticul.* 196, 15–27. doi: 10.1016/j.scienta.2015.09.013

Chance, B., and Maehly, A. C. (1955). Assay of catalase and peroxidase. *Methods Enzymol.* 2, 764–775. doi: 10.1016/S0076-6879(55)02300-8

Chen, S., Jin, W., Liu, A., Zhang, S., Liu, D., Wang, F., et al. (2013). Arbuscular mycorrhizal fungi (AMF) increase growth and secondary metabolism in cucumber subjected to low temperature stress. *Sci. Hortic.* 160, 222–229. doi: 10.1016/j.scienta.2013.05.039

Chevenet, F., Brun, C., Banuls, A. L., Jacq, B., and Christen, R. (2006). TreeDyn: towards dynamic graphics and annotations for analyses of trees. *BMC Bioinformatics* 7:439. doi: 10.1186/1471-2105-7-439

Choshali, A. H., Rezaee, S., Jamali, S., Zamanizadeh, H. R., and Rejali, F. (2019). Investigation of peroxidase and polyphenol oxidase enzymes quantitative changes in sensitive and tolerant cucumber to root knot nematode, due to mycorrhizal fungus. *Appl. Entomol. Phytopathol.* 87, 1–11. doi: 10.22092/jaep.2018.120132.1202

Collange, B., Navarrete, M., Peyre, G., Mateille, T., and Tchamitchian, M. (2011). Root-knot nematode (*Meloidogyne*) management in vegetable crop production: the challenge of an agronomic system analysis. *Crop Prot.* 30, 1251–1262. doi: 10.1016/j.cropro.2011.04.016

da Silva Campos, M. A. (2020). Bioprotection by arbuscular mycorrhizal fungi in plants infected with *Meloidogyne* nematodes: a sustainable alternative. *Crop Prot.* 135, 105–203. doi: 10.1016/j.cropro.2020.105203

Damalas, C. A., and Eleftherohorinos, I. G. (2011). Pesticide exposure, safety issues, and risk assessment indicators. *Int. J. Environ. Res. Public Health* 8, 1402–1419. doi: 10.3390/ijerph8051402

Deka, H., Deka, S., Baruah, C. K., Das, J., Hoque, S., and Sarma, N. S. (2011). Vermicomposting of distillation waste of citronella plant (*Cymbopogon winterianus* Jowitt.) employing *Eudrilus eugeniae*. *Bioresour. Technol.* 102, 6944–6950. doi: 10.1016/j.biortech.2011.04.027

Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32, 1792–1797. doi: 10.1093/nar/gkh340

Fabiyi, O. A. (2021). Sustainable management of *Meloidogyne incognita* infecting carrot (*Daucus carota*): green synthesis of silver nanoparticles with *Cnidoscolus aconitifolius*. *Vegetos* 34, 277–285. doi: 10.1007/s42535-021-00216-y

Fellbaum, C. R., Mensah, J. A., Pfeffer, P. E., Kiers, E. T., and Bücking, H. (2012). The role of carbon in fungal nutrient uptake and transport: implications for resource exchange in the arbuscular mycorrhizal symbiosis. *Plant Signal. Behav.* 7, 1509–1512. doi: 10.4161/psb.22015

Gao, X., Guo, H., Zhang, Q., Guo, H., Zhang, L., and Zhang, C. (2020). Arbuscular mycorrhizal fungi (AMF) enhanced the growth, yield, fiber quality and phosphorus regulation in upland cotton (*Gossypium hirsutum* L.). *Sci. Rep.* 10, 2084–2012. doi: 10.1038/s41598-020-59180-3

Gerdemann, J. W., and Nicholson, T. H. (1963). Spore and mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. *Trans. Br. Mycol. Soc.* 46, 235–244. doi: 10.1016/S0007-1536(63)80079-0

Giovannetti, M., and Mosse, B. (1980). An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. *New Phytol.* 84, 489–500. doi: 10.1111/j.1469-8137.1980.tb04556.x

Hemmati, S., and Saeedizadeh, A. (2019). Root-knot nematode, *Meloidogyne javanica*, in response to soil fertilization. *Braz. J. Biol.* 80, 621–630. doi: 10.1590/1519-6984.218195

Hepper, C. M., and Mosse, B. (1980). "Vesicular arbuscular mycorrhiza in root organ cultures" in *Tissue culture methods for plant pathologists*. eds. D. S. Ingram and J. P. Helgeson, 161–171.

Hunt, D., and Handoo, Z. (2009). Taxonomy, identification and principal species. In: *Root- knot nematodes*, R. N. Perry, M. Moens and J. L. Starr Eds. London: CABI. pp. 55–88.

Hussain, N., Abbasi, T., and Abbasi, S. A. (2016). Vermiremediation of an invasive and pernicious weed salvinia (*Salvinia molesta*). *Ecol. Eng.* 91, 432–440. doi: 10.1016/j.ecoleng.2016.03.010

Hussain, M. A., Mukhtar, T., and Kayani, M. Z. (2011). Efficacy evaluation of *Azadirachta indica, Calotropis procera, Datura stramonium* and *Tagetes erecta* against root-knot nematodes *Meloidogyne incognita*. *Pak. J. Bot.* 43, 197–204.

Kayania, M. Z., Mukhtar, T., and Hussain, M. A. (2012). Evaluation of nematicidal effects of *Cannabis sativa* L. and *Zanthoxylum alatum* Roxb. Against root-knot nematodes, *Meloidogyne Incognta*. *Crop Prot.* 39, 52–56. doi: 10.1016/j.cropro.2012.04.005

Khan, F., Asif, M., Khan, A., Tariq, M., and Siddiqui, M. A. (2018). Screening of carrot cultivars against root-knot nematode *Meloidogyne incognita*. *Indian Phytopathol.* 71, 415–421. doi: 10.1007/s42360-018-0052-9

Khan, M. H., Meghvansi, M. K., Gupta, R., Veer, V., and Singh, L. (2014). Foliar spray with vermiwash modifies the arbuscular mycorrhizal dependency and nutrient stoichiometry of bhut jolokia (*Capsicum assamicum*). *PLoS One* 9:e92318. doi: 10.1371/journal.pone.0092318

Khorshidi, M., Bahadori, F., and Behnamnia, M. (2013). The effects of arbuscular mycorrhizal fungi (*Glomus intraradices*) and vermicompost application on yield and nutrient uptake in garden thyme (*Thymus vulgaris* L.) under field conditions. *Int. J. Agric. Crop Sci.* 5, 1191–1194.

Koske, R. E., and Tessier, B. (1983). A convient, permanent slide mounting medium. *Mycol. Soc. Am. Newsl.* 34:59.

Kumar, S., Kumar, R., and Sood, P. (2021). *Role of microbial enriched vermicompost in plant-parasitic nematode management*. In: *Nematodes-recent advances, management and new perspectives*. IntechOpen, London.

Kumar, D., Satheesh, K. P., and Rajendran, N. M. (2014). Evaluation of vermicompost maturity using scanning electron microscopy and paper chromatography analysis. *J. Agric. Food Chem.* 62, 2738–2741. doi: 10.1021/jf4054403

Letunic, I., and Bork, P. (2016). Interactive tree of life (iTOL) v3: an online tool for the display and annotation of phylogenetic and other trees. *Nucleic Acids Res.* 44, W242–W245. doi: 10.1093/nar/gkw290

Liu, M., Zhu, C., and Wang, C. (2020). Vermicompost assisted arbuscular mycorrhizal fungi to transfer ^{15}N from crop residues to lettuce. *Plant Soil* 456, 175–187. doi: 10.1007/s11104-020-04711-0

Lv, B., Xing, M., Yang, J., Qi, W., and Lu, Y. (2013). Chemical and spectroscopic characterization of water extractable organic matter during vermicomposting of cattle dung. *Bioresour. Technol.* 132, 320–326. doi: 10.1016/j.biortech.2013.01.006

MacKinney, G. (1941). Absorption of light by chlorophyll solutions. *J. Biol. Chem.* 140, 315–322. doi: 10.1016/S0021-9258(18)51320-X

Mayer, A. M., Harel, E., and Shaul, R. B. (1965). Assay of catechol oxidase a critical comparison of methods. *Phytochemistry* 5, 783–789.

Megueni, C., Tchuenteu, T. L., Noubissie, E., Maimouna, A., and Bachirou, H. (2017). Field productivity of carrot (*Daucus carota* L.) in Adamawa Cameroon and chemical properties of roots according to chicken manure pre-treatments and vivianite powder. *J. Agric. Vet. Sci.* 10, 16–23. doi: 10.9790/2380-1005011623

Meng, L., Srivastava, A. K., Kuča, K., Giri, B., Rahman, M. M., and Wu, Q. (2021). Interaction between earthworms and arbuscular mycorrhizal fungi in plants: A review. *Phyton* 90, 687–699. doi: 10.32604/phyton.2021.015427

Mohamed, A. S., Ali, A. A. M., and Ibrahim, D. S. S. (2019). Potential of vermicompost and vermicompost tea to improve yield and quality of Kalamata olive trees infected with root-knot nematode, *Meloidogyne incognita*. *World J. Agric. Sci.* 15, 414–424. doi: 10.5829/idosi.wjas.2019.414.424

Mondal, S., Ghosh, S., and Mukherjee, A. (2021). Application of biochar and vermicompost against the rice root-knot nematode (*Meloidogyne graminicola*): an eco-friendly approach in nematode management. *J. Plant Dis. Prot.* 128, 819–829. doi: 10.1007/s41348-021-00433-2

Morte, A., Lovisolo, C., and Schubert, A. (2000). Effect of drought stress on growth and water relations of the mycorrhizal association *Helianthemum almeriense-Tertezia claveryi*. *Mycorrhiza* 10, 115–119. doi: 10.1007/s005720000066

Mosse, B., and Hayman, D. S. (1971). Plant growth responses to vesicular arbuscular mycorrhiza: II. In unsterilized field soils. *New Phytol.* 70, 29–34. doi: 10.1111/j.1469-8137.1971.tb02505.x

Nadler, S. A., Bolotin, E., and Stock, S. P. (2006). Phylogenetic relationships of *Steinernema* Travassos, 1927 (Nematoda: Cephalobina: Steinernematidae) based on nuclear, mitochondrial and morphological data. *Syst. Parasitol.* 63, 161–181. doi: 10.1007/s11230-005-9009-3

Naeeni, N. F., Moghadam, A. R. L., Moradi, P., Rezaei, M., and Abdoosi, V. (2017). Effect of vermicompost and mycorrhiza fungi on yield and growth of milk thistle and antioxidant system activity. *Iran J. Plant Physiol.* 7, 2063–2074. doi: 10.22034/IJPP.2017.533560

Nafady, N. A., Sultan, R., El-Zawahry, A. M., Mostafa, Y. S., Alamri, S., and Mostafa, R. G. (2022). Effective and promising strategy in management of tomato root-knot nematodes by *Trichoderma harzianum* and arbuscular mycorrhizae. *Agronomy* 12:315. doi: 10.3390/agronomy12020315

Nagesh, M., and Reddy, P. P. (2004). Biochemical changes in *Glomus fasciculatum* colonized roots of *Lycopersicon esculentum* in presence of *Meloidogyne incognita*. *Indian J. Exp. Biol.* 42, 721–727.

Navarro, J. M., Perez-Tornero, O., and Morte, A. (2014). Alleviation of salt stress in citrus seedlings inoculated with arbuscular mycorrhizal fungi depends on the root stock salt tolerance. *J. Plant Physiol.* 171, 76–85. doi: 10.1016/j.jplph.2013.06.006

Oka, Y. (2010). Mechanisms of nematode suppression by organic soil amendments-a review. *Appl. Soil Ecol.* 44, 101–115. doi: 10.1016/j.apsoil.2009.11.003

Oliveira, M. S., Campos, M. A., and Silva, F. S. (2015). Arbuscular mycorrhizal fungi and vermicompost to maximize the production of foliar biomolecules in *Passiflora alata* Curtis seedlings. *J. Sci. Food Agric.* 95, 522–528. doi: 10.1002/jsfa.6767

Pereira, M. G., and Arruda, M. A. Z. (2003). Vermicompost as a natural absorbent material. Characterization and potentialities for cadmium absorption. *J. Braz. Chem. Soc.* 14, 39–47. doi: 10.1590/S0103-50532003000100007

Plassard, C., and Dell, B. (2010). Phosphorus nutrition of mycorrhizal trees. *Tree Physiol.* 30, 1129–1139. doi: 10.1093/treephys/tpq063

Porter, W. M. (1979). The "most probable number" method of enumerating infective propagules of vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol. Soc.* 55, 158–161.

Prasad, G. G., Ravichandra, N. G., Narasimhamurthy, T. N., Kumar, C. P., and Yadahalli, P. (2014). Management of *Meloidogyne incognita* infecting carrot by using bioagents. *J. Biopest.* 7, 144–150.

Rajasekaran, S., and Nagarajan, S. M. (2004). Occurrence and histochemical studies on VAM fungi in some medicinal plants. *Asian J. Microbiol. Biotechnol. Environ. Sci.* 6, 553–556.

Rajasekaran, S., Nagarajan, S. M., Arumugam, K., Sravanamuthu, R., and Balamurugan, S. (2006). Effect of dual inoculation (AM fungi and *Rhizobium*) on chlorophyll content of *Arachis hypogaea* L. cv. *TMV-2. Plant Arch.* 6, 671–672.

Rajiv, P., Rajeshwari, S., and Venckatesh, R. (2013). Fourier transform-infrared spectroscopy and gas chromatography-mass spectroscopy: reliable techniques for analysis of Parthenium mediated vermicompost. *Spectrochim Acta Mol. Biomol. Spectrosc.* 116, 642–645. doi: 10.1016/j.saa.2013.08.012

Rana, A., Yadav, A., Bhat, A. H., Chaubey, A. K., and Malhotra, S. K. (2020). Techniques to Conduct Morphological and Molecular Investigations on Nematodes in *Experimental Protocols in Biotechnology*. eds. Gupta N., Gupta V. New York, NY: Springer Protocols Handbooks, Humana.

Ravindran, B., Dinesh, S. L., John Kennedy, L., and Sekaran, G. (2008). Vermicomposting of solid waste generated from leather industries using epigeic earthworm *Eisenia fetida*. *Appl. Biochem. Biotechnol.* 151, 480–488. doi: 10.1007/s12010-008-8222-3

Ravindran, B., Sravani, R., Mandal, A. B., Contreras-Ramos, S. M., and Sekaran, G. (2013). Instrumental evidence for biodegradation of tannery waste during vermicomposting process using *Eudrilus eugeniae*. *J. Therm. Anal. Calorim.* 111, 1675–1684. doi: 10.1007/s10973-011-2081-9

Rehman, F., Khan, F. A., and Badruddin, S. M. A. (2012). "Role of phenolics in plant defense against insect herbivory" in *Chemistry of phytopotentials: Health, energy and environmental perspectives* (Berlin, Heidelberg: Springer), 309–313.

Rivero, J., Gamir, J., Aroca, R., Pozo, M. J., and Flors, V. (2015). Metabolic transition in mycorrhizal tomato roots. *Front. Microbiol.* 6:598. doi: 10.3389/fmicb.2015.00598

Rostami, M., Karegar, A., and Ghorbani, A. (2022). Effects of arugula vermicompost on the root-knot nematode (*Meloidogyne javanica*) and the promotion of resistance genes in tomato plants. *Plant Pathol. J.* 38, 261–271. doi: 10.5423/PPJ.OA.01.2022.0006

Schenck, N. C., and Pervez, Y. (1990). *A manual of vesicular arbuscular mycorrhizal fungi, INVAM 3*. Gainsville, Florida University of Florida, 286 pp.

Schouteden, N., De Waele, D., Panis, B., and Vos, C. M. (2015). Arbuscular mycorrhizal fungi for the biocontrol of plant-parasitic nematodes: a review of the mechanisms involved. *Front. Microbiol.* 6:1280. doi: 10.3389/fmicb.2015.01280

Sebumpan, R., Guiritan, K. R., Suan, M., Abapo, C. J., Bhat, A. H., Machado, R. A. R., et al. (2022). Morphological and molecular identification of *Trichoderma asperellum* isolated from a dragon fruit farm in the southern Philippines and its pathogenicity against the larvae of the super worm, *Zophobas morio* (Fabricius, 1776) (Coleoptera: Tenebrionidae). *Egypt. J. Biol. Pest Control.* 32:47. doi: 10.1186/s41938-022-00548-0

Sen, B., and Chandra, T. S. (2007). Chemolytic and solid-state spectroscopic evaluation of organic matter transformation during vermicomposting of sugar industry wastes. *Bioresour. Technol.* 98, 1680–1683. doi: 10.1016/j.biortech.2006.06.007

Serfoji, P., Rajeshkumar, S., and Selvaraj, T. (2010). Management of root-knot nematode, *Meloidogyne incognita* on tomato c.v Pusa ruby. By using vermicompost, AM fungus, *Glomus aggregatum* and mycorrhiza helper bacterium, *Bacillus coagulans*. *Agric. Technol.* 6, 37–45.

Shamshiri, M., and Fattahi, M. E. (2016). Effects of arbuscular mycorrhizal fungi on photosystem II activity of three pistachio rootstocks under salt stress as probed by the OJIP-test. *Russ. J. Plant Physiol.* 63, 101–110. doi: 10.1134/S1021443716010155

Sharma, K., and Garg, V. K. (2018). Comparative analysis of vermicompost quality produced from rice straw and paper waste employing earthworm *Eisenia fetida* (Sav.). *Bioresour. Technol.* 250, 708–715. doi: 10.1016/j.biortech.2017.11.101

Sharma, I. P., and Sharma, A. K. (2017). Physiological and biochemical changes in tomato cultivar PT-3 with dual inoculation of mycorrhiza and PGPR against root-knot nematode. *Symbiosis* 71, 175–183. doi: 10.1007/s13199-016-0423-x

Shi-Chua, L., Yonga, J., Ma-bob, L., Wen-Xuc, Z., Nand, X., and Hui-Huib, Z. (2019). Improving plant growth and alleviating photosynthetic inhibition from salt stress using AMF in alfalfa seedlings. *J. Plant Inter.* 14, 482–491. doi: 10.1080/17429145.2019.1662101

Siddiqui, Z. A., and Akhtar, M. S. (2007). Effects of AM fungi and organic fertilizers on the reproduction of the nematode *Meloidogyne incognita* and on the growth and water loss of tomato. *Biol. Fertil. Soils* 43, 603–609. doi: 10.1007/s00374-006-0131-4

Singleton, V. L., and Rossi, J. A. (1965). Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. *Am. J. Enol. Vitic.* 16, 144–158. doi: 10.5344/ajev.1965.16.3.144

Sivakumar, P. V., Palanisamy, K., and Lenin, M. (2020). Potential role of arbuscular mycorrizhal fungi (amf) and vermicompost (vc) on the maturation of agriculture crops - a review. *S. Asian J. Life Sci.* 8, 24–37. doi: 10.17582/journal.sajls/2020/8.2.24.37

Smith, S. E., and Read, D. J. (2010). *Mycorrhizal Symbiosis; academic press: Cambridge*, MA, USA. ISBN978-0-08-055934-6.

Southey, J. F. (1986). *Laboratory methods for work with plant and soil nematodes*. Ministry of Agric. Fisheries and Food, Her Majesties Stationary Office, London, p. 202.

Srivastava, V., Goel, G., and Thakur, V. K. (2020). Analysis and advanced characterization of municipal solid waste vermicompost maturity for a green environment. *J. Environ. Manag.* 255:109914. doi: 10.1016/j.jenvman.2019.109914

Tamura, K., Stecher, G., and Kumar, S. (2021). MEGA11: molecular evolutionary genetics analysis version 11. *Mol. Biol. Evol.* 38, 3022–3027. doi: 10.1093/molbev/msab120

Trappe, J. M. (1982). Synoptic keys to genera and species of Zygomyccetes Mycorrhizal fungi. *Phytopathology* 72, 1102–1108.

Tuominen, A. (2013). Defensive strategies in *Geranium sylvaticum*, part 2: roles of water-soluble tannins, flavonoids and phenolic acids against natural enemies. *Phytochemistry* 95, 408–420. doi: 10.1016/j.phytochem.2013.07.029

Tyagi, J., Chaudhary, P., Jyotsana, , Bhagwati, U., Bhandari, G., and Chaudhary, A. (2022a). "Impact of endophytic fungi in biotic stress management" in *Plant protection: From chemicals to Biologicals*. eds. R. Soni, D. Suyal and R. Goel (Berlin, Boston: De Gruyter), 447–462.

Tyagi, J., Chaudhary, P., Mishra, A., Khatwani, M., Dey, S., and Varma, A. (2022b). Role of endophytes in abiotic stress tolerance: with special emphasis on *Serendipita indica*. *Int. J. Environ. Res.* 16:62. doi: 10.1007/s41742-022-00439-0

Unuofin, F. O., and Mnkeni, P. N. S. (2014). Optimization of *Eisenia fetida* stocking density for the bioconversion of rock phosphate enriched cow dung-waste paper mixtures. *Waste Manag.* 34, 2000–2006. doi: 10.1016/j.wasman.2014.05.018

Vagelas, I., and Gowen, S. R. (2012). Control of *Fusarium oxysporum* and root-knot nematodes (*Meloidogyne* spp.) with *Pseudomonas oryzihabitans*. *Pak. J. Phytopathol.* 24, 32–38.

Vos, C. M., Tesfahun, A. N., Panis, B., DeWaele, D., and Elsen, A. (2012). Arbuscular mycorrhizal fungi induce systemic resistance in tomato against these sedentary nematode *Meloidogyne incognita* and the migratory nematode *Pratylenchus penetrans*. *Appl. Soil Ecol.* 61, 1–6. doi: 10.1016/j.apsoil.2012.04.007

Wang, L., Chen, X., and Tang, Z. (2022). Arbuscular mycorrhizal symbioses improved biomass allocation and reproductive investment of cherry tomato after root-knot nematodes infection. *Plant Soil* 482, 513–527. doi: 10.1007/s11104-022-05708-7

Xiao, Z., Liu, M., Jiang, L., Chen, X., Griffiths, B. S., and Li, H. (2016). Vermicompost increases defense against root-knot nematode (*Meloidogyne incognita*) in tomato plants. *Appl. Soil Ecol.* 105, 177–186. doi: 10.1016/j.apsoil.2016.04.003

Xu, C., and Mou, B. (2016). Vermicompost affects soil properties and spinach growth, physiology, and nutritional value. *Hort. Sci.* 51, 847–855. doi: 10.21273/HORTSCI.51.7.847

Yadav, A., and Garg, V. K. (2015). Influence of vermi-fortification on chickpea (*Cicer arietinum* L.) growth and photosynthetic pigments. *Int. J. Recycl. Org. Waste Agricult.* 4, 299–305. doi: 10.1007/s40093-015-0109-z

Yadav, K. D., Sharma, D., and Prasad, R. (2022). "5 - challenges and opportunities for disposal of floral waste in developing countries by using composting method" in *Advanced Organic Waste Management*. eds. C. Hussain and S. Hait, pp. 55–77.

Yang, Y., Tang, M., Sulpice, R., Chen, H., Tian, S., and Ban, Y. (2014). Arbuscular mycorrhizal fungi alter fractal dimension characteristics of *Robinia pseudoacacia* L. seedlings through regulating plant growth, leaf water status, photosynthesis, and nutrient concentration under drought stress. *J. Plant Growth Regul.* 33, 612–625. doi: 10.1007/s00344-013-9410-0

Zhang, W., Han, D. Y., Dick, W. A., Davis, K. R., and Hoitink, H. A. J. (1998). Compost and compost water extract-induced systemic acquired resistance in and compost water extract-induced systemic acquired resistance in cucumber and Arabidopsis. *Phytopathology* 88, 450–455. doi: 10.1094/PHYTO.1998.88.5.450

Zhu, X. C., Song, F. B., Liu, S. Q., Liu, T. D., and Zhou, X. (2012). Arbuscular mycorrhizae improve photosynthesis and water status of *Zea mays* L. under drought stress. *Plant Soil Environ.* 58, 186–191. doi: 10.17221/23/2011-PSE

Zulhipri, E., and Purwanto, A. (2021). "Development of technology vermicompost production for the coffee plant industry" in *3rd international conference on research and learning of physics (ICRLP). J. Physics: Conf. Ser. No. 012020*, vol. *1876* (Padang: IOP Publishing Ltd.), 012020.

frontiers | Frontiers in Microbiology

TYPE Review
PUBLISHED 14 June 2023
DOI 10.3389/fmicb.2023.1174532

OPEN ACCESS

EDITED BY
Ravinder Kumar,
Central Potato Research Institute (ICAR), India

REVIEWED BY
Shaikhul Islam,
Bangladesh Agricultural Research Council, Bangladesh
Bartholomew Saanu Adeleke,
Olusegun Agagu University of Science and Technology, Nigeria
Lata Jain,
ICAR-National Institute of Biotic Stress Management, India

*CORRESPONDENCE
Nazia Manzar
✉ naziamanzar786@gmail.com
Pawan Kumar Sharma
✉ pawan112000@gmail.com

RECEIVED 27 February 2023
ACCEPTED 18 April 2023
PUBLISHED 14 June 2023

CITATION
Kashyap AS, Manzar N, Meshram S and Sharma PK (2023) Screening microbial inoculants and their interventions for cross-kingdom management of wilt disease of solanaceous crops- a step toward sustainable agriculture.
Front. Microbiol. 14:1174532.
doi: 10.3389/fmicb.2023.1174532

Screening microbial inoculants and their interventions for cross-kingdom management of wilt disease of solanaceous crops- a step toward sustainable agriculture

Abhijeet Shankar Kashyap[1], Nazia Manzar[2]*, Shweta Meshram[3] and Pawan Kumar Sharma[2]*

[1]Molecular Biology Lab, ICAR-National Bureau of Agriculturally Important Microorganisms, Maunath Bhanjan, India, [2]Plant Pathology Lab, ICAR-National Bureau of Agriculturally Important Microorganisms, Maunath Bhanjan, India, [3]Department of Plant Pathology, Lovely Professional University, Phagwara, Punjab, India

Microbial inoculants may be called magical bullets because they are small in size but have a huge impact on plant life and humans. The screening of these beneficial microbes will give us an evergreen technology to manage harmful diseases of cross-kingdom crops. The production of these crops is reducing as a result of multiple biotic factors and among them the bacterial wilt disease triggered by *Ralstonia solanacearum* is the most important in solanaceous crops. The examination of the diversity of bioinoculants has shown that more microbial species have biocontrol activity against soil-borne pathogens. Reduced crop output, lower yields, and greater cost of cultivation are among the major issues caused by diseases in agriculture around the world. It is universally true that soil-borne disease epidemics pose a greater threat to crops. These necessitate the use of eco-friendly microbial bioinoculants. This review article provides an overview of plant growth-promoting microorganisms bioinoculants, their various characteristics, biochemical and molecular screening insights, and modes of action and interaction. The discussion is concluded with a brief overview of potential future possibilities for the sustainable development of agriculture. This review will be useful for students and researchers to obtain existing knowledge of microbial inoculants, their activities, and their mechanisms, which will facilitate the development of environmentally friendly management strategies for cross-kingdom plant diseases.

KEYWORDS

bioinoculants, evergreen technology, nanotechnology, sustainable agriculture, magical microbial bullets, plan growth promoting microorganism, soil born pathogen

Introduction

The world population growth is increasing at an alarming rate, hence global food output must quadruple by 2050 to meet the needs of a growing population. The predictions made thus far are significantly lower than what we require. It is estimated that worldwide food production is reduced by 36% due to plant diseases, insects, and weeds, with diseases alone reducing yields

by 14%. (Agrios, 2005; Manzar et al., 2021a,b; Kashyap et al., 2022b). As a result, reducing the prevalence of plant diseases benefits agricultural output. Soil-borne diseases account for 10–20% of annual yield losses and are more detrimental to agricultural output than seed-borne or air-borne diseases (USDA, 2003).

Solanaceous crops are crucial to both the global economy and the diet of humans. They are known by the name "Nightshades" as well. All continents, with the exception of Antarctica, are home to members of this family. With 2,700 species and 98 genera, the Solanaceae family has the most diversity in terms of habitat, morphology, and ecology. Many regularly cultivated species are found in the Solanaceae family. The most significant genus in the Solanaceae family is "Solanum, "which comprises edible plants like potatoes, tomatoes, brinjal, chili, and capsicum. They can flourish in a variety of environments, from subtropical to tropical. They are plagued by a range of diseases in these various climatic situations and one among them being bacterial wilt caused by the bacterium *Ralstonia solanacearum*. It is one of the most serious diseases discovered to date because it causes host plants to wilt quickly and fatally. The pathogen has a vast host range of more than 200 species, is present around the world, and has a detrimental economic impact (Mansfield et al., 2012). Depending on the host, cultivar, temperature, soil type, cropping pattern, and strain, direct yield losses caused by *R. solanacearum* might vary greatly. For instance, yield losses for the tomato range from 0 to 91%, for the potato from 33 to 90%, for tobacco from 10 to 30%, for bananas from 80 to 100%, and for groundnuts from 10 to 20% (Elphinstone, 2005).

Bacterial wilt and geographical distribution

At the end of the 19th century, bacterial wilt disease was first reported on peppers tomatoes, potatoes, groundnuts, and tobacco in the southern USA and Asia, as well as the continent of South America (Seleim et al., 2014). The pathogen is infectious in soil and soilless culture resulting in the wilt of plants in the Solanaceae family. It is globally distributed in diverse climatic conditions (tropical, subtropical, and a few warm temperate regions, Hayward, 1991; Prameela and Rajamma, 2020). Twenty-five percent of the total area under vegetables is of solanaceous vegetables, primarily eggplants, chilies, and tomatoes. In India, the pathogen has been reported on various solanaceous vegetables including chili, tomato, potato, and brinjal from several states. It is reported from both the plains and plateau region of the west coast from Trivandrum in Kerala to Khera in Gujarat, Deccan and the central plateau of Karnataka, the North Eastern Hills region of India, Madhya Pradesh, Himachal Pradesh, Western Maharastra, Punjab, Tamil Nadu, West Bengal, Odisha, Jammu and Kashmir, Tamil Nadu, the Chotanagpur plateau area of Jharkhand, Uttarakhand, Bihar, and the eastern plains of Assam (Singh et al., 2010). *Ralstonia solanacearum* causes a 20–50 percent loss of solanaceous vegetable production in India each year (Singh et al., 2014). It has been recorded that wilt disease has destroyed 1.53 million hectares of tomato crops in around 80 countries, with a total worldwide loss of more than $950 million per year (Elphinstone, 2005). Solanaceous vegetable crops are mainly affected by *R. solanacearum*, such as summer-grown tomatoes, plain brinjal and tomatoes, and hill potatoes. Bacterial wilt losses range from 20 to 100% (Shekhawat et al., 2000) and 2–95% in tomatoes (Mishra, 1995; Singh et al., 2010; Yuliar et al., 2015). Extensive research was conducted on the use of physical, chemical, biological, and cultural techniques to manage bacterial wilt. Approximately 24% of the studies were concerned with breeding aspects, pathogen's diversity, distribution, and host range (22%), detection and diagnosis of the pathogen (4%), pathogenicity and host-pathogen interactions (17%), epidemiology and ecology (3%), disease management and control (18%), and biological control (10%). There were more studies on disease management aspects like biological control of bacterial wilt (54%), followed by cultural practices (21%), chemical methods (8%), and physical methods (6%). Additionally, integrated pest management was the topic of some studies (11%) (Yuliar et al., 2015). This result revealed that biological control was of interest to many researchers. Kanyagha (2021) reported limited success even with the commitment of farmers to follow integrated disease management strategies such as cultural norms, the use of resistant cultivars, and crop rotation. The use of chemicals is a challenging task to manage bacterial wilt disease because the pathogen is localized within the xylem and is able to persist in the soil for a long time (Yuliar et al., 2015). Hartman and Elphinstone (1994) tested a bactericide in Taiwan and reported that chemical management by antibiotics (Penicillin, Tetracycline, Ampicillin, and Streptomycin) and soil fumigation causes limited suppression of the wilt pathogen. Biological control is a possible non-chemical means for plant disease management. Substantial research has been done on the management of major diseases of plants through biological control. In the recent past, the applications of microbial inoculants to combat soil-borne pathogens and increase crop yields have acquired significance (Elnahal et al., 2022). To attain sustainable yields, beneficial microorganisms can be an essential part of the management strategy. Plant growth-promoting rhizobacteria (PGPR) help in promoting the growth of plants and also protect the plants from devastating plant pathogens. The PGPR belong to the genera *Pseudomonas*, *Azospirillum*, *Clostridium*, *Arthrobacter*, and *Serratia* (Kloepper and Schroth, 1978; Hurek and Reinhold-Hurek, 2003). *Pseudomonas fluorescens* and other species have been reported to be effective in managing soil-borne plant pathogens through their biocontrol activity (Mohammed et al., 2020). The *Pseudomonads* is a major rhizobacteria group having biocontrol potential (Li et al., 2012). *Pseudomonas* spp. is prevalent in agricultural soils. Substantial progress has been made in characterizing the root colonization process by *Pseudomonads*, the abiotic and biotic factors affecting colonization, bacterial traits and genes contributing to the competence of the rhizosphere, and the processes of pathogen suppression (Sivasakthi et al., 2017). Pseudomonads have been reported to suppress soil-borne pathogens (Tao et al., 2020). Since humans consume vegetables in their less processed or unprocessed forms, quality control and safety are of utmost importance in vegetable cultivation. The controlled environment of a greenhouse makes it easier to incorporate PGPR and many different BCE strains have been identified and are ready for deployment (Singh et al., 2017), with some having already been tested successfully in greenhouse experiments (Liu et al., 2013). For example, Pseudomonas fluorescens is being studied as a possible helpful biocontrol agent, while Bacillus spp. has emerged as an essential microbe for the prevention of diseases in the field (Miljakovi et al., 2020). These particular isolates *Pseudomonas stutzeri*, *Bacillus subtilis*, and *Bacillus amyloliquefaciens* have been isolated and demonstrated to be successful in root colonization. In addition, *Phytophthora capsici*, a disease that affects cucumber plants,

is greatly inhibited by these isolates (Islam et al., 2016). *Bacillus subtilis* was found to be efficient in preventing fruit infections caused by *Penicillium* spp. and *Rhizopus stolonifer* during the post-harvest stage. This was achieved by applying *Bacillus subtilis* to the fruit (Punja et al., 2016). In greenhouse conditions, *Fusarium* wilt caused by the fungus *Fusarium oxysporum* can be significantly inhibited by using *Bacillus amyloliquefaciens* isolates (Gowtham et al., 2016). These case studies show the efficacy of PGPR as BCAs in simulated lab settings. This ensures the viability and efficiency of PGPR for industrial horticulture by giving validity to its usage in greenhouse production systems (Jiao et al., 2021).

In the past, researchers have demonstrated that certain promising BCAs have the potential to be useful in the management of bacterial wilt disease. They may be avirulent strains of pathogens or different species of *Bacillus*, *Pseudomonas,* and *Streptomyces* spp. (Kurabachew and Wydra, 2014). The amount of research that is being done on *Bacillus* species, specifically on *Bacillus amyloliquefaciens*, is rising (Hu et al., 2010; Wei et al., 2011; Ding et al., 2013; Tan et al., 2013a,b; Chen et al., 2014; Yuan et al., 2014). Interesting methods for isolating rhizobacteria that stimulate plant development have been reported. Isolates taken from the rhizosphere of diseased plants were more effective at reducing disease incidence than those taken from healthy plants, as shown by Huang et al. (2015). The researchers found that the antagonists' biocontrol efficacies were linked to the antagonists' abilities to colonize plant roots but not to exhibit antibiosis in vitro. This finding suggests that root colonization plays an important role in disease suppression. Milagrosa and Balaki (1999) found that the incidence of wilting caused by *P. solanacearum* in potatoes was lower when Bokashi and effective microorganisms (EM) concentrate was applied alone or combined with inorganic fertilizer than the untreated control. Among the biocontrol agents, EM and Bokashi were found to be the best in the suppression of *R. solanacearum* (Lwin and Ranamukhaarachchi, 2006). Different bacteria and actinomycetes, viz., *B. megaterium*, *B. mesentericus*, *B. mycoides*, and *B. subtilis* have been reported to be effective against *R. solanacearum* (Doan and Nguyen, 2006). In contrast, Shekhawat et al. (1993) suggested that the biocontrol potential of fluorescent *Pseudomonads* be evaluated against the bacterial wilt pathogen. Various rhizobacteria are active in the rhizosphere and they play an important part in suppressing the *R. solanacearum* population and its activity. Different antagonisms have different ways of producing advantageous effects. According to Jagadeesh et al. (2001), RBG 114, Arthrobacter RBE 201, and *P. fluorescens* CHAO, the reference strain, were able to control the disease by 83.33 percent against pathogens. The combined application of biocontrol agents like *P. putida, Bacillus pumilus,* and Actigard (acibenzolar S-methyl) was more effective against *R. solanacearum* than against the untreated control (Anith et al., 2004). Various cross-kingdom biological control agents having plant growth and protection ability studied by different research groups are shown in Table 1.

Biochemical characterization of biocontrol agents

Various biochemical and phenotypic methods have been used to characterize fluorescent *Pseudomonad* isolates. The genus *Pseudomonas* is described as an aerobic cell rod shaped like a gram-negative and is associated with plants, with *P. aeruginosa*, *P. fluorescens*, *P. aureofaciens,* and *P. putida* being important organisms. Most of the experiments were performed to classify fluorescent *Pseudomonads* (Krieg and Holt, 1984). *P. aeruginosa* forms a light cluster among the *Pseudomonads* community and develops at 41°C. The organisms are again categorized into separate subgroups and biovars based on similarities (Barrett et al., 1986). Therefore, it is possible to identify fairly and economically sustainable bioagents easily by different biochemical tests (Weller et al., 2002). The colonies of *P. fluorescens* give bluish-green fluorescens under UV light. *Pseudomonas* species are morphologically short rods and develop yellow-green diffusible pigmenton King's B medium except for *P. putida.* Mulla et al. (2013) found that *P. fluorescens* strains isolated from the soil of various agro-climate zones were gram-negative, rod-shaped and motile, and developed Bluish green smooth colonies that fluoresced under UV light and in King's B broth produced water soluble and fluorescent bluish-green pigmentation. The positive effect of gelatin liquefaction and levan formation was observed in all isolates. The isolates were indole negative and positive. The positive effect of gelatin liquefaction and levan formation was observed in all isolates. Indole negative was observed because they did not develop a red layer at the top of the medium of tryptophan broth and was positive for catalase as shown by the development of air bubbles with the addition of hydrogen peroxide. The bacterial strains isolated from the rhizosphere of medicinal and aromatic plants were described by Malleswari (2014) as *Bacillus* sp. gram-positive, white colonies with flat edges, large, smooth, and a high nutrient agar center developed. Isolates were positive for the use of citrate and sorbitol and negative for the use of lysine ornithine, urease, deamination of phenylalanine, nitrate, glucose, and adonitol, as well as the development of H_2S. Arabinose, lactose, indole, Voges-Proskauer, gelatinase, methyl red test, and catalase activities showed a positive test.

Identification of microbial inoculants by molecular techniques

Microorganisms are being identified through genotypic and phenotypic characterization. 16SrRNA was used as a marker for the identification of bacteria and deciphering their phylogenetic relationship. The 16SrRNA is present among all bacteria; the gene function has not changed over time and the 16SrRNA gene (1,500 bp) is sufficient for accurate identification (Patel, 2001). Fungal inoculants were characterized using ITS, GAPDH, LSU, and Tef genomic regions (Manzar et al., 2022a; Kashyap et al., 2023). Zinniel et al. (2002) reported six endophytic bacteria that had colonized a range of host plants and identified them as *Bacillus* sp. using 16S rRNA genotyping. Phytopathogenic bacteria were severely restricted in their growth by the bacterial strain J12, which was isolated from the rhizosphere soil of tomato plants. Based on the 16SrRNA gene sequence, *P. brassicacearum* was distinguished from *R. solanacearum* (Zhou et al., 2016).

Rhizobacteria in the management of biotic stress in plants

Through various modes of action, plant growth-promoting rhizobacteria contribute to improving plant fitness. Direct and

TABLE 1 Research shows that various cross-kingdom microbiota support plant growth promotion and disease suppression in solanaceous crops.

Cross kingdom microbiota	Host	Targeted pathogen	Mode of action	References
Bacillus velezensis strain FJAT-46737	Tomato	*Ralstonia solanacearum*	FJAT-46737's suppressive actions were linked to lipopeptide secretion, particularly the fengycin concentration.	Chen et al. (2020)
Bacillus amyloliquefaciens	Tomato	*Ralstonia solanacearum*		Chun et al. (2017)
Bacillus amyloliquefaciens SQR-7 and SQR-101 and *B. methylotrophicus* SQR-29	Tobacco	*Ralstonia solanacearum*	Indole acetic acid and siderophores production	Yuan et al. (2014)
*Ralstoniapickettii*QL-A6	Tomato	*Ralstonia solanacearum*	Competition	Wei et al. (2013)
Pseudomonas monteilii(A) + *Glomus fasciculatum*(B)	*Coleus forskohlii*	*Ralstonia solanacearum*	Nutrient uptake and reduced the pathogen epidemic	Singh et al. (2013)
Brevibacillus brevis L-25 + *Streptomyces roche*L-9 + Organic fertilizer	Tobacco	*Ralstonia solanacearum*	Reducedroot colonization of Ralstonia	Liu et al. (2013)
Bacillus amyloliquefaciens+ bio-organic fertilizer (BIO23) *B. subtilis* + bio-organic fertilizer (BIO36)	Potato	*Ralstonia solanacearum*	Plant growth promotion activities	Ding et al. (2013)
Bacillus sp. (RCh6) *Pseudomonas mallei* (RBG4)	Brinjal	*Ralstonia solanacearum*	Inhibitory compounds and siderophores	Ramesh and Phadke (2012)
B. amyloliquefaciens QL-5, QL-18 + organic fertilizer	Tomato	*Ralstonia solanacearum*	Decreased root colonization	Wei et al. (2011)
B. amyloliquefaciens Bg-C31	Capsicum	*Ralstonia solanacearum*	Antimicrobial proteins	Hu et al. (2010)
B. vallismortis ExTN-1	Tomato, potato, and black pepper	*Ralstonia solanacearum*	Induction of systemic resistance	Thanh et al. (2009)
Bacillus amyloliquefaciens	Tomato	Tomato molt virus		Oteino et al. (2015)
Bacillus amyloliquefaciens Ba13	Tomato	Tomato yellow leaf curl virus	PR1, PR2, and PR3 gene	Guo et al. (2016)
Bacillus subtilis	Tomato, jujube, litchi, and apple	Volatile compounds production inhibits the mycelial growth of *Botrytis cinerea*, *Colletotrichum gloeosporioides, Penicillium expansum, Moniliniafructicola,* and *Alternaria alternata*		Gao et al. (2017)
Bacillus amyloliquefaciens FZB42	Tomato, Tobacco, Cucumber, Cotton, and Lettuce	*Phytophthora nicotianae*, *Rhizoctonia solani*	Defense-related genes, secondary metabolites production surfactin,and bacillomycin D	Chowdhury et al. (2015)
Bacillus cereus C1L	Tobacco and Maize	*Botrytis cinerea*, *Cochliobolus heterostrophus*	Induction of ISR via volatile compounds	Huang et al. (2012)
Bacillus circulans, Cladosporium herbarum	*Brassica juncea*	–	Phosphate solubilization	Oteino et al. (2015)
Bacillus mucilaginosus	*Piper nigrum, Cucumis sativus*	–	potassium intake capacity	Liu et al. (2012)
Bacillus subtilis	*Brassica juncea*		Support Nickel accumulation	Oyedele and Samuel (2014) and Prathap and Kumari (2015)
Bacillus circulans, Cladosporium herbarum	*Vigna radiate*	–	Phosphate solubilization	Oteino et al. (2015)

(Continued)

TABLE 1 (Continued)

Cross kingdom microbiota	Host	Targeted pathogen	Mode of action	References
Bacillus licheniformis	*Piper nigrum*	–	Biocontrol activity	Kumar et al. (2015)
Bacillus subtilis	Tobacco	*Ralstonia solanacearum*		Tahir et al. (2017)
*Paenibacilluspolymyxa*E681	*Sesamum indicum*	*Alternaria sesame*	Prevention from fungal disease	Ryu et al. (2006)
Pseudomonas aeruginosa	*Cicer arietinum*	-	Stimulate potassium and phosphorus uptake	Ahemad and Kibret (2014)
Pseudomonas aeruginosa, *Bacillus subtilis*	*Vigna radiate*	Root-knot formation	Management of root-knot disease	Ahemad and Kibret (2014) and Ngumbi and Kloepper (2016)
Pseudomonas cepacian	*Cucumis sativus*	*Pythium ultimum*	Manage *Pythium ultimum*	Montano et al. (2014)
Pseudomonas cepacian	*Gossypium hirsutum*	*Rhizoctonia solani*	Protection against *Rhizoctonia solani* virus	Montano et al. (2014)
Pseudomonas fluorescens	*Medicago sativa*		Increase metabolism, sequester cadmium from solution, and degrade trichloroethylene	Ramadan et al. (2016)
Pseudomonas fluorescens PTA-CT2	Grapevine	*Plasmoparaviticola*, *Botrytis cinerea*	Activation of SA, JA, and ABA	Lakkis et al. (2019)
Pseudomonas aeruginosa 7NSK2	Rice	*Magnaporthe grisea*; *Rhizoctonia solani*, *Botrytis cinerea*	Induction of ISR; ROS (inhibition of the mycelial growth and spore germination)	De Meyer et al. (1999a,b) and De Vleesschauwer et al. (2006)
Pseudomonas putida	*Arabidopsis thaliana*	Herbicide tolerance	Improve utilization of plant secondary metabolites	Ahemad and Khan (2012)
Streptomyces griseorubiginosus LJS06	*Cucumis sativus*	Cucumber anthracnose	Inhibit conidial germination	Chai et al. (2022)
Pseudomonas sp. *WCS417r*	*Dianthus caryophyllus*	*Fusarium* wilt	Disease suppression	Van Peer and Schippers (1992) and Sharma and Kaur (2010)
Bacillus sp.	*Capsicum annum*	*Colletotrichum capsica*	Increasing activities of defense-related enzymes (PAL, POX, PPO, LOX, and chitinase) lead to decreased anthracnose incidence.	Jayapala et al. (2019)

indirect strategies were typically used by rhizobacteria; these mechanisms are covered in more detail below.

Direct mechanisms of PGPR: Phosphate solubilization; Phytohormone production.

Indirect mechanisms of PGPR: Cyanide production; Siderophore production; Induced systematic resistance; Volatile compounds produced by PGPR.

Direct mechanisms of PGPR

Phosphate solubilization

Phosphorus contributes to the biomass construction of micronutrients, the metabolic process of energy transfer, macromolecular biosynthesis, signal transduction, respiration chain reactions, and photosynthesis (Shenoy and Kalagudi, 2005). Rhizobacteria that are capable of phosphate solubilization play an essential part in the accumulation and conversion of phosphate to plant roots (Bechtaoui et al., 2020). The enzyme phytase is in charge of liberating the phosphorus that has been bound in soil organic molecules like seeds or pollen and was preserved as phytate (inositol polyphosphate). Phytates are a useful source of phosphorous, making up 60–80% of the P in soil. Strong and stable ester linkages seen in phytates make them readily hydrolyzable by PSR. During vegetative growth, phosphorus is primarily absorbed and this absorbed form of phosphorus is found in seeds and fruits (Batool and Iqbal, 2019). Research has shown that the application of *Enterobacter*, *Bacillus*, *Agrobacterium*, *Trichoderma*, *Pseudomonas*, *Glomus*, and *Aspergillus*, as well as phosphate-solubilizing microbes to soils, roots, and fertilizers releases soluble phosphorus, stimulates growth, and protects plants from infection by pathogens (Liu X. et al., 2019; Liu Z. et al., 2019; Hii et al., 2020; Nacoon et al., 2020; Manzar et al., 2021a,b, 2022b; Kirui et al., 2022).

Phytohormone production by rhizobacteria

Phytohormones play a major role in maintaining plant growth. They act as molecular signals under varying environmental conditions that restrict the growth of the plant. Root-associated microbes such as symbiotic or endophytic bacteria strongly influence the production of phytohormones and promote seed germination, root development, vascular tissue development, shoot elongation, flowering, and complete plant growth (Sgroy et al., 2009; Antar et al., 2021). Root growth is promoted by auxins produced by PGPRs (e.g., Ahemad and Kibret, 2014; Afzal et al., 2015). Numerous research works suggest that hormones may be used to improve plant stress tolerance and promote growth. These include auxin in rice (Etesami and Beattie, 2017), cytokinins in wheat (Kudoyarova et al., 2014), abscisic acid in corn (Sgroy et al., 2009), and gibberellins in cucumber, tomato, immature radish, and rice (Kang et al., 2009). In plants, hormone levels can be controlled by microbes that generate plant growth regulators. These plant growth regulators exert effects that are similar to those caused by the application of exogenous plant phytohormones (Turan et al., 2009). Auxins and cytokinins are examples of phytohormones produced by microbes that are similar to plant-synthesized phytohormones. These microbe-produced phytohormones regulate plant hormone levels, which in turn affect the biochemical elicitation of defensive pathways (Backer et al., 2018).

Indirect mechanism

Cyanide production

A volatile metabolite hydrocyanic acid (HCN) is deemed to play an important part in the biocontrol of soil-borne pathogens (Siddiqui, 2006). Cyanide ions are primarily metabolized by thiocyanate. As an HCN, the cyanide ion is exhaled and metabolized to other compounds to some extent. HCN restricts electron movements, thus destroying the energy supply to the cells, resulting in the death of the microbial invaders. It regulates the enzyme function and natural receptors by reversible inhibition mechanisms (Corbett, 1974). Various researchers have documented the production of hydrocyanic acid (HCN) from *P. aeruginosa*, *P. fluorescens*, and rhizobacteria (Ahmad et al., 2008). Voisard et al. (1989) showed that the *P. flourescens* strain CHAO involves HCN in biological regulation. Root hair formation was stimulated by the cyanide-producing strain CHAO, suggesting that the strain brought about the alteration of the physiological activities of the plant. They further noted that three biosynthetic genes encode the enzyme HCN synthase (henA, henB, and henC).

Siderophore-mediated biocontrol

Siderophores are secondary metabolites that have low molecular weight and the ability to chelate iron. They are peptide molecules with side chains and functional groups that are composed of small compounds that can transport ferric ions through cell membranes with great affinity (Hofte et al., 1991; Raymond et al., 2015; Niehus et al., 2017). They also inhibit plant pathogens by competing with them for iron (Duijff et al., 1997). Rhizobacterial strains produce siderophores to chelate iron from the rhizosphere condition which is not soluble in water, therefore, not available for bacteria under iron-limiting conditions (Ghavami et al., 2017). *Pseudomonas fluorescens* produce siderophores under iron-limiting conditions in the Chrome Azurol medium. The production of siderophore, yellow color with a golden periphery, showed a positive result in casamino and succinate medium (Suryakala et al., 2004). The work with pyoverdin, a class of siderophores produced by fluorescent pseudomonads, provides evidence to support the siderophore theory of rhizobacteria's biological regulation (Demange et al., 1987). Pyoverdin produced by *P. aeruginosa* 7 NSK 2 was reported by Hofte et al. (1991), which increased the yield of cucumber, spinach, barley, maize, and wheat. Suryakala et al. (2004) indicated that siderophores of the tri-hyobroxamate group could be used against plant pathogens as effective biocontrol compounds. Zhou et al. (2016) reported that 2,4-DAPG, HCN, siderophores, and protease produced by *P. brassicacearum* J12 inhibited pathogen growth, thereby, revealing its potential in the biocontrol of tomato bacterial wilt. Karimi et al. (2012) stated that bacterial isolates are capable of being isolated. *Bacillus subtilis* (Bl, B6, B28, B40, B99, and BIOS), *P. putida* (P9 and PIO), and *P. aeuroginosa* (Pll, PI2, P66, and PI 12) differed in the synthesis of hydrogen cyanide, siderophore, protease, and indole acetic acid. Yu et al. (2011) have reported that *B. subtilis* CAS 15 isolated from the rhizospheric pepper soil in Hainan, China, produced siderophore on CAS agar plate and was found to be promising in promoting plant growth and biological control against *Fusarium* wilt of pepper.

Induced systemic resistance

Plant growth-promoting rhizobacteria (PGPR) are beneficial rhizobacteria that protect plants from pathogens by triggering the plant's immune system to react strongly to the invasion (Figure 1). The bacteria that cause ISRs have the ability to alter the morphological, physiological, and molecular reactions of plants. Over the past ten years, a lot of studies have been done on the mechanisms of microbial signals, plant receptors, and hormone signaling pathways that are involved in PGPR-induced ISR in plants. In terms of the mechanism associated with *Bacillus* spp. Elicitation of ISR. Investigations show that ISR is associated with ultra-structural and cytochemical changes in plants during the pathogen attack (Kloepper et al., 2004). There are a number of metabolic changes that occur in the host during ISR that ultimately result in the manufacture of defense-related molecules to be used against challenging pathogens. When a pathogen threatens, the priming action of PGPR activates cellular defense responses such as an oxidative burst, cell wall strengthening, the activation of defense-related genes, and the buildup of secondary metabolites (Conrath et al., 2006).

Several species of *Bacillus,* viz., *B. amyloliquefaciens*, B. *subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, and *B. mycoides* have been reported to induce ISR and protect plants against pathogen attacks (Beneduzi et al., 2012; Garcia-Gutierrez et al., 2013; Pieterse et al., 2014; Kashyap et al., 2021). According to Kashyap et al. (2021), induced systemic resistance (ISR) is a promising method for managing plant diseases that can successfully protect a plant against the respective plant diseases such as tomato wilt and chili wilt. The treatment of chili plants with *Bacillus subtilis* KA9 and *Pseudomonas fluorescens* PDS1 resulted in increased defense enzyme activities and resulted in the induction of resistance in chili against *Ralstonia solanacearum*. According to Yadav et al. (2017) PAL and PPO are the major ISR-based enzymes in plants and their activities are related to plant resistance. It was, therefore, important to find out whether tomato plants had improved resistance

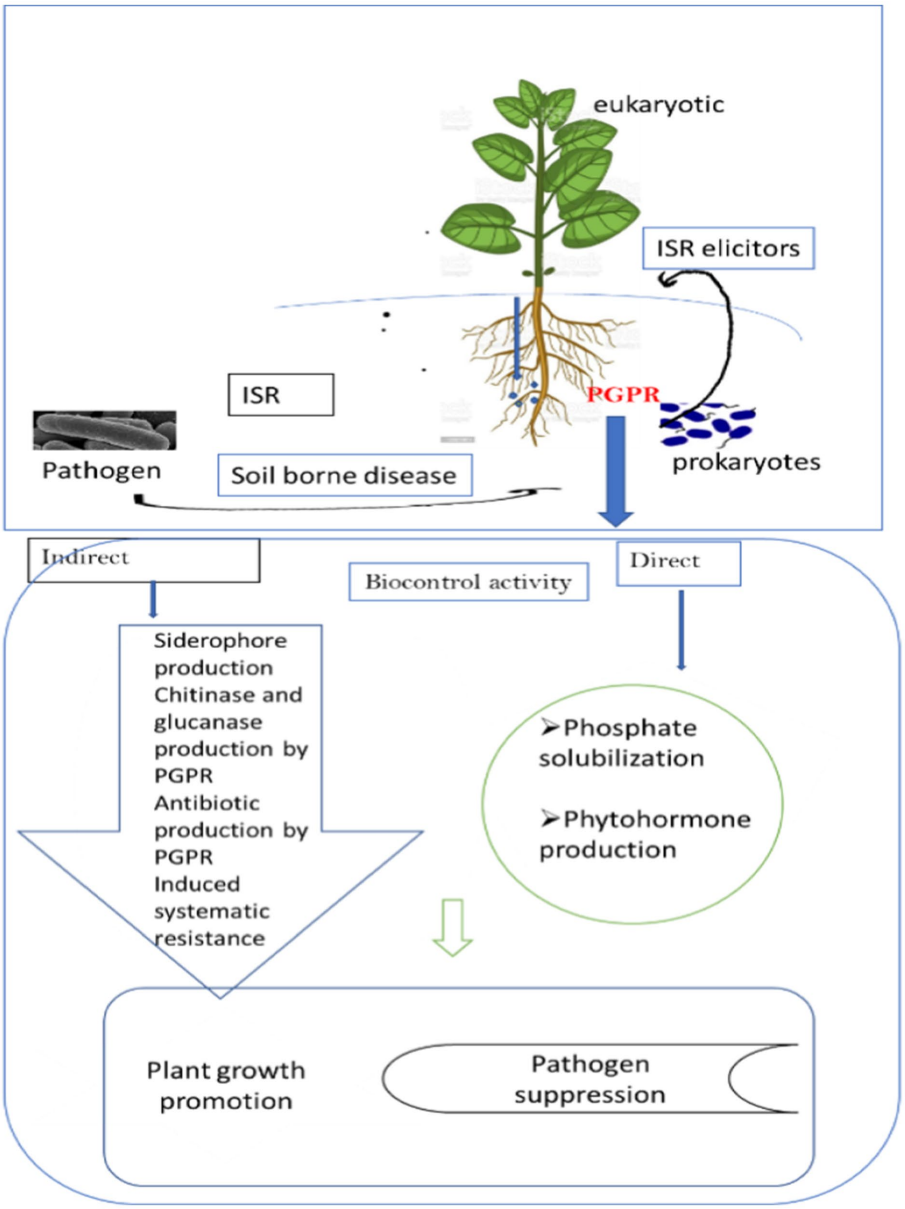


FIGURE 1
Cross-kingdom microbiota boosting systemic resistance in plants to manage plant diseases.

to infection with *R. solanacearum* after treatment with *B. amyloliquefaciens* DSBA-11, which mediates an oxidant/antioxidant system. Instead of increasing their development, ISR is linked to an increase in sensitivity to these hormones, which could activate a slightly separate set of defense genes. Choudhary et al. (2007) reported that after exposure to biotic stimuli by different PGPRs, ISR is induced, and plants acquire increased levels of resistance to pathogens. Recently, research has found that certain strains of *Bacillus* can regulate the gene expression of antioxidants genes such as CaPR1, CaPR4, and CaPR10 in their hosts, hence, triggering ISR against the pepper bacterial spot disease (Ma et al., 2018).

Tan et al. (2013a,b) reported resistance induction by *B. amyloliquefaciens* in tomatoes which provides protection against bacterial wilt. Research has found that CM-2 and T-5 *B. amyloliquefaciens* strains were antagonistic to *R. solanacearum* under greenhouse conditions and produced bioorganic fertilizers to control tomato wilt. The use of bioorganic fertilizers considerably reduced the tomato wilt incidence (63–74%), encouraged plant growth, and reduced the rhizosphere RS population relative to the control population. In the tomato rhizosphere, both strains of CM-2 and T-5 applied with bioorganic fertilizer application survived well. The use of *Bacillus amyloliquefaciens* (SN13) was found to enhance tolerance through a higher defense response against *Rhizoctonia solani* in cotton. The colonized plants showed altered phytohormone signaling, ongoing elicitor maintenance, and synthesis of secondary metabolites (Srivastava et al., 2016). *Enterobacter asburiae* strains were reported to increase the expression of defense-related genes and antioxidant enzymes, as well as other defensive enzymes (PPO, SOD, PAL, catalase, and PO) to protect the plant from tomato yellow leaf curl viruses (Li et al., 2016). PGPR colonization led to improved plant

physiology, tissue health, and increased development of flowers and seeds (Kumar, 2016).

Plant genes modulated by PGPR

Plant growth promotion and its protection against many biotic and abiotic stresses are brought about by PGPR through the modulation of plants. The proteome analysis of PGPR-treated leaves showed increased expression of RuBisCo protein (Kandasamy et al., 2009). RuBisCo plays a role in photosynthesis and accumulation of chlorophyll, thus treated plants have increased photosynthetic rate and, hence, better growth (Agrios, 2005). Another protein that is responsive to PGPR is the chaperone, a stress-related protein. PGPR-treated plants show the induced expression of Nucleoside diphosphate kinases (NDKs). There are reports stating the role of NDKS in wounding, heat shock, and oxidative stress (Harris et al., 1994; Moisyadi et al., 1994; Moon et al., 2003). Thus, the NDKs play a role in primary metabolic function and regulatory function too. Rhizobacteria SN13 provides stress tolerance against *Rhizoctonia solani* (a necrotrophic fungus) and bacterial mycolytic enzymes. They create a balance between ROS and ROS scavengers by induced expression of ferric reductases and defense response by increased expression of terpene synthase (Srivastava et al., 2016). Soil inoculation with PGPR improves the yield and nutrient uptake of crops by inducing the expression of various phosphate and nitrate transporter genes in absence of organic phosphorus and nitrogen (Saia, 2015). As PGPR modulates gene expression in plants to promote their growth, this study aims to understand the molecular mechanism involved in the modulation of gene expression. This investigation was conducted based on the view that not only the bacterium was promoting the growth of the plant but it too was also getting benefitted. The improved growth of the plant will provide better care and shelter to the bacteria too. The interaction between pathogens and host plants causes some changes in the activity of certain enzymes, including phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, lipoxygenase, superoxide dismutase, and −1,3-glucanase (Kavitha and Umesha, 2008; Manzar et al., 2021a,b). These enzymes determine the degree of host resistance. They participate in biosynthetic wall-related activities such as phenol, lignification, polymerization of hydroxyproline-rich glycoproteins, control of cell wall elongation, and wound healing that improve antimicrobial effectiveness (Belkhadir et al., 2004).

Yang et al. (2009) reported a group of plant growth-promoting rhizobacteria (PGPR) bacteria that showed an increase in crop growth. PGPR produce antagonistic compounds which help to reduce plant disease directly. The indirect control of plant disease is through the elicitation of induced systemic resistance (ISR). The ISR elicited by PGPR has been deciphered in the model plant *Arabidopsis*; however, it is not well characterized in pepper. Bacillus cereus strain BS107 induced ISR against *Xanthomonas axonopodis* pv. *vesicatoria* in pepper leaves and its priming effect on plant defense genes as an ISR mechanism was assessed in order to understand the mechanism of ISR in agricultural plants. To systemically prime the expression of *Capsicum annum* pathogenesis-protein 4 and CaPR1, strain BS107 was administered to the roots of pepper plants. This was verified by quantitative-reverse transcriptase PCR. The study corroborated that rhizobacterium has a priming effect on the expression of pepper defense genes that take part in ISR. *Bacillus thuringiensis* has been shown by Hyakumachi et al. (2013) as a possible biological control agent for plant disease suppression. The bacterial wilt disease-suppressing activity of *B. thuringiensis* in this research has been observed in tomato plants. It was found that challenge-inoculation of tomato plants with *R. solanacearum* after cell-free filtrate (CF) pre-treatment resulted in clearly decreased growth of *R. solanacearum* in stem tissues and there was induced expression of defense-related genes such as acidic chitinase, β-1, 3-glucanase, andPR-1 in stem and leaf tissues. In addition, resistance to direct inoculation with *R. solanacearum* was observed in the stem tissues of tomato plants when their roots were pre-treated with CF. Taken together, these findings indicate the CF treatment of tomato roots. *B. thuringiensis*, by systemic activation of the plant defense system, suppresses bacterial wilt. Jayanna and Umesha (2017) analyzed the accumulation of differentially expressed defense genes in susceptible and resistant cultivars of tomatoes by qRT-PCR. It was found that as against the control, there was upregulation of gene expression of defense genes in the resistant tomato cultivar. The upregulation was significantly increased upon the inoculation of *R. solanacearum*. There was a down-regulation of defense genes in susceptible cultivars as compared to the control. However, C8-HSL treatment resulted in upregulation. Thus, the results reveal that C8-HSL can induce significant defense genes in resistant and susceptible tomato cultivars.

Pseudomonas putida (RA) strain MTCC5279 has been shown to possess multiple advantageous traits, including P-solubilization, siderophore production, and indole acetic acid (IAA) production, all of which stimulate plant growth and alter the physiological, biochemical, cellular, and molecular responses of plants (Jatan et al., 2020). Roots of *P. putida* inoculated *Arabidopsis* plants were collected, and microRNA expression was examined. From sequencing the control and RA-inoculated libraries, 293 known and 67 potential new miRNAs were found. Following RA-inoculation, as compared to the control group, stem-loop quantitative real-time PCR verified the differential expression of 15 well-characterized miRNAs. Multiple biological, cellular, and molecular processes were found to be influenced by miRNAs both previously discovered and hypothesized. Additional evidence supporting R's central function in developmental regulation comes from an inverse relationship between the expression of RA-responsive miRNAs and their target genes.

Volatiles and other factors

Besides direct surface-to-surface communication, PGPRs and plant interaction also take place through volatiles. Low polarity and high vapor pressure are characteristics of volatiles generated by microorganisms, which facilitates their diffusion in soil and over extensive atmospheric distances (Vespermann et al., 2007). Using PGPRs that produce volatile compounds can be an effective way to control plant diseases, particularly post-harvest diseases (Arrebola et al., 2010). PGPR-produced volatiles can positively or negatively impact both plants and plant pathogens (Table 2).

Ryu et al. (2003) showed that *Bacillus* sp. strains GB03 and IN937produced 2,3-butanediol and its precursor acetoin that stimulate plant growth. However, volatiles from the same species inhibited Arabidopsis growth in another experiment conducted later

by Ryu et al. (2005). This inhibition was dependent on the distance between the plant's Bacillus strains and the specimen, indicating that the amount of chemical released may have an impact on the inhibitory action (Ryu et al., 2005). Kashyap et al. (2022a) revealed that *B. subtilis* KA9 and *P. fluorescens* PDS1 VOCs pyrazine compounds significantly increased defensive enzyme activity and overexpressed the antioxidant genes related to plant defense to manage the *Ralstonia* under *in vitro* conditions.

TABLE 2 Volatile compounds produced by Rhizoxbacteria acted as growth inhibitors for plantpathogens.

Rhizobacteria	Volatile compounds	Controlled plant pathogen	References
Bacillus spp.	Albuterol, Methylphosphonic acid,Methyl-3-buten-1-ol, 1,3-Propanediol, 2-methyl-, dipropanoate, Silanediol, dimethyl,2-Benzenediol,3,5-bis (1,1-dimethylethyl), Cyclotetrasiloxane, octamethyl-1-Octanol,2-butylBenzoic acid	*Botrytis cinerea, Colletotrichum gloeosporioides, Penicillium expansum, Moniliniafructicola,* and *Alternaria alternata*	Tahir et al. (2017)
Pseudomonas spp.	Toluene, Ethyl benzene, *m*-xylene, Benzothiazole,2-decanol,2-tridecanol,1-undecanol,Dimethyl disulfide, Ethanone 1-(2-furanyl)-Benzaldehyde, Naphthalene, 1-methyl,Dodecane,1-nonene	*R. solanacearum*	Raza et al. (2016a, b, c)
Bacillus amyloliquefaciens	2,3,6-Trimethyl-phenol Pentadecane Tetradecane	*Fusarium oxysporum*	Yuan et al. (2012)
	2,3-Butanediol	*Erwinia carotovora* subsp. *Carotovora*	Ryu et al. (2004)
	3-Pentanol	*Xanthomonas axonopodis* pv. *Vesicatoria*	Choi H. K. et al. (2014) and Choi Y. J. et al. (2014)
	2,5-Dimethyl pyrazine 2-Dodecanone	Antifungal activity against *Fusarium* sp. and *Colletotrichum gloeosporioides*	Guevara-Avendaño et al. (2014)
	2-Tetradecanone	Oomyceticidal activity against *Phytophthora cinnamomi*	Guevara-Avendaño et al. (2014)
	3-Pentanol	Induction of systemic resistance in pepper against *Xanthomonas axonopodis* pv. *Vesicatoria*	Choi H. K. et al. (2014) and Choi Y. J. et al. (2014)
Bacillus amyloliquefaciens SQR-9	Butylated hydroxy toluene, *p*-Xylene, 2-Nonanone, 2-Undecanone, 2-Dodecanone, 2-Tridecanone, Undecanal, Heptadecane, Oleic acid	*Ralstonia solanacearum*	Raza et al. (2016a, b, c)
Burkholderia ambifaria	Dimethyldisulfide 2-Undecanone dimethyltrisulfide 4-Octanone Methylmethanethiosulfonate Phenylpropanon	*Rhizoctonia solani Alternaria alternata*	Groenhagen et al. (2013)
Burkholderia tropica	Limonene Alpha-pinene Ocimene	*Colletotrichum gloeosporioides, Fusarium culmorum, Fusarium oxysporum, Athelia rolfsi*	Tenorio-Salgado et al. (2013)
Burkholderia gladioli	Limonene	*Fusarium oxysporum and Rhizoctonia solani*	Elshafie et al. (2012)
Pseudomonas fluorescens	(+) Monoterpenes (α-pinene, terpinolene, 4-carene, limonene, ocimeneeucalyptol, and lilac aldehyde A), sesquiterpenes (*α*-bergamotene, *α*-farnesene, nerolidol and farnesol)		
Pseudomonas fluorescens WR-1	Toluene, Ethyl benzene, *m*-XyleneBenzothiazole	*Ralstonia solanacearum*	Raza et al. (2016a, b, c
Bacillus subtilis	Benzaldehyde, Nonanal, Benzothiazole, Acetophenone	Antibacterial activity against *Clavibacter michiganensis* ssp. *sepedonicus*	Rajer et al. (2017)

(Continued)

TABLE 2 (Continued)

Rhizobacteria	Volatile compounds	Controlled plant pathogen	References
Pseudomonas putida	1-Undecene Dimethyldisulfide	Antifungal activity against *B. cinerea*, *Fusarium equiseti*, *F. oxysporum*, *F. solani*, *M. phaseolina*, *R. solani*, *R. necatrix*, *S. sclerotiourm,* and *V. dahliae* Oomyceticidal activity against *P. cactorum*, *P. nicotianae,* and *P. ultimum*	Giorgio et al. (2015)
Pseudomonas stutzeri	Dimethyl disulfide	Antifungal activity against *B. cinerea* tomato growth promotion	Rojas-Solís et al. (2018)
Streptomyces fimicarius	Phenylethyl Alcohol Ethyl phenylacetate Methyl anthranilate α-Copaene Caryophyllene Methyl salicylate 4-Ethylphenol	Oomyceticidal activity against *P. litchi*	Xing et al. (2007)

Bacillus amyloliquefaciens strain SQR-9 showed significant efficiency against the tomato wilt pathogen *Ralstonia solanacearum* by producing 22 volatile organic compounds. A lack of inhibition was observed in the case of treatment with a bacterium that did not produce VOCs, Additionally, the VOCs strongly hindered *R. solanacearum* ability to colonize tomato roots and develop its motility features, exopolysaccharide and antioxidant enzyme production, biofilm formation, and other traits (Raza et al., 2016a,b,c). Kim et al. (2010) isolated a *Bacillus subtilis* strain from *Bacillus subtilis* CMB32 by HPLC to monitor the anthracnose disease caused by *Colletotrichum gloeosporioides* and also studied the development of biosurfactant lipopeptides such as Fengycin, Iturin A, and Surfactin A. Gond et al. (2015) on the other hand (2015) investigated endophytic *Bacillus* spp. that produced antifungal lipopeptides in maize and induced the expression of the host defense gene. Mubarak et al. (2015) standardized a procedure for the identification and quantification of surfactin using high-performance liquid chromatography (HPLC) from the *Bacillus* strain (2015). The cumulative elution time of the surfactin peaks obtained was found to be four times faster than the numerous methods previously described. Fine separation of surfactin in the standard sample (98 percent purity) and surfactin in the fermentation broth was possible using the method described here. Bio-control strains produce VOCs, promote the growth of plants, and inhibit pathogens via the induction of systemic resistance in plants (Raza et al., 2016a,b). Bacterial genera like *Pseudomonas*, *Bacillus*, *Stenotrophomonas*, and *Serratia* produce VOCs that have a beneficial impact on plants. The bacterial VOCs serve as triggers for the plant ISR (Sharifi and Ryu, 2016). Increased disease resistance, abiotic stress tolerance, and plant biomass are all mediated by the VoCs from PGPR strains, either directly or indirectly. A wide range of soil microorganisms emit VOCs, which is a trait shared by a large number of them (Kanchiswamy et al., 2015).

Antimicrobial peptides

Bacillus spp. suppress plant pathogens and reduce disease incidence in plants through various mechanisms, viz., production of antibiotics, lysis of cells, induced resistance to the pathogen, and competition for food and space. The bacteria produce antibiotics such as iturinA, bacillomycin D, Surfactin, polyketides antibiotics, bacteriocins (Rea et al., 2010), cyclic lipopeptides (Ramarathnam et al., 2007), polyketides mcrolectine (Chen et al., 2009), and phospholipid (Tamehiro et al., 2002), to suppress the bacterial pathogens. *B. amyloliquefaciens* produce polyketides, *viz,* difficidin, bacillaene, and macrolectin, having antibacterial properties. *B. amyloliquefaciens* and *B. subtilis* produce dificid which is a highly unsaturated 22-membred macro cyclicpolyene lactone phosphate ester. The *dfn* gene sequence exhibits a reasonable co-linearity with the polyketides structure to deduce a biosynthetic module (Chen et al., 2006). The bacillaene gene cluster is assigned to synthesize the bacillaene polyketides (Chen et al., 2009). *B. amyloliquefacins* FZB42 also produces another polyketide macrolactin that has a macrolide-like structure. Macrolactin has a 24-membered lactone ring which contains three separate diene structure elements (Gustafson et al., 1989). Macrolactin is effective against bacterial pathogens (Chen et al., 2009 a). Polyketides difficidin, bacillaene (Hofemeister et al., 2004), and macrolactin (Jaruchoktaweechai et al., 2000) are found in the genome of *B. amyloliquefaciens* FZB 42 and these gene clusters are involved in the polyketides synthesis together, spanning nearly 200 kb (Koumoutsi, 2004). When compared to *B. amyloliquefaciens* FZB42 (340 kb, 8.5%), the genetic capacity for synthesis of antibiotics in strain *B. subtilis* 168 is lower (180 kb, 4–5% of the whole genome) (Chen et al., 2009). The biosynthetic pathway for peptides determines whether the active antimicrobial compounds are ribosomally synthesized (lantibiotics or bacteriocins) or non-ribosomally generated (lipopeptides and polyketides) (Stein, 2005). Antibacterial peptides with inter-residual thioether bonds, known as lantibiotics, are synthesized by the ribosome and further modified after crossing international borders (Abriouel et al., 2011). These antimicrobial peptides (AMPs) have a high degree of specificity for the target microorganisms and have advantages in multiple terms of agronomical, pathological, and economical practices to secure sustainability in agriculture (Figure 2).

This Review manuscript shows multiple functions of microbial inoculants and their screening is based on biochemical, molecular,

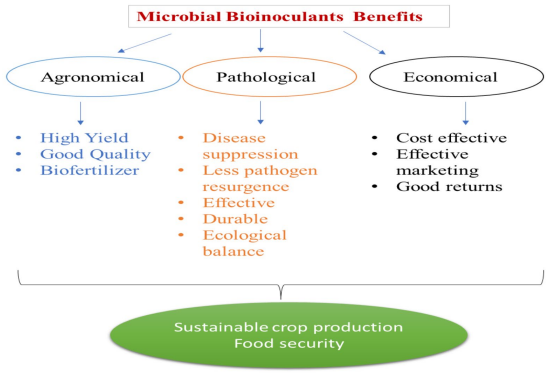


FIGURE 2
Advantages of microbial inoculants in terms of agronomical, pathological, and economical practices to secure sustainability in agriculture.

volatile, mode, and nature of actions. Such eco-friendly bioinoculant screening will be the next evergreen technology for the sustainability of agriculture in this 21st era where we are facing global warming and population blasts. Microbes may be used as magic bullets in the coming days to shoot out multiple problems of cross-kingdom plant diseases.

Author contributions

AK: manuscript preparation, writing, and editing. NM: supervision and editing. SM: figures construction and literature search. PS: supervision and funding. All authors contributed to the article and approved the submitted version.

Funding

This study was supported by the ICAR-NBAIM, Mau.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

Afzal, I., Shinwari, Z. K., and Iqrar, I. (2015). Selective isolation and characterization of agriculturally beneficial endophytic bacteria from wild hemp using canola. *Pak. J. Bot.* 47, 1999–2008.

Agrios, G.N. (2005). *Plant Pathology 5th*. Academic Press: San Diego, CA, 952.

Ahemad, M., and Khan, M. S. (2012). Evaluation of plant-growth-promoting activities of rhizobacterium *Pseudomonas putida* under herbicide stress. *Ann. Microbiol.* 62, 1531–1540. doi: 10.1007/s13213-011-0407-2

Ahemad, M., and Kibret, M. (2014). Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. *J. King Saud Univ. Sci.* 26, 1–20. doi: 10.1016/j.jksus.2013.05.001

Ahmad, F., Ahmad, I., and Khan, M. S. (2008). Screening of free living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiol. Res.* 163, 173–181. doi: 10.1016/j.micres.2006.04.001

Anith, K. N., Momol, M. T., Kloepper, J. W., Marios, J. J., Olson, S. M., and Jones, J. B. (2004). Efficacy of plant growth-promoting rhizobacteria, acibenzolar-s-methyl and soil amendment for integrated management of bacterial wilt on tomato. *Plant Dis.* 88, 669–673. doi: 10.1094/PDIS.2004.88.6.669

Antar, M., Gopal, P., Msimbira, L. A., Naamala, J., Nazari, M., Overbeek, W., et al. (2021). "Inter-organismal signaling in the rhizosphere" in *Rhizosphere biology: interactions between microbes and plants* (Singapore: Springer), 255–293.

Arrebola, E., Sivakumar, D., and Korsten, L. (2010). Effect of volatile compounds produced by *Bacillus* strains on postharvest decay in citrus. *Biol. Control* 53, 122–128. doi: 10.1016/j.biocontrol.2009.11.010

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., et al. (2018). Smith Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Front. Plant Sci.* 9:1473. doi: 10.3389/fpls.2018.01473

Bakker, W. A. B., and Schippers, B. (1987). Schippers microbial cyanide production in the rhizosphere in relation to potato yield reduction and *Pseudomonas* spp-mediated plant growth-stimulation. *Soil Biol. Biochem.* 19, 451–457. doi: 10.1016/0038-0717(87)90037-X

Barrett, E. L., Solanes, R. E., Tang, J. S., and Palleroni, N. J. (1986). *Pseudomonas fluorescens* biovar V: its resolution into distinct component groups and the relationship of these groups to other *P. fluorescens* biovars, to *P. putida*, and to psychrotrophic pseudomonads associated with food spoilage. *J. Gen. Microbiol.* 132, 2709–2721. doi: 10.1099/00221287-132-10-2709

Batool, S., and Iqbal, A. (2019). Phosphate solubilizing rhizobacteria as alternative of chemical fertilizer for growth and yield of *Triticum aestivum* (Var. Galaxy 2013). *Saudi J. Biol. Sci.* 26, 1400–1410. doi: 10.1016/j.sjbs.2018.05.024

Bechtaoui, N., Rabiu, M. K., Raklami, A., Oufdou, K., Hafidi, M., and Jemo, M. (2021). Phosphate-dependent regulation of growth and stresses management in plants. *Front. Plant Sci.* 12:679916. doi: 10.3389/fpls.2021.679916

Bechtaoui, N., Raklami, A., Benidire, L., Tahiri, A., Göttfert, M., and Oufdou, K. (2020). Effects of PGPR co-inoculation on growth, phosphorus nutrition and phosphatase/phytase activities of faba bean under different phosphorus availability conditions. *Polish J. Environ. Stud.* 29, 1557–1565. doi: 10.15244/pjoes/110345

Belkhadir, Y., Subramaniam, R., and Dangl, J. L. (2004). Plant disease resistance protein signaling: NBS–LRR proteins and their partners. *Curr. Opin. Plant Biol.* 7, 391–399. doi: 10.1016/j.pbi.2004.05.009

Beneduzi, A., Ambrosini, A., and Passaglia, L. M. (2012). Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. *Genet. Mol. Biol.* 35, 1044–1051. doi: 10.1590/S1415-47572012000600020

Chai, C. H., Hong, C. F., and Huang, J. W. (2022). Identification and characterization of a multifunctional biocontrol agent, *Streptomyces griseorubiginosus* LJS06, against cucumber anthracnose. *Front. Microbiol.* 13:923276. doi: 10.3389/fmicb.2022.923276

Chen, Y. Y., Lin, Y. M., Chao, T. C., Wang, J. F., Liu, A. C., Ho, F. I., et al. (2009). Virus-induced gene silencing reveals the involvement of ethylene-, salicylic acid- and mitogen-activated protein kinase-related defense pathways in the resistance of tomato to bacterial wilt. *Physiol. Plant.* 136, 324–335. doi: 10.1111/j.1399-3054.2009.01226.x

Chen, D., Liu, X., Li, C., Tian, W., Shen, Q., and Shen, B. (2014). Isolation of *Bacillus amyloliquefaciens*S20 and its application in control of eggplant bacterial wilt. *J. Environ. Manag.* 137, 120–127. doi: 10.1016/j.jenvman.2014.01.043

Chen, X. H., Vater, J., Piel, J., Franke, P., Scholz, R., Schneider, K., et al. (2006). Structural and functional characterization of three polyketide synthase gene clusters in *Bacillus amyloliquefaciens* FZB42. *J. Bacteriol.* 188, 4024–4036. doi: 10.1128/JB.00052-06

Chen, M., Wang, J., Liu, B., Zhu, Y., Xiao, R., Yang, W., et al. (2020). Biocontrol of tomato bacterial wilt by the new strain *Bacillus velezensis* FJAT-46737 and its lipopeptides. *BMC Microbiol.* 20:160. doi: 10.1186/s12866-020-01851-2

Cho, S. M., Shin, S. H., Kim, K. S., Kim, Y. C., Eun, M. Y., and Cho, B. H. (2004). Enhanced expression of a gene encoding a nucleoside diphosphate kinase 1 (OsNDPK1) in rice plants upon infection with bacterial pathogens. *Mol. Cells* 18, 390–395.

Choi, Y. J., Lee, J., Jang, Y. S., and Lee, S. Y. (2014). Metabolic engineering of microorganisms for the production of higher alcohols. *MBio* 5, e01524–e01514. doi: 10.1128/mBio.01524-14

Choi, H. K., Song, G. C., Yi, H.-S., and Ryu, C.-M. (2014). Field evaluation of the bacterial volatile derivative 3-pentanol in priming for induced resistance in pepper. *J. Chem. Ecol.* 40, 882–892. doi: 10.1007/s10886-014-0488-z

Choudhary, D. K., Prakash, A., and Johri, B. N. (2007). Induced systemic resistance (ISR) in plants: mechanism of action. *Indian J. Microbiol.* 47, 289–297. doi: 10.1007/s12088-007-0054-2

Chowdhury, S. P., Hartmann, A., Gao, X. W., and Borriss, R. (2015). Biocontrol mechanism by root-associated *Bacillus amyloliquefaciens* FZB42-a review. *Front. Microbiol.* 6:780. doi: 10.3389/fmicb.2015.00780

Chun, B. H., Kim, K. H., Jeon, H. H., Lee, S. H., and Jeon, C. O. (2017). Pan-genomic and transcriptomic analyses of *Leuconostoc mesenteroides* provide insights into its genomic and metabolic features and roles in kimchi fermentation. *Sci. Rep.* 7:11504. doi: 10.1038/s41598-017-12016-z

Conrath, U., Beckers, G. J., Flors, V., García-Agustín, P., Jakab, G., Mauch, F., et al. (2006). Priming: getting ready for battle. *Mol. Plant Microbe Interact.* 19, 1062–1071. doi: 10.1094/MPMI-19-1062

Corbett, J. R. (1974). "Pesticide design" in *The Biochemical Mode of Action of Pesticides* (London: Academic Press, Inc), 44–86.

De Meyer, G., Audenaert, K., and Höfte, M. (1999a). *Pseudomonas aeruginosa* 7NSK2-induced systemic resistance in tobacco depends on in planta salicylic acid accumulation but is not associated with PR1a expression. *Eur. J. Plant Pathol.* 105, 513–517. doi: 10.1023/A:1008741015912

De Meyer, G., Capiau, K., Audenaert, K., Buchala, A., Metraux, J. P., and Hofte, M. (1999b). Nanogram amounts of salicylic acid produced by the rhizobacterium Pseudomonas aeruginosa 7NSK2 activate the systemic acquired resistance pathway in bean. *Mol. Plant-Microbe Interact.* 12, 450–458. doi: 10.1094/MPMI.1999.12.5.450

De Vleesschauwer, D., Cornelis, P., and Höfte, M. (2006). Redox-active pyocyanin secreted by *Pseudomonas aeruginosa* 7NSK2 triggers systemic resistance to *Magnaporthe grisea* but enhances *Rhizoctonia solani* susceptibility in rice. *Mol. Plant Microbe Interact.* 19, 1406–1419. doi: 10.1094/MPMI-19-1406

Demange, P., Wenderbaum, S., Bateman, A., Dell, A., and Abdallah, M. A. (1987) Bacterial siderophores: structure and physicochemical properties of pyoverdins and related compounds. In: G. Winkleman, HelmD. Van Der and J. B. Neilands (Eds) *Iron transport in microbes, plants and animals*. VCH, Chemie.

Ding, C., Shen, Q., Zhang, R., and Chen, W. (2013). Evaluation of rhizosphere bacteria and derived bio-organic fertilizers as potential biocontrol agents against bacterial wilt (*Ralstonia solanacearum*) of potato. *Plant Soil* 366, 453–466. doi: 10.1007/s11104-012-1425-y

Doan, T. T., and Nguyen, T. H. (2006, 2005). "Status of research on biological control of tomato and groundnut bacterial wilt in Vietnam" in *1st International Symposium on Blogical Control of Bacterial Plant Diseases*. eds. W. Zeller and C. Ulrich (Germany: Darmstadt), 105–111.

Duijff, B. J., Gianinazzi-Pearson, V., and Lemanceau, P. (1997). Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol Pseudomonas fluorescens strain WCS417r. *New Phytologist*. 135, 325–334. doi: 10.1046/j.1469-8137.1997.00646.x

Elnahal, A. S. M., el-Saadony, M. T., Saad, A. M., Desoky, E.-S. M., el-Tahan, A. M., Rady, M. M., et al. (2022). The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: a review. *Eur. J. Plant Pathol.* 162, 759–792. doi: 10.1007/s10658-021-02393-7

Elphinstone, J. G. (2005). "The current bacterial wilt situation: a global overview" in *Bacterial Wilt Disease and the Ralstonia solanacearum Species Complex*. eds. C. Allen, P. Prior and A. C. Hayward (St. Paul, MN: American Phytopathological Society Press), 9–28.

Elshafie, H. S., Camele, I., Racioppi, R., Scrano, L., Iacobellis, N. S., and Bufo, S. A. (2012). *In vitro* antifungal activity of *Burkholderia gladioli* pv. *agaricicola* against some phytopathogenic fungi. *Int. J. Mol. Sci.* 13, 16291–16302. doi: 10.3390/ijms131216291

Etesami, H., and Beattie, G. A. (2017). "Plant-microbe interactions in adaptation of agricultural crops to abiotic stress conditions" in *Probiotics and plant health*. eds. V. Kumar, M. Kumar, S. Sharma and R. Prasad (Singapore: Springer), 163–200.

Gao, Z. F., Zhang, B. J., Liu, H. P., Han, J. C., and Zhang, Y. J. (2017). Identification of endophytic *Bacillus velezensis* ZSY-1 strain and antifungal activity of its volatile compounds against *Alternaria solani* and *Botrytis cinerea*. *Biol. Control* 105, 27–39. doi: 10.1016/j.biocontrol.2016.11.007

Garcia-Gutierrez, L., Zeriouh, H., Romero, D., Cubero, J., de Vicente, A., and Pérez-Garcia, A. (2013). The antagonistic strain *Bacillus subtilis* UMAF6639 also confers protection to melon plants against cucurbit powdery mildew by activation of jasmonate- and salicylic acid-dependent defense responses. *MicrobBiotechnol.* 6, 264–274. doi: 10.1111/1751-7915.12028

Ghavami, N., Alikhani, H. A., Pourbabaei, A. A., and Besharati, H. (2017). Effects of two new siderophore-producing rhizobacteria on growth and iron content of maize and canola plants. *J. Plant Nutr.* 40, 736–746. doi: 10.1080/01904167.2016.1262409

Giorgio, A., De Stradis, A., Lo, C. P., and Iacobellis, N. S. (2015). Biocide effects of volatile organic compounds produced by potential biocontrol rhizobacteria on *Sclerotinia sclerotiorum*. *Front. Microbiol.* 6:1056. doi: 10.3389/fmicb.2015.01056

Gond, S. K., Bergen, M. S., Torres, M. S., and White, J. F. Jr. (2015). *Endophytic Bacillus* spp. produce antifungal lipopeptides and induce host defence gene expression in maize. *Microbiol. Res.* 172, 79–87. doi: 10.1016/j.micres.2014.11.004

Gowtham, H. G., Hariprasad, P., Chandra Nayak, S., and Niranjana, S. R. (2016). Application of rhizobacteria antagonistic to *Fusarium oxysporum* f. sp. *lycopersici* for the management of *Fusarium* wilt in tomato. *Rhizosphere* 2, 72–74. doi: 10.1016/j.rhisph.2016.07.008

Groenhagen, U., Baumgartner, R., Bailly, A., Gardiner, A., Eberl, L., Schulz, S., et al. (2013). Production of Bioactive Volatiles by Different *Burkholderia ambifaria* Strains. *J. Chem. Ecol.* 39, 892–906. doi: 10.1007/s10886-013-0315-y

Guevara-Avendaño, E., Mauricio, L. R., Pablo, O. A., Lourdes, G. I. A., Ángel, T., and María, M. H. (2014). Effect of rhizobacteria indole producing on the development of *Capsicum annuum* var. Jalapeño M. *Int. Res. J. Biological Sci.* 3, 22–27.

Guo, M., Liu, J. H., Ma, X., Luo, D. X., Gong, Z. H., and Lu, M. H. (2016). The plant heat stress transcription factors (HSFs): structure, regulation, and function in response to abiotic stresses. *Front. Plant Sci.* 7:114. doi: 10.3389/fpls.2016.00114

Gustafson, K., Roman, M., and Fenical, W. (1989). The macrolactins, a novel class of antiviral and cytotoxic macrolides from a deep-sea marine bacterium. *J. Am. Chem. Soc.* 111, 7519–7524. doi: 10.1021/ja00201a036

Harris, N., Taylor, J., and Roberts, J. (1994). Isolation of a mRNA encoding a nucleoside diphosphate kinase from tomato that is up-regulated by wounding. *Plant Mol. Biol.* 25, 739–742. doi: 10.1007/BF00029611

Hartman, G. L., and Elphinstone, J. G. (1994). "Advances in the control of *Pseudomonas solanacearum* race 1 in major food crops" in *Bacterial wilt: The disease and its causal agent, Pseudomonas solanacearum*. eds. A. C. Hayward and G. L. Hartman (Wallingford, UK: CAB International), 157–177.

Hayward, A. C. (1964). Characteristics of *Pseudomonas solanacearum*. *J. Appl. Bacteriol.* 27, 265–277. doi: 10.1111/j.1365-2672.1964.tb04912.x

Hayward, A. C. (1991). Biology and epidemiology of bacterial wilt caused by Pseudomonas solanacearum annual review of phytopathol. *Annu. Rev. Phytopathol.* 29, 65–87. doi: 10.1146/annurev.py.29.090191.000433

Hii, Y. S., San, C. Y., Lau, S. W., and Danquah, M. K. (2020). Isolation and characterisation of phosphate solubilizing microorganisms from peat. *Biocatal. Agric. Biotechnol.* 26:101643. doi: 10.1016/j.bcab.2020.101643

Hofemeister, J., Conrad, B., Adler, B., Hofemeister, B., Feesche, J., Kucheryava, N. G., et al. (2004). Genetic analysis of the biosynthesis of non-ribosomal peptide and polyketide-like antibiotics, iron uptake and biofilm formation by *Bacillus subtilis* A1/3. *Mol. Gen. Genomics.* 272, 363–378. doi: 10.1007/s00438-004-1056-y

Hofte, M., Boelens, J., and Vstraete, W. (1991). Seed protection and promotion of seedling emergence by the plant growth beneficial Pseudomonas Strains 7NSK2 and ANP15. *Soil Biol. Biochem.* 23, 407–410. doi: 10.1016/0038-0717(91)90001-Z

Hu, H. Q., Li, X. S., and He, H. (2010). Characterization of an antimicrobial material from a newly isolated *Bacillus amyloliquefaciens* from mangrove for biocontrol of capsicum bacterial wilt. *Biol. Control* 54, 359–365. doi: 10.1016/j.biocontrol.2010.06.015

Huang, C. J., Tsay, J. F., Chan, S. Y., Yang, H. P., Wu, W. S., and Chen, C. Y. (2012). Dimethyl disulfide is an induced systemic resistance elicitor produced by *Bacillus cereus* C1L. *Pest Manag. Sci.* 68, 1306–1310. doi: 10.1002/ps.3301

Huang, X. F., Zhou, D. M., Guo, J. H., Manter, D. K., Reardon, K. F., and Vivanco, J. M. (2015). Bacillus spp. from rainforest soil promotes plant growth under limited nitrogen conditions. *J. Appl. Microbiol.* 118, 672–684. doi: 10.1111/jam.12720

Hurek, T., and Reinhold-Hurek, B. (2003). *Azoarcus* sp. strain BH72 as a model for nitrogen-fixing grass endophytes. *J. Biotechnol.* 106, 169–178. doi: 10.1016/j.jbiotec.2003.07.010

Hyakumachi, M., Nishimura, M., Arakawa, T., Asano, S., Yoshida, S., Tsushima, S., et al. (2013). *Bacillus thuringiensis* suppresses bacterial wilt disease caused by *Ralstonia solanacearum* with systemic induction of defense-related gene expression in tomato. *Microb. Envir.* 28, 128–134. doi: 10.1264/jsme2.ME12162

Islam, S., Akanda, A. M., Prova, A., Islam, M. T., and Hossain, M. M. (2016). Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect on plant growth promotion and disease suppression. *Front. Microbiol.* 6:1360.

Jagadeesh, K. S., Kullarni, J. H., and Krishnaraj, P. U. (2001). Evaluation of the role of fluorescent siderophore in the biological control of bacterial wilt in tomato using Tn 5 mutants of fluorescent *Pseudomonas* sp. *Curr. Sci.* 81:882.

Jaruchoktaweechai, C. S., Suwanboriux, K., Tanasupawatt, S., Kittakoop, P., and Menasveta, P. (2000). New macrolactins from a marine *Bacillus* sp. Sc026. *J. Nat. Prod.* 63, 984–986. doi: 10.1021/np990605c

Jatan, R. R., Chauhan, P. S., and Lata, C. (2020). High-throughput sequencing and expression analysis suggest the involvement of pseudomonas putida RA-Responsive microRNAs in growth and development of Arabidopsis. *Int. J. Mol. Sci.* 21:5468. doi: 10.3390/ijms21155468

Jayanna, S. K., and Umesha, S. (2017). Enhancement of the expression of defense genes in tomato against *Ralstonia solanacearum* by N-octanoyl L-homoserine lactone. *Afr. J. Microbiol. Res.* 11, 194–203.

Jayapala, N., Mallikarjunaiah, N., and Puttaswamy, H. (2019). *Rhizobacteria Bacillus* spp. induce resistance against anthracnose disease in chili (*Capsicum annuum* L.) through activating host defense response. *Egypt. J. Biol. Pest Control* 29:45. doi: 10.1186/s41938-019-0148-2

Jiao, X., Takishita, Y., Zhou, G., and Smith, D. L. (2021). Plant associated Rhizobacteria for biocontrol and plant growth enhancement. *Front. Plant Sci.* 12:634796. doi: 10.3389/fpls.2021.634796

Kanchiswamy, C. N., Malnoy, M., and Maffei, M. E. (2015). Chemical diversity of microbial volatiles and their potential for plant growth and productivity. *Front. Plant Sci.* 6:151. doi: 10.3389/fpls.2015.00151

Kandasamy, S., Loganathan, K., Muthuraj, R., Duraisamy, S., Seetharaman, S., Thiruvengadam, R., et al. (2009). Understanding the molecular basis of plant growth promotional effect of *Pseudomonas fluorescens* on rice through protein profiling. *Proteome Sci.* 7:47. doi: 10.1186/1477-5956-7-47

Kang, S. M., Joo, G. J., Hamayun, M., Na, C. I., Shin, D. H., Kim, H. Y., et al. (2009). Gibberellin production and phosphate solubilization by newly isolated strain of *Acinetobacter calcoaceticus* and its effect on plant growth. *Biotechnol. Lett.* 31, 277–281. doi: 10.1007/s10529-008-9867-2

Kanyagha, H. E. (2021). *Characterization of Ralstonia Spp. in Tanzania and potential integrated pest-management strategies for managing bacterial wilt in tomatoes*. USA: The Ohio State University.

Karimi, A., Sadeghi, P. A., Dahaji, Y., Dalvand, M., and Omidvari, M. K. N. (2012). Biocontrol activity of salt tolerant Streptomyces isolates against phytopathogens causing root rot of sugar beet. *Biocontrol Sci Technol* 22, 333–349.

Kashyap, A. S., Manzar, N., Ahamad, F., Tilgam, J., Sharma, P. K., and Saxena, A. K. (2022b). First report of root rot disease in green gram (*Vigna radiata*) caused by *Ectophoma multirostrata* in India. *Plant Dis* 106:2256. doi: 10.1094/PDIS-11-21-2400-PDN

Kashyap, A. S., Manzar, N., Maurya, A., Mishra, D. D., Singh, R. P., and Sharma, P. K. (2023). Development of diagnostic markers and applied for genetic diversity study and population structure of *Bipolaris sorokiniana* associated with leaf blight complex of wheat. *J. Fungi* 9:153. doi: 10.3390/jof9020153

Kashyap, A. S., Manzar, N., Nebapure, S. M., Rajawat, M. V. S., Deo, M. M., Singh, J. P., et al. (2022a). Unraveling microbial volatile elicitors using a transparent methodology for induction of systemic resistance and regulation of antioxidant genes at expression levels in chili against bacterial wilt disease. *Antioxidants* 11:404. doi: 10.3390/antiox11020404

Kashyap, A. S., Manzar, N., Rajawat, M. V. S., Kesharwani, A. K., Singh, R. P., Dubey, S. C., et al. (2021). Screening and biocontrol potential of Rhizobacteria native to Gangetic plains and hilly regions to induce systemic resistance and promote plant growth in Chilli against bacterial wilt disease. *Plan. Theory* 10:2125. doi: 10.3390/plants10102125

Kavitha, R., and Umesha, S. (2008). Regulation of defense-related enzymes associated with bacterial spot resistance in tomato. *Phytoparasitica* 36, 144–159. doi: 10.1007/BF02981327

Kim, P. I., Ryu, J., and Kim, Y. H. (2010). Production of biosurfactant lipopeptides Iturin A, fengycin and surfactin A from Bacillus subtilis CMB32 for control of *Colletotrichum gloeosporioides*. *J. Microbiol. Biotechnol.* 20, 138–145. doi: 10.4014/jmb.0905.05007

Kirui, C. K., Njeru, E. M., and Runo, S. (2022). Diversity and phosphate solubilization efficiency of phosphate solubilizing bacteria isolated from semi-arid agroecosystems of Eastern Kenya. *Microbiol Insights* 15, 1–12. doi: 10.1177/11786361221088991

Kloepper, J. W., Ryu, C. M., and Zhang, S. (2004). Induced systemic resistance and promotion of plant growth by *Bacillus* spp. *Phytopathology* 94, 1259–1266. doi: 10.1094/PHYTO.2004.94.11.1259

Kloepper, J. W., and Schroth, M. N. (1978). *Plant growth-promoting rhizobacteria on radishes Proceedings of the 4th international conference on plant pathogenic bacteria. 2*. Station de PathologieVegetale et Phytobacteriologie, INRA, Angers, France. 879–882.

Koumoutsi, A. (2004). Structural and functional characterization of gene clusters directing non-ribosomal synthesis of bioactive cyclic lipopeptides in *Bacillus amyloliquefaciens* strain FZB42. *J. Bacteriol.* 186, 1084–1096. doi: 10.1128/JB.186.4.1084-1096.2004

Krieg, N. R., and Holt, J. G. (1984). *Bergey's manual of systematic bacteriology*. Williams and Wilkins, Baltimore, London.

Kudoyarova, G. R., Korobova, A. V., Akhiyarova, G. R., Arkhipova, T. N., Zaytsev, D. Y., Prinsen, E., et al. (2014). Accumulation of cytokinins in roots and their export to the shoots of durum wheat plants treated with the protonophore carbonyl cyanide m-chlorophenylhydrazone (CCCP). *J. Exp. Bot.* 65, 2287–2294. doi: 10.1093/jxb/eru113

Kumar, A. (2016). Phosphate solubilizing bacteria in agriculture biotechnology: diversity, mechanism and their role in plant growth and crop yield. *Int. J. Adv. Res.* 4, 116–124. doi: 10.21474/IJAR01/111

Kumar, S., Agarwal, M., Dheeman, S., and Maheshwari, D. K. (2015). "Exploitation of phytohormone-producing PGPR in development of multispecies bioinoculant formulation" in *Bacterial metabolites in sustainable agroecosystem*. ed. D. K. Maheshwari, Springer.

Kurabachew, H., and Wydra, K. (2014). Induction of systemic resistance and defense related enzymes after elicitation of resistance by rhizobacteria and silicon application against *Ralstonia solanacearum* in tomato (*Solanum lycopersicum*). *Crop Prot.* 57, 1–7. doi: 10.1016/j.cropro.2013.10.021

Lakkis, S., Trotel-Aziz, P., Rabenoelina, F., Schwarzenberg, A., Nguema-Ona, E., Clément, C., et al. (2019). Strengthening grapevine resistance by *Pseudomonas fluorescens* PTA-CT2 relies on distinct defense pathways in susceptible and partially resistant genotypes to Downy Mildew and Gray Mold Diseases. *Front. Plant Sci.* 10:1112. doi: 10.3389/fpls.2019.01112

Li, H., Ding, X., Wang, C., Ke, H., Wu, Z., Wang, Y., et al. (2016). Control of tomato yellow leaf curl virus disease by *Enterobacter* asburiaeBQ9 as a result of priming plant resistance in tomatoes. *Turk. J. Biol.* 40, 150–159. doi: 10.3906/biy-1502-12

Li, S. B., Fang, M., Zhou, R. C., and Huang, J. (2012). Characterization and evaluation of the endophyte Bacillus B014 as a potential biocontrol agent for the control of *Xanthomonas axonopodis* pv. *dieffenbachiae* induced blight of Anthurium. *Biol. Control* 63, 9–16. doi: 10.1016/j.biocontrol.2012.06.002

Liu, X., Jiang, X., He, X., Zhao, W., Cao, Y., Guo, T., et al. (2019). Phosphate-solubilizing Pseudomonas sp. strain P34-L promotes wheat growth by colonizing the wheat rhizosphere and improving the wheat root system and soil phosphorus nutritional status. *J. Plant Growth Regul.* 38, 1314–1324. doi: 10.1007/s00344-019-09935-8

Liu, D., Lian, B., and Dong, H. (2012). Isolation of *Paenibacillus* spp. and assessment of its potential for enhancing mineral weathering. *Geo Microbiol. J.* 29, 413–421.

Liu, Y., Shi, J., Feng, Y., Yang, X., Li, X., and Shen, Q. (2013). Tobacco bacterial wilt can be biologically controlled by the application of antagonistic strains in combination with organic fertilizer. *Biol. Fertil. Soils* 49, 447–464. doi: 10.1007/s00374-012-0740-z

Liu, Z., Shi, L., Weng, Y., Zou, H., Li, X., Yang, S., et al. (2019). ChiIV3 acts as a novel target of WRKY40 to mediate pepper immunity against *Ralstonia solanacearum* infection. *Mol. Plant-Microbe Interact.* 32, 1121–1133. doi: 10.1094/MPMI-11-18-0313-R

Lwin, M., and Ranamukhaarachchi, S. L. (2006). Development of biological control of *Ralstonia solanacearum* through antagonistic microbial populations. *Int. J. Agric. Biol.* 8, 657–660.

Ma, L., Zhang, H.-Y., Zhou, X.-K., Yang, C.-G., Zheng, S.-C., Duo, J.-L., et al. (2018). Biological control tobacco bacterial wilt and black shank and root colonization by bio-organic fertilizer containing bacterium *Pseudomonas aeruginosa* NXHG29. *Appl. Soil Ecol.* 129, 136–144. doi: 10.1016/j.apsoil.2018.05.011

Malleswari, D. (2014). In vitro antagonistic activity of diverse bacterial isolates against *Macrophomina phaseolina* (Tassi) Goid. *Int. J. Curr. Microbiol. App. Sci.* 3, 755–763.

Mansfield, J., Genin, S., Magori, S., Citovsky, V., Sriariyanum, M., Ronald, P., et al. (2012). Top 10 plant pathogenic bacteria in molecular plant pathology. *Mol. Plant Pathol.* 13, 614–629. doi: 10.1111/j.1364-3703.2012.00804.x

Manzar, N., Kashyap, A. S., Goutam, R. S., Rajawat, M. V. S., Sharma, P. K., Sharma, S. K., et al. (2022b). Trichoderma: advent of versatile biocontrol agent, its secrets and insights into mechanism of biocontrol potential. *Sustainability* 14:12786. doi: 10.3390/su141912786

Manzar, N., Kashyap, A. S., Maurya, A., Rajawat, M. V. S., Sharma, P. K., Srivastava, A. K., et al. (2022a). Multi-gene phylogenetic approach for identification and diversity analysis of *Bipolaris maydis* and *Curvularia lunata* isolates causing foliar blight of *Zea mays*. *J Fungi* 8:802. doi: 10.3390/jof8080802

Manzar, N., Kashyap, A. S., Sharma, P. K., and Saxena, A. K. (2021a). First report of leaf spot of maize caused by *Curvularia geniculata* in India. *Plant Dis.* 105:4155. doi: 10.1094/PDIS-03-21-0637-PDN

Manzar, N., Singh, Y., Kashyap, A. S., Sahu, P. K., Rajawat, S. M. V., Bhowmik, A., et al. (2021b). Biocontrol potential of native *Trichoderma* spp. against anthracnose of great millet (*Sorghum bicolour* L.) from Tarai and hill regions of India. *Biol. Control* 152:104474. doi: 10.1016/j.biocontrol.2020.104474

Milagrosa, S. P., and Balaki, E. T. (1999). Influence of Bokashi organic fertilizer and effective microorganisms (EM) on growth and yield of field grown vegetables. In: Y. D. A. Senanayake and U. R. Sangakkara (Eds.), Proceeding of fix international conference on Kyusei nature farming, International nature farming research center, Atami, Japan, 84–92

Miljakovi, D., Marinkovi, J., and Baleevi-Tubi, S. (2020). The significance of *Bacillus* spp. in disease suppression and growth promotion of field and vegetable crops. *Microorganisms* 8:1037. doi: 10.3390/microorganisms8071037

Mishra, A. (1995). Assessment of yield loss due to wilting in some popular tomato cultivars. *Env. Ecol.* 13:287.

Mohammed, A. F., Oloyede, A. R., and Odeseye, A. O. (2020). Biological control of bacterial wilt of tomato caused by *Ralstonia solanacearum* using *Pseudomonas* species isolated from the rhizosphere of tomato plants. *Arch. Phytopathol. Plant Protect.* 53, 1–16. doi: 10.1080/03235408.2020.1715756

Moisyadi, S., Dharmasiri, S., Harrington, H. M., and Lukas, T. J. (1994). Characterization of a low molecular mass autohosphorylated protein in cultured sugarcane cells and its identifications as a nucleoside diphosphate kinase. *Plant Physiol.* 104, 1401–1409. doi: 10.1104/pp.104.4.1401

Montano, F. P., Villegas, C. A., Bellogia, R. A., Cerro, P. D., Espuny, M. R., Guerrero, I. J., et al. (2014). Plant growth promotation in cereals and leguminous

agricultural important plants from microorganisms' capacities to crop production. *Microbiol. Res.* 169, 325–336. doi: 10.1016/j.micres.2013.09.011

Moon, H., Lee, B., Choi, G., Shin, D., Prasad, D. T., Lee, O., et al. (2003). NDP kinase 2 interacts with two oxidative stress-activated MAPKs to regulate cellular redox state and enhances multiple stress tolerance in transgenic plants. *Proc. Natl. Acad. Sci. U. S. A.* 100, 358–363. doi: 10.1073/pnas.252641899

Mubarak, M. Q. E., Hassan, A. R., Hamid, A. A., Khalil, S., and Isa, M. H. M. (2015). A simple and effective isocratic HPLC method for fast identification and quantification of surfactin. *Sains Malays.* 44, 115–120. doi: 10.17576/jsm-2015-4401-16

Mulla, S. R., Sandeep, C. P., Salimath, J., Varsha, P., Suresh, C. K., and Priyadarsini, R. I. (2013). Effect of *Pseudomonas fluorescens* isolated from various agroclimatic zones of Karnataka on *Rauwolfia serpentina*. *Int J Pharm Sci* 5, 141–146.

Nacoon, S., Jogloy, S., Riddech, N., Mongkolthanaruk, W., Kuyper, T. W., and Boonlue, S. (2020). Interaction between phosphate solubilizing bacteria and arbuscular mycorrhizal fungi on growth promotion and tuber inulin content of *Helianthus tuberosus* L. *Sci. Rep.* 10, 1–10. doi: 10.1038/s41598-020-61846-x

Ngumbi, E., and Kloepper, J. (2016). Bacterial-mediated drought tolerance: current and future prospects. *Appl. Soil Ecol.* 105, 109–125. doi: 10.1016/j.apsoil.2016.04.009

Niehus, R., Picot, A., Oliveira, N. M., Mitri, S., and Foster, K. R. (2017). The evolution of siderophore production as a competitive trait. *Evolution* 71, 1443–1455. doi: 10.1111/evo.13230

Oteino, N., Lally, R. D., Kiwanuka, S., Lloyd, A., Ryan, D., Germaine, K. J., et al. (2015). Plant growth promotion induced by phosphate solubilizing endophytic *Pseudomonas* isolates. *Front. Microbiol.* 6:745. doi: 10.3389/fmicb.2015.00745

Oyedele, A. O., and Samuel, T. (2014). Antifungal activities of *Bacillus subtilis* isolated from some condiments and soil. *Afr. J. Microbiol. Res.* 8, 1841–1849. doi: 10.5897/AJMR2013.6162

Patel, J. B. (2001). 16S rRNA gene sequencing for bacterial pathogen identification in the clinical laboratory. *Mol. Diagn.* 6, 313–321. doi: 10.1007/BF03262067

Pieterse, C. M., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C., and Bakker, P. A. (2014). Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* 52, 347–375. doi: 10.1146/annurev-phyto-082712-102340

Prameela, T. P., and Rajamma, S. B. (2020). Bacterial wilt of ginger (*Zingiber officinale* Rosc.) incited by *Ralstoniapseudosolanacearum*-A review based on pathogen diversity, diagnostics and management. *J. Plant Pathol.* 102, 709–719.

Prathap, M., and Kumari, R. B. D. (2015). A Critical review on plant growth promoting rhizobacteria. *J. Plant Pathol. Microbiol.* 6, 1–4.

Punja, Z. K., Rodriguez, G., and Tirajoh, A. (2016). Effects of *Bacillus subtilis* strain QST 713 and storage temperatures on post-harvest disease development on greenhouse tomatoes. *Crop Prot.* 84, 98–104. doi: 10.1016/j.cropro.2016.02.011

Rajer, F. U., Wu, H., Xie, Y., Xie, S., Raza, W., Tahir, H. A. S., et al. (2017). Volatile organic compounds produced by a soil-isolate, *Bacillus subtilis* FA26 induce adverse ultra-structural changes to the cells of *Clavibacter michiganensis* ssp. *sepedonicus*, the causal agent of bacterial ring rot of potato. *Microbiology (Reading).* 163, 523–530. doi: 10.1099/mic.0.000451

Ramadan, E. M., AbdelHafez, A. A., Hassan, E. A., and Saber, F. M. (2016). Plant growth promoting rhizobacteria and their potential for biocontrol of phytopathogens. *Afr. J. Microbiol. Res.* 10, 486–504.

Ramarathnam, R., Bo, S., Chem, Y., Fernando, W. G. D., Xuewen, G., and de Kievit, T. (2007). Molecular and biochemical detection of fengycin and bacillomycin D producing *Bacillus* spp., antagonistic to fungal pathogens of canola and wheat. *Can. J. Microbiol.* 53, 901–911. doi: 10.1139/W07-049

Ramesh, R., and Phadke, G. S. (2012). Rhizosphere and endophytic bacteria for the suppression of eggplant wilt caused by *Ralstonia solanacearum*. *Crop Prot.* 37, 35–41. doi: 10.1016/j.cropro.2012.02.008

Raymond, K. N., Allred, B. E., and Sia, A. K. (2015). Coordination chemistry of microbial iron transport. *Acc. Chem. Res.* 48, 2496–2505. doi: 10.1021/acs.accounts.5b00301

Raza, W., Ling, N., Liu, D., Wei, Z., Huang, Q., and Shen, Q. (2016a). Volatile organic compounds produced by Pseudomonas fluorescensWR-1 restrict the growth and virulence traits of *Ralstonia solanacearum*. *Microbiol. Res.* 192, 103–113. doi: 10.1016/j.micres.2016.05.014

Raza, W., Ling, N., Yang, L., Huang, Q., and Shen, Q. (2016b). Response of tomato wilt pathogen *Ralstonia solanacearum* to the volatile organic compounds produced by a biocontrol strain *Bacillus amyloliquefaciens* SQR-9. *Sci. Rep.* 6:24856. doi: 10.1038/srep24856

Raza, W., Yousaf, S., and Rajer, F. U. (2016c). Plant growth promoting activity of volatile organic compounds produced by Bio-control strains. *Sci. Lett.* 4, 40–43.

Rea, M. C., Sit, C. S., Claytona, E., Connor, P. M., Whittal, R. M., Zheng, J., et al. (2010). Thuricin CD, a post-translationally modified bacteriocin with a narrow spectrum of activity against *Clostridium difficile*. *Proc. Natl. Acad. Sci. U. S. A.* 107, 9352–9357. doi: 10.1073/pnas.0913554107

Rojas-Solís, D., Zetter-Salmón, E., Contreras-Pérez, M., del Carmen Rocha-Granados, M., Macía-Rodríguez, L., and Santoyo, G. (2018). *Pseudomonas stutzeri* E25 and *Stenotrophomonas maltophilia* CR71 endophytes produce antifungal volatile organic compounds and exhibit additive plant growth-promoting effects. *Biocat. Agri. Biotechnol.* 13, 46–52. doi: 10.1016/j.bcab.2017.11.007

Ryu, C., Farag, M. A., Hu, C., Reddy, M. S., Wei, H., and Pare, P. W. (2003). Bacterial volatiles promote growth in Arabidopsis. *PNAS* 100, 4927–4932. doi: 10.1073/pnas.0730845100

Ryu, C. M., Farag, M. A., Hu, C. H., Reddy, M. S., Kloepper, J. W., and Paré, P. W. (2004). Bacterial volatiles induce systemic resistance in Arabidopsis. *Plant Physiol.* 134, 1017–1026. doi: 10.1104/pp.103.026583

Ryu, C.-M., Hu, C.-H., Locy, R. D., and Kloepper, J. W. (2005). Study of mechanisms for plant growth promotion elicited by rhizobacteria in Arabidopsis thaliana. *Plant Soil.* 268, 285–292.

Ryu, C.-M., Kim, J., Choi, O., Kim, S. H., and Park, C.-S. (2006). Improvement of biological control capacity of *Paenibacillus polymyxa* E681 by seed pelleting on sesame. *Biol. Control* 39, 282–289. doi: 10.1016/j.biocontrol.2006.04.014

Saia, S. (2015). Soil inoculation with symbiotic microorganisms promotes plant growth and nutrient transporter genes expression in durum wheat. *Front. Plant Sci.* 6:202.

Seleim, M. A. A., Abo-Elyousr, K. A. M., Abd-El-Moneem, K. M., and Saead, F. A. (2014). First report of bacterial wilt caused by *Ralstonia solanacearum* biovar 2 race 1 on tomato in Egypt. *J. Plant Pathol.* 30, 299–303. doi: 10.5423/PPJ.NT.10.2013.0101

Sgroy, V., Cassan, F., Masciarelli, O., Del Papa, M. F., and Lagares, A. (2009). Luna isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. *Appl. Microbiol. Biotechnol.* 85, 85371–85381.

Sharifi, R., and Ryu, C. M. (2016). Are bacterial volatile compounds poisonous odors to a fungal pathogen *Botrytis cinerea*, Alarm signals to Arabidopsis seedlings for eliciting induced resistance, or both. *Front. Microbiol.* 7, 1–10.

Sharma, S., and Kaur, M. (2010). Antimicrobial activities of rhizobacterial strains of *Pseudomonas* and *Bacillus* strains isolated from rhizosphere soil of carnation (*Dianthus caryophyllus* cv. Sunrise). *Indian J. Microbiol.* 50, 229–232. doi: 10.1007/s12088-010-0045-6

Shekhawat, G. S., Chakrabarti, S. K., Kishore, V., Sunaina, V., and Gadewar, A. V. (1993). "Possibilities of biological management of potato bacterial wilt with strains of Bacillus sp., Bacillus subtilis, Pseudomonas fluorescens and Actinomycetes" in *Bacterial Wilt 327–30. ACIAR Proceedings*. eds. G. L. Hartman and A. C. Hayward, vol. *45* (Camera: Australian Centre for International Agricultural Research)

Shekhawat, G. S., Gadewar, A. V., and Chakrabarti, S. K. (2000). Potato bacterial wilt in India. *Technical Bullet* 38, 56–57.

Shenoy, V. V., and Kalagudi, G. M. (2005). Enhancing plant phosphorus use efficiency for sustainable cropping. *Biotechnol. Adv.* 23, 501–513. doi: 10.1016/j.biotechadv.2005.01.004

Siddiqui, Z. (2006). PGPR: Prospective Biocontrol Agents of Plant Pathogens. *Biocontrol. Biofertil.* 111–142.

Sivasakthi, S., Saranraj, P., and Sivasakthivelan, P. (2017). Biological nitrogen fixation by Azotobacter sp.—a review. *Indo. Asian. J. Multidiscip. Res.* 3, 1274–1284. doi: 10.22192/iajmr.2017.3.5.6

Singh, D., Chaudhary, G., and Yadav, D. K. (2017). Genetic diversity of Indian isolates of *Ralstonia solanacearum* causing bacterial wilt of eggplant (*Solanum melongena*). *Indian J. Agric. Sci.* 87, 1466–1475.

Singh, D., Shweta, S., Yadav, D. K., Sharma, J. P., Srivastava, D. K., Lal, H. C., et al. (2010). Characterization of biovar/races of *Ralstonia solanacearum*, the incitant of bacterial wilt in solanaceous crops. *Indian Phytopath* 63, 261–265.

Singh, S., Singh, D. R., Kumar, K., and Birah, A. (2014). Eco-friendly management modules for bacterial wilt (Ralstonia solanacearum) of tomato for protected cultivation in a tropical island ecosystem. *Biol. Agric. Hortic.* 30, 219–227. doi: 10.1080/01448765.2014.913263

Singh, R., Soni, S. K., and Kalra, A. (2013). Synergy between *Glomus fasciculatum* and beneficial *Pseudomonas* in reducing root diseases and improving yield and forskolin content in Coleus forskohlii Brig, under organic field condition. *Mycorrhiza* 23, 35–44. doi: 10.1007/s00572-012-0447-x

Srivastava, S., Bist, V., Srivastava, S., Singh, P. C., Trivedi, P. K., and Asif, M. H. (2016). Unraveling aspects of *Bacillus amyloliquefaciens* mediated enhanced production of rice under biotic stress of *Rhizoctonia solani*. *Front. Plant Sci.* 7:587. doi: 10.3389/fpls.2016.00587

Stein, T. (2005). Bacillus subtilis antibiotics: structures, syntheses and specific functions. *Mol. Microbiol.* 56, 845–857. doi: 10.1111/j.1365-2958.2005.04587.x

Suryakala, D., Maheshwaridevi, P. V., and Lakshmi, K. V. (2004). Chemical characterization and *in vitro* antibiosis of siderophores of rhizosphere fluorescent *pseudomonads*. *Indian J. Microbiol.* 44, 105–108.

Tahir, H. A. S., Gu, Q., Wu, H., Raza, W., Hanif, A., and Wu, L. (2017). Plant growth promotion by volatile organic compounds produced by *Bacillus subtilis* SYST2. *Front. Mol. Biol.* 8, 1–11.

Tamehiro, N., Okamoto, H. Y., Okamoto, S., Ubukata, M., Hamada, M., Naganawa, H., et al. (2002). Bacilysocin, a novel phospholipid antibiotic produced by *Bacillus subtilis*. *Antimicrob. Agents Chemother.* 46, 315–320. doi: 10.1128/AAC.46.2.315-320.2002

Tan, S., Dong, Y., Liao, H., Huang, J., Song, S., Xu, Y., et al. (2013a). Antagonistic bacterium *Bacillus amyloliquefaciens* induces resistance and controls the bacterial wilt of tomato. *Pest Manag. Sci.* 69, 1245–1252. doi: 10.1002/ps.3491

Tan, S., Yang, C., Mei, X., Shen, S., Raza, W., and Shen, Q. (2013b). The effect of organic acids from tomato root exudates on rhizosphere colonization of *Bacillus amyloliquefaciens* T-5. *Appl. Soil Ecol.* 64, 15–22. doi: 10.1016/j.apsoil.2012.10.011

Tao, C., Li, R., Xiong, Z. S., Shen, Z., Liu, S., Wang, B., et al. (2020). Bio-organic fertilizers stimulate indigenous soil *Pseudomonas* populations to enhance plant disease suppression. *Microbiome* 8, 1–14. doi: 10.1186/s40168-020-00892-z

Tenorio-Salgado, S., Tinoco, R., Vazquez-Duhalt, R., Caballero-Mellado, J., and Perez-Rueda, E. (2013). Identification of volatile compounds produced by the bacterium *Burkholderia tropica* that inhibit the growth of fungal pathogens. *Bioengineered* 4, 236–243. doi: 10.4161/bioe.23808

Thanh, D. T., Tarn, L. T. T., Hanh, N. T., Tuyen, N. H., Lee, S. Y., and Park, K.-S. (2009). Biological control of soilborne diseases on tomato, potato and black pepper by selected PGPR in the greenhouse and field in Vietnam. *Plant Pathol. J.* 25, 263–269. doi: 10.5423/PPJ.2009.25.3.263

Turan, M. A., Awad-Alkarim, A. H., Taban, N., and Taban, S. (2009). Effect of salt stress on growth, stomatal resistance, proline and chlorophyll concentrations on maize plant. *Afr. J. Agric. Res.* 4, 893–897.

USDA. (2003). Biological control of Fusarium wilt and other soilborne pathogenic fungi. Available at: http://www.ars.usda.gov/research/projects/projects.htm?ACCN_NO=406590&fy=2003

Van Peer, R., and Schippers, B. (1992). Lipopolysaccharides of plant-growth promoting Pseudomonas sp. strain WCS417r induce resistance in carnation to Fusarium wilt. *Neth. J. Plant Pathol.* 98, 129–139. doi: 10.1007/BF01996325

Vespermann, A., Kai, M., and Piechulla, B. (2007). Rhizobacterial volatiles affect the growth of fungi and Arabidopsis thaliana. *Appl. Environ. Microbiol.* 73, 5639–5641. doi: 10.1128/AEM.01078-07

Voisard, C., Keel, C., Haas, D., and Dèfago, G. (1989). Cyanide production by Pseudomonas fluorescens helps suppress black rot of tobacco under gnotobiotic conditions. *EMBO J.* 8, 351–358. doi: 10.1002/j.1460-2075.1989.tb03384.x

Wei, Z., Huang, J., Tan, S., Mei, X., Shen, Q., and Xu, Y. (2013). The congeneric strain *Ralstoniapicketti* QL-A6 of *Ralstonia solanacearum* as an effective biocontrol agent for bacterial wilt of tomato. *Biol. Control* 65, 278–285. doi: 10.1016/j.biocontrol.2012.12.010

Wei, Z., Yang, X., Yin, S., Shen, Q., Ran, W., and Xu, Y. (2011). Efficacy of *Bacillus*-fortified organic fertilizer in controlling bacterial wilt of tomato in the field. *Appl. Soil Ecol.* 48, 152–159. doi: 10.1016/j.apsoil.2011.03.013

Weller, D. M., Raaijmakers, J. M., McSpadden, B. B. G., and Thomashow, L. S. (2002). Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu. Rev. Phytopathol.* 40, 308–348.

Xing, Y., Jia, W., and Zhang, J. (2007). AtMEK1 mediates stress-induced gene expression of CAT1 catalase by triggering H_2O_2 production in Arabidopsis. *J. Exp. Bot.* 58, 2969–2981. doi: 10.1093/jxb/erm144

Yadav, D. K., Singh, D., and Kumar, N. (2017). Induction of Defense-related Enzymes by *Bacillus amyloliquefaciens* DSBA-11 in resistant and susceptible cultivars of tomato against bacterial wilt disease. *Int. J. Agric. Res.* 12, 172–180. doi: 10.3923/ijar.2017.172.180

Yang, J., Kloepper, J. W., and Ryu, C. M. (2009). Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci.* 14, 1–4. doi: 10.1016/j.tplants.2008.10.004

Yu, X., Ai, C., Xin, L., and Zhou, G. (2011). The siderophore-producing *Bacterium*, *Bacillus subtilis* CAS15, Has a biocontrol effect on *Fusarium* wilt and promotes the growth of pepper. *Eur. J. Soil Biol.* 47, 138–145. doi: 10.1016/j.ejsobi.2010.11.001

Yuan, S., Cohen, D. B., Ravel, J., Abdo, Z., and Forney, L. J. (2012). Evaluation of methods for the extraction and purification of DNA from the human microbiome. *PLoS One* 7:e33865. doi: 10.1371/journal.pone.0033865

Yuan, S., Wang, L., Wu, K., Shi, J., Wang, M., Yang, X., et al. (2014). Evaluation of *Bacillus*-fortified organic fertilizer for controlling tobacco bacterial wilt in greenhouse and field experiments. *Appl. Soil Ecol.* 75, 86–94. doi: 10.1016/j.apsoil.2013.11.004

Yuliar, N., Nion, Y. A., and Toyota, K. (2015). Recent trends in control methods for bacterial wilt diseases caused by *Ralstonia solanacearum*. *Microbes Environ.* 30, 1–11. doi: 10.1264/jsme2.ME14144

Zhou, C., Ma, Z. Y., Zhu, L., Xiao, X., Xie, Y., Zhu, J., et al. (2016). Rhizobacterial strain *Bacillus megaterium* bofc15 induces cellular polyamine changes that improve plant growth and drought resistance. *Int. J. Mol. Sci.* 17:976. doi: 10.3390/ijms17060976

Zinniel, D. K., Lambrecht, P., Harris, N. B., Feng, Z., Kuczmarski, D., Higley, P., et al. (2002). Isolation and characterization of endophytic colonizing bacteria from agronomic crops and prairie plants. *Appl. Environ. Microbiol.* 68, 2198–2208. doi: 10.1128/AEM.68.5.2198-2208.2002

frontiers | Frontiers in Microbiology

TYPE Review
PUBLISHED 19 July 2023
DOI 10.3389/fmicb.2023.1214870

OPEN ACCESS

EDITED BY
Parul Chaudhary,
Graphic Era Hill University, India

REVIEWED BY
Bartholomew Saanu Adeleke,
Olusegun Agagu University of Science and Technology, Nigeria
Sami Abou Fayssal,
University of Forestry, Sofia, Bulgaria

*CORRESPONDENCE
Geeta Bhandari
✉ geet33n@gmail.com
Sumira Malik
✉ smalik@rnc.amity.edu
Petr Slama
✉ petr.slama@mendelu.cz

RECEIVED 30 April 2023
ACCEPTED 28 June 2023
PUBLISHED 19 July 2023

CITATION
Bhandari G, Gangola S, Dhasmana A, Rajput V, Gupta S, Malik S and Slama P (2023) Nano-biochar: recent progress, challenges, and opportunities for sustainable environmental remediation.
Front. Microbiol. 14:1214870.
doi: 10.3389/fmicb.2023.1214870

Nano-biochar: recent progress, challenges, and opportunities for sustainable environmental remediation

Geeta Bhandari[1]*, Saurabh Gangola[2], Archna Dhasmana[1], Vishal Rajput[1], Sanjay Gupta[1], Sumira Malik[3,4]* and Petr Slama[5]*

[1]Department of Biosciences, Himalayan School of Biosciences, Swami Rama Himalayan University, Dehradun, India, [2]School of Agriculture, Graphic Era Hill University, Bhimtal Campus, Uttarakhand, India, [3]Amity Institute of Biotechnology, Amity University Jharkhand, Ranchi, Jharkhand, India, [4]Guru Nanak College of Pharmaceutical Sciences, Dehradun, Uttarakhand, India, [5]Laboratory of Animal Immunology and Biotechnology, Department of Animal Morphology, Physiology and Genetics, Faculty of AgriSciences, Mendel University in Brno, Brno, Czechia

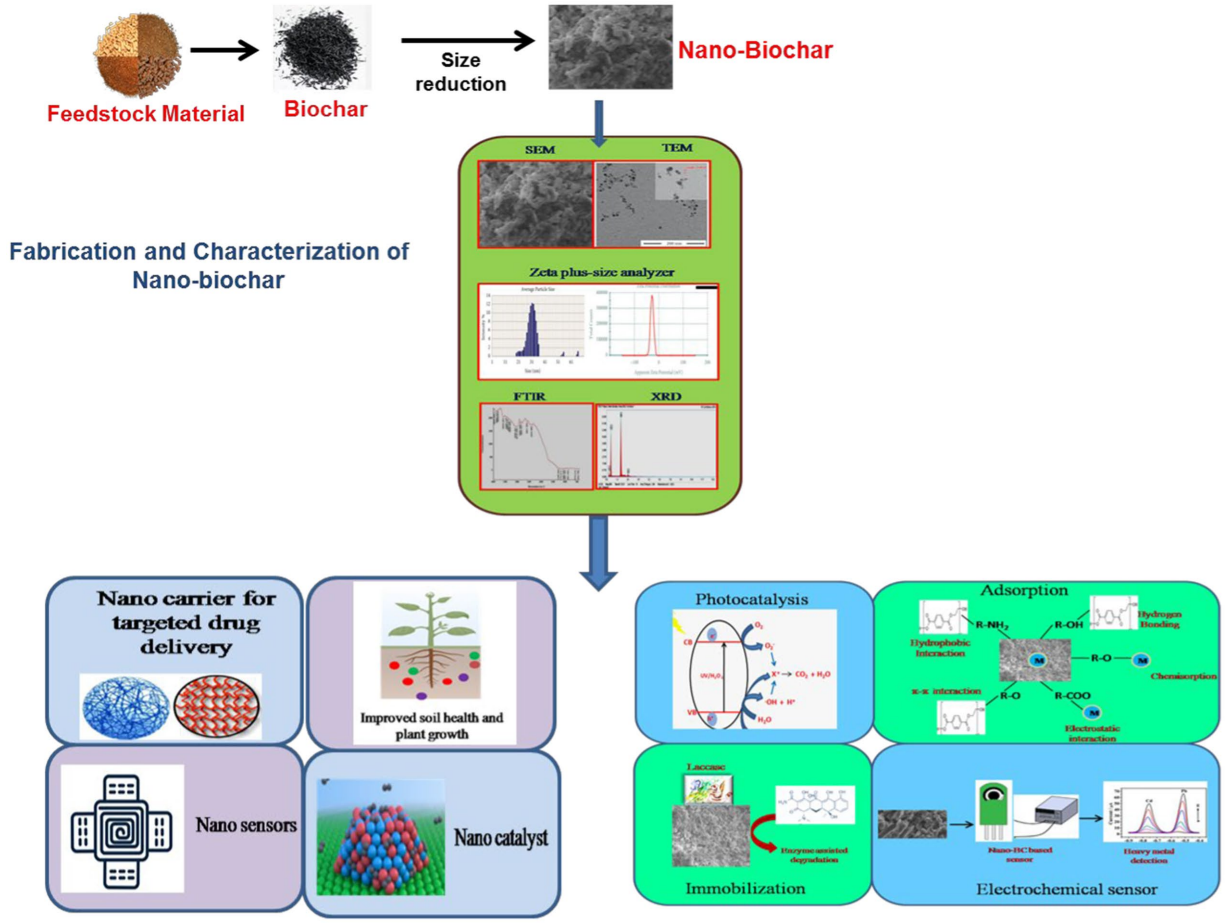
Biochar is a carbonaceous by-product of lignocellulosic biomass developed by various thermochemical processes. Biochar can be transformed into "nano-biochar" by size reduction to nano-meters level. Nano-biochar presents remarkable physico-chemical behavior in comparison to macro-biochar including; higher stability, unique nanostructure, higher catalytic ability, larger specific surface area, higher porosity, improved surface functionality, and surface active sites. Nano-biochar efficiently regulates the transport and absorption of vital micro- and macro-nutrients, in addition to toxic contaminants (heavy metals, pesticides, antibiotics). However an extensive understanding of the recent nano-biochar studies is essential for large scale implementations, including development, physico-chemical properties and targeted use. Nano-biochar toxicity on different organisms and its in-direct effect on humans is an important issue of concern and needs to be extensively evaluated for large scale applications. This review provides a detailed insight on nanobiochar research for (1) development methodologies, (2) compositions and properties, (3) characterization methods, (4) potentiality as emerging sorbent, photocatalyst, enzyme carrier for environmental application, and (5) environmental concerns.

KEYWORDS

Nano-biochar, biochar, nanotechnology, environmental pollution, remediation

1. Introduction

Extensive industrialization, urbanization, and modern agricultural methods have resulted in accumulation of innumerous toxic compounds (pesticides, pharmaceutical and personal care products, antibiotics, hormones, organic compounds, nano-compounds, endocrine disruptors, steroids, surfactants and their metabolites, industrial additives, and heavy metals) in the different environmental matrices (Bhatt et al., 2022; Gangola et al., 2022). Anthropogenic activities such as healthcare, industries, power plants, oil refineries, mining, improper waste treatment, agriculture and household activities can lead to build-up of pollutants ranging from 1 μg/kg to 10 mg/kg in the different environments (Zhou et al., 2021). Furthermore, aquatic and soil sediments also function as potent sink for innumerous hydrophobic compounds (polychlorinated biphenyl, poly-and perfluoroalkyl compounds, and organochloride insecticides) (Bhatt et al.,



GRAPHICAL ABSTRACT
Fabrication, characterization, and applications of Nano-biochar.

2022). The immoderate enhancement in the amount of such contaminants in the environment has alarmed the scientific and regulatory bodies across the globe due to acute and chronic human health toxicities. With time, various physico-chemical and biological processes such as adsorption, advanced oxidation methods, sonocatalysis, nano-filtration/reverse osmosis and bioremediation have been developed for efficient treatment of contaminated environments (Amusat et al., 2021). However, majority of these advanced methods are energy and cost extensive and release more toxic secondary by-products in the environment. The sustainable, eco-friendly nature, easy operation, and low cost of bioremediation in comparison with traditional and advanced physico-chemical methods have resulted in the establishment of bioremediation technologies recently (Bhatt et al., 2020; Suresh et al., 2022). Nonetheless, limitations such as dynamic microbial habitat fluctuation, reproducibility, cross contamination with other contaminants, and interfacial physical and biogeochemical methods in the soil-aquatic shift may render biodegradation slow and inefficient (Mukherjee et al., 2022).

Several authors have recently concentrated on the utilization of nano-compounds for the development of better remediation methods (Mahmoud et al., 2022; Rajput et al., 2022). Due to distinct physical characters of nano-materials such as excellent surface-to-volume proportion, higher reactivity, ability modify surface chemistry, smaller intra-particle diffusion distance, higher contaminant removal efficiency, stable nature and reusable and recyclable capacity, nanobiotechnology has recently received great attention for environmental applications recently (Xia et al., 2022). Biochar (BC) is a carbon containing solid compound fabricated by pyrolytic degradation of biomass (agricultural, animal and solid waste) in the absolute vacuum conditions (Bolan et al., 2022). It is generally produced using different thermochemical methods; fast and slow pyrolysis, flash and hydrothermal carbonization, gasification and torrefaction (Bolan et al., 2022; Mukherjee et al., 2022). Biochar has shown a substantial ability to remediate pollutants since it is cheap accessibility of feedstock, economical, and desirable physicochemical surface properties (Xiao et al., 2021). Among these physicochemical properties, the biodegradable nature plays a crucial role especially in agricultural activities (Širić et al., 2022). The synthesis and applications of biochar have however also faced few hurdles due to low catalysis, inadequate pore size and surface area, deficiency of simple and chemical-free functionalization processes (Li et al., 2019a).

Recently, studies on the production of nano-biochar (nano-BC) for environmental and agriculture applications has been documented (Nath et al., 2019; Li et al., 2019b; Rajput et al., 2022). Carbonization results in fabrication of micro-sized BC with size 1 µm-1 nm referred to as "dissolved" or "nano-BC." The elemental composition, aromatic/polar nature, cation exchange capacity, crystalline form, graphitic nature, pH, specific surface area, pore size, stability,

temperature-dependent dispersibility and zeta potential of nano-BC vary in comparison with bulk-BC (Ramanayaka et al., 2020a). Colloidal and nano-BC possess features such as surface hydrophobicity, nano-scale size, significantly high specific surface area, micro-porous structure, diverse surface functionality (hydroxyl, carboxy, lactonyl) and thus significantly enhance the adsorption and immobilization capability of nano-BC for different pollutants, including heavy metals, pesticides, PCBs, PAHs, and others (Nath et al., 2019; Mahmoud et al., 2022). Nano-BC assisted adsorption for the removal of toxicants from water bodies have been developed recently, which also enable for both "C" sequestration in addition to remediation (Xia et al., 2022).

Furthermore, due to high porosity, surface functionality and larger surface-to-volume ratio, nano-BC functions as an excellent immobilization material for enzymes and can thus function as a nanocatalyst in bioremediation (Naghdi et al., 2018). The chemical and physical properties of nano-BC dictate its ability to remove various pollutants, which are dependent on feedstock material, production method, pyrolysis temperature, and other pre-or post-treatment methods (Xia et al., 2022). Thus, nano-BC, with its unique features and applications, opens up new avenues for a long-term, cost-effective, and sustainable solution to environmental pollution. Therefore, the present review provides updated information on the methodologies for fabrication and characterization of nano-BC and its application for managing hazardous contaminants in the environment. Furthermore, for future research, an extensive appraisal of the potentiality of nano-BC-assisted contaminant removal is presented.

2. Production of nanobiochar

Nano-BC is a novel nano-sized carbonaceous material generally manufactured using green and energy-saving nanotechnology methods. Nano-BC differs from macrochar by of possessing higher specific surface area, higher porosity, lower hydrodynamic radius, stronger negative zeta potential, better oxygen-consisting surface functional groups, and lower carbon defects (Qin et al., 2018; Ramanayaka et al., 2020a). The most widely employed feedstocks for fabrication of nano-BC include animal wastes, municipal wastes, lignocellulosic agricultural wastes (grass, palm, peanut shell, rice husk and straw, sugar cane bagasse, bamboo, and soy bean stover), woody forest residues and sewage sludge. Initially the biomass is transformed into bulk-BC followed by size reduction through various fractionation approaches to produce nano-BC (Figure 1).

2.1. Preparation of bulk biochar

Biochar is fabricated from lignocellulosic biomass using thermo-chemical approaches such as pyrolysis (slow and fast), torrefaction, carbonization (hydrothermal or flash), and gasification (Amusat et al., 2021). The feedstock material is thermochemically or pyrolytically decomposed at 350–700°C in vacuum (<1% O_2) for the generation of BC. Slow pyrolysis is an eco-friendly process commonly employed for BC fabrication and results in high yield of bio-oil and 35% yield of dry mass (Tomczyk et al., 2020). Zhang et al. (2017) used slow pyrolytically produced BC for soil remediation and sorption of different pollutants from wastewater. For biofuel production, fast pyrolysis is favored over other processes; gasification is primarily employed for the synthesis of syngas, which subsequently produces heat and energy. Additionally, lignocellulosic material caused higher BC yield than municipal solid waste (Ashiq et al., 2019). To expedite the nano-BC production the employment of BC produced by traditional thermochemical methods is advised, while optimizing the quality of biomass materials through transforming them to nano-particles. The traditional methods produce BC with different yields and elemental constitution (C, H, O). Biomass normally becomes more carbonized as treatment intensity increases, which corresponds to an elevation in C composition but a reduction in O and H composition. Additionally, BC is modified physically and chemically for a variety of purposes to enhance its functionality. Steam coating, chemical oxidation, acidic/basic treatment, CO_2 activation, saturation with native and artificial nano-materials is used for chemically modifying BC (Song et al., 2022).

2.2. Conversion of bulk biochar to nanobiochar

Nano-BC inherently forms while synthesizing macro-BC, however its output is limited (<2.0% from peanut shell-derived BC) (Liu et al., 2018). It is thus necessary to undergo a size reduction process in order to enhance the amount of nano-BC (Table 1). The production of nanomaterials can be performed by top-down or bottom-up processes. In the top-down process, the size of the macro BC is minimized to nanoscale; whereas in the bottom-up method, the nanomaterial is amassed from the atomic level. Top–down methods such as grinding, cutting, centrifugation and etching are used for the fabrication of nano-BC in an economical manner. Lonappan et al. (2016), Dong et al. (2018), Lian et al. (2020), and Ramanayaka et al. (2020a) have employed grinders for reducing the size of macro-BC to nanoscale. The bottom up method includes disintegration by ball milling or sonication and carbonization. Ball milling enables fabrication of nano-BC with improved properties without destroying its crystal structure (Amusat et al., 2021). Ball-milling has received great attention because of its low cost and energy demand during manufacturing, eco-friendly nature and wide range of application. The ball milling method disintegrates bulk-BC into nanoscale by the colliding it between metallic balls. The desired particle size may be attained by regulating the aggregation and modifying the ball sample ratio and milling time. There are two ways to ball mill BC at the nanoscale: wet and dry techniques. The wet approach is more preferred due to synthesis of nano-BC with superior dispersivity, higher surface functionality, eco-friendly and less labor intensive approach (Yuan et al., 2020). Ball milling method effectively tailors nano-BC characteristics by enhancing surface area, decreasing material size, improving surface oxygen functionality, and increasing sorption and photocatalytic efficacy (Lyu et al., 2017, 2018; Naghdi et al., 2017; Wang et al., 2018). Nano-BC with particle size smaller than 100 nm was fabricated within 30 h using planetary ball milling method (Richard et al., 2016). Naghdi et al. (2019) suggested a pre-treatment of BC at 80°C for 24 h before conversion to nano-BC using planetary ball milling within 100 min. The pre-conditioning subdued the agglomeration of nano-particles and reduced the size of BC from 212 to 60 nm. Double-disc milling is also an alternative method for nano-BC fabrication; however it demands high operational costs. Among the different ball mill methods, vibrating disc milling produces

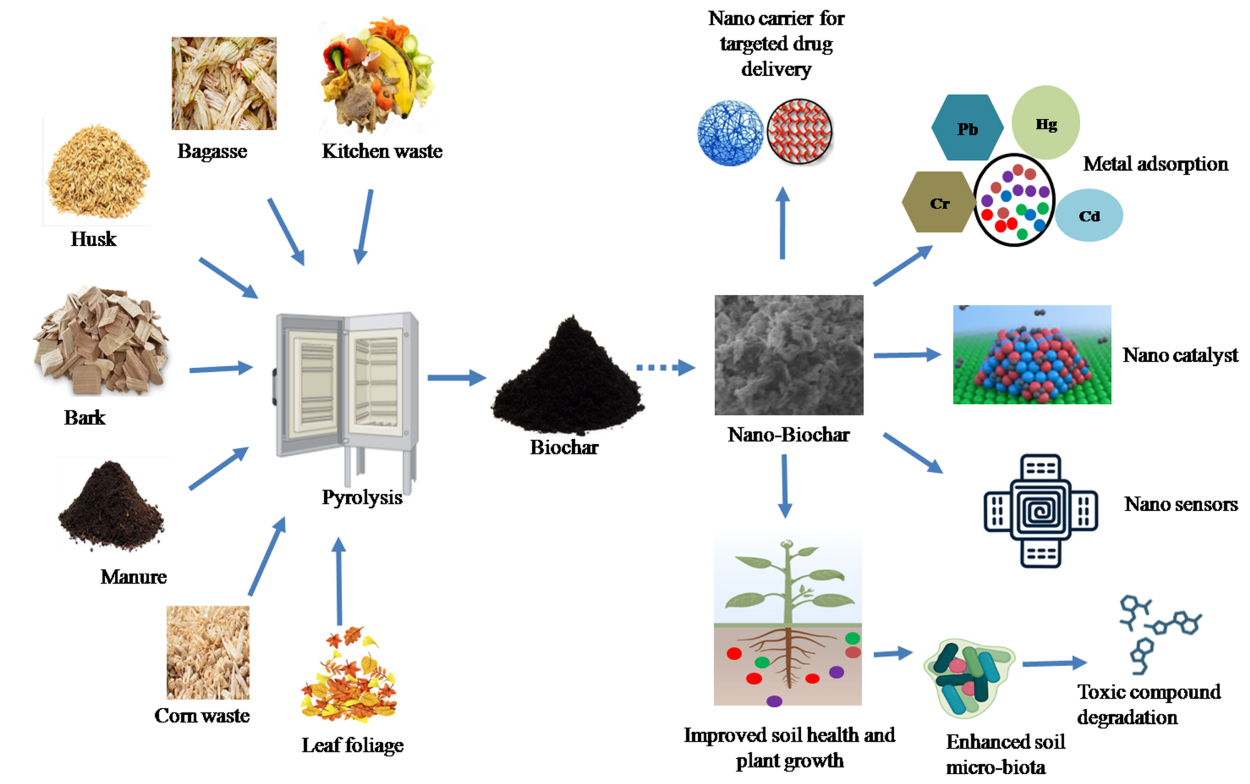


FIGURE 1
Different feedstock material for fabrication of nano-BC and its wide applications.

greater quantities of nano-BC with consistent size and shape due to attrition and shear stress (Karinkanta et al., 2018). Several studies have reported fabrication of nano-BC in a controlled environment using process parameters such as milling period of 120–1,200 min, number of balls from 25 to 800, ball weight from 0.5 to 100 g, and ball size from 3/4 to 15 mm. Ma et al. (2022) optimized the process parameters for synthesis of ball-milled nano-BC by regulating grinding time, rotating speed, and ball-to-powder mass ratio. The BC mixtures must be subsequently dispersed in different solvents post milling to improve particle distribution before separation (Song et al., 2022). The pre-treatment at 80°C however enables the reduction in size aggregation, but is a high-cost method thus restricting its scale-up. Iron oxides can be also added into BC for suppressing the agglomeration of particles and enhancing their distribution (Li et al., 2020a). Ball milling is a high atom economy method and generates nano-scale biodegradable products using renewable sources by limiting the usage of hazardous chemical-assisted procedures.

Among physical methods, sonication is an efficient method for production of nano-BC by employing high-energy ultrasonic radiations to disintegrate BC in suspension. The microporous region in BC increases due to shock waves resulting in opening of clogged pores and exfoliating the carbon structure. The small exfoliated particles then adhere to the surface or embed in the pores of BC resulting in nano-BC production (Liu et al., 2018). The uniformity in nano-BC surface and the development of porosity without obstruction are two prime benefits of sonication (Yang Y. et al., 2020). Few investigations also reported the generation of nano-BC from waste lignin carbonization as a post or pre-treatment with milling for enhancing the surface features and size of nano-BC with subsequent removal of impregnating salts (Jiang et al., 2020; Makshut et al., 2020). Guo et al. (2020) employed hydrothermal reaction for fabricating nano-BC from agricultural waste biomass. Soybean straw and animal wastes were employed as feedstock and digested with acids in a high-pressure hydrothermal reactor. Furthermore, multiple rounds of centrifugation are also employed for separating highly dispersed nano-BC particles (Ullmann et al., 2017). Different feedstock material and pyrolytic conditions, centrifugation period (2–30 min) and rotational speed (3,500–1,000 rpm) were used to prepare nano-BC (Anupama and Khare, 2021).

2.3. Functionalization of nano biochar

The intrinsic characters of nano-BC can be readily modified thus providing a platform for the easy modification for wide applicability in different sectors. Surface fictionalization using amination, sulfonation and oxidation improves the performance of BC-based nanomaterials (Nath et al., 2019). It has been observed that employment of different combination of pure and acid mixtures (H_2SO_4, HNO_3, and HCl) for surface functionalization increased carboxylic group formation with concurrent laccase adsorption (Naghdi et al., 2017). Similarly, Fe_3O_4 engineered nano-BC has a greater surface area and adsorption site owing to mesoporous structure (Nath et al., 2019). Cellulosic nanocrystal derived nano-BC was modified with ZnO and it displayed greater active sites and functioned as potent photo-catalysts for phenol removal (Zhang et al., 2021). Nano-BC obtained from artichoke leaves was base-modified with NaOH and employed for removal of metformin hydrochloride. The results revealed the existence of COOH, OH, and C=C groups and higher elimination rates of metformin by

TABLE 1 Different approaches for synthesis of nano-biochar and its wide applications.

Feedstock	Methodology	Nano-BC characteristics	Application	Performance	References
Pine wood	Planetary ball miller	Nano-BC (60 ± 20 nm)	Elimination of carbamazepine	95% removal of carbamazepine	Naghdi et al. (2019)
Rice husk	Ball milled nano-BC treated by one-pot pyrolytic method	Iron oxide permeated mesoporous nano-BC	Adsorbent for As	>90% adsorption of As	Nath et al. (2019)
Microcrystalline cellulose	*In situ* precipitation and carbonization	ZnO modified nano-BC	Photocatalyst for elimination of Phenol	99.8% removal of phenol within 90 min	Zhang et al. (2020)
Wheat straw	Ball-milled at 700°C	Magnetic nano-BC	Adsorbent for f tetracycline and Hg	Adsorption rate of 268.3 mg g^{-1}(tetracycline) and 127.4 mg g^{-1} (Hg)	Li et al. (2020a)
Soybean straw and cattle manure	Digestion of the bulk-BC in high pressure and acidic conditions in a hydrothermal reactor	BC nanodots, (4–5 nm)	–	–	Guo et al. (2020)
Wood BC (a by-product of *Gliricidia sepium* gasification)	pre-treated BC (at – 80°C for 3 days) in ethanol media was disc milled	Graphitic nano-BC (surface area of 28 m^2/g and high surface functionality)	Elimination of oxytetracycline, glyphosate, Cr (VI) and cadmium (Cd (II))	High partition coefficient in comparison to other adsorbents for the elimination of contaminants	Ramanayaka et al. (2020a)
Wood BC (a by-product of *Gliricidia sepium* gasification)	pre-treated BC (at – 80°C for 3 days) in ethanol media was disc milled	Graphitic nano-BC (surface area of 28 m^2/g and high surface functionality)	Adsorbent for Oxytetracycline	A two-step sorption with sorption rate of 16.9 and 113.2 mg g^{-1}	Ramanayaka et al. (2020b)
Oil palm	Pyrolysis-carbonization of $FeCl_3$ pre-treated biomass at 500°C and sulfonation	Sulphonated magnetic nano-BC in amorphous phase with crystallite Fe_3O_4	Acid catalyst	High catalytic activity in comparison to commercial catalysts for esterification	Jenie et al. (2020)
Waste lignin	High temperature carbonization	Nano-BC (vesicular, specific surface area of 83.41 m^2/g)	Alternative of carbon black	Renewable filler of styrene-butadiene rubber	Jiang et al. (2020)
Cynodon dactylon (L.) pers. residues	Hydrothermal and co-precipitation method	Amino-substituted silica-coated nano-BC (0 nm size, spherical shape and superparamagnetic nature)	Adsorbent for Cu^{2+} and Pb^{2+}	Adsorption rate of 220.4 mg g^{-1} (Cu^{2+}) and 180.5 mg g^{-1} (Pb^{2+})	Vishnu et al. (2021)
Wheat	Impregnation	Wheat nano-BC	Nanofertilizer	Slow release OF nitrate, phosphate, potassium and sodium	Khan et al. (2021)
Cynara scolymus L. leaves	Pyrolysis at 350°C for 1 h	Ecofriendly nano-BC	Nanoadsorbent for Cd and Sm by microwave sorption	Sorption rates of 1,150 µmol g^{-1} (Cd^{2+}) and 650 µmol g^{-1} (Sm^{3+})	Mahmoud et al. (2021)
Orange peel	Hydrothermal carbonization	Graphene based nano-BC (10–100 nm, high surface functionality, fluorescent and high water-dispersion)	Biocompatible nanocarrier	Capable of targeted cancer therapy	Iannazzo et al. (2022)
Orange peel waste derived hydrochar	Hydrothermal carbonization	Nano-BC	Electrochemical sensor	Detection of sulfites and nitrites in wastewater	Ferlazzo et al. (2023)
Goat manure	Ball miller	Nano-BC (0 nm and high surface functionality)	Nanofertilizer	Improved soil microflora, soil health, and wheat production	Rashid et al. (2023)
Cynara scolymus leaves	Gentle milling and surface modification with Amberlite cation exchanger (ACE) IR-120	Immobilized ACE nano-BC (18.74–23.70 nm)	Nanobiosorbent	Removal rates of 91.74–98.19% (Pb^{2+}) and 96.27–99.14% (methylene blue)	Mahmoud et al. (2023)

modified nano-BC in comparison with pristine nano-BC (Mahmoud et al., 2020). Ethylenediamine functionalized nano-BC was employed as an effective nano-sorbent for removing prednisolone and Cr(VI) (Mahmoud et al., 2022). The significance of magnetic nano-BC for treating tetracycline and Hg(II) polluted wastewater was assessed by Li et al. (2019b). The modified nano-BC exhibited high removal rates

(>99%) for both tetracycline and Hg(II) (Li et al., 2019b). The employment of pristine BC imposes some limitations on the adsorption efficacy for various contaminants due to low surface functionality and pore size. The surface modification of BC by different approaches improves the surface area, furnishes additional surface functional groups and adsorption sites. Thus, functionalized BC is a promising potential substitute for treating wide range of contaminants.

3. Inherent properties of nano-BC and their characterization

The intrinsic properties of nano-BC are significant in their selection for wide applications. Plant derived nano-BC have large aromatic cluster size and high oxygen surface functionality resulting in higher affinity and coordinate binding of organic pollutants and heavy metals (Figure 2). Nano-BC fabricated from municipal wastes have abundant carbonate, sulfate and aluminosilicate groups, which enable heavy metal complexation and co-precipitation (Song et al., 2019). Likewise, the degree and type of functional groups and porosity influence nano-BC efficacy as a nano-adsorbent and nano-catalyst. The graphitic and amorphous character of BC (hardness and abrasion resistance) can influence the fabrication, characters and morphological and physiological diversity of nano-BC (Anupama and Khare, 2021). Nano-BC synthesized by bulk-BC fabricated at high-temperature has a higher carbon amount, bulk density, and extractable cations such as Ca, Fe, K, Mg, Mn, P, and Zn (Nath et al., 2019). The carbon amount of nano-BC derived from coconut fibers (90–94%) was greater than that of nano-BC from sewage sludge (4%). Generally, the nano-BC has comparatively greater ash content and lower aromatic and carbonized carbon content than the macro-BC (Wang et al., 2013).

The duration and operating temperature of pyrolysis affect the properties of fabricated nano-BC. An increase in pyrolysis temperature increases nano-BC size owing to improved solid density of micro-BC, resulting in the synthesis of large particle (Zhou et al., 2017). Likewise, increasing pyrolysis duration facilitates the transformation of less dense disordered carbon to small particles that form denser mass fractal architectures (Nath et al., 2019). Nano-BC synthesized at lower temperatures (300–400°C) have smaller surface areas (5.6–47.2 m^2g^{-1}), but nano-BC synthesized at higher temperatures (450–600°C), possess higher surface area (342–430 m^2g^{-1}) due to devolatilization of biomass and generation of surface porosity (Ramanayaka et al., 2020a). The surface area of nano-BC produced by ball milling, sonication, carbonization and centrifugation were in ranges of 3.67–1736, 0.76–264, 9.08–173, and 21.7–253 m^2g^{-1}, respectively (Anupama and Khare, 2021). The zeta potential describes the charge on nano-BC surface and stabilizes the efficiency of nano-BC colloidal solution. The higher zeta potential exhibits lesser particle aggregation and increased dispersion. Nano-BC display greater zeta potential (19.4 to 87 mv) as compared to bulk-BC indicating that nano-BC possesses higher degree of dispersity and colloidal stability.

4. Application of nano-BC in environmental remediation

Biochar is recognized as a carbon-negative source since it produces energy while sequestering carbon and has emerged as a potential technology for dealing with several environmental challenges (Jiang et al., 2023). Moreover, the generation of eco-friendly energy and electrodes having enhanced properties using nano-BC is also being explored. Recently, nano-BC is being explored for diverse

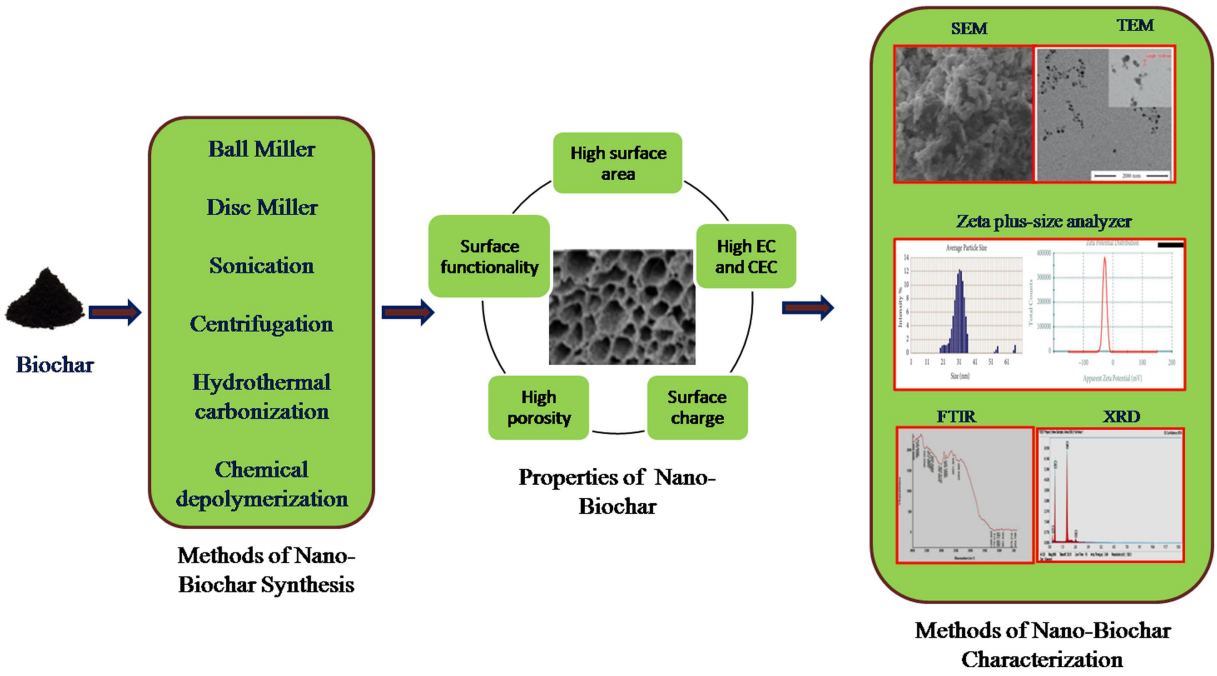


FIGURE 2
The different approaches for synthesis of nano-BC and its method of characterization.

environmental applications including carbon sequestration, energy generation and treatment of emerging contaminants (agrochemicals, pharmaceuticals, inorganic and organic compounds) from contaminated sites (Figure 3). Nano-BC functions as an excellent adsorbent and thus displays remarkable adsorption capacity for wide range of contaminants (Tables 2, 3). Furthermore, nano-BC also accelerates the breakdown of organic compounds through catalytic electronic shifts like a biocatalyst (Yang et al., 2017).

4.1. Nano-biochar as an adsorbent

Nano-BC has demonstrated exceptional adsorption capability of hazardous organic and inorganic compounds, personal care products, pharmaceutically active compounds, insecticides, and heavy metals from various environmental matrices (Ma et al., 2022; Jiang et al., 2023; Mahmoud et al., 2023). The excellent sorption ability of nano-BC is due to the generation of a stable colloidal solution, greater surface areas, porosity, and surface charge. Chemical and physical adsorption, precipitation, and ion-exchange are the three primary process described for the adsorption of inorganic pollutants on nano-BC (Amusat et al., 2021). The carboxyl, phenol and hydroxyl groups present on nano-BC surface assist in chemi-sorption of contaminants by exchanging anionic ions with cationic contaminants. Physi-sorption occurs due to electrostatic and Van der Waals interactions among the freely mobile electrons of surface aromatic functional groups of the derived nano-BC, ultimately resulting in non-covalent attraction with C=C bonds (Amusat et al., 2021). Precipitation is also considered as one of the primary processes of sorption of inorganic contaminants. It generally involves heavy metal ion precipitation onto the nano-BC surface either in solid form or in the solvent during the adsorption process. The adsorption of organic contaminants by nano-BC consists of different sorption mechanisms including; electrostatic and hydrophobic interaction, ion exchange and pore–filling (Rajput et al., 2022). Moreover physical sorption is regarded as an initial removal mechanism indicating that nano-BC may transport and subsequently desorb the toxic contaminants from aquatic environment. High temperature pyrolysis enhances the specific surface area and void structure richness of nano-BC and reduces hydrophilic surface functional groups and thus physic-sorption is the prominent mechanism for adsorption. However, the surface area of low-temperature pyrolyzed nano-BC is comparatively low and hydrophilic surface functional groups are high, suggesting chemi-sorption to be the dominant mechanism of adsorption (Jiang et al., 2023).

4.2. Nano-biochar as an adsorbent for removal of inorganic compounds

Elbehiry et al. (2022) studied the mono-and multi-sorption of metals (Cd, Cr, and Ni) on water hyacinths and black tea derived

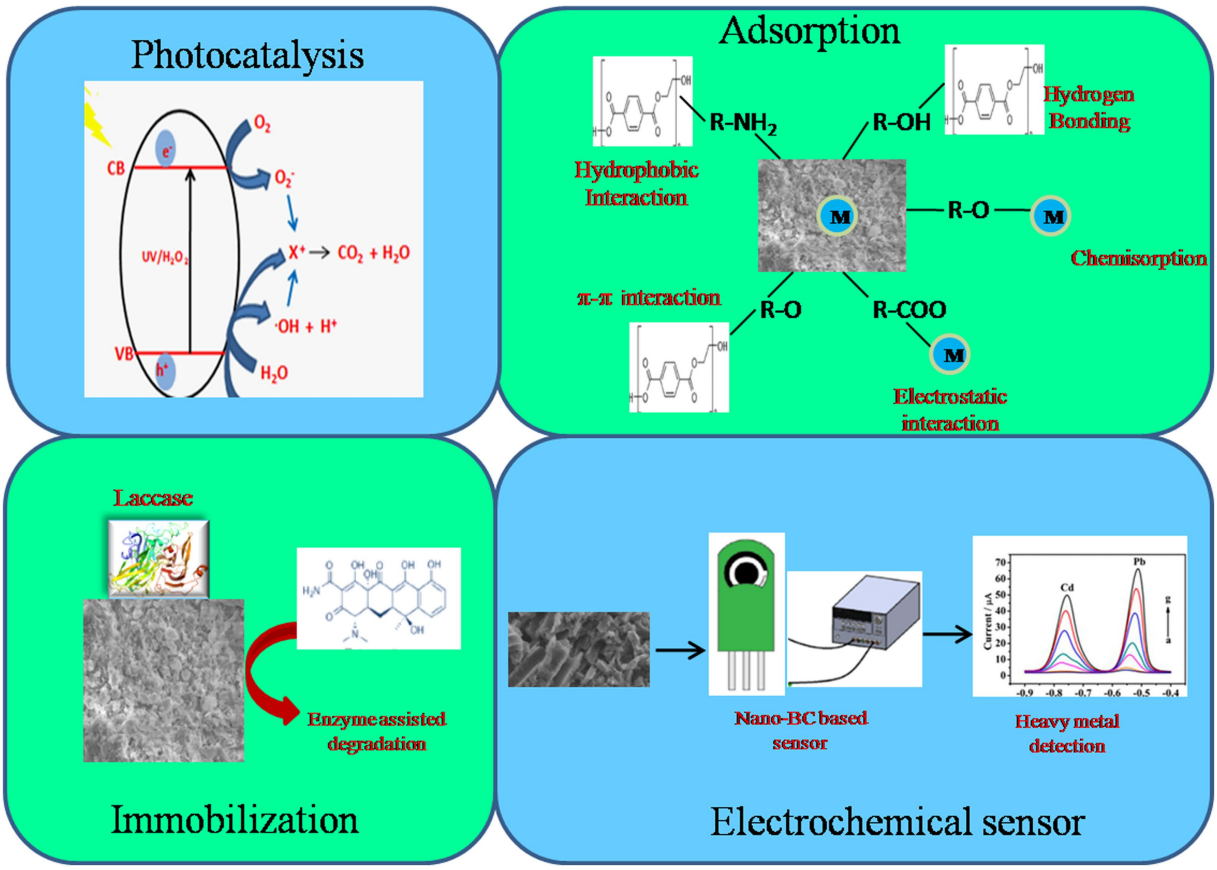


FIGURE 3
Application of nano-BC in remediation of environment pollutants and their mechanism.

TABLE 2 Applications of nano-BC for heavy metal adsorption from contaminated environments.

Nano-BC type	Contaminants	Performance	References
Nanosized rice-husk biochar	Fluoride (3–10 mg L^{-1})	90% removal within 60 min	Goswami and Kumar (2018)
Bark chips derived nano-BC	Cu^{2+}, Pb^{2+}, and Zn^{2+}	Sorption rate of 121.5, 336, and 134.6 mg g^{-1} for Cu^{2+}, Pb^{2+}, and Zn^{2+}, respectively	Arabyarmohammadi et al. (2018)
Wood chips derived nano-BC	Cu^{2+}	Adsorption rate of 22 mg g^{-1} for Cu^{2+}	Safari et al. (2019)
Rice hull derived nano-BC	Cd^{2+}	High sorption of Cd^{2+} and reduced uptake and phytotoxicity of Cd	Yue et al. (2019)
Ball milled wheat straw-Biochar	Pb^{2+}	Adsorption by ion exchange and precipitation with sorption rate of 134.68 mg g^{-1} for Pb^{2+}	Cao et al. (2019)
Rice straw and Palm leave nano-BC	NH^{4+} and H_2PO_4	Infinite adsorption capacity for NH^{4+} and H_2PO_4	Helal et al. (2019)
Nano-BC	Cd^{2+} (5–300 mgL^{-1}) Cr^{6+} (1–25 mgL^{-1})	Higher partition coefficient for the elimination of heavy metals	Ramanayaka et al. (2020a)
Hickory chips Ball-milled nano-BC	Sulfamethoxazole and Sulfapyridine	Removal rates of 83.3% (Sulfamethoxazole) and 89.6% (Sulfapyridine)	Huang et al. (2020)
CuO modified hickory wood chips ball-milled nano-BC	Reactive red dye	Adsorption rate of 1,399 mg g^{-1} for reactive red dye	Wei et al. (2020)
Rice straw nanobiochar (Nano BCs)	Antibiotic resistance genes-amp C, erm B	Adsorption of eDNA-Nano 700 (60%), Nano400 (31.3%)	Lian et al. (2020)
Pine wood nano-BC	Ni	Removal rate of 71% for Ni	Sajjadi et al. (2020)
Sludge derived nano-BC	Pb^{2+} (5 mg L^{-1})	Removal rate of 99.87% for Pb^{2+} at 0.5 g of nano-BC within 30 min	Makshut et al. (2020)
Cornstalk derived nano-BC	Cr^{6+}	Elimination rates of 49.6, 65.8, and 97.8% for Cr by Fe^0-nanobiochar composite consisting of biochar pyrolyzed at 300, 500, and 700°C respectively	Wang et al. (2020)
Ball milled woody nano-BC	Cd^{2+}	Adsorption rate of 1062.4 mg kg^{-1} for Cd^{2+}	Ramezanzadeh et al. (2021)
Ball milled phosphorus loaded Corn straw nano-BC	Cd^{2+} and Pb^{2+}	Adsorption rates of 8.7 mg g^{-1} (Cd^{2+}), 126.0 mg g^{-1} (Pb^{2+})	Zhang et al. (2022)

BC and nano-BC as a potent, economical and environmentally acceptable absorbents. The nano-BC eliminated >98.8% of Cr and Cd in mono-and competitive systems and the Freundlich isotherm model fitted most appropriately in the sorption kinetics (Elbehiry et al., 2022). The elimination of Cd(II) from an contaminated systems by nano-BC embedded in Ca-alginate beads and fabricated using ball-miller were reported (Wang et al., 2018). The improved surface functionality (oxygen-consisting groups) worked as effective sorption sites, promoting Cd(II)-calcium(II) ion exchange. The pH-dependent variations in Cd(II) sorption revealed the significance of oxygen-consisting surface groups (carboxylic, lactonic, and hydroxyl). The adsorption potential of nano-BC is determined by the surface area, humic acid, functional groups, and graphitic nature. Magnetic nano-BCs (nano zero-valent iron, iron sulfide, and iron oxide BC) display better functionality and magnetic properties that permit nano-BC recovery for recurrent usage. Improved chemical reduction, chemical precipitation, electrostatic interaction, surface complexation, ion exchange and radical activation due to synergistic effect of iron and nano-BC composites, better removal rate for wide range of pollutants are reported (Lyu et al., 2020a; Li et al., 2020b). Sisay et al. (2023) reported that Mg/Zr modified nano-BC derived from spent coffee grounds is an efficient sorbent for phosphate recovery and phosphorous release fertilizer. Furthermore, thiol-modified ball-milled BC demonstrated an improved Hg(II) elimination efficiency, with a sorption rate of 320.1 mg g^{-1}, as compared to unmilled BC (105.7 mg g^{-1}) (Lyu et al., 2020b). The amino-functional silica-coated magnetic nano-BC derived from *Cynodon dactylon* exhibited improved adsorption rates of 220.4 and 185.4 mg g^{-1} for Cu and Pb, respectively. The nano-composites also demonstrated a 15-fold reuse capability and highest elimination rates for Cu and Pb (Dhanya et al., 2022). The efficacy of ethylenediamine modified nano-BC in the elimination of Cr (VI) and prednisolone was investigated (Mahmoud et al., 2022). Electrostatic, hydrophobic and π-π interaction, ion exchange and complexation are the reported processes for Cr (VI) and prednisolone sorption onto the modified nano-BC. Similarly electrostatic interaction was involved in the elimination of anionic inorganic contaminants from aqueous systems by CuO modified nano-BC. CuO provides cationic sorption sites on surface of nano-BC for the contaminant binding and its subsequent elimination (Wei et al., 2020).

4.3. Nano-biochar as an adsorbent for treating organic compounds

Bulk-BC is the most commonly employed sorbent for treating a wide range of toxic contaminants (Yang F. et al., 2020). Nonetheless, nano-BC has an advantage above macro-BC due to larger specific

TABLE 3 Applications of nano-BC in remediation of organic pollutant contaminated environments.

Nano-BC type	Contaminants	Mode of action	Performance	References
Ball-Milled sugarcane bagasse nano-BC	Methylene blue (50 mg L^{-1})	Adsorption	Adsorption of methylene blue by π–π interaction and electrostatic attraction with sorption rate of 354 mg g^{-1}	Lyu et al. (2018)
Corn straw and rice husk derived nano-BC	Diethyl phthalate	Adsorption	Adsorption rate of 27.65–33.87 mg g^{-1} for diethyl phthalate	Ma et al. (2019)
Rice husk derived nano-BC	Toluene	Adsorption	Adsorption rate of 264 mg g^{-1} for toluene by nano-BC enriched in silicon	Shen and Zhang (2019)
Bamboo	Methylene blue	Adsorption	74% removal of methylene blue by nano-BC	Wang et al. (2019)
Chitosan-nanobiochar composite	–	Nano-biocatalyst	Encapsulated laccase retained 30% of the initial activity after 5 cycles	Naghdi et al. (2019)
Rice husk and wheat straw derived nano-BC	Galaxolide	Adsorption	Adsorption rates of 609–2,098 mg kg^{-1} for galaxolide	Zhang Q. et al. (2019)
Hickory wood	Acetone	Adsorption	Adsorption rate of 103.4 mg g^{-1} for acetone	Xiang et al. (2020)
Wheat straw derived nano-BC	Tetracycline	Adsorption	Tetracycline adsorption rate of nano-BC pyrolyzed at 700°C for was 268.3 mg g^{-1}	Li et al. (2020a,b)
Artichoke leaves derived nano-BC	Metformin hydrochloride (10 mg L^{-1})	Adsorption	Removal rates for metformin hydrochloride by modified nano-BC from tap water, wastewater and sea water was 87.0, 97.0, and 92.0%, respectively	Mahmoud et al. (2020)
Poplar woodchips derived nano-BC	Enrofloxacin	Photocatalytic degradation	Degradation rate of 80.2% for enrofloxacin by nano-BC pyrolyzed at 300°C	Xiao et al. (2020)
Date-palm derived nano-BC	Phosphate and nitrate	Adsorption	Highest monolayer sorption rates of 177.97 and 28.06 mg g^{-1} for phosphate and nitrate	Alagha et al. (2020)
ZnO modified nano-BC derived from cellulose nanocrystals	Phenol	Photocatalysis	Photocatalytic removal of 99.8% of phenol within 90 min	Zhang et al. (2021)
Wheat straw and rice husk derived nano-BC	Tetracycline	Adsorption and microbial degradation	Removal rate of 94.9–96% for tetracycline by nano-BC	Sun et al. (2022)
Amberlite cation exchanger (ACE) IR-120 modified *Cynara scolymus* derived nano-BC	Methylene blue	Adsorption	Removal rates of 96.27–99.14% for methylene blue	Mahmoud et al. (2023)
Mulberry waste derived nano-BC	Tetracycline	Adsorption	Removal rate of 103.7% for tetracycline	Yu et al. (2023)

surface area, higher negative Zeta-potential and greater surface functionality (Lian et al., 2018). Ball-milled BC displayed adsorption capabilities of 100.3 and 57.9 mg g^{-1} for removing antibiotics sulfamethoxazole and sulfapyridine, respectively (Huang et al., 2020). According to Shen et al. (2020), any changes in mechanical, physico-chemical, and morphological characters of nano-BC may improve its adsorption efficacy. Luong et al. (2020) described that the change in pH from acid to alkaline using a detergent (tween 80) can increase the sorption capacities of pinewood nano-BC by up to 63%. Xiao et al. (2020) reported that goethite modified peanut shell nano-BC exhibited intercalated hetero-structures and improved hetero-aggregation, which resulted in better adsorption rates. Few reports have employed nano-BC for efficiently removing oxytetracycline from aqueous systems (Li et al., 2020b; Ramanayaka et al., 2020b). The larger surface areas and higher oxygenic groups on nano-BC surface enabled remarkable removal of trichloroethylene with a degradation rate of 99.4% within 5 min, where nZVI-enhanced SO4• synthesis improved the degradation rate (Yan et al., 2015). The removal rate for dimethyl phthalate, diethyl phthalate, and dibutyl phthalate by BC-graphene nanosheets was substantially greater than that of bulk-BC. The aromatic groups on BC graphene nanosheets displayed π–π EDA linkages with the aromatic ring of dimethyl phthalate while hydrophobic groups are involved in dibutyl phthalate binding (Abdul et al., 2017).

The sorption of Cu(II), tylosin and sulfamethoxazole on nano-hydroxyapatite modified BC occurred due to electrostatic and π–π interaction, and hydrogen bonds (Li et al., 2020b). The occurrence of tylosin and/or sulfamethoxazole increased adsorption of Cu(II) significantly (Li et al., 2020b). Nano-BC obtained from hickory wood with specific surface area of 305 m^2 g^{-1} efficiently adsorbed various compounds (acetone, cyclohexane, chloroform, ethanol, and toluene) with an adsorption rate in the range of 23.4–103.4 mg/g (Xiang et al., 2020). The volatile organic compounds easily diffuse through the pores of nano-BC to reach the interior during sorption, reaching equilibrium after about 1 h. The physico-chemical, morphological and mechanical characters of nano-BC such as pore size, specific surface area, BC composition and contaminant characters are the most important factors in surface sorption (Xiang et al., 2020). The volatile

polar organic compounds (acetone, ethanol, and chloroform) are sorbed onto nano-BC by dipole–dipole interaction and hydrogen bonds. The sorption of weakly polar volatile organic compounds exhibited more heterogeneity than the sorption of polar compounds. Furthermore, due to stronger intermolecular forces, organic contaminants with high boiling points (ethanol, cyclohexane, and toluene) were efficiently sorbed by nano-BC. Thus, the sorption of volatile contaminants by ball-milled nano-BC is a highly potent alternative for removal of air pollutants and warranting detailed research into the mechanisms and critical factors (Anupama and Khare, 2021).

4.4. Nano-biochar as an immobilization material for enzymes/biocatalysts

Nano-BC can be utilized as an enzyme/microbe/biocatalyst carrier material for achieving continued breakdown of contaminants due to its high mobility and tunable surface chemistry (Table 4). Enzymatic catalysis is a sustainable process for degradation of pollutants and thus laccases immobilized nano-BC is being extensively employed for biodegradation of different contaminants. Oxygen functionalized nano-BC supported Lacasse was utilized for treating carbamazepine contamination (Naghdi et al., 2017). The acidic treatment introduced hydroxyl groups, with its subsequent oxidation to carboxyl groups. The degradation rates of >80% for carbamazepine with recyclability for 3 cycles at a comparative removal efficacy were reported (Naghdi et al., 2017). The immobilization process can be improved by addition of cross-linking compounds such as carbodiimide hydrochloride or glutaraldehyde (Naghdi et al., 2018). Naghdi et al. (2019) recently described a hydrogel technique for encapsulating laccase on nano-BC and chitosan. They reported that adding laccase onto nano-BC significantly improved its thermostability (4–70°C) during storage. Lonappan et al. (2018) used laccase immobilized nano-BC to completely remove (100%) diclofenac (2.5 mg L^{-1}) in 2 h, which was faster than laccase immobilized carbon nanotube (6 h), and 40% of the efficacy was retained post 5 cycles. More recently, laccase immobilized onto magnetic nano-BC was fabricated and employed for elimination of bisphenol A from aqueous environment (Zhang et al., 2020). The complete elimination of bisphenol A (25 mg L^{-1}) was reported within 75 min and 85% efficacy of the composite remained after 7 cycles. Cold-active toluene/*o*-xylene monooxygenase and catechol 1,2-dioxygenase were immobilized onto micro/nano-BC or chitosan and employed for petroleum hydrocarbon degradation (Miri et al., 2021). The results suggested that immobilization improved the storage stability of the enzymes (>50% recyclability after 1 month at 4°C) and degradative ability (>80% degradation of BTEX).

4.5. Nanobiochar as photocatalyst

In recent times nano-BC supported photocatalysts have been fabricated through different methods to photo-catalytically breakdown water pollutants (phenolics, dyes, pharmaceutically active components, antibiotics). The photocatalysis is dependent on the methods of nano-BC synthesis. BC is an excellent support for photocatalysts owing to its tunable functional groups, chemo-stability, and electrical conductance. BC as a photocatalytic support reduces e−/h + recombination and thus displays increased catalytic efficiency (Ahmaruzzaman, 2021). Recently, the nano-BC/ZnO photocatalyst derived from carbon/ZnO nanocomposite were employed for photocatalytic breakdown of phenol (Zhang et al., 2020). *In-situ* precipitation and carbonization were used to create the photocatalyst, with carbon nano-composites serving as both the template and the carbon source. These composites demonstrated remarkable stability and durability with photodegradation rate of 95% suggesting that the integration of carbon nano-composites could efficiently reduce the photo-corrosion of ZnO (Zhang et al., 2020). The BC caused a reduction in the band gap of ZnO through continuous electron/hole separation and transport, increasing phenol degradation rates. A unique core-shell P-laden BC/ZnO/g-C3N4 nano-composite was recently reported as an excellent catalyst for atrazine breakdown and a potential regulated-release nanofertilizer for enhancing P utilization rates (An et al., 2022). The results revealed the formation of a Z-shaped heterojunction between ZnO and g-C_3N_4 in Pbi-ZnO-g-C_3N_4. The authors suggested that BC functions as an electron-transfer agent promoting the disjunction of electron–hole pairs. Highest atrazine photodegradation rates of 85.3% within 260 min were reported (An et al., 2022).

4.6. Nano-biochar used in electrochemical biosensor

The electrochemical characteristics of nano-BC have recently received attention for its potential application as an alternative to carbon electrodes. The high adsorption capacity of nano-BC enables selective entrapment of chemicals to improve their concentration on electrode surface thus increasing the sensitiveness of electrochemical biosensors for detection (Table 4). The water-dispersible nature of nano-BC allows its use in film-forming methods for creating film electrodes with potent electrochemical applications (Plácido et al., 2019). In supercapacitors also, the electrode materials have recently been substituted with nano-BC due to its both meso and microporous structures having higher specific surface area resulting in improved performance. Biochar is also being used to replace cathode materials in batteries. Water dispersible nano-BC has been successfully used as an electrode material for Pb(II) and Cd(II) voltammetric sensors (Liu et al., 2016; Li et al., 2017). Li et al. (2017) investigated the impact of loading a hybrid of both bulk and nano-BC on the electrodes of a voltammetric sensor for detection of Pb^{2+}, and increased sensitivity and electric current (3.24–4.0 and 4.5 μA) were reported. Moreover, fluorescence assay confirmed that BC releases dissolved organic matter containing fluorescent humic compounds (Hernandez-Soriano et al., 2016). The fluorescent characters of nano-BC have also been exploited for development of fluorescent detectors for metals (Plácido et al., 2019). Nano-BC fabricated from sorghum and rice straw and dairy manure was utilized as a probe for heavy metal detection and the results revealed a 100, 66, 66, and 33% accuracy for Pb^{2+}, Ni^{2+}, Cu^{2+}, and Hg^{2+} detection, respectively, (Plácido et al., 2019). This was the initial report to suggest the application of nano-BC quenching data as a simple and accurate method for detection of toxic metal ions.

TABLE 4 Recent studies on application of nano-biochar and biochar based nano-composites.

Nano-composite	Application	Outcomes	References
Ball-milled wheat straw nano-BC	Adsorbent for removal of Cd^{2+}	Nano-BC acted as double-edged sword for Cd^{2+} adsorption on zeolite	Cao et al. (2023)
Ball-milled bone nano-BC	Adsorbent for removal of Cu^{2+}, Pb^{2+}, Cd^{2+} Mn^{2+}	Reduction in heavy metal bioavailability and improved N and P soil fertility	Xiao et al. (2023)
Ball-milled corn stalk nano-BC	Adsorbent for removal of Cd^{2+}	Adsorption by Precipitation and complexation; threefold enhanced adsorption of cadmium in comparison to bulk BC	Ma et al. (2022)
Metal oxides coated biochar nanocomposites	Adsorbent for removal of textile dyes in constructed wetlands	Significant removal of Reactive Golden Yellow Merl dye	Munir et al. (2023)
$CoFe_2O_4$-BC Nano-composite	Adsorbent for removal of Methylparaben	Adsorption rate of 85.6% for methylparaben; Vander Waals forces, H-bonding, and dipole interaction involved in adsorption	Fito and Nkambule (2023)
Zero-valent iron supported BC	Adsorbent for removal of Organochlorine pesticide	Removal efficiency up to 92%	Batool et al. (2022)
Ag/biochar nano-composites	Catalytic degradation of p-nitrophenol	98% degradation of p-nitrophenol to p-aminophenol	Behera et al. (2022)
Sugarcane pressmud nano-BC	Plant growth promotion in Cr contaminated soil	Reduced Cr toxicity and improved plant (black cumin) growth	Ramzan et al. (2023)
Ball milled BC	Electrochemical sensor for monitoring of Pb^{2+} and Cd^{2+}	Detection limit: 5.86 Fm, 0.883 aM for Pb^{2+} and Cd^{2+} respectively	Mao et al. (2022)
Ag–Cu/biochar	Removal of doxycycline	Removal rate of 81% after 6 repeated cycles	Hosny et al. (2022)
Copper/egg shell BC nano-composite	Electrochemical sensor for detection of nitrite	Broader linear range, detection limit:0.63 μM, and high sensitivity	Cao et al. (2020)
Nano-BC particle	Electrochemical immunosensor for detection of microcystin-LR toxin in water	Response time ≈ 5 min, detection limit: 17 pM	Yao et al. (2021)
ZnO BC nano-composite	Electrochemical sensor for detection of bisphenol A	Detection limit: 1×10^{-7} mol/L, detection sensitivity: 92 mA/M.	Hu et al. (2022)
BC nano-composites	Electrochemical sensor for detection of 17β-estradiol	Detection limit:11.30 nM	Dong et al. (2018)
Nano-BC and Bioinoculant	Mitigation of antibiotic resistance genes (ARG) in Cu contaminated soil	Impeded transport of ARGs in plant, reduced bioavailability of Cu, Improved plant growth	Duan et al. (2023)
Corn cob nano-BC	Laccase immobilization	Immobilization rate: 99.60% and activity: 22.54 U mg^{-1}	Borges et al. (2023)

Furthermore, functionalized magnetic baggase nano-BC was fabricated by combining carboxyl groups and enzymes for bisphenol A monitoring in aqueous systems, demonstrating high sensitiveness as well as excellent electrochemical activity. Dong et al. (2018) studied the possibility of loading nano-BC on glass carbon electrodes for 17-estradiol monitoring and the electric current increased from 0 to 1.5 μA at the 17-estradiol amount of 3 M. The transfer resistance was lowered from 495 to 325 Ω on loading electrodes with nano-BC fabricated at 800°C in comparison with pristine BC resulting in increased electrode conductance. Ball-milled BC modified carbon electrodes displayed remarkable electrochemical characters and electrocatalysis as indicated by conductance, peak-to-peak disjunction, resistivity, and charge transfer resistance (Lyu et al., 2019). He et al. (2020) employed tyrosinase immobilized magnetic nano-BC for detection of bisphenol A. The developed electrochemical biosensor demonstrated a monitoring range of 2.78 nM with a linear range of 0.01–1.01 M, and the sensitivity remained consistent after 8 cycles without signal reduction. The use of nano-BC in electrochemistry can be expanded into new fields such as biomass electrocatalysis, fuel cells, and CO_2 reduction. A novel electrochemical biosensor for detection of lead and cadmium was synthesized by fabricating a high conductance and contaminant specific electrode. Ball milled BC was employed as the conductive material having large conductance, oxygen rich functionality and pores of ion-imprinted polymer functioned as target interacting sites (Mao et al., 2022). The ion imprinted bulk-BC electrode was created by *in situ* electro-polymerization of L-Cysteine and template metal ions on glassy carbon-modified bulk-BC, followed by template removal. The electrode detected very low concentrations of lead and cadmium using anodic dissolved differential pulse voltammetry. The monitoring range of 5.86 fM and 0.883 aM, and linear ranges of 25 fM ~ 1 μM and 0.1 fM ~ 1 μM, respectively were reported. The electrodes displayed no interaction with other ionic and organic molecules, and could be recycled for 7 cycles without losing detection sensitivity (Mao et al., 2022). Ferlazzo et al. (2023) described an electrochemical biosensor fabricated by nano-BC for the detecting nitrites and sulfites in contaminated water bodies. The nano-BC was placed on a commercial screen-printed carbon electrode (SPCE). The fabricated sensor outperformed the normal

SPCE sensor in terms of detection limits and electrochemical oxidization of sulfites and nitrites in water (Ferlazzo et al., 2023).

5. Factors affecting performance of nano-BC for environmental remediation

The biogeochemical nature of nano-BC during contaminant elimination is influenced by a variety of physico-chemical parameters (Table 5). Nano-BC possessing high cationic surface groups allows improved ion exchange capacity of nano-BC with toxic metal ions. A higher concentration of aromatic groups on surface of nano-BC results in better π-π-interactions with organic contaminants (Jiang et al., 2023). The aggregation capability, suspension stability, and electrokinetic characters of nano-BC impact the sorption of contaminants that may be determined by the zeta potential (Filipinas et al., 2021). The surface functionality is also dependent on pyrolysis temperature used for BC synthesis and low pyrolytic temperature was found to have abundant surface functional groups, higher zeta potential and stronger colloidal stability (Xu et al., 2020). In case of metal ions, the valency, hydration area, electronegative nature and hydrolytic constant are the dominant parameters that influence the metal ion removal by nano-BC. Zhang et al. (2022) reported that the sorption rate of nano-BC for Pb^{2+} was significantly higher than that for Cd^{2+} in same treatment conditions. The authors suggested that variation in metal characteristics (hydration area, hydrolytic constant) and their affinity for binding sites are responsible for different sorption rates. For organic contaminants, groups such as polar, hydrophobic, aromatic, and molecular weight of the contaminant affect their interaction with nano-BC. In general, the sorption of highly hydrophobic compounds by carbonaceous compounds is slow (Choi et al., 2014). Galaxolide is a highly hydrophobic contaminant and therefore shows high sorption to ball milled nano-BC (Zhang Q. et al., 2019). Moreover, high molecular weight contaminants are hardly sorbed by nano-BC due to size exclusion and pore filling effect resulting in restriction of these compounds from entering small pores on nano-BC (Zhu et al., 2022). Nano-BC assisted remediation of contaminants is also influenced by environmental parameters including: pH, soil microbes, dissolved organic matter, root exudates and coexisting contaminants (Jiang et al., 2023). In lower pH environments, the surface functional groups of nano-BC get protonated to generate H^+. This causes competition between H^+ and cationic contaminants for sorption sites thus affecting nano-BC's sorption capability (Mahmoud et al., 2023). Wang et al. (2017) reported that co-existence of lead and p-nitrophenol improved the sorption of p-nitrophenol on nano-BC. In soil systems, carbon of nano-BC may functions as a source of nutrition to soil microbes, thus improving their metabolism and contaminant degradation

TABLE 5 Factors affecting the performance of nano-biochar for environmental applications.

Parameter	Impact on environmental application of nano-BC	References
Nano-BC synthesis method		
Ball milling	Fabricated Nano-BC has high specific surface area, pore volume	Anupama and Khare (2021)
Sonication	Better purity and uniform shape of nano-BC	
Centrifugation	High stability nano-BC colloids	
Chemical methods	Higher surface functionality of nano-BC	
Nano-BC properties		
Pyrolysis temperature	High pyrolysis temperature increases specific surface area of BC thus increasing adsorptive capacity	Liu et al. (2018) and Lyu et al. (2018)
	Increase in pyrolysis temperature decreases surface functionality and thus reduces adsorptive capacity	Xu et al. (2020)
	Increase in pyrolysis temperature increases the ash and carbon content of nano-BC	Jiang et al. (2023)
Zeta potential	Zeta potential of nano-BC < micro/macro-BC	Song et al. (2019)
Raw material	Hemicellulosic biomass> lignin results in higher specific surface area of nano-BC	Jiang et al. (2023)
Surface functionality	High cationic groups increase ion exchange capability with metal ions; more aromatic groups allow π–π interactions among nano-BC and organic contaminants	Jiang et al. (2023)
Pollutant characteristics		
Heavy metal	High hydration radius and hydrolysis constant of metal ion reduce their adsorption onto nano-BC; high electronegativity of metal ion result in better binding capacity onto nano-BC	Ni et al. (2019) and Zhang et al. (2022)
Organic contaminant	Highly polar organic contaminant readily adsorb onto nano-BC; more hydrophobic group lowers adsorption; large molecules are less readily adsorbed by nano-BC	Zhuang et al. (2021) and Zhu et al. (2022)
Environmental factors		
pH	Acidic pH reduces adsorptive capacity of nano-BC	Mahmoud et al. (2020)
Extracellular secretions by microbes	Extracellular polymers of microbes block the pores of nano-BC and thus reduce adsorption rate	Zhang et al. (2020)
Root exudates	Oxalic acid increase adsorption of phenanthrene by BC	Li et al. (2019)

efficacy (Mukherjee et al., 2022). The root exudates released from plant in contaminated soils can also impact the physical and chemical characteristics of nano-BC thus influencing its contaminant sorption ability (Li et al., 2019).

6. Challenges and environmental concern of N-BC

Nano-BC and colloidal BC possess high surface area, pore size, and surface functionality thus demonstrating remarkable contaminant removal efficiency as compared to pristine BC (Ramanayaka et al., 2020b). However there are several constraints to using native nano-BC in environmental applications including low yield and stability, easy mobilization, high agglomeration, uptake, accumulation, toxic nature and limitations in recovery (Liu et al., 2018). Functionalizing nano-BC with appropriate redox functional groups promotes its stability/suitability for contaminant removal in different environmental matrices but these studies are still in infancy and broad understanding is still necessary for on-site application. The inter-linkages among BC structure, oxygenic surface functional groups, feedstock types and pyrolytic parameters must be assessed for postulating molecular mechanisms of contaminant removal by electrochemical reaction pathways (Amusat et al., 2021). The technologies for large-scale fabrication of nano-BC need to be developed for achieving high yield of nano-BC for wide applications. The green and biogenic methods for fabricating nano-BC need to be investigated for reducing the risk of cross-contamination of chemicals used for synthesis during wastewater treatment. Nano-BC showed improved results when compared to the bulk-BC, however, the comparative performance to other nanomaterials and carbon based nanocompounds should be investigated further (Rajput et al., 2022). The economical assessment of the expenses is critical in evaluating the manufacture and deployment of the nano-BC for wide application. The lack of data on large level synthesis and employment of nano-BC makes estimating the economic aspect of nano-BC difficult. Furthermore, the utilization of wide range of raw feedstock material and different factors and processes for the fabrication of bulk-BC and the lack of standard procedures limit the cost analysis of nano-BC synthesis. The higher adsorption of contaminants and transportability of nano-BC, can cause the risk of cross-contamination of different ecosystems. High dispersion of nano–BC in natural aquatic systems can further expose different organisms to nanoparticle-associated risks (Freixa et al., 2018). The examination of toxic impact on respiratory system indicated a lower risk to human health (Dong et al., 2019). A very limited number of reports suggested the toxic impact of nano-BC and nanocarbon compounds on plant, mammals and soil microflora, thus in spite of their numerous benefits, the eco-toxicity must be investigated (Zhang K. et al., 2019; Rajput et al., 2022).

7. Conclusion

Nano-BC is an emerging and potential alternative to carbon-based nanomaterials for wide applicability in comparison to the pristine and bulk-BC. Nano-BC exhibits exceptional physicochemical characters such as high surface functionality and ease of surface modification. It is generally manufactured using ball miller, ultra-sonication, carbonization, centrifugation, and manual grinders. Ball milling is an economical, sustainable and green method, while ultrasonication is more energy-intensive and non-eco-friendly. Nonetheless, process optimization, eco-toxicity, and life cycle evaluation of nano-BC fabrication is necessary for individual process prior to its selection for commercial-scale synthesis. The distinctly minute size of nano-BC offers improved surface areas imparting it with the potential of applicability in environmental remediation. Nano-BC efficiently reduced toxic organic and inorganic pollutants from different environmental matrices as compared to bulk-BC. Nano-BC functions as detoxicant, playing vital part in waste management, reduction of soil erosion, and preventing nutrient loss from soil. The surface features of nano-BC allow it to function as carrier for the immobilizing enzymes, biocatalysts and microbes. Nano-BC is also a potential alternative to chemical electrode and thus functions as biosensor for detection and monitoring of toxic contaminants. Additionally the high surface area also provides habitat for microorganisms on nano-BC, thus understanding their interactions at molecular and genetic level can unfold new areas for hybrid remediation strategies, which however warrants future research. However, there is a considerable knowledge gap about the parameters of the nano-BC synthesis by different methods and their physicochemical characters. The optimization of process parameter for desirable properties (porosity, surface area and functionality and binding sites) and yield is required. Methods for rapid valorization of nano-BC and their transport and distribution into different ecosystems need to be studied for restricting the detrimental impact.

Author contributions

GB, AD, SGa, and VR: conceptualization and written the original draft. SGu, SM, and PS edited and revised the manuscript. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor PC declared a shared affiliation with the author SG at the time of review.

Publisher's note

References

Abdul, G., Zhu, X., and Chen, B. (2017). Structural characteristics of biochar–graphene nanosheet composites and their adsorption performance for phthalic acid esters. *Chem. Eng. J.* 319, 9–20. doi: 10.1016/j.cej.2017.02.074

Ahmaruzzaman, M. (2021). Biochar based nanocomposites for photocatalytic degradation of emerging organic pollutants from water and wastewater. *Mater. Res. Bull.* 140:111262. doi: 10.1016/j.materresbull.2021.111262

Alagha, O., Manzar, M. S., Zubair, M., Anil, I., and Muazu Qureshi, N. D. A. (2020). Comparative adsorptive removal of phosphate and nitrate from wastewater using biochar-MgAl LDH nanocomposites: coexisting anions effect and mechanistic studies. *Nano* 10:336. doi: 10.3390/nano10020336

Amusat, S. O., Kebede, T. G., Dube, S., and Nindi, M. M. (2021). Ball-milling synthesis of biochar and biochar–based nanocomposites and prospects for removal of emerging contaminants: a review. *J. Water Process Eng.* 41:101993. doi: 10.1016/j.jwpe.2021.101993

An, X., Wang, H., Dong, C., Jiang, P., Wu, Z., and Yu, B. (2022). Core-shell P-laden biochar/ZnO/g-C_3N_4 composite for enhanced photocatalytic degradation of atrazine and improved P slow-release performance. *J. Colloid Interface Sci.* 608, 2539–2548. doi: 10.1016/j.jcis.2021.10.166

Anupama, , and Khare, P. (2021). A comprehensive evaluation of inherent properties and applications of nano-biochar prepared from different methods and feedstocks. *J. Clean. Prod.* 320:128759. doi: 10.1016/j.jclepro.2021.128759

Arabyarmohammadi, H., Darban, A. K., Abdollahy, M., Yong, R., Ayati, B., Zirakjou, A., et al. (2018). Utilization of a novel chitosan/clay/biochar nanobiocomposite for immobilization of heavy metals in acid soil environment. *J. Polym. Environ.* 26, 2107–2119. doi: 10.1007/s10924-017-1102-6

Ashiq, A., Adassooriya, N. M., Sarkar, B., Rajapaksha, A. U., Ok, Y. S., and Vithanage, M. (2019). Municipal solid waste biochar-bentonite composite for the removal of antibiotic ciprofloxacin from aqueous media. *J. Environ. Manag.* 236, 428–435. doi: 10.1016/j.jenvman.2019.02.006

Batool, S., Shah, A. A., Bakar, A. F. A., Maah, M. J., and Bakar, N. K. A. (2022). Removal of organochlorine pesticides using zerovalent iron supported on biochar nanocomposite from *Nephelium lappaceum* (Rambutan) fruit peel waste. *Chemosphere* 289:133011. doi: 10.1016/j.chemosphere.2021.133011

Behera, M., Tiwari, N., Banerjee, S., Sheik, A. R., Kumar, M., Pal, M., et al. (2022). Ag/biochar nanocomposites demonstrate remarkable catalytic activity towards reduction of p-nitrophenol via restricted agglomeration and leaching characteristics. *Colloids Surf A Physicochem. Eng. Aspects.* 642:128616. doi: 10.1016/j.colsurfa.2022.128616

Bhatt, P., Bhandari, G., and Bilal, M. (2022). Occurrence, toxicity impacts and mitigation of emerging micropollutants in the aquatic environments: recent tendencies and perspectives. *J. Environ. Chem. Eng.* 10:107598. doi: 10.1016/j.jece.2022.107598

Bhatt, P., Gangola, S., Bhandari, G., Zhang, W., Maithani, D., Mishra, S., et al. (2020). New insights into degradation of synthetic pollutants in contaminated environment. *Chemosphere* 268:128827. doi: 10.1016/j.chemosphere.2020.128827

Bolan, N., Hoang, S. A., Beiyuan, J., Gupta, S., Hou, D., Karakoti, A., et al. (2022). Multifunctional applications of biochar beyond carbon storage. *Int. Matter. Rev.* 67, 150–200. doi: 10.1080/09506608.2021.1922047

Borges, J. F., Nascimento, P. A., Alves, A. N., Santos, M. P. F., Brito, M. J. P., Bonomo, R. C. F., et al. (2023). Laccase immobilization on activated carbon from hydrothermal carbonization of corn cob. *Waste Biomass Valor.* doi: 10.1007/s12649-023-02160-1

Cao, L., Kang, Z. W., Ding, Q., Zhang, X., Lin, H., Lin, M., et al. (2020). Rapid pyrolysis of cu^{2+}−polluted eggshell membrane into a functional Cu^{2+}-Cu^{+}/biochar for ultrasensitive electrochemical detection of nitrite in water. *Sci. Total Environ.* 723:138008. doi: 10.1016/j.scitotenv.2020.138008

Cao, X., Meng, Z., Sheng, L., Hu, X., Wang, T., Sun, X., et al. (2023). Double-edged sword effect of nano-biochar for Cd^{2+} adsorption on zeolite. *J. Environ. Chem. Eng.* 11:109901. doi: 10.1016/j.jece.2023.109901

Cao, Y., Xiao, W., Shen, G., Ji, G., Zhang, Y., Gao, C., et al. (2019). Carbonization and ball milling on the enhancement of Pb(II) adsorption by wheat straw: competitive effects of ion exchange and precipitation. *Bioresour. Technol.* 273, 70–76. doi: 10.1016/j.biortech.2018.10.065

Choi, Y. J., Cho, Y. M., and Luthy, R. G. (2014). *In situ* sequestration of hydrophobic organic contaminants in sediments under stagnant contact with activated carbon. 1. Column studies. *Environ. Sci. Technol.* 48, 1835–1842. doi: 10.1021/es403335g

Dhanya, V., Dhandapani, B., Vaishnavi, G., and Preethi, V. (2022). Synthesis of tri-metallic surface engineered nanobiochar from *Cynodon dactylon* residues in a single step - batch and column studies for the removal of copper and lead ions. *Chemosphere* 28:131572. doi: 10.1016/j.chemosphere.2021.131572

Dong, X., He, L., Liu, Y., and Piao, Y. (2018). Preparation of highly conductive biochar nanoparticles for rapid and sensitive detection of 17β-estradiol in water. *Electrochim. Acta* 292, 55–62. doi: 10.1016/j.electacta.2018.09.129

Dong, C., Lung, S., Chen, C., Lee, J., Chen, Y., Wang, W., et al. (2019). Assessment of the pulmonary toxic potential of nano-tobacco stem-pyrolyzed biochars. *Environ. Sci. Nano* 6, 1527–1535. doi: 10.1039/C8EN00968F

Duan, M., Li, Z., Yan, R., Zhou, B., Su, L., Li, M., et al. (2023). Mechanism for combined application of biochar and *Bacillus cereus* to reduce antibiotic resistance genes in copper contaminated soil and lettuce. *Sci. Total Environ.* 884:163422. doi: 10.1016/j.scitotenv.2023.163422

Elbehiry, F., Darweesh, M., Al-Anany, F. S., Khalifa, A. M., Almashad, A. A., El-Ramady, H., et al. (2022). Using biochar and Nanobiochar of water hyacinth and black tea waste in metals removal from aqueous solutions. *Sustainability* 14:10118. doi: 10.3390/su141610118

Ferlazzo, A., Bressi, V., Espro, C., Iannazzo, D., Piperopoulos, E., and Neri, G. (2023). Electrochemical determination of nitrites and sulfites by using waste-derived nanobiochar. *J. Electroana. Chem.* 928:117071. doi: 10.1016/j.jelechem.2022.117071

Filipinas, J. Q., Rivera, K. K. P., Ong, D. C., Pingul-Ong, S. M. B., Abarca, R. R. M., and de Luna, M. D. G. (2021). Removal of sodium diclofenac from aqueous solutions by rice hull biochar. *Biochar* 3, 189–200. doi: 10.1007/s42773-020-00079-7

Fito, J., and Nkambule, T. T. I. (2023). Synthesis of biochar-$CoFe_2O_4$ nanocomposite for adsorption of methylparaben from wastewater under full factorial experimental design. *Environ. Monit. Assess.* 195:241. doi: 10.1007/s10661-022-10819-w

Freixa, A., Acuña, V., Sanchís, J., Farré, M., Barceló, D., and Sabater, S. (2018). Ecotoxicological effects of carbon based nanomaterials in aquatic organisms. *Sci. Total Environ.* 619–620, 328–337. doi: 10.1016/j.scitotenv.2017.11.095

Gangola, S., Bhatt, P., Kumar, A. J., Bhandari, G., Joshi, S., Punetha, A., et al. (2022). Biotechnological tools to elucidate the mechanism of pesticide degradation in the environment. *Chemosphere* 296:133916. doi: 10.1016/j.chemosphere.2022.133916

Goswami, R., and Kumar, M. (2018). Removal of fluoride from aqueous solution using nanoscale rice husk biochar. *Groundw. Sustain. Dev.* 7, 446–451. doi: 10.1016/j.gsd.2017.12.010

Guo, F., Bao, L., Wang, H., Larson, S. L., Ballard, J. H., Knotek-Smith, H. M., et al. (2020). A simple method for the synthesis of biochar nanodots using hydrothermal reactor. *Methods X* 7:101022. doi: 10.1016/j.mex.2020.101022

He, L., Yang, Y., Kim, J., Yao, L., Dong, X., Li, T., et al. (2020). Multi-layered enzyme coating on highly conductive magnetic biochar nanoparticles for bisphenol a sensing in water. *Chem. Eng. J.* 384:123276. doi: 10.1016/j.cej.2019.123276

Helal, M. I. D., Husein, M. E., Walaa, G., and Mostafa, E. D. (2019). Characterization of agricultural residues-based nano biochar and its efficiency in adsorption/desorption of nutrients. *Int. J. Environ.* 8, 130–141,

Hernandez-Soriano, M. C., Kerré, B., Kopittke, P. M., Horemans, B., and Smolders, E. (2016). Biochar affects carbon composition and stability in soil: a combined spectroscopymicroscopy study. *Sci. Rep.* 6:25127. doi: 10.1038/srep25127

Hosny, M., Fawzy, M., and Eltaweil, A. S. (2022). Phytofabrication of bimetallic silver-copper/biochar nanocomposite for environmental and medical applications. *J. Environ. Manag.* 316:115238. doi: 10.1016/j.jenvman.2022.115238

Hu, J., Mao, D., Duan, P., Li, K., Lin, Y., Wang, X., et al. (2022). Green synthesis of ZnO/BC nanohybrid for fast and sensitive detection of bisphenol a in water. *Chemosensors* 10:163. doi: 10.3390/chemosensors10050163

Huang, J., Zimmerman, A. R., Chen, H., and Gao, B. (2020). Ball milled biochar effectively removes sulfamethoxazole and sulfapyridine antibiotics from water and wastewater. *Environ. Pollut.* 258:113809. doi: 10.1016/j.envpol.2019.113809

Iannazzo, D., Celesti, C., Espro, C., Ferlazzo, A., Giofrè, S. V., Scuderi, M., et al. (2022). Orange-peel-derived nanobiochar for targeted cancer therapy. *Pharmaceutics* 14:2249. doi: 10.3390/pharmaceutics14102249

Jenie, S. N. A., Kristiani, A., Khaerudini, D. S., and Takeishi, K. (2020). Sulfonated magnetic nanobiochar as heterogeneous acid catalyst for esterification reaction. *J. Environ. Chem. Eng.* 8:103912. doi: 10.1016/j.jece.2020.103912

Jiang, C., Bo, J., Xiao, X., Zhang, S., Wang, Z., Yan, G., et al. (2020). Converting waste lignin into nano-biochar as a renewable substitute of carbon black for reinforcing styrene-butadiene rubber. *Waste Manag.* 102, 732–742. doi: 10.1016/j.wasman.2019.11.019

Jiang, M., He, L., Niazi, N. K., Wang, H., Gustave, H., Vithanage, M., et al. (2023). Nanobiochar for the remediation of contaminated soil and water: challenges and opportunities. *Biochar* 5:2. doi: 10.1007/s42773-022-00201-x

Karinkanta, P., Ammala, A., Illikainen, M., and Niinimaki, J. (2018). Fine grinding of wood overview from wood breakage to applications. *Biomass Bioenergy* 113, 31–44. doi: 10.1016/j.biombioe.2018.03.007

Khan, H. A., Naqvi, S. R., Mehran, M. T., Khoja, A. H., Khan Niazi, M. B., Juchelková, D., et al. (2021). A performance evaluation study of nano-biochar as a potential slow-release nano-fertilizer from wheat straw residue for sustainable agriculture. *Chemosphere* 285:131382. doi: 10.1016/j.chemosphere.2021.131382

Li, R., Deng, H., Zhang, X., Wang, J. J., Awasthi, M. K., Wang, Q., et al. (2019a). High-efficiency removal of Pb (II) and humate by a CeO2-MoS2 hybrid magnetic biochar. *Bioresour. Technol.* 273, 335–340. doi: 10.1016/j.biortech.2018.10.053

Li, X., Song, Y., Bian, Y., Wang, F., Gu, C., Yang, X., et al. (2019). Effects of root exudates on the sorption of polycyclic aromatic hydrocarbons onto biochar. *Environ. Pollut. Bioavail.* 31, 156–165. doi: 10.1080/26395940.2019.1593054

Li, Z., Sun, Y., Yang, Y., Han, Y., Wang, T., Chen, J., et al. (2020a). Biochar supported nanoscale zero-valent iron as an efficient catalyst for organic degradation in groundwater. *J. Hazard. Mater.* 383:121240. doi: 10.1016/j.jhazmat.2019.121240

Li, Z., Wang, Z., Wu, X., Li, M., and Liu, X. (2020b). Competitive adsorption of tylosin, sulfamethoxazole and cu(II) on nano-hydrocyapatite modifed biochar in water. *Chemosphere* 240:124884. doi: 10.1016/j.chemosphere.2019.124884

Li, L., Zhang, L., Chen, Z., Huang, G., Liu, M., and Li, Y. (2017). Mass preparation of micro/nano-powders of biochar with water dispersibility and their potential application. *New J. Chem.* 41, 9649–9657. doi: 10.1039/C7NJ00742F

Li, R., Zhang, Y., Deng, H., Zhang, Z., Wang, J. J., and Shaheen, S. M. (2019b). Removing tetracycline and hg(II) with ball-milled magnetic nanobiochar and its potential on polluted irrigation water reclamation. *J. Haz. Mater.* 384:121095. doi: 10.1016/j.jhazmat.2019.121095

Lian, F., Yu, W., Wang, Z., and Xing, B. (2018). New insights into black carbon nanoparticle-induced dispersibility of goethite colloids and configuration-dependent sorption for phenanthrene. *Environ. Sci. Technol.* 53, 661–670. doi: 10.1021/acs.est.8b05066

Lian, F., Yu, W., Zhou, Q., Gu, S., Wang, Z., and Xing, B. (2020). Size matters: nano-biochar triggers decomposition and transformation inhibition of antibiotic resistance genes in aqueous environments. *Environ. Sci. Technol.* 54, 8821–8829. doi: 10.1021/acs.est.0c02227

Liu, G., Li, L., Zhang, K., Wang, X., Chang, J., Sheng, Y., et al. (2016). Facile preparation of water-processable biochar based on pitch pine and its electrochemical application for cadmium ion sensing. *Int. J. Electrochem. Sci.* 11, 1041–1054. doi: 10.1016/S1452-3981(23)15903-7

Liu, G., Zheng, H., Jiang, Z., Zhao, J., Wang, Z., Pan, B., et al. (2018). Formation and physicochemical characteristics of nano biochar: insight into chemical and colloidal stability. *Environ. Sci. Technol.* 52, 10369–10379. doi: 10.1021/acs.est.8b01481

Lonappan, L., Liu, Y., Rouissi, T., Pourcel, F., Brar, S. K., Verma, M., et al. (2018). Covalent immobilization of laccase on citric acid functionalized micro-biochars derived from different feedstock and removal of diclofenac. *Chem. Eng. J.* 351, 985–994. doi: 10.1016/j.cej.2018.06.157

Lonappan, L., Rouissi, T., Das, R. K., Brar, S. K., Ramirez, A. A., Verma, M., et al. (2016). Adsorption of methylene blue on biochar microparticles derived from different waste materials. *Waste Manag.* 49, 537–544. doi: 10.1016/j.wasman.2016.01.015

Luong, D. X., Bets, K. V., Algozeed, W. A., Stanford, M. G., Kittrell, C., Chen, W., et al. (2020). Gram-scale bottom-up flash graphene synthesis. *Nature* 577, 647–651. doi: 10.1038/s41586-020-1938-0

Lyu, H., Gao, B., He, F., Ding, C., Tang, J., and Crittenden, J. C. (2017). Ball-milled carbon nanomaterials for energy and environmental applications. *ACS Sustain. Chem. Eng.* 5, 9568–9585. doi: 10.1021/acssuschemeng.7b02170

Lyu, H., Gao, B., He, F., Zimmerman, A. R., Ding, C., Huang, H., et al. (2018). Effects of ball milling on the physicochemical and sorptive properties of biochar: experimental observations and governing mechanisms. *Environ. Pollut.* 233, 54–63. doi: 10.1016/j.envpol.2017.10.037

Lyu, H., Tang, J., Cui, M., Gao, B., and Shen, B. (2020b). Biochar/iron (BC/Fe) composites for soil and groundwater remediation: synthesis, applications, and mechanisms. *Chemosphere* 246:125609. doi: 10.1016/j.chemosphere.2019.125609

Lyu, H., Xia, S., Tang, J., Zhang, Y., Gao, B., and Shen, B. (2020a). Thiol-modified biochar synthesized by a facile ball-milling method for enhanced sorption of inorganic Hg2+ and organic CH3Hg+. *J. Hazard. Mater.* 384:121357. doi: 10.1016/j.jhazmat.2019.121357

Lyu, H., Yu, Z., Gao, B., He, F., Huang, J., Tang, J., et al. (2019). Ball-milled biochar for alternative carbon electrode. *Environ. Sci. Pollut. Res.* 26, 14693–14702. doi: 10.1007/s11356-019-04899-4

Ma, S., Jing, F., Sohi, S. P., and Chen, J. (2019). New insights into contrasting mechanisms for PAE adsorption on millimeter, micron-and nano-scale biochar. *Environ. Sci. Pollut. Res.* 26, 18636–18650. doi: 10.1007/s11356-019-05181-3

Ma, W., Xu, Y., Zhou, D., Wang, L., Liang, X., and Sun, Y. (2022). Development and optimization of high–performance nano–biochar for efficient removal cd in aqueous: absorption performance and interaction mechanisms. *Chem. Eng. Res. Des.* 189, 516–529. doi: 10.1016/j.cherd.2022.11.051

Mahmoud, M. E., Abou-Ali, S. A. A., and Elweshahy, S. M. T. (2021). Efficient and ultrafast removal of cd (II) and Sm (III) from water by leaves of *Cynara scolymus* derived biochar. *Mater. Res. Bull.* 141:111334. doi: 10.1016/j.materresbull.2021.111334

Mahmoud, M. E., El-Ghanam, A. M., and Saad, S. R. (2022). Sequential removal of chromium (VI) and prednisolone by nanobiochar-enriched-diamine derivative. *Biomass Conv. Bioref.* doi: 10.1007/s13399-022-02888-1

Mahmoud, M. E., El-Ghanam, A. M., Saad, S. R., and Mohamed, R. A. H. (2020). Promoted removal of metformin hydrochloride anti-diabetic drug from water by fabricated and modified nanobiochar from artichoke leaves. *Sus. Chem. Pharmacy* 18:100336. doi: 10.1016/j.scp.2020.100336

Mahmoud, S. E. M. E., Ursueguia, D., Mahmoud, M. E., Fatteh, T. M. A., and Diaz, E. (2023). Functional surface homogenization of nanobiochar with cation exchanger for improved removal performance of methylene blue and lead pollutants. *Biomass Conv. Bioref.* doi: 10.1007/s13399-023-04098-9

Makshut, N. A., Ngaini, Z., Wahi, R., Hussain, H., Mahmut, N. I., and Bahrin, N. Q. (2020). Nano-sized adsorbent from pyrolysed sago activated sludge for removal of Pb (II) from aqueous solution. *Pertanika J. Sci. Technol.* 28, 893–916,

Mao, D., Hu, J., Duan, P., Qin, C., and Piao, Y. (2022). Ultrasensitive and highly reusable electrochemical sensor with ion imprinted nanobiochar. *Sens. Actuat. B Chem.* 371:132490. doi: 10.1016/j.snb.2022.132490

Miri, S., Perez, J. A. E., Brar, S. K., Rouissi, T., and Martel, R. (2021). Sustainable production and co-immobilization of cold-active enzymes from *Pseudomonas* sp. for BTEX biodegradation. *Environ. Poll.* 285:117678. doi: 10.1016/j.envpol.2021.117678

Mukherjee, S., Sarkar, B., Aralappanavar, V. K., Mukhopadhyay, R., Basak, B. B., Srivastava, P., et al. (2022). Biochar-microorganism interactions for organic pollutant remediation: challenges and perspectives. *Environ. Poll.* 308:119609. doi: 10.1016/j.envpol.2022.119609

Munir, R., Ali, K., Naqvi, S. A. Z., Muneer, A., Bashir, M. Z., Maqsood, M. A., et al. (2023). Green metal oxides coated biochar nanocomposites preparation and its utilization in vertical flow constructed wetlands for reactive dye removal: performance and kinetics studies. *J. Contaminant Hydrol.* 256:104167. doi: 10.1016/j.jconhyd.2023.104167

Naghdi, M., Taheran, M., Brar, S. K., Kermanshahi-Pour, A., Verma, M., and Surampalli, R. Y. (2017). Immobilized laccase on oxygen functionalized nanobiochars through mineral acids treatment for removal of carbamazepine. *Sci. Total Environ.* 584–585, 393–401. doi: 10.1016/j.scitotenv.2017.01.021

Naghdi, M., Taheran, M., Brar, S. K., Kermanshahi-Pour, A., Verma, M., and Surampalli, R. Y. (2018). Pinewood nanobiochar: a unique carrier for the immobilization of crude laccase by covalent bonding. *Int. J. Biol. Macromol.* 115, 563–571. doi: 10.1016/j.ijbiomac.2018.04.105

Naghdi, M., Taheran, M., Brar, S. K., Kermanshahi-Pour, A., Verma, M., and Surampalli, R. Y. (2019). Fabrication of nanobiocatalyst using encapsulated laccase onto chitosan-nanobiochar composite. *Int. J. Biol. Macromol.* 124, 530–536. doi: 10.1016/j.ijbiomac.2018.11.234

Nath, B. K., Chaliha, C., and Kalita, E. (2019). Iron oxide permeated mesoporous rice-husk nanobiochar (IPMN) mediatedremoval of dissolved arsenic (as): chemometric modelling and adsorption dynamics. *J. Environ. Manag.* 246, 397–409. doi: 10.1016/j.jenvman.2019.06.008

Ni, B. J., Huan, Q. S., Wang, C., Ni, T. Y., Sun, J., and Wei, W. (2019). Competitive adsorption of heavy metals in aqueous solution onto biochar derived from anaerobically digested sludge. *Chemosphere* 219, 351–357. doi: 10.1016/j.chemosphere.2018.12.053

Plácido, J., Bustamante López, S., Meissner, K. E., Kelly, D. E., and Kelly, S. L. (2019). Multivariate analysis of biochar-derived carbonaceous nanomaterials for detection of heavy metal ions in aqueous systems. *Sci. Total Environ.* 688, 751–761. doi: 10.1016/j.scitotenv.2019.06.342

Qin, Y., Li, G., Gao, Y., Zhang, L., Ok, Y. S., and An, T. (2018). Persistent free radicals in carbon-based materials on transformation of refractory organic contaminants (ROCs) in water: a critical review. *Water Res.* 137, 130–143. doi: 10.1016/j.watres.2018.03.012

Rajput, V. D., Minkina, T., Ahmed, B., Singh, V. K., Mandzhieva, S., Sushkova, S., et al. (2022). Nano-biochar: a novel solution for sustainable agriculture and environmental remediation. *Environ. Res.* 210:112891. doi: 10.1016/j.envres.2022.112891

Ramanayaka, S., Kumar, M., Etampawala, T., and Vithanage, M. (2020b). Macro, colloidal and nanobiochar for oxytetracycline removal in synthetic hydrolyzed human urine. *Environ. Poll.* 267:115683. doi: 10.1016/j.envpol.2020.115683

Ramanayaka, S., Tsang, D. C. W., Hou, D., Ok, Y. S., and Vithanage, M. (2020a). Green synthesis of graphitic nanobiochar for the removal of emerging contaminants in aqueous media. *Sci. Total Environ.* 706:135725. doi: 10.1016/j.scitotenv.2019.135725

Ramezanzadeh, H., Reyhanitabar, A., Oustan, S., Mohammadi, M. H., and van der Zee, S. (2021). Enhanced sorption of cadmium by using biochar nanoparticles from ball milling in a sandy soil. *Eurasian Soil Sci.* 54, 201–211. doi: 10.1134/S1064229321020125

Ramzan, M., Zia, A., Naz, G., Shahid, M., Shah, A. A., and Farid, G. (2023). Effect of nanobiochar (nBC) on morpho-physio-biochemical responses of black cumin (*Nigella sativa* L.) in Cr-spiked soil. *Plant Physiol. Biochem.* 196, 859–867. doi: 10.1016/j.plaphy.2023.02.037

Rashid, M. I., Shah, G. A., Sadiq, M., Amin, N. U., Ali, A. M., Ondrasek, G., et al. (2023). Nanobiochar and copper oxide nanoparticles mixture synergistically increases soil nutrient availability and improves wheat production. *Plan. Theory* 12:1312. doi: 10.3390/plants12061312

Richard, S., Rajadurai, J. S., and Manikandan, V. (2016). Influence of particle size and particle loading on mechanical and dielectric properties of biochar particulate reinforced polymer nanocomposites. *Int. J. Polym. Anal. Charact.* 21, 462–477. doi: 10.1080/1023666X.2016.1168602

Safari, S., von Gunten, K., Alam, M. S., Hubmann, M., Blewett, T. A., Chi, Z., et al. (2019). Biochar colloids and their use in contaminants removal. *Biochar* 1, 151–162. doi: 10.1007/s42773-019-00014-5

Sajjadi, B., Chen, W. Y., Mattern, D. L., Hammer, N., and Dorris, A. (2020). Low-temperature acoustic-based activation of biochar for enhanced removal of heavy metals. *J. Water Process Eng.* 34:101166. doi: 10.1016/j.jwpe.2020.101166

Shen, Y., Shen, U., and Xiang, W. (2020). Role of nano-biochar in attenuating the allelopathic effect from *Imperata cylindrica* on rice seedlings. *Environ. Sci. Nano* 7, 116–126. doi: 10.1039/C9EN00828D

Shen, Y., and Zhang, N. (2019). Facile synthesis of porous carbons from silica-rich rice husk char for volatile organic compounds (VOCs) sorption. *Bioresour. Technol.* 282, 294–300. doi: 10.1016/j.biortech.2019.03.025

Širić, I., Eid, E. M., Taher, M. A., El-Morsy, M. H. E., Osman, H. E. M., Kumar, P., et al. (2022). Combined use of spent mushroom substrate biochar and PGPR improves growth, yield, and biochemical response of cauliflower (*Brassica oleracea var. botrytis*): a preliminary study on greenhouse cultivation. *Horticulturae* 8:830. doi: 10.3390/horticulturae8090830

Sisay, G. B., Atisme, T. B., Workie, Y. A., Negie, Z. W., and Mekonnen, M. L. (2023). Mg/Zr modified nanobiochar from spent coffee grounds for phosphate recovery and its application as a phosphorous release fertilizer. *Environ. Nanotechnol. Monit. Manag.* 19:100766. doi: 10.1016/j.enmm.2022.100766

Song, B., Cao, X., Gao, W., Aziz, S., Gao, S., Lam, C., et al. (2022). Preparation of nano-biochar from conventional biorefineries for high-value applications. *Renewable Sus. Energy Rev.* 157:112057. doi: 10.1016/j.rser.2021.112057

Song, B., Chen, M., Zhao, L., Qiu, H., and Cao, X. (2019). Physicochemical property and colloidal stability of micron-and nano-particle biochar derived from a variety of feedstock sources. *Sci. Total Environ.* 661, 685–695. doi: 10.1016/j.scitotenv.2019.01.193

Sun, Y., Lyu, H., Cheng, Z., Wang, Y., and Tang, J. (2022). Insight into the mechanisms of ball-milled biochar addition on soil tetracycline degradation enhancement: physicochemical properties and microbial community structure. *Chemosphere* 291:132691. doi: 10.1016/j.chemosphere.2021.132691

Suresh, R., Rajendran, S., Kumar, P. S., Dutta, K., and Vo, D. V. N. (2022). Current advances in microbial fuel cell technology toward removal of organic contaminants–a review. *Chemosphere* 287:132186. doi: 10.1016/j.chemosphere.2021.132186

Tomczyk, A., Sokołowska, Z., and Boguta, P. (2020). Biochar physicochemical properties: pyrolysis temperature and feedstock kind effects. *Rev. Environ. Sci. Biotechnol.* 19, 191–215. doi: 10.1007/s11157-020-09523-3

Ullmann, C., Babick, F., Koeber, R., and Stintz, M. (2017). Performance of analytical centrifugation for the particle size analysis of real-world materials. *Powder Technol.* 319, 261–270. doi: 10.1016/j.powtec.2017.06.057

Vishnu, D., Dhandapani, B., Vaishnavi, G., and Preethi, V. (2021). Synthesis of tri-metallic surface engineered nanobiochar from cynodon dactylon residues in a single step-batch and column studies for the removal of copper and lead ions. *Chemosphere* 286:131572. doi: 10.1016/j.chemosphere.2021.131572

Wang, H., Feng, M., Zhou, F., Huang, X., Tsang, D. C. W., and Zhang, W. (2017). Effects of atmospheric ageing under different temperatures on surface properties of sludge-derived biochar and metal/metalloid stabilization. *Chemosphere* 184, 176–184. doi: 10.1016/j.chemosphere.2017.05.175

Wang, B., Gao, B., and Wan, Y. (2018). Entrapment of ball-milled biochar in ca-alginate beads for the removal of aqueous cd (II). *J. Ind. Eng. Chem.* 61, 161–168. doi: 10.1016/j.jiec.2017.12.013

Wang, B., Gao, B., and Wan, Y. (2019). Comparative study of calcium alginate, ballmilled biochar, and their composites on aqueous methylene blue adsorption. *Environ. Sci. Pollut. Res.* 26, 11535–11541. doi: 10.1007/s11356-018-1497-1

Wang, K., Sun, Y., Tang, J., He, J., and Sun, H. (2020). Aqueous Cr(VI) removal by a novel ball milled Fe0-biochar composite: role of biochar electron transfer capacity under high pyrolysis temperature. *Chemosphere* 241:125044. doi: 10.1016/j.chemosphere.2019.125044

Wang, D., Zhang, W., Hao, X., and Zhou, D. (2013). Transport of biochar particles in saturated granular media: effects of pyrolysis temperature and particle size. *Environ. Sci. Technol.* 47, 821–828. doi: 10.1021/es303794d

Wei, X., Wang, X., Gao, B., Zou, W., and Dong, L. (2020). Facile ball-milling synthesis of CuO/biochar nanocomposites for efficient removal of reactive red 120. *ACS Omega* 5, 5748–5755. doi: 10.1021/acsomega.9b03787

Xia, C., Liang, Y., Li, X., Garalleh, H. A., Garaleh, M., Hill, J. M., et al. (2022). Remediation competence of nanoparticles amalgamated biochar (nanobiochar/nanocomposite) on pollutants: a review. *Environ. Res.* 218:114947. doi: 10.1016/j.envres.2022.114947

Xiang, W., Zhang, X., Chen, K., Fang, J., He, F., Hu, X., et al. (2020). Enhanced adsorption performance and governing mechanisms of ball-milled biochar for the removal of volatile organic compounds (VOCs). *Chem. Eng. J.* 385:123842. doi: 10.1016/j.cej.2019.123842

Xiao, J., Li, X., Cao, Y., and Chen, G. (2023). Does micro/nano biochar always good to phytoremediation? A case study from multiple metals contaminated acidic soil using Salix jiangsuensis '172'. *Carbon Res.* 2:21. doi: 10.1007/s44246-023-00053-5

Xiao, Y., Lyu, H., Tang, J., Wang, K., and Sun, H. (2020). Efects of ball milling on the photochemistry of biochar: enrofoxacin degradation and possible mechanisms. *Chem. Eng. J.* 384:123311. doi: 10.1016/j.cej.2019.123311

Xiao, Y., Raheem, A., Ding, L., Chen, W., Chen, X., Wang, F., et al. (2021). Pretreatment, modification and applications of sewage sludge-derived biochar for resource recovery-a review. *Chemosphere* 287:131969. doi: 10.1016/j.chemosphere.2021.131969

Xu, C. Y., Li, Q. R., Geng, Z. C., Hu, F. N., and Zhao, S. W. (2020). Surface properties and suspension stability of low-temperature pyrolyzed biochar nanoparticles: effects of solution chemistry and feedstock sources. *Chemosphere* 259:127510. doi: 10.1016/j.chemosphere.2020.127510

Yan, J., Han, L., Gao, W., Xue, S., and Chen, M. (2015). Biochar supported nanoscale zerovalent iron composite used as persulfate activator for removing trichloroethylene. *Bioresour. Technol.* 175, 269–274. doi: 10.1016/j.biortech.2014.10.103

Yang, J., Pignatello, J. J., Pan, B., and Xing, B. (2017). Degradation of p-nitrophenol by lignin and cellulose chars: H_2O_2-mediated reaction and direct reaction with the char. *Environ. Sci. Technol.* 51, 8972–8980. doi: 10.1021/acs.est.7b01087

Yang, F., Zhang, Q., Jian, H., Wang, C., Xing, B., Sun, H., et al. (2020). Effect of biochar-derived dissolved organic matter on adsorption of sulfamethoxazole and chloramphenicol. *J. Hazard. Mater.* 396:122598. doi: 10.1016/j.jhazmat.2020.122598

Yang, Y., Zhou, B., Hu, Z., and Lin, H. (2020). The effects of nano-biochar on maize growth in northern Shaanxi province on the loess plateau. *Appl. Ecol. Environ. Res.* 18, 2863–2877. doi: 10.15666/aeer/1802_28632877

Yao, L., He, L., Yang, Y., Zhang, Y., Liu, Z., Liang, L., et al. (2021). Nanobiochar paper based electrochemical immunosensor for fast and ultrasensitive detection of microcystin-LR. *Sci. Total Environ.* 750:141692. doi: 10.1016/j.scitotenv.2020.141692

Yu, Z., Ji, L., Zuo, Y., Zhang, F., Wei, C., Jiang, F., et al. (2023). Removal of tetracycline hydrochloride by ball-milled mulberry biochar. *Water Air Soil Pollut.* 234:211. doi: 10.1007/s11270-023-06223-w

Yuan, Y., Zhang, N., and Hu, X. (2020). Effects of wet and dry ball milling on the physicochemical properties of sawdust derived-biochar. *Instrum. Sci. Technol.* 48, 287–300. doi: 10.1080/10739149.2019.1708751

Yue, L., Lian, F., Han, Y., Bao, Q., Wang, Z., and Xing, B. (2019). The efect of biochar nanoparticles on rice plant growth and the uptake of heavy metals: implications for agronomic benefts and potential risk. *Sci. Total Environ.* 656, 9–18. doi: 10.1016/j.scitotenv.2018.11.364

Zhang, H., Chen, C., Gray, E. M., and Boyd, S. E. (2017). Effect of feedstock and pyrolysis temperature on properties of biochar governing end use efficacy. *Biomass Bioenergy* 105, 136–146. doi: 10.1016/j.biombioe.2017.06.024

Zhang, K., Mao, J., and Chen, B. (2019). Reconsideration of heterostructures of biochars: morphology, particle size, elemental composition, reactivity and toxicity. *Environ. Pollut.* 254:113017. doi: 10.1016/j.envpol.2019.113017

Zhang, Y., Piao, M., He, L., Yao, L., Piao, T., Liu, Z., et al. (2020). Immobilization of laccase on magnetically separable biochar for highly efficient removal of bisphenol a in water. *RSC Adv.* 10, 4795–4804. doi: 10.1039/C9RA08800H

Zhang, Q., Wang, J., Lyu, H., Zhao, Q., Jiang, L., and Liu, L. (2019). Ball-milled biochar for galaxolide removal: sorption performance and governing mechanisms. *Sci. Total Environ.* 659, 1537–1545. doi: 10.1016/j.scitotenv.2019.01.005

Zhang, P., Xue, B., Jiao, L., Meng, X., Zhang, L., Li, B., et al. (2022). Preparation of ballmilled phosphorus-loaded biochar and its highly efective remediation for cd-and Pb-contaminated alkaline soil. *Sci. Total Environ.* 813:152648. doi: 10.1016/j.scitotenv.2021.152648

Zhang, Y., Zhao, G., Xuan, Y., Gan, L., and Pan, M. (2021). Enhanced photocatalytic performance for phenol degradation using ZnO modified with nano-biochar derived from cellulose nanocrystals. *Cellulose* 28, 991–1009. doi: 10.1007/s10570-020-03581-0

Zhou, L., Huang, Y., Qiu, W., Sun, Z., Liu, Z., and Song, Z. (2017). Adsorption properties of nano-MnO2–biochar composites for copper in aqueous solution. *Molecules* 22:173. doi: 10.3390/molecules22010173

Zhou, Y., Qin, S., Verma, S., Sar, T., Sarsaiya, S., Ravindran, B., et al. (2021). Production and beneficial impact of biochar for environmental application: a comprehensive review. *Bioresour. Technol.* 337:125451. doi: 10.1016/j.biortech.2021.125451

Zhu, H. X., Liu, X. Y., Jiang, Y., Lin, H. D., and Yang, K. (2022). Sorption kinetics of 1,3,5-trini - trobenzene to biochars produced at various temperatures. *Biochar.* 4:32. doi: 10.1007/s42773-022-00157-y

Zhuang, Z., Wang, L., and Tang, J. (2021). Efficient removal of volatile organic com - pound by ball-milled biochars from different preparing conditions. *J. Hazard. Mater.* 406:124676. doi: 10.1016/j.jhazmat.2020.124676

frontiers | Frontiers in Microbiology

TYPE Original Research
PUBLISHED 20 July 2023
DOI 10.3389/fmicb.2023.1208591

OPEN ACCESS

EDITED BY
Shaohua Chen,
South China Agricultural University, China

REVIEWED BY
Abhijeet Shankar Kashyap,
National Bureau of Agriculturally Important Microorganisms (ICAR), India
Elsherbiny A. Elsherbiny,
Mansoura University, Egypt

*CORRESPONDENCE
Tuo Yao
✉ yaotuo@gsau.edu.cn
Guiqin Zhao
✉ zhaogq@gsau.edu.cn

RECEIVED 19 April 2023
ACCEPTED 30 June 2023
PUBLISHED 20 July 2023

CITATION
Zhang J, Yao T, Gong W, Gao Y and Zhao G (2023) Additive screening and formula optimization of microbial inhibitor having disease prevention and growth promotion effects on *Avena sativa*. *Front. Microbiol.* 14:1208591. doi: 10.3389/fmicb.2023.1208591

Additive screening and formula optimization of microbial inhibitor having disease prevention and growth promotion effects on *Avena sativa*

Jiangui Zhang[1,2], Tuo Yao[1,2]*, Wenlong Gong[1], Yamin Gao[1] and Guiqin Zhao[1,2]*

[1]College of Grassland Science, Gansu Agricultural University, Lanzhou, Gansu, China, [2]Key Laboratory of Grassland Ecosystem of Ministry of Education, Lanzhou, Gansu, China

In order to develop environment friendly microbial inhibitor that can also control disease and promote oat (*Avena sativa*) growth, the growth rate method and response surface methodology were used to screen wetting agents, preservatives and protective agents at optimal concentrations in this study. Antagonistic activity of the tested bacterium and cell-free fermentation liquid against pathogenic fungi was evaluated on potato dextrose agar (PDA) substratum plates by dual culture technique. Oxford cup method was used to measure antagonistic reaction between screened bacteria. According to each screened bacteria with 50 mL were mixed and cultured in Luria-bertani (LB) substratum. Additives of Wetting agents, UV-protectors, and preservatives were screened by single factor test on the growth concentration of screened mixed bacteria. Afterwards, the optimal additives and concentrations were screened by Box-Behnken method. The microbial inhibitor was detected according to national standards GB20287-2006 and tested on oat in a pot experiment. The results showed that: (1) Functional bacteria which including *Bacillus velezensis* and *Brevundimonas faecalis* had control effects of 50.00% to 83.29% on three pathogenic fungi, and their cell free-fermentation liquid could inhibit the growth of pathogenic fungi from 23.51% to 39.90%; (2) Tween-80 was most suitable as wetting agents for Mix biocontrol bacteria (MBB) with 1.00% mass fraction; Sorbitol was selected as UV protective agents for MBB with 0.50% mass fraction. And methyl paraben was used as a preservative for MBB, with 0.50% mass fraction; (3) The most effective adjuvant contained 14.96 mL/L Tween-80, 5.12 g/L methylparaben and 5.6 g/L sorbitol; and (4) The microbial inhibitor controlled 45.57% of oat root rot and increased plant height, root length and seedling biomass. This study provides a suitable environment for the protection of mixed biocontrol bacteria, and lays a foundation for the prevention and control of oat diseases, the promotion of growth and the improvement of quality.

KEYWORDS

mix biocontrol bacteria, additive screening, formulation optimization, *Avena sativa*, disease control, growth promotion

1. Introduction

Food security has always been a topic of concern. Unfortunately, in the past few years, pesticide pollution in the air, water, and soil and deaths caused by pesticides have been serious in various countries (Karunarathne et al., 2020). Pesticide poisoning often happens when chemical pesticides are used to control a pest, and it affects humans, wildlife, plants, and

beneficial insects (Wang et al., 2022). Therefore, a biological control strategy is an important alternative for this type of agriculture, and *Trichoderma* spp. and *Bacillus* spp. are well known as biological agents and have been applied to control root rot disease in many crops (Alamri et al., 2019). A microbial inhibitor has already applied to control root rot by seed dressing and plant spraying and to control plant diseases and plant growth promotion (O'Callaghan, 2016; Abbas et al., 2019). The problem is that most microbial agents are susceptible to ultraviolet, temperature, and sunlight (Compant et al., 2005; Kaewkham et al., 2016). The number of effective microorganisms in microbial inhibitors decreases and reduces their colonization on the crop root surface (Arora and Mishra, 2016). The reason for this problem is that, on the one hand, the biocontrol effect of the selected bacteria itself is not very high, but on the other hand, the protective effect of the adjuvant is insufficient. Therefore, it is imperative to screen bacteria with good biocontrol effect, and then through good additives, to ensure their role.

As the main components of biocontrol agents, microbial agents play important roles in the biological control of diseases. Common biocontrol bacteria include *Bacillus subtilis*, *Bacillus velezensis*, *Bacillus thuringiensis*, *Pseudomonas fluorescens*, *Trichoderma harzianum*, *Alternaria* spp., and *Streptomyces* (Duan et al., 2020; Müller and Behrendt, 2021). Microbial agents were found to have controlled 80% of root rot in ginseng in Jilin Province (Zhang et al., 2019). The application of microbial agents increases wheat yield by 7.7–24.2% (Chang et al., 2017). In Sweden, microbial agents increased the yield of wheat suffering from root rot by 26.37% (Al-Sadi, 2021). Additives can effectively protect the activities of microorganisms and improve the durability of microbial agents and even improve disease control effects (Yardin et al., 2000; Raymaekers et al., 2020). The use of a combination of lignosulfonate and polyethylene glycol additives in the formulation increased the survival of *Lysobacter capsici* cells living on grapevine leaves under field conditions by 10 times and caused a reduction of 71% in *Plasmopara viticola* attacks (Segarra et al., 2015). Common forms of additives include granules, suspension agents, water agents, and wettable powders (Shi et al., 2008; Yang et al., 2017). Additives commonly used in suspension agents are wetting agents, preservatives, and UV-protective agents (Shi et al., 2008). When 650 μL Tween-80, 164.58 mg sodium citrate, and 308.12 mg sodium lignosulfonate were added to 65 mL *Bacillus amyloliquefaciens* fermentation broth, they controlled 84.78% of apple rot (Sun C. H et al., 2017). The addition of 0.5% folic acid, 0.5% tyrosine, and 1% riboflavin in yeast reduced the mortality of ultraviolet (UV) irradiation yeast (Lahlali et al., 2011).

Cereal crops are the most important food crops, and their yield accounts for about 90%. Cereal root rot can occur during the whole growth period and reduce yield by 20–30%, even 50% in severely affected plots (Tunali et al., 2008; Gupta et al., 2017; Li et al., 2019). The main pathogens are *Bipolaris sorokiniana*, *Fusarium graminearum*, and *Fusarium equiseti* (Kazan and Gardiner, 2018; Al-Sadi, 2021). Oat is one of the eight major grain crops of cereal crops. Oat is a one-year-old cereal crop and the field incidence of oat root rot diseases is 4–15%, and the main pathogens are *F. avenaceum, F. solani, F. graminearum, Gibberella moniliformis*, and *Gibberella* acuminata (Yang et al., 2021). Root rot is mainly controlled by biological agents in central and northern America and northern Italy (Parikh and Adesemoye, 2018; Colombo et al., 2019), as well as in crop-planting areas in China (Sun, 2019). Although the effects of biological control are remarkable, some problems such as single composition, uneven distributions, poor UV resistance, and resultant pollution have also been reported (O'Brien, 2017; Brodeur et al., 2018). Thus, it is necessary to develop microbial biocontrol agents with high activity, long action time, UV protection, and uniform dispersion. Therefore, the objectives of this study are to (1) obtain biocontrol bacteria with high control effect of pathogenic fungi, (2) select the best protective agents for antagonistic bacteria, and (3) verify the effectiveness of the biocontrol agent on oat.

2. Materials and methods

2.1. Test strains and culture medium

The eight bacteria and three pathogenic fungi were provided by the laboratory of grassland microbiology, Gansu Agricultural University, China (Tables 1, 2). The tested bacteria were cultured in a Luria–Bertani (LB) medium, and the pathogenic fungi were cultured in a potato dextrose agar (PDA) medium.

2.2. Test reagents

The wetting agents consisted of Tween-20, Tween-80, and OP emulsifiers, purchased from Beijing Solarbio Technology Co. Ltd., China. The UV-protective agents were sodium alginate, sorbitol, and xanthan gum, ordered from Tianjin Tianchen Chemical Co. Ltd., China. The preservatives included methylparaben, ethylparaben, kaisong, and sodium citrate, purchased from Tianjin Guangfu Fine Chemical Co. Ltd., China. The protein peptone, yeast powder, agar, and glucose were purchased from Beijing Aobox Biotechnology Co. Ltd., China. The glucose and sodium chloride were purchased from Sinopharm Chemical Reagent Co. Ltd., China.

2.3. Screening bacteria and preparation of bacterial suspension

The antagonistic activity of the tested bacteria against pathogenic fungi was evaluated on PDA plates by the dual culture method. The tested bacteria were inoculated in a liquid LB medium at 25°C, 180 r/min for 24 h to achieve a 10^8 cfu/mL concentration. Pathogenic fungi were grown on a PDA medium at 25°C for 5 d. The mycelial disk (5 mm) was placed at the center of the PDA medium, and bacterial suspension (100 uL) was spotted at 2 cm juxtaposed from the fungal

TABLE 1 The basic information of pathogenic fungi includes name, host, location and gene sequence number.

Number	Strains	Host plant	Disease site	Gene bank sequence
PB1	*Bipolaris sorokiniana*	wheat	root	MW494590
PB6	*Fusarium avenaceum*	highland barley	root	MW494595
PB7	*Fusarium equiseti*	oat	root	MW494596

TABLE 2 The host, characteristics and references of the test bacteria.

Code	Strains	Host plant	Nitrogenase activity(C_2H_4 nmol/(mL·h))	Amount of dissolved phosphorus(mg/L)	Secreting plant hormones(mg/L)	Source
GAU24	*Bacillus velezensis*	*Polygonum viviparum*	–	–	36.57	Zhang (2019); Liu (2016)
GAU39	*Bacillus xiamenensis*	*Allium fistulosum*	28.86	362.60	1.71	Zhang (2019); Jiang et al. (2018)
GAU68	*Bacillus mycoides*	*Kobresia myosuroides*	3193.07	67.15	66.21	Liu (2016)
GAU85	*Serratia plymuthica*	*Medicago sativa*	110.45	75.22	15.30	Sun G. Z et al., 2017
GAU86	*Bacillus pumilus*	*Triticum aestivum*	–	200.02	54.36	Liu et al. (2011)
GAU88	*Brevundimonas faecalis*	*Medicago sativa*	75.34	132.60	47.25	Zhang (2019); Han et al. (2013)
GAU89	*Bacillus subtilis*	*Trifolium pratense*	497.70	103.50	10.56	Sun et al. (2015)
GAU117	*Bacillus* sp.	*Triticum aestivum*	–	202.00	–	Feng et al. (2009)

disk four times with four replicates. The plates were incubated at 28°C for 3–7 days. The percentage of growth inhibition (I) was calculated by measuring the distance between the edges of the bacterium and fungal colonies by the following calculation (Sun G. Z et al., 2017):

$$I(\%) = [(C - T) / (C - C_0] \times 100\%$$

where I represents the inhibition rate, C indicates the colony radius of the fungi in control, T is the colony semidiameter of the fungi in the dual culture, and C_0 means the radius of the test fungi agar disks.

To test the antifungal activity of the cell-free fermentation liquid (Sun G. Z et al., 2017), 2% (V/V) bacterial suspension was inoculated to the liquid LB medium and placed in a shaker at 28°C for 48 h at 180 r/min. The fermentation liquid was then centrifuged at 8000 r/min for 10 min and filtered by 0.22 μm filtration membranes. The media incorporating the filtrate at a volume fraction of 10% were inoculated with agar disks containing the tested fungi and sterile water (10% by volume, control) with three replicates and then incubated at 28°C for 3–7 days. The radius of mycelium growth of the fungi (mm) in both the treated (T) and control (C) petri dishes was measured in perpendicular directions until the fungi growth in the control dishes was almost complete. The percentage of growth inhibition (I) was calculated using the formula:

$$I(\%) = [(C - T) / (C - C_0] \times 100\%$$

where I represents the inhibition rate, C indicates the colony radius of the fungi in control, T is the colony semidiameter of the fungi in the dual culture, and C_0 means the radius of the test fungi agar disks.

The bacterium combination was screened by the Oxford cup method (Sun G. Z et al., 2017). The Oxford cup method means that the growth of bacteria in the range of the bacteriostatic concentration around the Oxford cup is inhibited, forming a transparent bacteriostatic ring. In all, 100 μL of filtrate of one bacterium and 100 μL sterile water (control) were dropped into the Oxford cup (diameter 7 mm) at the center of the solid LB agar culture containing 2% of another bacterium. The plates were observed for inhibition zone after 24 h of incubation at 28°C, and the experiment was replicated thrice (Sun G. Z et al., 2017). The selected bacterium was inoculated in 50 mL liquid LB and shaken at 180 r/min, 28°C for 72 h. Then, the fermentation of each seed strain with 50 mL was mixed in a flask containing 500 mL of liquid LB medium and shaken at 180 r/min, 28°C for 72 h, and then put in a 4-degrees refrigerator spare.

2.4. Additive selection and microbial agents making

To select different additives, a single additive was added to a flask containing 50 mL of liquid LB medium and 5 mL of mixed bacteria (Table 3), using no additive one as control, with five replicates. Then, the sealed flasks were put at 180 r/min, 28°C for 40 h, and OD_{600} was determined by an ultraviolet spectrophotometer every 4 hours to draw the growth curve of the mixed bacteria.

Based on the results of the single-additive experiment, the optimal wetting agent, UV-protection agent, preservative, and their concentration for the mixed bacteria were screened. The Box–Behnken design was used for the response surface analysis of the optimal additives and concentrations for the mixed bacteria growth (Barrera et al., 2019). The Box–Behnken central composite test was adopted using appropriate concentrations of different optimal additives as independent variables and the OD_{600} value of the mixed bacterial suspension as a response value. The quadratic regression was used to analyze the central composite test results to verify the fitting effect of the model, and the optimal combination of the concentration ratio of additives was determined.

To make the fungi inhibitor, the additives were added into a liquid LB medium containing mixed bacteria according to their best

10.3389/fmicb.2023.1208591

TABLE 3 Experimental design of different chemical additive concentration.

Auxiliary type	Chemical additives	Concentrations/ (%)				
Wetting agents	Tween-20	0.10	0.50	1.00	1.50	2.00
	Tween-80	0.10	0.50	1.00	1.50	2.00
	OP emulsifier	0.05	0.10	0.50	1.00	2.50
UV-protectors	Sodium alginate	0.10	0.50	1.00	2.50	5.00
	Xanthan gum	0.10	0.50	1.00	2.50	5.00
	Sorbitol	0.05	0.10	0.20	0.50	1.00
Preservatives	Methylparaben	0.05	0.10	0.50	1.00	1.50
	Ethylparaben	0.05	0.10	0.50	1.00	1.50
	Kathon	0.05	0.15	0.25	0.50	1.00
	Sodium citrate	0.05	0.10	0.50	1.00	1.50

combination and placed at 180 r/min at 28°C for 72 h before being stored at room temperature.

To detect the quality of the inhibitor, two sample were taken every 15 d until 90 days (Wang et al., 2021). One sample was diluted to 10^8 cfu/mL using sterile water, taken at 20 μL and coated on a solid LB medium with five replicates, and then incubated at 28°C for 48 h to count the number of living bacteria and contaminating microorganisms. The other sample was used to determine the pH. The calculation formula used is as follows:

$$\mathrm{BN}(\mathrm{cfu/mL}) = \mathrm{AN} \times \mathrm{DM} \times \mathrm{BV} / (\mathrm{SS} \times \mathrm{SA})$$

$$\mathrm{MR}(\%) = \mathrm{IC} / (\mathrm{IC} + \mathrm{LC}) \times 100\%$$

where BN represents the number of colonies, AN is the average bacteria count, DM means the dilution multiple, BV denotes the base liquid volume, SS indicates the sample volume, SA is the pipetting volume, MR means the mixed bacteria rate, IC indicates the microbial contaminant, and LC is the effective viable count.

2.5. Biocontrol efficacy evaluation of microbial inhibitor

To test the effectiveness of the fungi inhibitor, a pot experiment was conducted. Oat seeds were disinfected with 1% NaClO for 1 min, and 10 were seeded in each plastic pot (80 mm × 45 mm × 205 mm) containing farmland soils. The pots were put in an incubator (25°C/18°C, 16 h/ 8 h) for 1 w before being thinned to seven plants. The oat variety was Longyan 3, which was provided by the College of Grassland Science, Gansu Agricultural University, China.

The pathogenic fungi PB1 (*Bipolaris sorokiniana*), PB6 (*Fusarium avenaceum*), and PB7 (*Fusarium equiseti*) were scraped onto PDA plates and incubated at 25°C for 7 days; then, spores of the pathogenic fungi were dispersed into a 6 g/L carboxymethyl cellulose solution to produce a 10^7 cfu/mL spore suspension.

Two weeks after thinning, the 5 mL spore suspension and sterile water (control) were inoculated (Table 4) by the perfusion method

TABLE 4 Pot-experimental design.

Code	Control	Treatment
CK	PB (sterile water)	PB + MA (Microbial inhibitor)
T1	PB1 (*Bipolaris sorokiniana*)	PB1 + MA (*B. sorokiniana* + MA)
T6	PB6 (*Fusarium avenaceum*)	PB6 + MA (*F. avenaceum* + MA)
T7	PB7 (*Fusarium equiseti*)	PB7 + MA (*F. equiseti* + MA)

(Zheng et al., 2019). A five-milliliter microbial inhibitor (MA) was injected into each pot 7 days after inoculation. The root rot disease symptoms were recorded 21 days after the pathogenic fungi inoculation.

Six oat plants were selected for each treatment, and plant height, fresh biomass, and root length were determined. Disease was ranked according to Table 5, and disease incidence was calculated as per the following equation:

$$\mathrm{I}(\%) = \mathrm{TD} / \mathrm{TI} \times 100\%$$

$$\mathrm{DI} = \left[\sum(\mathrm{TL} \times \mathrm{RV}) / (\mathrm{TI} \times \mathrm{ML})\right] \times 100$$

$$\mathrm{CE}(\%) = (\mathrm{CI} - \mathrm{TI}) / \mathrm{CI} \times 100\%$$

where I means incidence, TD represents the total number of diseased plants, TI is the total number of plants investigated, DI denotes the disease index, TL signifies the total number of diseased plants at all levels, RV means the representative value, ML denotes the maximum disease level representation, CE represents the control effect, CI is the control disease index, and TI signifies treatment of the disease index.

2.6. Data analysis

The data of the inhibition of mycelial growth of the tested bacteria against the pathogenic fungi, the Box–Behnken central composite experiment, and the control effect of the microbial inhibitor on oat root diseases were analyzed using analysis of variance (ANOVA) for individual parameters on the basis of mean values to find out the significance at a 5% level. The standard errors of the mean and ANOVA statistics were calculated using SPSS 22.0. Design Expert was used for experimental design response surface optimization analysis, and Origin software was used for plotting.

3. Results

3.1. Effect of tested bacterium on the growth of pathogenic fungi

3.1.1. *In vitro* antifungal activity of tested bacterium and liquid cell-free fermentation

Different bacteria had different inhibition effects on pathogenic fungi growth (Figure 1). After 7-day cultivation, the antifungal activity

TABLE 5 Classification standard of root rot diseases.

Rank	Occurring degree	Representative value
1	disease-free	0
2	Disease spot accounts for 1%~5% of root surface area	1
3	Disease spot accounts for 6%~10% of root surface area	2
4	Disease spot accounts for 11%~20% of root surface area	3
5	Disease spot accounts for 21%~40% of root surface area	4
6	Disease spot accounts for 41%~60% of root surface area	5
7	Disease spot accounts for 61%~80% of root surface area	6
8	Disease spot accounts for more than 80% of root surface area	7

of the tested bacteria varied from 50.00 to 83.29%, whereas liquid cell-free fermentation showed a 8.35–39.90% inhibition rate (Table 6). Moreover, GAU88 had the highest antifungal activity on *Bipolaris sorokiniana* (83.29%) and *Fusarium avenaceum* (74.56%), while GAU68 was most effective (75.30%) on *Fusarium equiseti*. Among the eight bacteria, GAU24, GAU68, and GAU88 had better inhibitory effects on the three pathogenic fungi, while liquid cell-free fermentation of GAU24 and GAU88 also gave better performance.

3.1.2. Screening of bacterium combinations

Bacteriostatic ring was not observed after one day of bacteria in the Oxford cup, indicating a good growth. According to the result from Table 6, GAU24 and GAU88 were finally selected and tested for antagonism by the Oxford cup method, which showed no antagonism; thus, they could coexist (Figures 1D,E).

3.2. Screening of auxiliary agents for antifungal bacteria

3.2.1. Screening of the wetting agents

Wetting agents can increase the activity of mixed biocontrol bacteria (MBB). Different concentrations of Tween-20, Tween-80, and OP emulsifier had different influence on the growth activity of MBB (Figures 2A–C). MBB grew rapidly and then slowly with the prolonging culture. Tween-80 had little influence on MBB growth, while Tween-20 and OP emulsifier had strong inhibitory effects on the growth of MBB. After 12 h culture, the OD_{600} value of the OP emulsifier-treated MBB was 48.42% ($p<0.05$) lower than the control. After 24 h culture, the OD_{600} value of Tween-80-treated MBB was 5.80% higher than the control, and when its mass fraction was 1.00%, the OD_{600} value of MBB reached 1.471 (10.91% greater than the control, $p<0.05$) after 32 h culture. Therefore, Tween-80 was most suitable as a wetting agent for MBB with 1.00% mass fraction.

3.2.2. Screening of ultraviolet protective agents

Ultraviolet protection agents can reduce the ultraviolet damage of MBB and improve their activity. Different concentrations of sodium alginate, sorbitol, and xanthan gum had different effects on the growth activity of MBB (Figures 2D–F). With the increase of culture time, the growth of MBB increased and then decreased after adding sodium alginate, sorbitol, and xanthan gum. After 28 h culture, xanthan gum inhibited MBB growth, as indicated by the much lower OD_{600} value than that of the control. When the mass fraction of sorbitol was 0.50%, the MBB's OD_{600} value was higher than that of the control (1.411 vs. 1.296, $p<0.05$) after 40 h culture. Thus, sorbitol was selected as a UV-protective agent for MBB with 0.50% mass fraction.

3.2.3. Screening of preservatives

Preservatives can reduce bacterial contamination and prolong the storage time of MBB. Adding different concentrations of methylparaben, ethylparaben, Kathon, and sodium citrate had different effects on the growth of MBB (Figures 2G–J). With the increase of culture time, compared with the control, Kathon and ethylparaben inhibited MBB, and Kathon was the most effective inhibitor. However, low concentrations of methylparaben and sodium citrate promoted MBB growth. At 0.50% mass fraction of methylparaben, the OD_{600} value of MBB was 8.82% greater than that of the control ($p<0.05$). Therefore, methylparaben was used as a preservative for MBB with 0.50% mass fraction.

3.3. The ratio optimization of additives

Based on a single-factor test, a 3×3 response surface analysis experiment was conducted for the mixed biocontrol agents (Table 7). According to the Box–Behnken central composite experiment (Table 8), 750 μL Tween-80, 300 mg sorbitol, and 300 mg methylparaben were added into the mixed biocontrol bacterial suspension, and the highest OD_{600} value was 1.51. Data regression analysis was performed using the RSA program, and the regression equation models between the OD_{600} value and three influencing factors were as following:

$$Y = 1.45 + Y_1 + Y_2 + Y_3$$

$$Y_1 = 0.071A + 0.061B + 0.083C$$

$$Y_2 = -0.050AB + 0.14AC - 0.058BC$$

$$Y_3 = -0.054A^2 - 0.094B^2 - 0.19C^2$$

where A, B, and C were Tween-80, sorbitol, and methylparaben, respectively.

The regression model was significant ($p<0.0001$, Table 9). Three different types of additives had significant effects on the growth of MBB. The equation's lack fit was $0.9748>0.05$, indicating a stable model with accurate predicted value. The coefficient of determination $R^2=0.9759$, showing a good fitting degree. The influence of each additive on the OD_{600} value of MBB activity could be judged by the *F* value. The greater the F value, the greater the influence.

The response surface is a three-dimensional surface figure composed of response values and tested factors. Figure 3 shows that

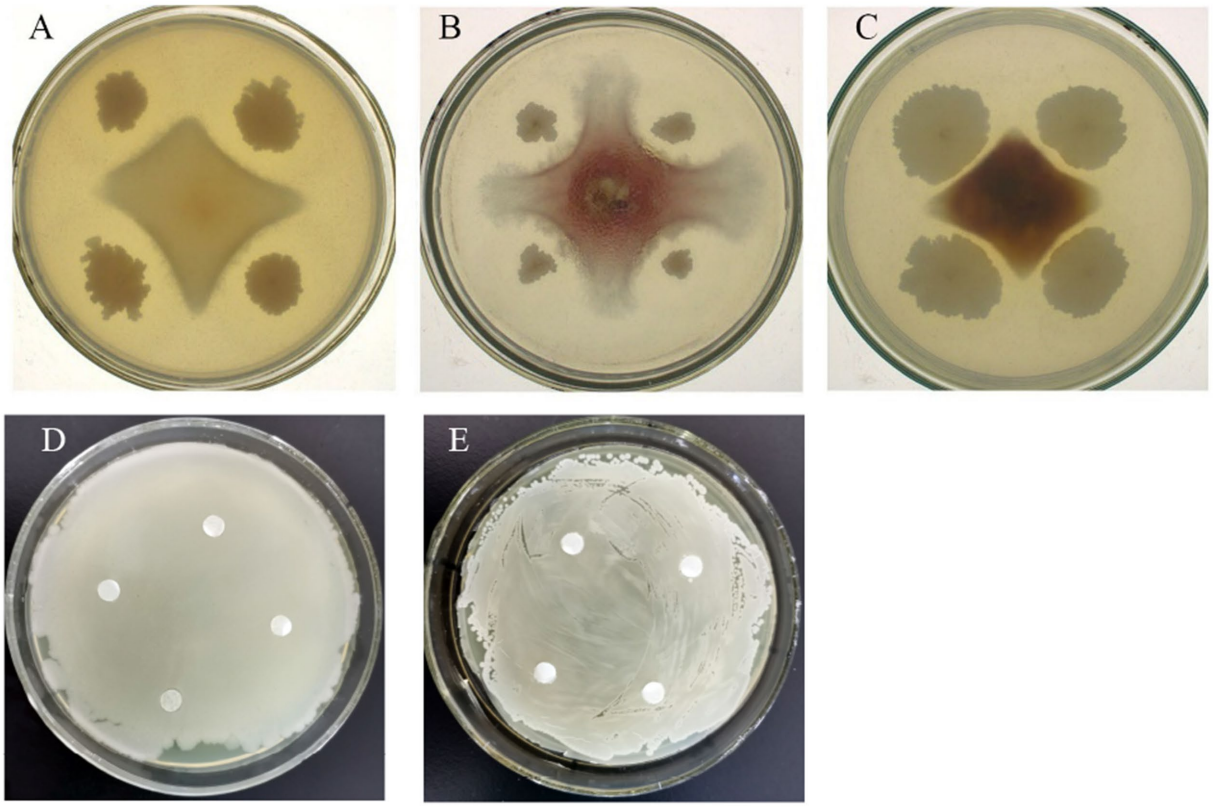


FIGURE 1
Confrontation between two strains (part). **A** represented the inhibitory effect of GAU88 (*Brevundimonas faecalis*) on *Bipolaris sorokiniana*; **B** was the inhibitory effect of GAU39 (*Bacillus xiamenensis*) on *Fusarium avenaceum*; **C** meant the inhibitory effect of GAU24 (*Bacillus velezensis*) on *Fusarium equiseti*; **D** and **E** denoted the co-growth effect of GAU24 (*B. velezensis*) on GAU88 (*B. faecalis*).

TABLE 6 Inhibition of mycelial growth of the tested bacteria against pathogenic fungi.

Strain n_O.	PB1	PB6	PB7	PB1	PB6	PB7
		m			n	
GAU24	64.15 ± 2.05c	50.00 ± 2.20d	63.48 ± 0.95 cd	34.85 ± 1.19b	25.05 ± 1.39a	26.47 ± 0.93b
GAU39	0.00 ± 0.00d	56.12 ± 2.25c	67.78 ± 1.41bc	0.00 ± 0.00c	15.13 ± 1.28b	8.35 ± 1.06d
GAU68	0.00 ± 0.00d	62.24 ± 2.01b	75.30 ± 1.18a	0.00 ± 0.00c	8.37 ± 0.49c	8.53 ± 0.80d
GAU85	0.00 ± 0.00d	0.00 ± 0.00e	62.41 ± 0.94d	0.00 ± 0.00c	0.00 ± 0.00d	22.51 ± 1.01c
GAU86	67.47 ± 1.22b	0.00 ± 0.00e	0.00 ± 0.00e	32.64 ± 1.15b	0.00 ± 0.00d	0.00 ± 0.00e
GAU88	83.29 ± 2.05a	74.56 ± 1.09a	64.55 ± 0.61bcd	39.90 ± 1.85a	23.51 ± 0.67a	31.37 ± 1.59a
GAU89	0.00 ± 0.00d	64.29 ± 1.77b	68.85 ± 1.70b	0.00 ± 0.00c	18.27 ± 1.22b	0.00 ± 0.00e
GAU117	0.00 ± 0.00d	54.08 ± 2.01c	60.24 ± 1.19d	0.00 ± 0.00c	0.00 ± 0.00d	0.00 ± 0.00e

PB1 was Bipolaris sorokiniana; PB6 meant Fusarium avenaceum; PB7 denoted Fusarium equiseti; GAU24 signified Bacillus velezensis, GAU39 was Bacillus xiamenensis, GAU68 indicated Bacillus mycoides Serratia, GAU85 signified Serratia plymuthica, GAU86 meant Bacillus pumilus, GAU88 was Brevundimonas faecalis, GAU89 was Bacillus subtilis, GAU117 represented Bacillus sp. The letter m antifungal activity of tested bacterium. The n antifungal activity of cell-free fermentation liquid. Values in the table are mean ± SE. Different letters within the same column indicate significant difference at $P < 0.05$ level by Duncan's test.

Tween-80 and methylparaben had the strongest interaction. The Design-Expert 10 software gave the optimal combination formula, i.e., 14.96 mL/L Tween-80, 5.60 g/L sorbitol, and 5.12 g/L methylparaben, under which the OD_{600} value of MBB was 1.53, very close to the result shown in Table 8 (1.51 OD_{600} value), thus indicating an accurate and reliable result of the response surface method.

3.4. Quality inspection of microbial inhibitor

3.4.1. Living bacteria count of microbial inhibitor

As the storage time of the microbial inhibitor prolonged, the living bacteria count decreased (Figure 4A). It was 5.10×10^9 cfu/mL on the

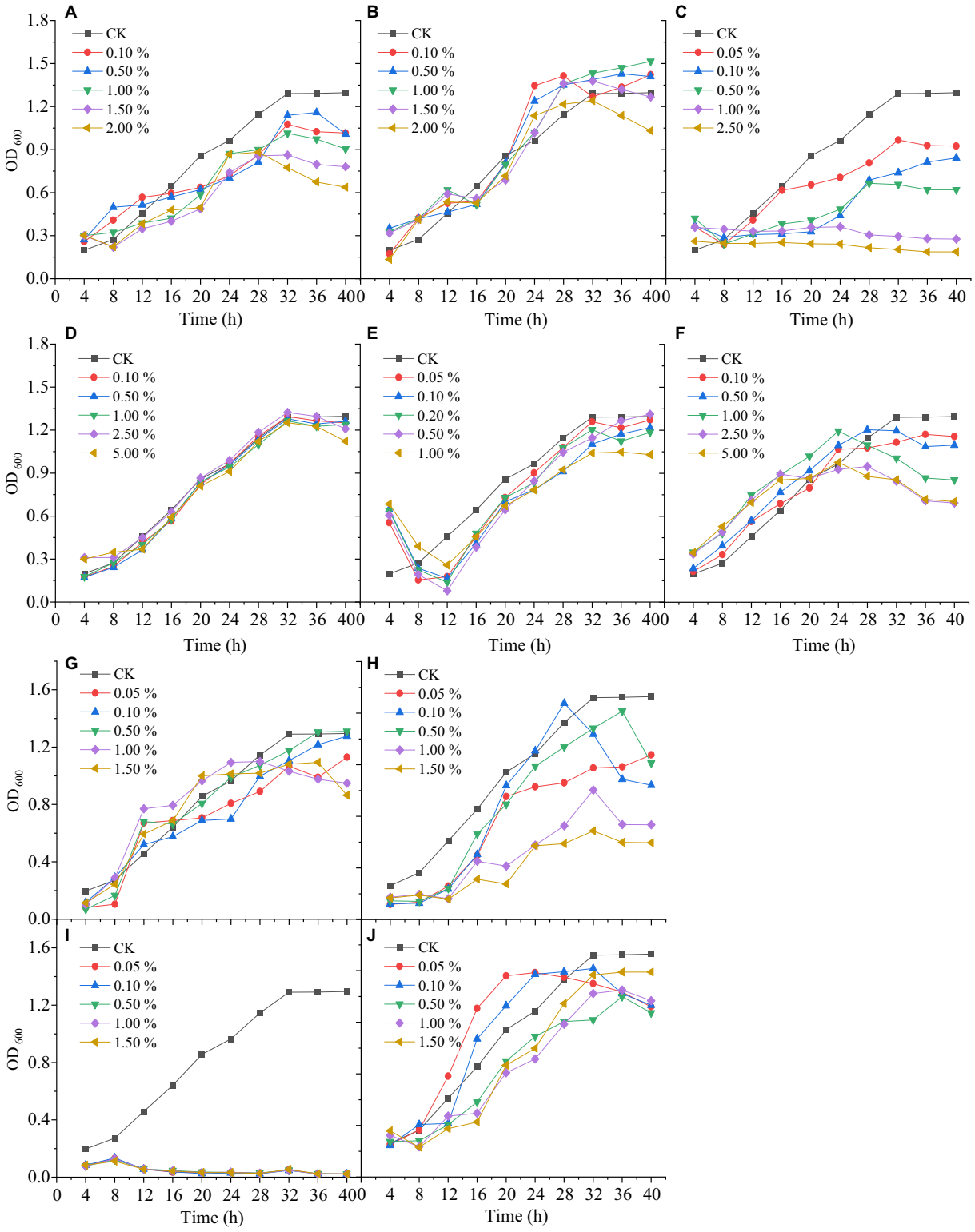


FIGURE 2
Effect of different types and concentrations of auxiliary agents on mixed biocontrol strains growth. **A:** Tween-20; **B:** Tween-80; **C:** OP emulsifier; **D:** sodium alginate; **E:** sorbitol; **F:** xanthan gum; **G:** methyl paraben; **H:** ethyl paraben; **I:** kathon; **J:** sodium citrate.

15th day, which was 5.46 times that on the 30th day and 16.45 times that on the 90th day. The living bacteria count was 3.10×10^9 cfu/mL on the 90th day, still much greater than that required by China National Standard GB 20287–2006 (1.00×10^8 cfu/mL).

3.4.2. The number and rate of contaminating microorganisms in microbial inhibitor

With the increase of the storage time of the microbial inhibitor, the number of contaminating microorganisms was 6.28×10^5 cfu/mL

on the 90th day(Figure 4B), which was 1.14 times that on the 60th day ($p < 0.05$). However, the contaminating microorganism count was far less than 10^4 cfu/mL (GB 20287–2006). Moreover, the mixed bacteria rate on the 90th day was 2.22 times that on the 60th day and 1.19 times that on the 75th day (Figure 4C), but it was still much lower than required by GB 20287–2006 (3.0×10^6 cfu/mL).

3.4.3. pH value of microbial inhibitor

The pH of the microbial inhibitor increased initially and then decreased with the increasing storage time (Figure 4D). It was 7.55 on the 15th day, then declined to 7.46 on the 30th day, and rose up to 7.58 on the 90th day. This range is in accordance with GB 20287–2006.

3.5. Control effect of microbial inhibitor on oat root diseases and growth of oat

The incidence of three pathogenic fungi on oat roots was 34.71% (T1), 30.02% (T7), and 25.84% (T6) (Table 10). The highest disease index was 27.68 from T1. The highest control effect of the microbial inhibitor was observed in T6 (68.44%), followed by T7 (52.96%) and T1 (48.70%). Accordingly, the best plant growth was obtained in the T6 treatment with a taller plant ($p < 0.05$), longer root length, and greater biomass (Figure 5).

TABLE 7 The test factor levels of the Box–Behnken.

Code	Factor		Factor levels	
		-1	0	1
A	Tween-80 /%	0.50	1.00	1.50
B	Sorbitol /%	0.20	0.50	1.00
C	Methylparaben /%	0.10	0.50	1.00

4. Discussion

Some biocontrol bacteria produce resistant substances against pathogens and play important roles in disease biocontrol (Compant et al., 2005; Kaewkham et al., 2016). *Bacillus velezensis*, *Bacillus xiamenensis*, *Bacillus mycoides*, and *Brevundimonas faecalis* significantly inhibited the growth of the three pathogens in this study. Similar results were also reported by Ait-Kaki et al. (2014), who obtained 60.00 and 61.00% inhibitory rates of *B. velezensis* isolated from *Calendula officinalis* against *F. oxysporum* and *Botrytis cinerea*, respectively. Moreover, 66.00 and 56.00% inhibitory rates of *B. velezensis* isolated from *Cucumis sativus* against *F. oxysporum* were obtained by Liu et al. (2017). *Streptomyces* sp., *Saccharothrix* sp., and *Nocardpsis* sp. isolated from the rhizosphere of *Solanum tuberosum* were shown to significantly inhibit the mycelial growth of *Phytophthora infestans* with a 35.02–79.20% inhibitory rate (Feng et al., 2022). Bacteria isolated from rice leaves have antagonistic effects on *Rhizoctonia solani* and inhibit disease spot extension *in vitro* (Shrestha et al., 2016). Inhibitory rates as high as 73.82, 66.81, and 85.71% of biocontrol bacteria on *Sclerotinia sclerotiorum*, *F. oxysporum*, and *R. solani*, respectively, were reported (Sun G. Z et al., 2017). In this study, cell-free fermentation liquid of biocontrol bacteria also inhibited the growth of the pathogenic fungi. The fermentation broth of GAU88 had inhibitory effects on *B. sorokiniana* (PB1) and *F. avenaceum* (PB6), with inhibitory rates of 39.90 and 31.37%, respectively; even higher inhibitory rates (67.00 and 54.00%) of the

TABLE 8 Box–Behnken central composite experiment.

Number	Factors			
	A: Tween-80/μL	B: Sorbitol/mg	C: Methylparaben /mg	Y: OD_{600} value
1	550	500	100	1.21 ± 0.01f
2	550	500	300	1.25 ± 0.01e
3	350	500	200	1.35 ± 0.03d
4	550	300	200	1.48 ± 0.02b
5	350	300	300	1.08 ± 0.03i
6	350	300	100	1.18 ± 0.02 g
7	550	300	200	1.49 ± 0.01b
8	550	300	200	1.37 ± 0.03d
9	750	300	300	1.51 ± 0.01a
10	550	300	200	1.49 ± 0.01b
11	750	100	200	1.36 ± 0.02d
12	750	500	200	1.38 ± 0.02d
13	550	300	200	1.44 ± 0.03c
14	550	100	300	1.24 ± 0.01e
15	750	300	100	1.06 ± 0.03i
16	350	100	200	1.13 ± 0.03 h
17	550	100	100	0.97 ± 0.04j

Different letters within the same column indicate significant difference at $p < 0.05$ level by Duncan's test.

10.3389/fmicb.2023.1208591

TABLE 9 Variance analysis of the regression equation.

Source	Sum of squares	*DF*	Mean square	*F*	*P*(Prob) > F	*P*(Prob) > F
Model	0.45	9	0.050	31.43	<0.0001	**
A	0.041	1	0.041	25.74	0.0018	**
B	0.030	1	0.030	19.02	0.0042	**
C	0.054	1	0.054	34.51	0.0008	**
AB	0.010	1	0.010	6.34	0.0496	*
AC	0.076	1	0.076	47.93	0.0003	**
BC	0.013	1	0.013	8.38	0.0284	*
A^2	0.013	1	0.013	7.93	0.0415	*
B^2	0.038	1	0.038	23.83	0.0022	**
C^2	0.16	1	0.16	98.37	<0.0001	**
Residual	0.011	7	0.001			
Lack of fit	0.0005	3	0.00017	0.067	0.9748	ns
Pure error Lack of fit	0.011	4	1.83			
Cor total	0.46	16				
Adj R^2	0.9759					

DF represented degree of freedom; **represented significant at $p < 0.01$; *represented significant at $p < 0.05$; ns represented not significant at $p > 0.05$.

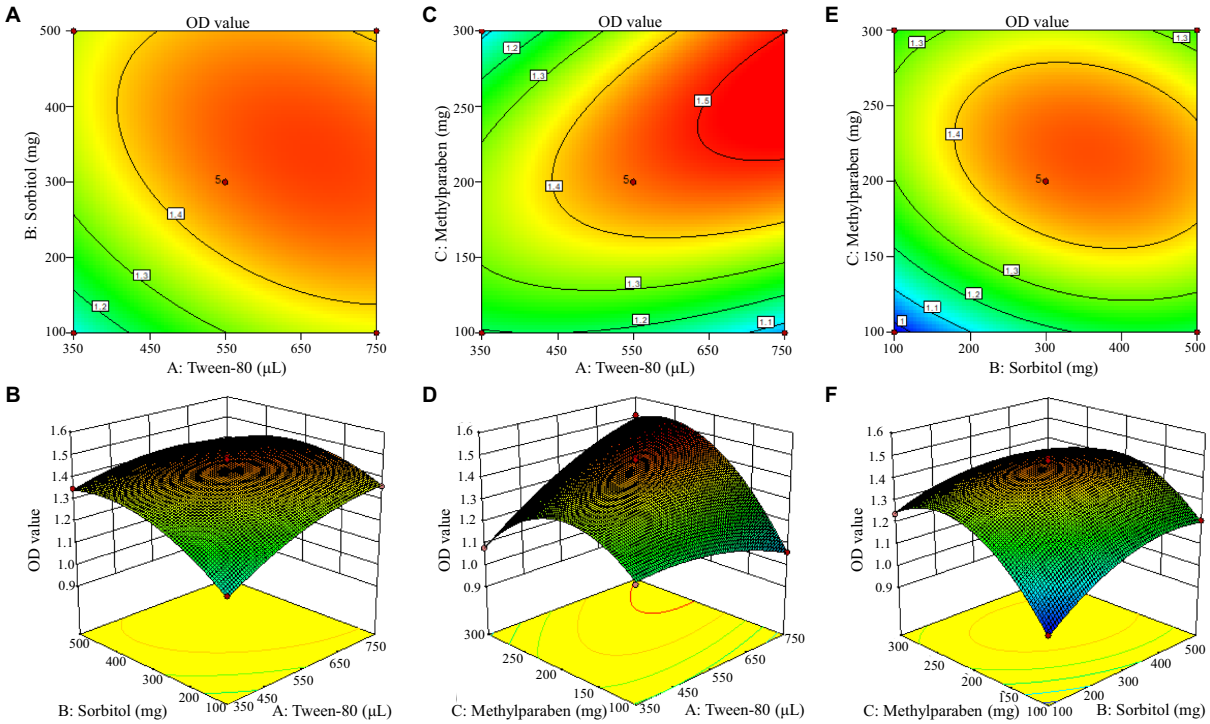


FIGURE 3
Contour plot (up) and surface (down) of mutual-influence for the selected adjuvant. Letter in the figure, **A** was contour plot and **B** meant surface of mutual-influence for the tween-80 and sorbitol; **C** denoted contour plot and **D** indicated surface of mutual-influence for the tween-80 and methylparaben; **E** was contour plot and **F** meant surface of mutual-influence for the sorbitol and methylparaben.

cell-free fermentation liquid of *B. velezensis* isolated from *Cucumis sativus* against *F. oxysporum* have been observed (Liu et al., 2017). *Bacillus* and *Brevundimonas* may produce antimicrobial proteins (Kim et al., 2017) and lipopeptide antibiotics (Peypoux et al., 1978, 1999; Vanittanakom et al., 1986) and secrete growth hormones (Meng et al., 2016; Yaashikaa et al., 2020), pyoverdine, and NH_3 (Meng et al., 2016). It can be seen that biocontrol bacteria have a good inhibitory effect on the growth of pathogenic fungi. In order to make biocontrol bacteria play a better role, it is a good choice to add preservatives, protective agents, and wetting agents to them.

Biocontrol bacteria are viable microorganisms and sensitive to UV, extreme temperature, light, and other environmental factors (Liu

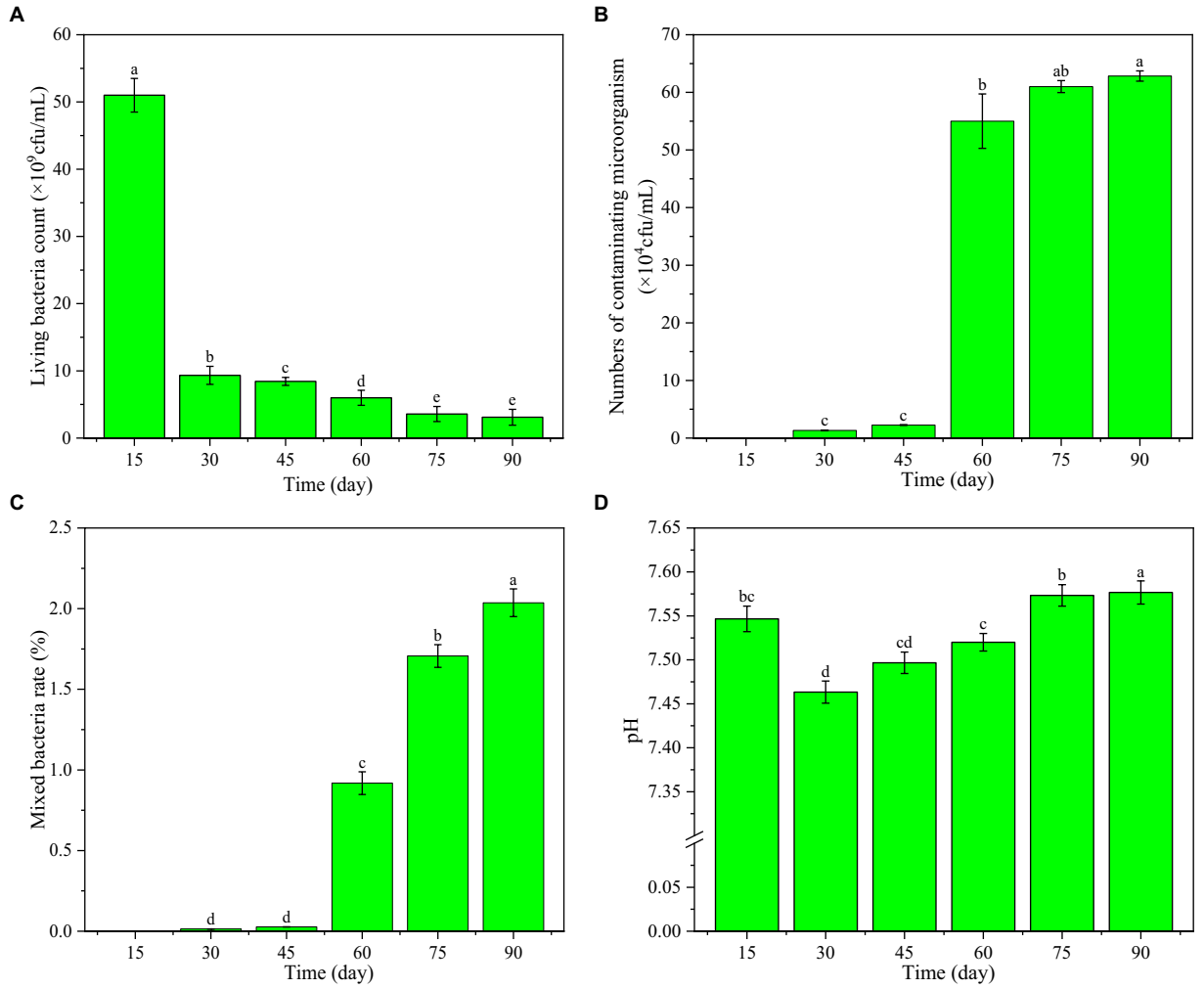


FIGURE 4
Effect of storage time on the main indexes of microbial inhibitor. Different letters within different storage time indicate significant difference at $p<0.05$ level by Duncan's test.

TABLE 10 Control effect of microbial inhibitor on oat root diseases.

Code	Incidence(%)	Disease index	Control effect(%)
T1 (*Bipolaris sorokiniana*)	34.71 ± 1.94a	27.68 ± 0.55a	48.70 ± 0.57c
T6 (*Fusarium avenaceum*)	25.84 ± 0.35c	16.98 ± 0.38c	68.44 ± 0.47a
T7 (*Fusarium equiseti*)	30.02 ± 0.75b	23.28 ± 0.61b	52.96 ± 1.15b

Different letters within the same column indicate significant difference at $p < 0.05$ level by Duncan's test.

and Xing, 2016). To reduce these impacts and prolong the shelf life of microbial preparations, it is necessary to add appropriate protective additives (Arora and Mishra, 2016). At present, most auxiliary additives are chemically synthesized, and so the compatibility of the additives with living microorganisms should be fully considered. The addition of Tween-80 to the culture medium of *Streptomyces padanus* was demonstrated to enhance the inhibitory effect of *S. padanus* against cucumber downy mildew (Fan et al., 2019). Furthermore, the addition of 0.1% Tween-80 to laboratory growth media increased the growth rate of planktonic *Staphylococcus aureus* batch cultures, and it also increased the total biomass when *S. aureus* was grown as biofilms (Nielsen et al., 2016). Studies have shown that sorbitol may act as an antioxidant to scavenge reactive oxygen species and precisely regulate the balance of reactive oxygen species under the synergistic effect of antioxidant enzyme systems (SOD, POD, CAT) (Smirnoff and Cumbes, 1989). Parabens are a class of compounds primarily used as antimicrobial preservatives in pharmaceutical products, cosmetics, and foodstuffs (Nguyen et al., 2021). It was shown that in a control of grape downy mildew, a combination of corn steep liquor, lignosulfonate, and polyethylene glycol in *Lysobacter capsici* formula increased the survival rate of *L. capsici* in the field and reduced the occurrence of disease by 71%; in addition, the authors also admitted that the required quantities limited the usefulness of that particular formulation (Segarra et al., 2015). In this study, adding 1.00% Tween-80, 0.50% sorbitol, and 0.50% methylparaben to 50 mL of mixed fermentation had no inhibitory effects, indicating that the developed biocontrol bacteria had good compatibility with the additives. During the growth of biocontrol bacteria, their viable counts decrease due to the decline of nutrients and oxygen and the production of lactic acid,

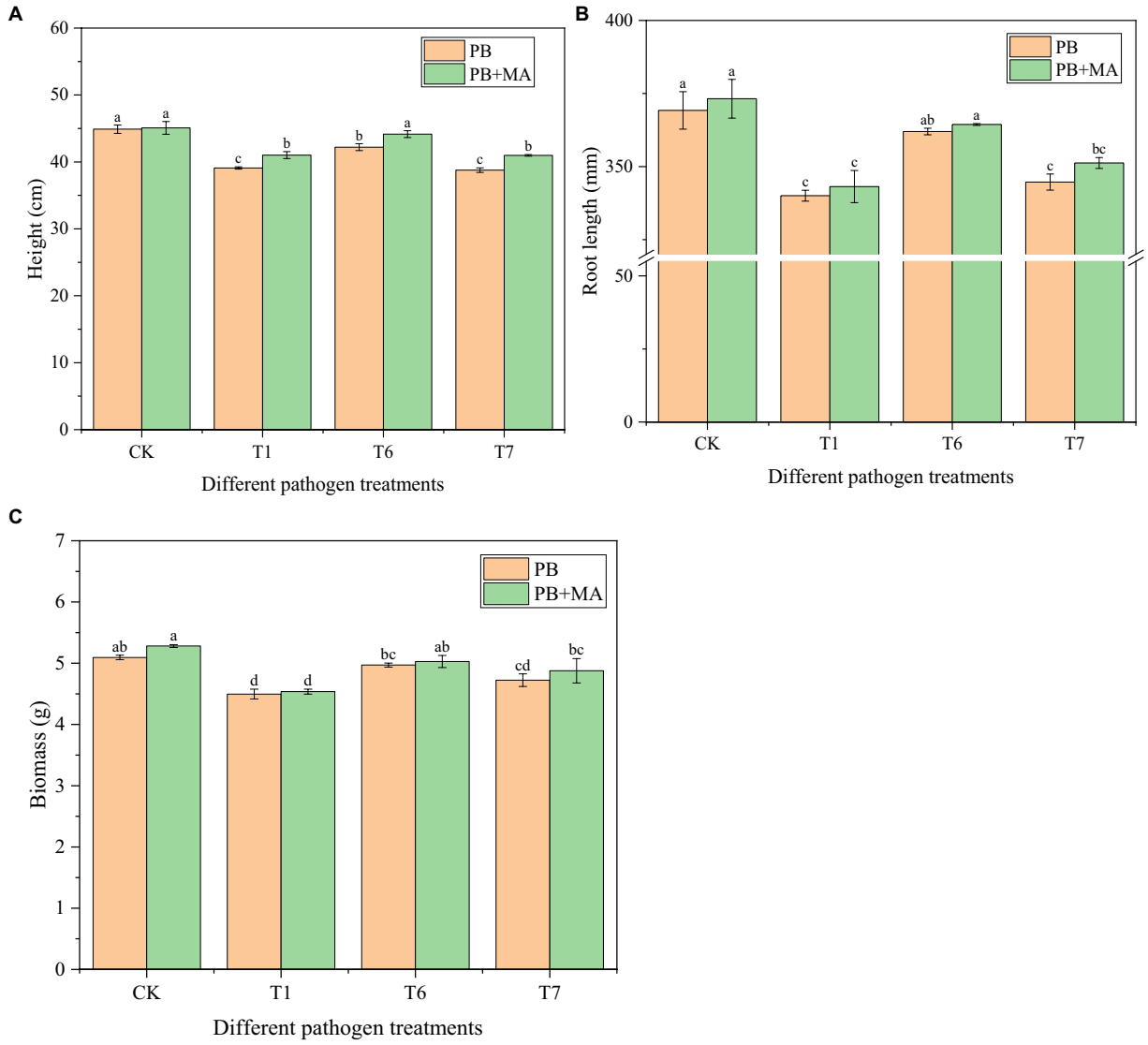


FIGURE 5
Effect of microbial inhibitor on oat seedling stage growth. PB in CK and in T treatment represent sterile water and pathogenic fungi respectively; MA was microbial inhibitor. Different letters within the treatment indicate significant difference at $p < 0.05$ level by Duncan's test.

causing fluctuation of the pH (Wong et al., 2019). The microbial inhibitor developed in this study was in compliance with the China National Standards of Agricultural Microbial Agents (GB 20287–2006) in terms of living bacteria counts, contaminating microorganism counts, undesirable mixed bacteria rate, and pH.

To test the effectiveness of the developed microbial inhibitor, the pathogenic fungi and microbial inhibitor were inoculated on oat, and the results showed as a control effect as high as 68.44%, much higher than that of *Bacillus cereus* on tobacco bacterial wilt (31.43%, Wu et al., 2020). *Pseudomonas brassicacearum*, *Pseudomonas putida*, *Paenibacillus peoriae*, and *Bacillus licheniformis* isolated from potato have been shown to reduce potato disease occurrence by 27–55% (Bahmani et al., 2021). Plant growth-promoting rhizo-bacteria may interact with plants directly by increasing the availability of essential nutrients (nitrogen, phosphorus, and iron), production and regulation of compounds involved in plant growth (phytohormones), and stress hormonal status (ethylene levels by ACC-deaminase). They may also indirectly affect plants by protecting them against diseases through competition with pathogens for highly limited nutrients, biocontrol of pathogens through the production of aseptic-activity compounds, synthesis of fungal cell-wall-lysing enzymes, and the induction of systemic responses in host plants (Olenska et al., 2020). In this study, although the microbial inhibitor showed good control effects on the different pathogenic fungi in the pot experiments, their effects in fields need further study.

5. Conclusion

In conclusion, this study comprehensively analyzed the additive screening and formula optimization of a microbial inhibitor with disease prevention and growth promotion effects on *Avena sativa*. *B. velezensis* GAU24 and *B. faecalis* GAU88 had good inhibitory effects on *B. sorokiniana*, *F. avenaceum*, and *F. equiseti* and could

be used to make the biocontrol agent. Their optimal additives consisted of 1.00% wetting agent Tween-80, 0.50% UV-protective agent sorbitol, and 0.50% preservative methylparaben, and the optimal combination formula was 14.96 mL/L Tween-80, 5.6 g/L sorbitol, and 5.12 g/L methylparaben. When used on oat, it could control 48.70–68.44% of root rot. In addition, the developed microbial inoculants have disease prevention and growth-promoting effects on plants. This study provides a suitable environment for the protection of mixed biocontrol bacteria and lays a foundation for the prevention and control of oat diseases, the promotion of growth, and the improvement of quality.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

JZ, TY, and GZ designed the experiments and contributed to the writing and revision of the manuscript. JZ performed the experiments, being assisted by WG and YG, analyzed the data, and wrote the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by China Agriculture Research System (CARS-07-C-1) and Excellent Doctoral Program Foundation of Gansu Province (22JR5RA841).

Acknowledgments

The authors thank Qi Li, Xiaolei Yang, and Yanshan Yang for their assistance during the pot experiment.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Abbas, A., Khan, S. U., Khan, W. U., Saleh, T. A., Khan, M. H., Ullah, S., et al. (2019). Antagonist effects of strains of *Bacillus* spp. against *Rhizoctonia solani* for their protection against several plant diseases: alternatives to chemical pesticides. Science. *Direct* 342, 124–135. doi: 10.1016/j.crvi.2019.05.002

Ait-Kaki, A., Kacem-Chaouche, N., Ongena, M., Kara-Ali, M., Dehimat, L., Kahlat, K., et al. (2014). In vitro and in vivo characterization of plant growth promoting *Bacillus* strains isolated from extreme environments of eastern Algeria. *Appl. Biochem. Biotechnol.* 172, 1735–1746. doi: 10.1007/s12010-013-0617-0

Alamri, S., Hashem, M., Moustafa, Y., Nafady, N., and Abo-Elyousr, K. (2019). Biological control of root rot in lettuce caused by *Exserohilum rostratum* and *fusarium oxysporum* via induction of the defense mechanism. *Biol. Control* 128, 76–84. doi: 10.1016/j.biocontrol.2018.09.014

Al-Sadi, A. M. (2021). *Bipolaris sorokiniana*-induced black point, common root rot, and spot blotch diseases of wheat: a review. *Front. Cell. Infect. Microbiol.* 11:584899. doi: 10.3389/fcimb.2021.584899

Arora, N. K., and Mishra, J. (2016). Prospecting the roles of metabolites and additives in future bioformulations for sustainable agriculture. *Appl. Soil Ecol.* 107, 405–407. doi: 10.1016/j.apsoil.2016.05.020

Bahmani, K., Hasanzadeh, N., Harighi, B., and Marefat, A. L. (2021). Isolation and identifcation of endophytic bacteria from potato tissues and their effects as biological control agents against bacterial wilt. *Physiol. Mol. Plant Pathol.* 116:101692. doi: 10.1016/J.PMPP.2021.101692

Barrera, M. C., Gómez, M. I., and Bermúdez, J. C. (2019). Towards the production of fungal biocontrol candidates using inert supports: a case of study of *Trichoderma asperellum* in a pilot fixed bed fermenter. *Biocontrol Sci. Tech.* 29, 162–184. doi: 10.1080/09583157.2018.1542486

Brodeur, J., Abram, P. K., Heimpel, G. E., and Messing, R. H. (2018). Trends in biological control: public interest, international networking and research direction. *BioControl* 63, 11–26. doi: 10.1007/s10526-017-9850-8

Chang, N., Zhang, X. J., Ma, L. L., Shi, J. J., Jia, W., Qi, Y. Z., et al. (2017). Effects of microbial agents on wheat growth and soil-borne diseases prevention. *Crop J.* 1, 155–160. doi: 10.16035/j.issn.1001-7283.2017.01.028

Colombo, E. M., Kunova, A., Pizzatti, C., Saracchi, M., Cortesi, P., and Pasquali, M. (2019). Selection of an endophytic *Streptomyces* sp. strain DEF09 from wheat roots as a biocontrol agent against *fusarium graminearum*. *Front. Microbiol.* 10:2356. doi: 10.10.3389/fmicb.2019.02356

Compant, S., Duffy, B., Nowak, J., Clément, C., and Barka, E. A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Appl. Environ. Microbiol.* 71, 4951–4959. doi: 10.1128/AEM.71.9.4951–4959.2005

Duan, Y. J., Chen, J., He, W., Chen, J. J., Pang, Z. C., Hu, H. G., et al. (2020). Fermentation optimization and disease suppression ability of a *Streptomyces* ma. FS-4 from banana rhizosphere soil. *BMC Microbiol.* 20:24. doi: 10.1186/s12866-019-1688-z

Fan, Y. T., Chung, K. R., and Huang, J. W. (2019). Fungichromin production by *Streptomyces padanus* PMS-702 for controlling cucumber downy mildew. *Plant Pathol. J.* 35, 341–350. doi: 10.5423/PPJ.OA.03.2019.0057

Feng, R. Z., Yao, T., Zhou, W. H., and Long, R. J. (2009). Effects of different habitats and insoluble phosphates on phosphate solubilizing activity of four phosphate solubilizing bacteria. *Chin. J. Appl. Environ.* 15, 856–860. doi: 10.3724/SP.J.1145.2009.00856

Feng, S., Jin, L., Tang, S. C., Jian, Y. F., and Li, Z. G. (2022). Combination of rhizosphere bacteria isolated from resistant potato plants for biocontrol of potato late blight. *Pest Manag. Sci.* 78, 166–176. doi: 10.1002/ps.661

Gupta, A. K., Raj, R., Choudhary, R., Singh, S. P., and Solanki, I. S. (2017). Effect of mineral nutrients, seed treatment and foliar fungicides on spot blotch (*Bipolaris sorokiniana*) severity and agronomic performance of wheat (*Triticum aestivum*) in hot-humid environment of eastern Gangetic plain in India. *Indian J. Agric. Sci.* 87, 505–511. doi: 10.56093/ijas.v87i4.69419

Han, H. W., Sun, L. N., Yao, T., Rong, L. Y., Liu, Q. H., Lu, H., et al. (2013). Effects of bio-fertilizers with different PGPR strain combinations on yield and quality of alfalfa. *Acta Prataculturae Sin.* 22, 104–112. doi: 10.11686/cyxb20130512

Jiang, Y. M., Gao, Y. M., Yao, T., Duan, Q. B., Zhao, D. Q., Li, Z. X., et al. (2018). Effect of plant growth–promoting rhinoacteria on the growth of Uraria crinita and ×*Triticale Wittmack*. *Pratacultural Sci.* 35, 1910–1918. doi: 10.11829/j.issn.1001-0629.2017-0432

Kaewkham, T., Hynes, R. K., and Siri, B. (2016). The effect of accelerated seed ageing on cucumber germination following seed treatment with fungicides and microbial biocontrol agents for managing gummy stem blight by *Didymella bryoniae*. *Biocontrol Sci. Tech.* 26, 1048–1061. doi: 10.1080/09583157.2016.1183189

Karunarathne, A., Gunnell, D., Konradsen, F., and Eddleston, M. (2020). How many premature deaths from pesticide suicide have occurred since the agricultural green revolution? *Clin. Toxicol.* 58, 227–232. doi: 10.1080/15563650.2019.1662433

Kazan, K., and Gardiner, D. M. (2018). Fusarium crown rot caused by *fusarium pseudograminearum* in cereal crops: recent progress and future prospects. *Mol. Plant Pathol.* 19, 1547–1562. doi: 10.1111/mpp.12639

Kim, S. Y., Lee, S. Y., Weon, H. Y., Sang, M. K., and Song, J. (2017). Complete genome sequence of *Bacillus velezensis* M75, a biocontrol agent against fungal plant pathogens, isolated from cotton waste. *J. Biotechnol.* 241, 112–115. doi: 10.1016/j.jbiotec.2016.11.023

Lahlali, R., Brostaux, Y., and Jijakli, M. H. (2011). Control of apple blue mold by the antagonistic yeast pichia anomala strain k: screening of UV protectants for preharvest application. *Plant Dis.* 95, 311–316. doi: 10.1094/PDIS-04-10-0265

Li, Q. Y., Xu, Q. Q., Jiang, Y. M., Niu, J. S., Xu, K. G., and He, R. S. (2019). The correlation between wheat black point and agronomic traits in the North China plain. *Crop Prot.* 119, 17–23. doi: 10.1016/j.cropro.2019.01.004

Liu, D. Y., Li, M., Sun, W. X., and Liu, R. J. (2017). Screening and antibiosis study of PGPR strains against *fusarium oxysporum*. *Acta Phytopathologica Sinica.* 47, 704–715. doi: 10.13926/j.cnki.apps.000067

Liu, Q. H., Yao, T., Ma, C., and Li, X. G. (2011). Cultural conditions for mixed culture of phosphate solubilizing and nitrogen fixing bacteria. *Grassland Turf.* 31, 1–13. doi: 10.3969/j.issn.1009-5500.2011.06.004

Liu, T. (2016). *Evaluating and identifying of plant growth promoting rhizobacteria of dominant alpine meadows. [dissertation/master's thesis]*. (Lanzhou: Gansu Agricultural University).

Liu, Z. H., and Xing, X. K. (2016). Research progress in microbial pesticide adjuvants. *Geneomics and Appl. Biol.* 35, 2109–2113. doi: 10.13417/j.gab.035.002109

Meng, Q., Jiang, H., and Hao, J. J. (2016). Effects of *Bacillus velezensis* strain BAC03 in promoting plant growth. *Biol. Control* 98, 18–26. doi: 10.1016/j.biocontrol.2016.03.010

Müller, T., and Behrendt, U. (2021). Exploiting the biocontrol potential of plant-associated pseudomonads–a step towards pesticide-free agriculture? *Biol. Control* 155:104538. doi: 10.1016/j.biocontrol.2021.104538

Nguyen, V. H., Thi, L. P., Chandana, P. S., Do, H. T., Pham, T. H., Lee, T., et al. (2021). The degradation of paraben preservatives: recent progress and sustainable approaches toward photocatalysis. *Chemophere.* 276:130163. doi: 10.1016/j.chemosphere.2021.130163

Nielsen, C. K., Kjems, J., Mygind, T., Snabe, T., and Meyer, R. L. (2016). Effects of tween 80 on growth and biofilm formation in laboratory media. *Front. Microbiol.* 7:1878. doi: 10.3389/fmicb.2016.01878

O'Brien, P. A. (2017). Biological control of plant diseases. *Australas. Plant Pathol.* 46, 293–304. doi: 10.1007/s13313-017-0481-4

O'Callaghan, M. (2016). Microbial inoculation of seed for improved crop performance: issues and opportunities. *Appl. Microbiol. Biotechnol.* 100, 5729–5746. doi: 10.1007/s00253-016-7590-9

Olenska, E., Malek, W., Wojcik, I., Swiecicka, I., Thijs, S., and Vangronsveld, J. (2020). Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: a methodical review. *Sci. Total Environ.* 743:140682. doi: 10.1016/j.scitotenv.2020.140682

Parikh, L., and Adesemoye, A. (2018). Impact of delivery method on the efficacy of biological control agents and the virulence of *fusarium* root rot pathogens in the greenhouse. *Biocontrol Sci. Tech.* 28, 1191–1202. doi: 10.1080/09583157.2018.1520198

Peypoux, F., Bonmatin, J. M., and Wallach, J. (1999). Recent trends in the biochemistry of surfactin. *Appl. Microbiol. Biotechnol.* 51, 553–563. doi: 10.1007/s002530051432

Peypoux, F., Guinand, M., Michel, G., Delcambe, L., Das, B. C., and Lederer, E. (1978). Structure of iturine a, a peptidolipid antibiotic from *Bacillus subtilis*. *Biochemistry* 17, 3992–3996. doi: 10.1021/bi00612a018

Raymaekers, K., Ponet, L., Holtappels, D., Berckmans, B., and Cammue, B. P. (2020). Screening for novel biocontrol agents applicable in plant disease management-a review. *Biol. Control* 144:104240. doi: 10.1016/j.biocontrol.2020.104240

Segarra, G., Puopolo, G., Giovannini, O., and Pertot, I. (2015). Stepwise flow diagram for the development of formulations of non spore-forming bacteria against foliar pathogens: the case of *Lysobacter capsici* AZ78. *J. Biotechnol.* 216, 56–64. doi: 10.1016/j.jbiotec.2015.10.004

Shi, W. B., Zhang, L. L., and Feng, M. G. (2008). Field trials of four formulations of *Beauveria bassiana* and *Metarhizium anisoplae* for control of cotton spider mites (Acari: Tetranychidae) in the Tarim Basin of China. *Biol. Control* 45, 48–55. doi: 10.1016/j.biocontrol.2007.11.006

Shrestha, B. K., Karki, H. S., Groth, D. E., Jungkhun, N., and Ham, J. H. (2016). Biological control activities of rice-associated *bacillus* sp. strains against sheath blight and bacterial panicle blight of rice. *PLoS One* 11:e0146764. doi: 10.1371/journal.pone.0146764

Smirnoff, N., and Cumbes, Q. J. (1989). Hydroxyl radical scavenging activity of compatible solutes. *Phytochemistry* 28, 1057–1060. doi: 10.1016/0031-9422(89)80182-7

Sun, C. H., Hou, B. H., Zhang, S. W., Xue, Y. Y., Zhang, W. J., and Xu, B. L. (2017). Screening and optimizing of the adjuvant and carriers for the bio-control agent *Bacillus amyloliquefaciens* TS-1203. *Chinese J. Pesticide Sci.* 19, 254–265. doi: 10.16801/j.issn.1008-7303.2017.0034

Sun, G. Z., Hou, D., Yue, H. Z., Zhao, G. Q., Yao, T., Chai, X. H., et al. (2015). Screening of bacteria antagonizing *Alternaria solani* and its inhibitory effects. *Grassland Turf.* 35, 32–36, 43. doi: 10.3969/j.issn.1009-5500.2015.01.006

Sun, G. Z., Yao, T., Feng, C. J., Chen, L., Li, J. H., and Wang, L. D. (2017). Identification and biocontrol potential of antagonistic bacteria strains against *Sclerotinia sclerotiorum* and their growth-promoting effects on *Brassica napus*. *Biol. Control* 104, 35–43. doi: 10.1016/J.Biocontrol.2016.10.008

Sun, X. P. (2019). Research progress on green control of root rot in China. *Hans J. Agricul. Sci.* 9, 1193–1196. doi: 10.12677/HJAS.2019.912170

Tunali, B., Nicol, J. M., Hodson, D., Uckun, Z., Buyuk, O., Erdurmus, D., et al. (2008). Root and crown rot fungi associated with spring, facultative, and winter wheat in Turkey. *Plant Dis.* 92, 1299–1306. doi: 10.1094/PDIS-92-9-1299

Vanittanakom, N., Loeffler, W., Koch, U., and Jung, G. (1986). Fengycin a novel antifungal lipopeptide antibiotic produced by *Bacillus subtilis* F-29-3. *J. Antibiot.* 39, 888–901. doi: 10.7164/antibiotics.39.888

Wang, X. J., Chi, Y., and Li, F. (2022). Exploring China stepping into the dawn of chemical pesticide-free agriculture in 2050. *Front. Plant Sci.* 13:942117. doi: 10.3389/fpls.2022.942117

Wang, Y. Y., Yuan, S. K., Nong, X. Q., and Li, M. (2021). Current situation of standards for quality control, risk assessment and application technology of microbial pesticides in China. *Agrochemicals.* 60, 872–877. doi: 10.16820/j.cnki.1006-0413.2021.12.003

Wong, C. K., Saidi, N. B., Vadamalai, G., Teh, C. Y., and Zulperi, D. (2019). Effect of bioformulations on the biocontrol efficacy, microbial viability and storage stability of a consortium of biocontrol agents against fusarium wilt of banana. *J. Appl. Microbiol.* 127, 544–555. doi: 10.1111/jam.14310

Wu, X. Z., Li, H. L., Wang, Y., and Zhang, X. B. (2020). Effects of bio-organic fertiliser fortified by *Bacillus cereus* QJ-1 on tobacco bacterial wilt control and soil quality improvement. *Biocontrol Sci. Tech.* 30, 351–369. doi: 10.1080/09583157.2020.1711870

Yaashikaa, P. R., Senthil, P. K., Varjani, S., Tamilselvi, S., and Saravanan, A. (2020). Formulation and combinatorial effect of *Pseudomonas fluorescens* and *Bacillus coagulans* as biocontrol agents. *Biocatal. Agric. Biotechnol.* 30:101868. doi: 10.1016/j.bcab.2020.101868

Yang, L., Liang, J., and Zhang, X. Y. (2017). Development and application methods for poplar canker biocontrol agents. *Bangladesh J. Bot.* 46, 1225–1232.

Yang, Y. S., Yao, T., Zhang, J. G., Bai, J., Han, D. R., Li, Q., et al. (2021). Isolation, identification and pathogenicity of pathogenic fungi of oat root rot. *Grassland and lawn.* 41, 60–69. doi: 10.13817/j.cnki.cyycp.2021.02.009

Yardin, M. R., Kennedy, I. R., and Thies, J. E. (2000). Development of high quality carrier materials for field delivery of key microorganisms used as bio-fertilisers and bio-pesticides. *Radiation Phy. Chemistry.* 57, 565–568. doi: 10.1016/S0969-806X(99)00480-6

Zhang, J. (2019) *Antibacterial characteristics of excellent biocontrol bacteria and development of microorganism inoculant. [dissertation/master's thesis]*. (Lanzhou: Gansu Agricultural University).

Zhang, J., Wan, L. X., and Lu, L. Z. (2019). Study on the control effect of microbial agents on ginseng root rot in stubble fields. *Ginseng Study.* 31, 27–30. doi: 10.19403/j.cnki.1671-1521.2019.04.008

Zheng, D. D., Niu, S. Q., Zhou, X., Wang, Y., Zhu, X. T., Kong, W. B., et al. (2019). Screening, identification and control of composite biocontrol actinomycetes against Astragalus root rot. *J. Ecol.* 38, 753–761. doi: 10.13292/j.1000-4890.201903.006

frontiers | Frontiers in Microbiology

TYPE Original Research
PUBLISHED 26 July 2023
DOI 10.3389/fmicb.2023.1212349

OPEN ACCESS

EDITED BY
Parul Chaudhary,
Graphic Era Hill University, India

REVIEWED BY
Kumar Pranaw,
University of Warsaw, Poland
Anuj Rana,
Chaudhary Charan Singh Haryana Agricultural University, India
Sami Abou Fayssal,
University of Forestry, Sofia, Bulgaria

*CORRESPONDENCE
Rajeev Kaushik
✉ Rajeev_micro@iari.res.in

RECEIVED 26 April 2023
ACCEPTED 30 June 2023
PUBLISHED 26 July 2023

CITATION
Naitam MG, Ramakrishnan B, Grover M and Kaushik R (2023) Rhizosphere-dwelling halophilic archaea: a potential candidate for alleviating salinity-associated stress in agriculture. *Front. Microbiol.* 14:1212349. doi: 10.3389/fmicb.2023.1212349

Rhizosphere-dwelling halophilic archaea: a potential candidate for alleviating salinity-associated stress in agriculture

Mayur G. Naitam[1], B. Ramakrishnan[1], Monendra Grover[2] and Rajeev Kaushik [1]*

[1]Division of Microbiology, ICAR-Indian Agricultural Research Institute, New Delhi, India, [2]Center for Agricultural Bioinformatics, ICAR-Indian Agricultural Statistical Research Institute, New Delhi, India

Salinity is a serious environmental factor that impedes crop growth and drastically reduces yield. This study aimed to investigate the potential of halophilic archaea isolated from the Rann of Kutch to alleviate the negative impact of salinity on crop growth and yield. The halophilic archaea, which demonstrated high tolerance to salinity levels up to 4.5 M, were evaluated for their ability to promote plant growth in both salt-tolerant and salt-susceptible wheat cultivars. Our assessment focused on their capacity to solubilize essential nutrients, including phosphorus (14-61 mg L^{-1}), potassium (37-78 mg L^{-1}), and zinc (8-17 mg L^{-1}), as well as their production of the phytohormone IAA (17.30 to 49.3 μg ml^{-1}). To conduct the experiments, five wheat cultivars (two salt-tolerant and three salt-susceptible) were grown in triplicates using soft MS agar tubes (50 ml) and pots containing 10 kg of soil with an electrical conductivity (EC) of 8 dSm^{-1}. Data were collected at specific time points: 21 days after sowing (DAS) for the MS agar experiment, 45 DAS for the pot experiment, and at the time of harvest. In the presence of haloarchaea, the inoculated treatments exhibited significant increases in total protein (46%), sugar (27%), and chlorophyll (31%) levels compared to the un-inoculated control. Furthermore, the inoculation led to an elevated accumulation of osmolyte proline (31.51%) and total carbohydrates (27.85%) while substantially reducing the activity of antioxidant enzymes such as SOD, catalase, and peroxidase by 57–76%, respectively. Notably, the inoculated treatments also showed improved plant vegetative growth parameters compared to the un-inoculated treatments. Interestingly, the positive effects of the halophilic archaea were more pronounced in the susceptible wheat cultivars than in the tolerant cultivars. These findings highlight the growth-promoting abilities of the halophilic archaeon *Halolamina pelagica* CDK2 and its potential to mitigate the detrimental effects of salinity. Consequently, further evaluation of this halophilic archaeon under field conditions is warranted to explore its potential use in the development of microbial inoculants.

KEYWORDS

halophilic archaea, wheat, salinity alleviation, abiotic stress, plant growth promotion

1. Introduction

Salinity is one of the most detrimental kinds of abiotic stress that affects agricultural productivity and food security (Sardar et al., 2023). Soil salinity causes several morphological, physiological, and molecular changes in crop plants which result in decreased growth and productivity. The enhanced production of reactive oxygen species

in plants under oxidative stress induced by salinity causes damage to the cell membrane, proteins, lipids, and nucleic acids and triggers programmed cell death (Gill and Tuteja, 2010; Calanca, 2017). Globally, an estimated 20% of arable soil is affected by salinity at the moment, and that number may rise to 50% by 2050 due to a variety of factors, including the lack of effective mitigation practices (Rakshit et al., 2020). Efficient resource management and crop improvement for the development of better cultivars can aid in the reduction of salinity stress. To reduce salinity stress in agriculture, commonly practiced strategies include soil and irrigation management, selecting and breeding salt-tolerant crop varieties, implementing agronomic practices, such as mulching, crop rotation, and intercropping, leaching excess salts, and employing biotechnological interventions to develop and utilize salt-tolerant plant varieties (Ondrasek et al., 2022). Given the time-consuming and expensive nature of current strategies, it is crucial to develop cost-effective and easily adaptable biological methods to manage agricultural stress. These methods can have direct implications in the near future. Microorganisms could play an important role in this regard if we take advantage of their unique properties. Not only microbial inoculation can help in the control of different stresses, but also it can trigger plant development and production and the improvement of soil fertility (Chaudhary et al., 2023). These include salinity tolerance, the ability to thrive in varying water conditions, production of plant growth-promoting hormones, nutrient cycling, siderophore production, volatile organic compound production, ACC deaminase activity, antioxidant capabilities, and the ability to produce osmolytes. They also interact with other microbes and crops, thereby helping plants withstand multiple stresses simultaneously (Sharma et al., 2021; Suman et al., 2022). In this regard, the ability of bacterial inoculants to alleviate biotic and abiotic stresses in plants is well documented and demonstrated, but the members of the domain Archaea are still under explored (Naitam and Kaushik, 2021).

Prokaryotes from the domain Archaea have long been considered native inhabitants of ecological niches with extreme conditions of temperature, acidity, alkalinity, and salinity (Gubry-Rangin et al., 2010; Naitam and Kaushik, 2021). However, this notion of a scientific community has changed since the advent of next-generation genome sequencing techniques (metagenomics and metatranscriptomics) that have revolutionized the study of microbial diversity (Oren, 2014; Yadav et al., 2017). In recent decades, archaea have also been isolated from a wide range of ecological niches that have normal environmental conditions; these include arable and barren lands, plant rhizosphere, freshwater lakes, sediments, humans, and animals' guts (Kumar et al., 2009; Gubry-Rangin et al., 2010; Yadav et al., 2019; Jung et al., 2020; Akinola and Babalola, 2021; Hu et al., 2021). Archaea also constitute a significant proportion of microbiomes, phytobiomes, and various plant-associated ecosystems (Jung et al., 2020). Archaea can play a potential role in improving crop production and sustainability in arid and semi-arid (Alori et al., 2020). Few studies reported the presence of archaea and their role in improving plant growth. Thaumarchaeota was reported as dominant phyla in the rhizospheric soils of native alpine trees of the Qinghai-Tibetan Plateau along with some unclassified archaeal groups as keystone species. The results suggested that the archaeal community structure in rhizospheric soil is simple as opposed to bulk soils (Zhang et al., 2020). Cultivar-specific variation (rhizospheric effect) in the archaeal community was observed in tomatoes; however, a many-fold reduction in the archaeal community was observed during vertical transmission in the F1 generation (Taffner et al., 2020). The archaeal community in tomato rhizosphere studies was dominated by Thaumarchaeota and Euryarchaeota (Taffner et al., 2020).

Among archaea, the halophilic archaea belonging to the class Halobacteria and phylum Euryarchaeota have significant economic importance due to their wider adaptability to salinity levels for growth (1.5 M NaCl to saturation) (Oren, 2014; Naitam and Kaushik, 2021). Halophilic archaea are natural inhabitants of the hypersaline environment of salt lake and salt evaporation ponds (Oren, 2014, 2019). Halophilic archaea *Haloferax* sp. strain NARS9, isolated from the solar salterns from the coast of Jeddah, Saudi Arabia, ameliorated the cobalt heavy metal stress and improved grain yield in wheat (Hagagy et al., 2023). Halophilic archaea found in the rhizosphere of plants in high-salinity areas can be assessed for their potential to alleviate salinity stress and enhance crop growth and productivity in cultivated regions affected by salinity. In the pursuit of exploring such possibilities, 28 halophilic archaea were isolated and characterized from bulk soil, water bodies, and rhizosphere of wild vegetation in the saline desert of Rann of Kutch, Gujarat, India. The salinity levels in this region ranged from 1.19 to 106.7 dSm-1, and the pH varied from 7.40 to 10.15 (Yadav et al., 2015). Most of the isolates belonged to 16 genera, viz. *Halobacterium*, *Halococcus, Halolamina, Haladaptatus, Haloarcula, Haloferax, Halogeometricum, Halopenitus, Halosarcina, Halostagnicola, Haloterrigena, Halorubrum, Natrialba, Natrinema, Natronoarchaeum,* and *Natronomonas*. In many of the isolates belonging to these 16 genera, solubilization of inorganic phosphorous was reported (Yadav et al., 2015). Studies on the population dynamics of halophilic archaea in different samples revealed seasonal variation. The highest and lowest diversity and population of archaea were observed in winter and autumn, respectively, whereas some of the archaea were season-specific (Yadav et al., 2019). Furthermore, in lab-scale studies, we observed stimulation of Wheat and Bajara germination upon inoculation of some of these isolates of halophilic archaea in a saline soft agar medium having electrical conductivity (EC) ranging from 6.8 to 8.4 dSm^{-1}.

Hence, a hypothesis can be proposed that halophilic archaea inhabiting the rhizosphere of wild vegetation in hypersaline soils of Rann of Kutch, Gujarat, India, may have developed a mutualistic relationship with the plant system. It is likely that they assist in the establishment and growth of the plants by mitigating the detrimental effects of salinity. However, to date, very few significant findings are available which can prove that halophilic archaea can promote plant growth by alleviating the harmful effects of salinity.

Based on soil EC, the saline soils are classified as slightly saline (4.0–8.0 dSm^{-1}), moderately saline (8–30 dSm^{-1}), and strong saline (>30.0 dSm^{-1}) (Gorji et al., 2020). The optimal range of soil EC for the growth of crops ranges from 1 to 2 dSm^{-1}, and an increase in soil EC from slightly to strongly saline significantly reduces crop growth and productivity (Sadaty and Nazari, 2021). The EC of soil in different regions of Rann of Kutch varies from

1.19 to 106.7 dSm^{-1} (Yadav et al., 2019). The halophilic archaea in our previous study were isolated from barren soil (EC >75.25 dSm^{-1}) and rhizosphere of wild vegetation growing in soil having EC ranging from 4.79 to 34.2 dSm^{-1} (Yadav et al., 2019). In this study, the ability of halophilic archaeal isolates to thrive in moderately saline soil was examined. Additionally, their potential as bioinoculants for enhancing wheat growth was explored through nutrient solubilization, phytohormone production, and mitigation of salinity-induced oxidative stress.

2. Materials and methods

2.1. Procurement of halophilic archaea and quantification of their growth

In total, 28 halophilic archaea previously isolated from the rhizosphere of wild plants growing in the hypersaline region of the Rann of Kutch, Gujarat, India, were procured from the microbial culture collection of the Division of Microbiology, Indian Agricultural Research Institute, New Delhi, India. All the isolates were cultured in the liquid broth of a modified DSMZ 1184 medium, and their growth was quantified in terms of μg protein ml^{-1}. The composition of the DSMZ 1184 growth medium was modified and standardized for culturing of halophilic archaea inhabiting plant rhizosphere. The modified media used in this study was called the halophilic rhizospheric archaea (HRA) medium. Its composition per liter included the following: 1.0 g of sodium pyruvate, 1.0 g of yeast extract, 80.0 g of NaCl, 32.5 g of $MgCl_2.6H_2O$, 50.8 g of $MgSO_4.7H_2O$, 5.0 g of KCl, 0.25 g of $NaHCO_3$, 1.0 g of $NaNO_3$, 0.8 g of $CaCl_2.2H_2O$, 0.05 g of KH_2PO_4, 0.03 g of NH_4Cl, traces of $FeSO_4.7H_2O$, traces of $MnSO_4.7H_2O$, and 20 g of agar. pH was adjusted to 7.4 with a 1 M Tris base, and the final EC of the media was 119.8 dSm^{-1}. The stock solution of NaHCO3 and sodium pyruvate was filter-sterilized and added aseptically to the autoclaved HRA medium. Approximately 1 ml of actively growing inoculum containing 10^8 CFU ml^{-1} of the respective isolates was inoculated in the 50 ml HRA broth and incubated at 37 °C at 130 rpm. After 10 d of incubation, the 5 ml of culture broth was centrifuged at 7,500 *g* for 10 min, and the pellet was used for quantification of protein by Bradford's method (Marion, 1976). The amount of protein in the culture was extrapolated by comparison with a standard curve prepared using different concentrations of bovine serum albumin (BSA).

2.2. Evaluation of PGP attributes

2.2.1. Solubilization of P, K, and Zn

All 28 halophilic archaeal isolates were assessed qualitatively and quantitatively for solubilization of phosphorus (P), potassium (K), and zinc (Zn). The HRA medium was modified by adding 5.0 g L^{-1} tricalcium phosphate to estimate P solubilization (HPS medium), and KCl was replaced with 5.0 g L^{-1} potassium aluminum silicate to estimate K solubilization (HKS medium). Similarly, Zn solubilization was quantified using two sets of HRA medium supplemented with zinc oxide and zinc carbonate, respectively (added at 1.0 gL^{-1}) (HZS medium). For qualitative estimation of P, K, and Zn solubilization, 10 μl of log phase cultures were spot-inoculated on respective modified HRA agar and incubated at 37 °C. The formation of the halo zone around colonies was recorded periodically until the 10th day of incubation and the D/D ratio was calculated, i.e., the diameter of the zone of solubilization/colony diameter. The cultures which solubilized the P, K, and Zn with a D/D ratio higher than one were selected for quantifying the extent of their solubilization. For this, 1 ml inoculum (10^8 CFU ml^{-1}) of the selected cultures was inoculated in 50 ml (for P solubilization) and 100 ml (for K and Zn solubilization) of respective HRA broth and incubated at 37 °C at 130 rpm. After 10 d of incubation, the pH of the culture broth was recorded and subjected to centrifugation at 10, 000 *g* for 5 min. The supernatant was used for quantitative estimation of soluble P, K, and Zn by the ascorbic acid method (Yadav et al., 2015), flame photometer (Banerjee and Prasad, 2020), and atomic absorption spectrophotometer (ZEEnit 700 P, Analytik Jena, Gmbh) (Saravanan et al., 2004), respectively. The experiment was performed in triplicates, and un-inoculated control was maintained.

2.2.2. Quantification of indole-3-acetic acid production

The production of indole-3-acetic acid (IAA) by 28 isolates of halophilic archaea was quantified by culturing them in HRA broth supplemented with L-tryptophane (at 500μg ml^{-1}). The 50 ml broth was inoculated with 1 ml of actively growing inoculum (10^8 CFU ml^{-1}) and incubated at 37 °C for 10 d at 130 rpm. Following incubation, the culture was centrifuged at 5,500 *g* for 10 min, and 2 ml supernatant was used for spectrophotometric estimation of IAA production by Salkowski's reagent method (Goswami et al., 2014). The concentration of IAA in the samples was inferred by comparison with the standard curve. The un-inoculated medium was used as blank, and the experiment was conducted in triplicates.

2.3. Growth and PGPR studies in soil extract medium

2.3.1. Preparation of HSE medium

Plant growth-promoting rhizobacteria (PGPR) play a big role in the mitigation of abiotic stresses by improving the expansion of soil colonization by plant roots. This can be reflected in higher affordability to retain the needed nutrients for plant growth and development (Širić et al., 2022). To determine whether the halophilic archaea can grow in soils having slight (4.0 to 8.0 dsm^{-1}) to moderate (8.0 to 30.0 dsm^{-1}) salinity, a modified halophilic broth was prepared using soil extract, where the water component was replaced with soil extract. The soil extract was prepared from the soil sample collected from a wheat field (15 cm depth) located at the village Chhapra Khera (29°40′42.3″N and 77°02′50.7″E), Karnal, Haryana, India. The soil was sandy loam in texture with an EC of 6.2 dsm^{-1}, pH 8.1, total carbon: 0.48 %, total nitrogen: 0.051%, exchangeable K: 173.61 mg Kg^{-1}, and available P: 4.21 mg Kg^{-1}. For the preparation of soil extract, 400 g of fine soil was mixed with 1600 ml of tap water and

mixed thoroughly to make a uniform solution. The mixture was heated at 121°C for 15 min. After cooling to room temperature, the mixture was filtered through a sterile muslin cloth followed by filter paper (Whatman No. 1). The filtrate was used as a water component in the preparation of halophilic broth. The HRA broth was modified to develop halophilic soil extract (HSE) broth having EC and nutrient mineral composition (gL^{-1}) as shown in Table 1. The composition of major mineral ingredients (NaCl, $MgCl_2.6H_2O$, $MgSO_4.7H_2O$, KCl, $NaHCO_3$, $NaNO_3$, and $CaCl_2.2H_2O$) was subjected to change to achieve desired EC levels, and the composition of remaining minor mineral nutrients (KH_2PO_4, NH_4Cl, FeSO4.7H2O, and MnSO4.7H2O) was kept constant. The medium was denoted as HSE-1 to HSE-9 (EC: 7.13–30.84 dsm^{-1}). HRA medium (EC: 119.8 dsm^{-1}) was used as a reference control for comparing the growth and PGP properties of selected halophilic archaea. The HSE broth (HSE-1 to HSE-9) was used to quantify the growth and PGP attributes of *H. pelagica* CDK2.

2.3.2. Growth, nutrient solubilization (p, k, and zn), and IAA production by a selected halophilic archaeon in different strength HSE broth

Based on the results of the experiment as described in Section 2.2, the best performing halophilic archaeon was selected for evaluating its growth, nutrient solubilization (P, K, and Zn) potential, and IAA production at different strengths of EC in HSE broth. The growth was quantified by estimating protein by Bradford's protein assay (Marion, 1976) as described above in Section 2.1. For quantifying IAA production and the solubilization of P, K, and Zn, the HSE broth was amended with tryptophan, tricalcium phosphate, potassium aluminum silicate, ZnO, and $ZnCO_3$ similarly as described above in Section 2.1 for the modification of HRA medium. The quantification of IAA production and P, K, and Zn solubilization was carried out as per the method described in Section 2.1.

2.3.3. Inoculum preparation for in planta studies

The inoculum for *in planta* studies was raised by culturing *H. pelagica* CDK2 in 250 ml of HRA1 broth for 15 days. The exponentially growing culture was centrifuged at 7,500 *g* for 15 min, and the supernatant was discarded. The pellet was washed twice with phosphate buffer saline (PBS) whose electrical conductivity was maintained at 8 dSm^{-1}. The washed pellet was suspended in PBS (prepared using soil extract instead of water; EC: 8dsm^{-1}) to maintain the cell density of $\sim 10^9$ cells ml^{-1}. The PBS with archaeal cells was mixed with charcoal (sterilized at 121°C for 20 min for 3 consecutive days and buffered with calcium carbonate) and homogenized. This mixture was air-dried overnight at room temperature under sterile conditions and was coated over wheat seeds immediately before sowing in the pots. For the soft mineral salt agar experiment, the seeds were soaked directly in the PBS with archaeal cell suspension for 30 min and were sown in the soft agar tubes.

2.3.4. Soft agar experiment

Five wheat cultivars, namely two tolerant (K65 and KRL210) and three susceptible (HD2380, HD3086, and HD2687), were procured from ICAR-Indian Institute of Wheat and Barley Research, Karnal, India. A 21-day wheat-halophilic archaea interaction experiment was carried out in soft agar test tubes under controlled conditions to assess the effect of inoculating *H. pelagica* CDK2 on seed germination. Seeds of all the wheat cultivars were treated with cells of *H. pelagica* CDK2 suspended in PBS (halophilic archaeal soil extract phosphate buffer saline suspension; EC: 8 dsm^{-1}) for 30 min. The mineral salt soil extract soft agar (MSSE) was prepared by dissolving various macro- and micronutrients, vitamins, and amino acids in previously prepared soil extract as per composition. The composition of MSSE was as follows: a) macronutrients (mg L^{-1}): 1650.0 NH4NO3, 332.0 $CaCl_2$, 180.690 $MgSO_4$, 1900.0 KNO3, and 170.0 KH_2PO_4, b) micronutrients (mg L^{-1}): 6.20 H_3BO_3, 0.025 $CoCl_2.6H_2O$, 0.025 $CuSO_4{\cdot}5H_2O$, 37.30 disodium EDTA dihydrate, 27.800 $FeSO_4.7H_2O$, 16.90 $MnSO_4{\cdot}H_2O$, 0.213 $Na_2MoO_4{\cdot}2H_2O$, 0.830 KI, 8.60, and $ZnSO_4.7H_2O$, c) vitamins (mg L^{-1}): 100.0 myoinositol, 0.50 nicotinic acid, 0.50 pyridoxine HCl, and 0.10 thiamine HCl, and d) amino acid (mg L^{-1}): 2.00 glycine and agar 8.0 gL^{-1} (pH 6.8 and EC: 8 dSm^{-1}). The treated seeds were placed in a 50 ml test tube having 35 ml of MSSE soft agar medium (Filek et al., 2010). The tubes were incubated in the dark until seed germination and were later transferred to a glasshouse of Phytotron facility, IARI, New Delhi, under controlled conditions (glasshouse conditions were as follows; temperature: 20-24° C, humidity: 50%, and white LED lights, 15000 lux with 10 h of daily illumination). The un-inoculated control was maintained, and the experiment was carried out in three replications. Observations on vegetative growth were recorded after 21 days of incubation.

2.3.5. Mesocosm study for plant–microbe interaction

The wheat–*H. pelagica* CDK2 interaction was further evaluated in a pot experiment to verify the effect of inoculating *H. pelagica* CDKA on wheat growth and yield parameters in an un-sterile rooting medium. The study was conducted in the net house of the Division of Microbiology, ICAR-Indian Agricultural Research Institute, New Delhi. The treatment included two salt-tolerant (K65 and KRL210) and three susceptible (HD2380, HD3086, and HD2687) wheat cultivars in triplicates. The seeds were coated with the halophilic archaeal-charcoal-based inoculum (as described in section 2.4) and were sown in 14-inch pots each containing 10 kg of un-sterile soil. The electrical conductivity of the soil was maintained at 8 dSm^{-1} using a mineral salt solution. An un-inoculated control was maintained for all the wheat cultivars in triplicates. The pots were fertilized with the recommended dose of NPK (120:60:60). The full dose of P, K, and 50% of N was applied as a basal dose before sowing. The remaining half dose of nitrogen was applied in 2 split doses at 21 d and 45 d. Observations on vegetative growth, osmolyte accumulation, and biochemical and yield parameters were recorded after 45 days of sowing and at the time of harvesting.

TABLE 1 Composition and salinity levels (EC) of halophilic soil extract (HSE) broth.

Halophilic soil extract broth	Electrical conductivity (dSm^{-1})	Media mineral composition (g L^{-1})						
		NaCl	$MgCl_2.6H_2O$	$MgSO_4.7H_2O$	KCl	$NaHCO_3$	$NaNO_3$	$CaCl_2.2H_2O$
HSE-1	7.13	8.00	3.25	5.08	0.50	0.0250	0.100	0.08
HSE-2	9.73	8.88	3.61	5.64	0.555	0.0277	0.111	0.088
HSE-3	12.20	10.00	4.06	6.35	0.625	0.0310	0.125	0.100
HSE-4	16.59	11.40	4.64	7.25	0.71	0.0357	0.140	0.114
HSE-5	18.46	13.33	5.41	8.46	0.83	0.0416	0.166	0.133
HSE-6	21.29	16.00	6.50	10.16	1.00	0.050	0.200	0.16
HSE-7	24.8	20.00	8.125	12.7	1.25	0.0625	0.250	0.20
HSE-8	27.63	26.60	10.83	16.93	1.66	0.083	0.330	0.266
HSE-9	30.84	40.00	16.25	25.4	2.50	0.125	0.500	0.40
[1]HRA-control	119.8	80.00	32.5	52.8	5.00	0.250	1.00	0.80

[1]HRA, halophilic rhizospheric archaea medium.

2.4. Estimation of vegetative and biochemical parameters

2.4.1. Vegetative parameters

The shoot and root length (cm) and shoot and root biomass (g) were measured manually using standard laboratory protocols. The plants at 21 d from MSSE and at 45 d from pot experiments were sampled destructively. The roots were washed thoroughly with water to remove adhering medium and soil, respectively. The above-ground part (shoots) was separated from the roots and allowed to air dry for 1 h. The fresh weight (biomass) and the length of the shoot and roots were measured manually with a balance and sliding caliper, respectively.

2.4.2. Quantification of crude protein

Crude protein was extracted from 100 mg wheat leaves homogenized with the 5 ml salt-alkaline phosphate extraction buffer (0.1 M NaOH in 3.5% NaCl; pH 7.4). The homogenate was incubated at 60 °C for 90 min followed by centrifugation at 4,000 *g* for 20 min at room temperature. A total of 1 ml of supernatant was used for the quantification of crude protein following Bradford's quantitative protein extraction method (Marion, 1976). The protein content was expressed as μg protein mg^{-1} of wheat tissue. The quantity of protein in the sample was extrapolated from a standard curve prepared using different concentrations of bovine serum albumin (BSA).

2.4.3. Quantification of total chlorophyll

Chlorophyll from the leaf sample was estimated using the DMSO method (Blanke, 1992). A 100 mg fresh plant leaf sample was placed in a 100 ml volumetric flask containing 10 ml DMSO (Dimethyl sulfoxide). The flask was allowed to stand overnight before measuring the spectroscopic absorbance at 663 and 645 nm. DMSO without leaf sample was used as blank, and un-inoculated wheat leaf was used as control. The total chlorophyll content of the wheat leaf was calculated using the formula given below.

$$mg\ of\ chlorophyll\ g^{-1}\ leaf\ tissue = 20.2\,(A645) + 8.02\,(A663)^{*}\frac{volume\ of\ DMSO}{1000^{*}weight\ of\ leaf\ sample}$$

2.4.4. Quantification of total sugars and proline accumulation

Total sugars in wheat leaf samples were quantified using the phenol-sulfuric acid method (Dubois et al., 1951). D-glucose was used as a standard for the preparation of the standard curve, and a run without a sample was used as a blank. The amount of proline synthesized in wheat seedlings in response to salinity stress was estimated using an acid ninhydrin-sulfosalicylic acid method as described by Ábrahám and László Erdei (2010). A blank was run without the sample, and a standard graph was prepared using L-proline.

2.4.5. Quantification of antioxidant enzyme activity

The antioxidant enzymes, such as ascorbate peroxidase (APox), catalase (CAT), and superoxide dismutase (SOD) accumulation, were quantified in wheat leaves. The enzyme extract was prepared by freezing 1 g of wheat leaf sample in liquid nitrogen to arrest the proteolytic activity followed by grinding with 10 ml of extraction buffer (0.1 M phosphate buffer, pH 7.5, containing 0.5 mM EDTA with 1 mM ascorbic acid). The mixture was passed through four-layered muslin cloth followed by centrifugation at 15,000 *g* for 20 min. The resultant filtrate was used as an enzyme in the enzyme assay. The APox activity was determined by measuring the decrease in ascorbic acid content as described by Nakano and Asada (1981).

Superoxide dismutase activity was quantified by measuring the decrease in the absorbance of formazan generated by superoxide radicles and nitroblue tetrazolium (NBT) dye as per the method described by Dhindsa et al. (1981). A unit of SOD activity was expressed as the amount of enzyme, which reduced the absorbance to 50% as compared to tubes lacking enzyme. Catalase antioxidant enzyme activity was analyzed by calculating the amount of H_2O_2 decomposed by comparing it to a standard curve of known concentrations of hydrogen peroxide (Aebi, 1984).

2.4.6. Estimation of root architecture parameters at harvesting

Analysis of changes in root physiological parameters at the harvesting was performed using a root scanner LA2400 Instruments REGENT, equipped with WinRhizo software. Freshly harvested roots were washed under running tap water to remove all the soil particles attached to the roots. After washing, the roots were kept immersed in water in a 500 ml beaker and taken for root imaging. Roots were placed horizontally on the scanner block filled with a minimal amount of distilled water to keep the roots submerged. The entangling of roots was removed using the forceps.

2.5. Quantification of yield parameters at harvest

To quantify yield parameters, such as grain yield per plant and grains per spike, the plants were harvested after grain filling and drying. The spikes were manually separated from the harvested plants, and the data for grain content per spike were recorded. The grains separated from spikes of a single plant were combined to extrapolate grain yield per plant manually.

2.6. Statistical analysis of data

All the experiments were carried out in triplicates, and statistical analysis was performed using WASP 2.0 (Web Agri Stat Package, Indian Council of Agricultural Research, India). The data were subjected to ANOVA, and the least significant differences (LSDs) at $P \leq 0.05$ and $P \leq 0.01$ for *in planta* and *in vitro* studies, respectively, among means were compared using standard deviation.

3. Results

3.1. Growth of halophilic archaea in halophilic broth

All 28 halophilic archaeal isolates exhibited growth in the HRA broth. The production of protein after 10 days varied significantly among these isolates (Supplementary Table 1). The protein production in the halophilic broth ranged from 122.371 μg ml^{-1} to 271.80 μg ml^{-1}. The highest protein production was observed in *Halococcus hamelinensis* IARI-SNS2 (271.8 μg ml^{-1}), followed by *Halococcus* sp. IARI-BGAK2 (268.94 μg ml^{-1}), *Natrialba* sp. IARI-SGAB2 (257.51 μg ml^{-1}), *Halolamina pelagica* CDK2 (252.65 ± 8.33 μg ml^{-1}), *Haloferax volcanii* IARI-CFAB4 (254.08 ± 1.81 μg ml^{-1}), and *Halogeometricum borinquense* IARI-WRAK9 (255.22 ± 7.96 μg ml^{-1}). The protein production of *H. pelagica* IARI-CDK2, *H. volcanii* IARI-CFAB4, and *H. borinquense* IARI-WRAK9 did not significantly differ from each other (252.65, 253.08, and 255.22 μg ml^{-1}, respectively). The lowest growth in terms of protein production was observed in *Natrinema altunense* IARI-WRAK5 (122.37 μg ml^{-1}).

3.2. Quantification of plant growth-promoting properties of halophilic archaea

3.2.1. Qualitative estimation of P, K, and Zn solubilization

Based on the halo zone formation observed around spot-inoculated colonies in specific solubilization media (HPS, HKS, and HZS medium), we qualitatively assessed the ability of 28 halophilic archaea to solubilize phosphorus (P), potassium (K), and zinc (Zn) (Supplementary Table 2). Among the isolates, 17 showed significant zones of P solubilization. The highest D/D ratio (cm) for P solubilization was observed in *H. pelagica* CDK2 (1.8), followed by *Halobacterium* sp. IARI-SNS3 (1.75), *Natronoarchaeum mannanilyticum* IARI-SSAB3 (1.6), *H. borinquense* IARI-WRAK9 (1.6), *Halolamina pelagica* IARI-CSK1 (1.6), and *Natronomonas pharaonis* IARI-MAAB4 (1.6). The halophilic archaea *N. mannanilyticum* IARI-SSAB3, *H. borinquense* IARI-WRAK9, *H. pelagica* IARI-CSK1, and *N. pharaonis* IARI-MAAB4 exhibited similar D/D ratios for P solubilization. Conversely, the lowest D/D ratio was observed in *Halorubrum* sp. IARI-WRAB4 (1.16), followed by *Halostagnicola kamekurae* IARI-TWAK7 (1.2) and *Halosarcina* sp. IARI-WRAB3 (1.25), respectively. Furthermore, 21 isolates displayed significant K solubilization zones, with D/D ratios ranging from 1.25 to 1.68. The highest D/D ratios for K solubilization were recorded in *Haloterrigena* sp. IARI-SOAB2, *N. pharaonis* IARI-MAAB4, and *H. pelagica* CDK2 (1.68, 1.66, and 1.65, respectively). In contrast, only a few isolates demonstrated the ability to solubilize Zn, with six isolates solubilizing ZnO and three isolates solubilizing ZnCO3 in the respective HZS medium. The D/D ratio for all the Zn solubilizing isolates was just above 1, indicating the formation of very small clearing zones around the spot-inoculated colonies.

3.2.2. Quantitative estimation of P, K, and Zn solubilization and effect on medium ph

We conducted quantification of P solubilization and measured the reduction in pH of the medium for the selected 17 isolates, grown in HPS broth. On the 10th day of growth, a significant decrease in pH was observed, ranging from 3.6 to 4.8, compared to the initial pH of 7.2. The greatest reduction in pH was observed in *Haloarcula tradensis* IARI-WRAK3 and *H. pelagica* CDK2 (pH: 3.6), while the least reduction occurred in *Halorubrum* sp. IARI-WRAB4 and *Haloarcula argentinensis* IARI-SOAB1 (pH: 4.8) (Figure 1A). Regarding P solubilization in HPS broth, the values

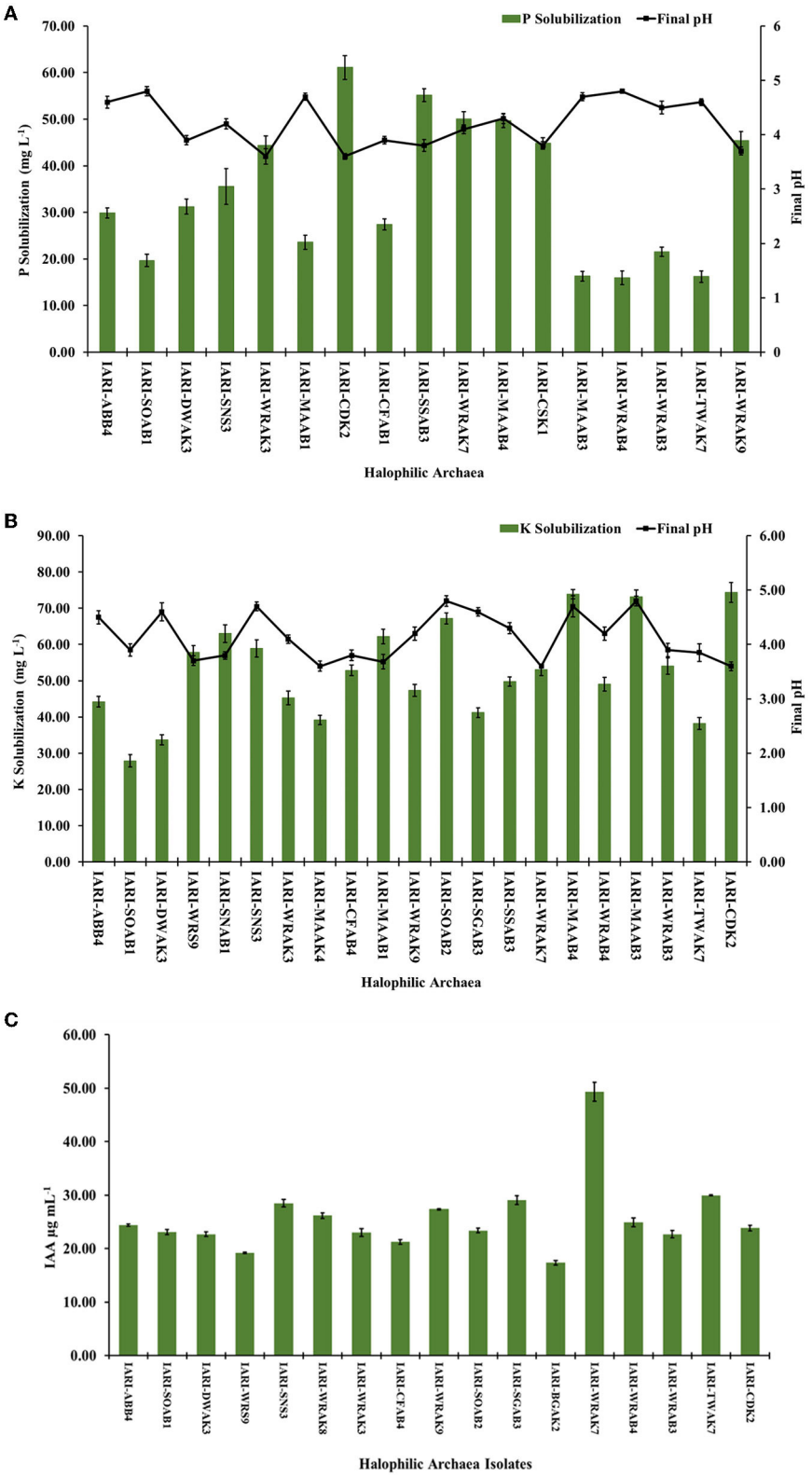


FIGURE 1
Quantification of **(A)** P and **(B)** K solubilization and reduction in pH of the respective modified HRA media by selected isolates of halophilic archaea after 10 d of growth (LSD $p \leq 0.05$: for P and K solubilization between isolates is 2.98 and 2.544, respectively; for pH reduction: for P and K solubilization between isolates is 0.133 and 0.165, respectively); **(C)** quantification of indole acetic acid production by the selected halophilic archaea isolates grown in HRA broth supplemented with L-tryptophane (LSD $p \leq 0.05$: 1.46; error bar denotes standard deviation from the mean).

TABLE 2 Quantification of growth (protein mg ml^{-1}), nutrient solubilization (P, K, and Zn), and indole acetic acid production by *Halolamina pelagica* CDK2 in different strength halophilic soil extract (HSE) broth.

HSE Broth	Electrical conductivity (dSm^{-1})	Growth (protein mg ml^{-1})			Nutrient solubilization (mg L^{-1})*				IAA* production (μg ml^{-1})
		8 d	15 d	21 d	P	K	ZnO	$ZnCO_3$	
HSE-1	7.13	15.22 ± 0.02	28.25 ± 0.89	46.11 ± 0.86	8.12 ± 0.20	ND	ND	ND	2.64 ± 0.03
HSE-2	9.73	29.01 ± 0.52	32.14 ± 0.90	56.14 ± 0.48	9.24 ± 0.30	3.67 ± 0.04	ND	ND	3.63 ± 0.11
HSE-3	12.20	43.70 ± 0.59	51.97 ± 0.69	86.17 ± 0.22	10.48 ± 0.60	4.92 ± 0.12	ND	ND	4.92 ± 0.15
HSE-4	16.59	52.85 ± 0.54	66.91 ± 0.52	97.71 ± 1.97	12.89 ± 0.30	8.41 ± 0.37	1.25 ± 0.02	ND	5.89 ± 0.12
HSE-5	18.46	51.60 ± 1.63	80.77 ± 0.49	103.11 ± 4.26	14.76 ± 0.27	12.49 ± 0.42	1.7 ± 0.03	ND	7.01 ± 0.032
HSE-6	21.29	59.85 ± 1.34	86.68 ± 3.18	110.65 ± 2.92	17.16 ± 0.41	18.38 ± 0.58	1.93 ± 0.03	ND	8.02 ± 0.11
HSE-7	24.8	70.69 ± 2.14	103.45 ± 2.45	122.48 ± 0.10	22.63 ± 0.70	21.35 ± 0.20	2.31 ± 0.04	ND	11.63 ± 0.35
HSE-8	27.63	106.77 ± 0.65	143.25 ± 5.57	171.08 ± 6.22	27.71 ± 0.88	27.11 ± 0.41	2.96 ± 0.05	ND	15.42 ± 0.40
HSE-9	30.84	193.31 ± 5.32	209.34 ± 7.45	246.48 ± 8.35	31.44 ± 1.17	42.09 ± 1.44	3.54 ± 0.10	2.47 ± 0.02	16.98 ± 0.20
**HRA-control	119.8	220.80 ± 2.35	243.25 ± 10.40	263.45 ± 10.10	61.10 ± 2.56	74.36 ± 2.74	7.21 ± 0.29	5.27 ± 0.12	23.85 ± 0.52
LSD$p \leq 0.01$		Factor A (EC Level): 5.206; Factor B (Days of incubation: 2.859; Interaction (AxB): 9.027	1.23	1.78	2.17	0.012	0.55		

*The nutrient solubilization (P, K, and Zn mg L^{-1}) and IAA μg ml^{-1} were quantified after 10 d of incubation. *HRA, halophilic rhizospheric archaea medium.

ranged from 15.98 ± 1.46 to 61.10 ± 2.56 mg L^{-1} among the 17 isolates. *H. pelagica* IARI-CDK2 demonstrated the highest P solubilization, significantly measuring 61.10 ± 2.56 mg L^{-1}. Close behind were *N. mannanilyticum* IARI-SSAB3 with 55.17 ± 1.36 mg L^{-1}, *Halogeometricum rufum* IARI-WRAK7 with 50.04 ± 1.56 mg L^{-1}, and *N. pharaonis* IARI-MAAB4 with 49.69 ± 1.45 mg L^{-1} (as depicted in Figure 1A). Conversely, the lowest P solubilization was observed in *Halorubrum* sp. IARI-WRAB4 (15.98 ± 1.46 mg L^{-1}), *H. kamekurae* IARI-TWAK7 (16.20 ± 1.21 mg L^{-1}), *Halopenitus persicus* IARI-MAAB3 (16.30 ± 1.06 mg L^{-1}), and *H. argentinensis* IARI-SOAB1 (19.68 ± 1.35 mg L^{-1}) (Figure 1A).

Similarly, a significant reduction in the pH of HKS broth was observed on the 10th day of incubation, compared to the initial pH of 7.4, during the solubilization of P. The highest pH reduction was observed in *Haloferax* sp. IARI-MAAK4, *H. rufum* IARI-WRAK7, and *H. pelagica* CDK2 (pH: 3.6), followed by *Haloferax alexandrinus* IARI-MAAB1 (pH: 3.68) and *Natrinema* sp. IARI-WRS9 (pH: 3.7) (as depicted in Figure 1B). Conversely, the least decrease in pH was observed in *Halopenitus persicus* IARI-MAAB3 and *Haloterrigena hispanica* IARI-SGAB3 (pH: 4.8), followed by *Halobacterium* sp. IARI-SNS3 and *N. pharaonis* IARI-MAAB4 (pH: 4.7) (refer to Figure 1B). For potassium solubilization in HKS broth, the halophilic archaea exhibited a range of solubilization from 27.89 ± 0.30 to 74.36 ± 2.74 mg L^{-1}. *H. pelagica* CDK2 (74.36 ± 2.74 mg L^{-1}), *N. pharaonis* IARI-MAAB4 (73.85 ± 1.26 mg L^{-1}), and *H. persicus* IARI-MAAB3 (73.16 ± 1.84 mg L^{-1}) solubilized a significantly high amount of K. On the other hand, *H. argentinensis* IARI-SOAB1 (27.89 ± 0.30 mg L^{-1}), *Haloarcula* sp. IARI-DWAK3 (33.64 ± 0.39 mg L^{-1}), and *H. kamekurae* IARI-TWAK7 (38.19 ± 0.06 mg L^{-1}) solubilized a significantly low amount of K (Figure 1B).

The solubilization of Zn by six isolates in the HZS medium using ZnO as the source ranged from 4.96 ± 0.03 mg L^{-1} to 7.21 ± 0.29 mg L^{-1}. Additionally, in the HZS medium with ZnCO3 as the source, three positive isolates exhibited Zn solubilization ranging from 4.91 ± 0.15 to 5.84 ± 0.25 mg L^{-1}. Notably, *H. borinquense* IARI-WRAK9, *H. pelagica* CDK2, and *Natrinema pallidum* IARI-WRAK8 were capable of solubilizing both insoluble sources of Zn (ZnO and ZnCO3), whereas *H. alexandrinus* IARI-MAAB1, *N. pharaonis* IARI-MAAB4, and *Halorubrum* sp. IARI-WRAB4 solubilized only ZnO. Among the ZnO-containing HZS media, *H. pelagica* CDK2 exhibited the maximum quantity of

Zn solubilization (7.21 ± 0.29 mg L^{-1}), which was statistically comparable to *Halorubrum* sp. IARI-WRAB4 (7.14 ± 0.21 mg L^{-1}) and significantly higher than IARI-MAAB4 (5.72 ± 0.09 mg L^{-1}), IARI-MAAB1 (5.28 ± 0.98 mg L^{-1}), IARI-WRAK8 (5.4 ± 0.20 mg L^{-1}), and IARI-WRAK9 (4.96 ± 0.23 mg L^{-1}). In contrast, *N. pallidum* IARI-WRAK8 exhibited the highest solubilization of Zn in the HZS media containing ZnCO3 (5.84 ± 0.25 mg L^{-1}), which was significantly higher than the solubilization by *H. pelagica* IARI-CDK2 (5.27 ± 0.12 mg L^{-1}) and IARI-WRAK9 (4.91 ± 0.15 mg L^{-1}). A significant reduction in pH was observed in the HRA medium containing ZnO and ZnCO3 compared to the initial pH of 7.4, ranging from 3.6 ± 0.15 to 4.2 ± 0.13.

3.2.3. Phytohormone production (IAA production)

The ability of all halophilic archaea isolates to produce the phytohormone IAA (indole-3-acetic acid) was assessed by culturing them in HRA media supplemented with tryptophan. Out of the isolates, 17 exhibited significant production of IAA, ranging from 17.33 ± 0.43 μg ml^{-1} to 49.31 ± 1.79 μg ml^{-1} (Figure 1C). Among them, the highest amount of IAA was produced by *H. rufum* IARI-WRAK7 (49.31 ± 1.79 μg ml^{-1}), which was significantly greater than the IAA production of all other isolates. Following closely were *H. kamekurae* IARI-TWAK7 (29.97 ± 0.79 μg ml^{-1}), *H. hispanica* IARI-SGAB3 (29.06 ± 0.82 μg ml^{-1}), and IARI-SNS3 (28.49 μg ml^{-1}). The isolate *Halolamina pelagica* CDK2, which exhibited significant solubilization of P, K, and Zn, also produced IAA (23.86 ± 0.52 μg ml^{-1}). On the other hand, *Halococcus* sp. IARI-BGAK2 produced the lowest amount of IAA, which was significantly measured at 17.33 ± 0.43 μg ml^{-1}.

3.2.4. Quantification of growth and plant growth-promoting properties of a selected halophilic archaeon in halophilic soil extract broth having different salinity concentrations

Based on the obtained results, *H. pelagica* CDK2 was chosen for further investigation. The study aimed to assess its ability to thrive in lower electrical conductivity (EC) conditions, compared to its natural habitat with EC ranging from 75.25 to 106.7 dSm^{-1}. Additionally, the study aimed to evaluate its potential in enhancing wheat growth by managing nutrient availability and mitigating salinity stress. A modified growth medium suitable for halophilic organisms, supplemented with soil extract (HSE), was utilized. The HSE medium was prepared with different levels of EC, as shown in Table 1. The growth and plant growth-promoting (PGP) attributes of *H. pelagica* CDK2 were quantified at 8-, 15-, and 21-day intervals, as outlined in Table 2. Observations revealed that *H. pelagica* CDK2 exhibited growth even at the lowest EC of 7.13 dSm^{-1}. Protein production by the haloarchaeon increased significantly as the electrical conductivity (EC) of the HSE broth increased (Table 2). Notably, at the highest EC level of 119.8 dSm^{-1}, *H. pelagica* CDK2 produced the highest amount of protein throughout the incubation period. Specifically, protein production reached 220.80 ± 2.35 μg ml^{-1}, 243.25 ± 10.40 μg ml^{-1}, and 263.45 ± 10.10 μg ml^{-1} at 8, 15, and 21 days, respectively (Table 2 and Figure 2A).

H. pelagica CDK2 exhibited the ability to solubilize insoluble tricalcium phosphate across various salinity levels, ranging from EC: 7.13 to 30.84 dSm^{-1} (HSE-1 to HSE-9). The solubilization of phosphorus (P) in different EC levels of HSE broth ranged from 8.12 ± 0.19 mg L^{-1} (EC: 7.13 dSm^{-1}) to 31.44 ± 1.17 mg L^{-1} (EC: 30.84 dSm^{-1}) after 10 days. The lowest values of P solubilization in HSE-1 broth (EC: 7.13 dSm^{-1}) were statistically similar to those observed in HSE-2, with a P solubilization of 8.12 ± 0.20 mg L^{-1} at an EC of 9.73 dSm^{-1}. However, a significant increase in P solubilization was observed as the EC level increased from 12.20 to 30.84 dSm^{-1}. The highest solubilization, reaching 31.44 ± 1.17 mg L^{-1}, was observed in HSE-9 with an EC of 30.84 dSm^{-1}. It is worth noting that the P solubilization in HSE-9 was significantly lower compared to the solubilization observed in the control HRA media (61.10 ± 2.56 mg L^{-1}) with an EC of 119.8 dSm^{-1} (Table 2). A similar pattern was observed for potassium (K) solubilization, with the exception that *H. pelagica* CDK2 did not exhibit K solubilization in the HSE-1 medium with the lowest EC of 7.13 dSm^{-1}. However, K solubilization began at a level of 3.67 ± 0.036 mg L^{-1} in HSE-2 with an EC of 9.73 dSm^{-1}, and this was statistically similar to the K solubilization (4.92 ± 0.12 mg L^{-1}) observed in HSE-3 with an EC of 12.20 dSm^{-1}. A significant increase in K solubilization was observed as the EC increased from 16.59 to 30.84 dSm^{-1}, reaching a maximum yield of 42.09 ± 1.44 mg L^{-1} in HSE-9 medium with an EC of 30.84 dSm^{-1}. However, this value was significantly lower than the K solubilization observed in the control HRA medium (74.36 ± 2.74 mg L^{-1}) with an EC of 119.8 dSm^{-1} (Table 2).

In contrast to P and K solubilization, the solubilization of zinc (Zn) by *H. pelagica* CDK2 in HSE media using ZnO as the source of Zn was not observed at lower EC levels of 7.13, 9.73, and 12.20 dSm^{-1} (HSE broth 1, 2, and 3, respectively). Solubilization of ZnO was statistically similar (ranging from 1.25 ± 0.02 to 2.96 ± 0.05 mg L^{-1}) in media with ECs ranging from 16.59 to 27.63 dSm^{-1} (HSE-4 to HSE-8). The maximum solubilization of zinc oxide (ZnO) was observed in the medium with an EC of 30.84 dSm^{-1}, specifically in the HSE-9 medium, with a solubilization level of 3.54 ± 0.10 mg L^{-1}. However, this value was significantly lower than the solubilization observed in the control HRA medium with an EC of 119.8 dSm^{-1}. Furthermore, *H. pelagica* CDK2 did not exhibit solubilization of zinc carbonate (ZnCO3) at any of the lower EC levels. It only showed solubilization in the medium with an EC of 30.84 dSm^{-1}, with a solubilization level of 2.47 ± 0.015 mg L^{-1}. Again, this value was significantly lower than the solubilization observed in the control HRA medium with an EC of 119.8 dSm^{-1} (Table 2).

The production of indole acetic acid (IAA) was observed at all EC levels in different HSE broths. There was a significant increase in indole-3-acetic acid (IAA) production with each subsequent increase in the electrical conductivity (EC) level, as indicated in Table 2. The IAA production in HSE broth supplemented with tryptophan ranged from 2.64 ± 0.027 μg ml^{-1} in HSE-1 medium with an EC of 7.13 dSm^{-1} to 16.98 ± 0.20 μg ml^{-1} in HSE-9 medium with an EC of 30.84 dSm^{-1} on the 10th day of incubation. Notably, the IAA production in the control HRA medium (23.85 ± 0.52 μg ml^{-1}) was significantly higher compared

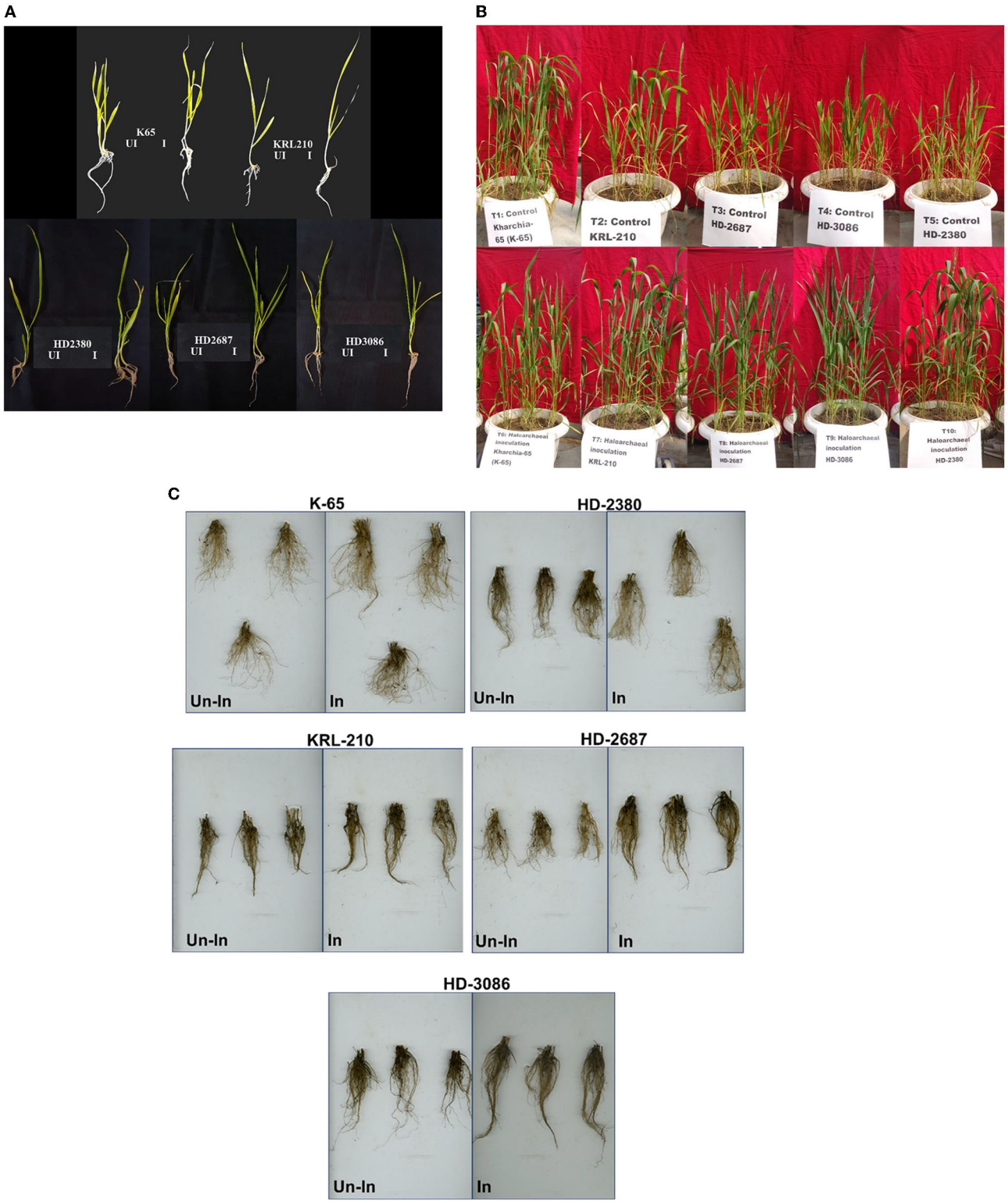


FIGURE 2
Wheat seedlings growth as influenced by inoculation of *Halolamina pelagica* CDK2 **(A)** at 21st day of seed germination in soft agar having EC of 8 dS m-1, **(B)** effect of inoculating *Halolamina pelagica* CDK2 on the growth of different wheat cultivars at 45th d of seed germination, and **(C)** effect of inoculating *Halolamina pelagica* CDK2 on root architecture of different wheat cultivars at harvesting (Un-In: un-inoculated; In: inoculated).

to the values observed in the HSE-9 medium (16.98 ± 0.20 μg ml^{-1}) (Table 2).

3.2.5. Effect of *H. pelagica* CDK2 inoculation on germination parameters of different wheat cultivars in MS-soft agar

Inoculation of the halophilic archaea *H. pelagica* CDK2 had a significant positive impact on the germination and initial vegetative growth of all wheat cultivars grown in soft agar (EC 8 dSm^{-1}) compared to the un-inoculated control (Figure 2A). The germination time of the inoculated wheat cultivars was significantly reduced by 2 to 3 days compared to the germination observed on the 8th day in the un-inoculated control treatment. Among the inoculated treatments, wheat cultivar K65 exhibited the fastest germination on the 5th day, followed by germination on the 6th day for all other cultivars. On the 21st day of germination, shoot and root growth parameters were measured (Supplementary Table 3). Inoculation resulted in a significant increase in the total shoot weight and length of all wheat cultivars compared to their respective un-inoculated treatments. The maximum percent increase in shoot weight due to inoculation was observed in wheat cultivar HD2687 (21.23%), followed by HD2380 (18.48%), K65 (16.96%), HD3086 (15.93%), and KRL210 (13.78%) compared to their respective un-inoculated wheat cultivars. Similarly, the maximum percent increase in shoot length due to inoculation was observed in wheat cultivar K65 (25.19%), followed by HD3086 (21.45%), HD2687 (18.80%), HD2380 (17.82%), and KRL210 (15.24%) compared to their respective un-inoculated wheat cultivars.

Likewise, inoculation of *H. pelagica* CDK2 in different wheat cultivars significantly improved the root growth parameters compared to their respective un-inoculated wheat cultivars. Inoculation significantly increased the percent root weight of wheat cultivar K65 by 67.18%, followed by HD3086 (47.06%), HD2687 (46.56%), KRL210 (42.30%), and HD2380 (42.22%) compared to their respective un-inoculated wheat cultivars. The number of lateral roots also increased compared to the un-inoculated control (Figure 2A). A similar effect was observed on total root length, and inoculation of *H. pelagica* CDK2 significantly increased the percent root length of wheat cultivar HD2380 by 39.93%, followed by HD2687 (37.81%), HD3086 (33.53%), K65 (16.45%), and KRL210 (14.62%) compared to their respective un-inoculated wheat cultivars.

3.3. Pot evaluation of the effect of inoculating *H. pelagica* CDK2 in different wheat cultivars

3.3.1. Shoot and root parameters on the 45th day of seed germination

Inoculation with *H. pelagica* CDK2 significantly increased the fresh shoot biomass and shoot length of all wheat cultivars compared to their respective un-inoculated treatments on the 45th day after seed germination (Table 3). The wheat cultivar HD3086 showed the maximum percent increase in shoot biomass due to inoculation (47.13%), followed by HD2380 (32.44%), KRL210

TABLE 3 Quantification of vegetative growth and yield parameters in different wheat cultivars (pot experiment) as influenced by inoculation of *H. pelagica* CDK2.

Cultivars	Root biomass (g)		Shoot biomass (g)		Root length (cm)		Shoot height (cm)		Grains per spike		Grain yield (g/plant)	
	UI**	I	UI	I	UI	I	UI	I	UI	I	UI	I
K65	3.09 ± 0.57	4.13 ± 0.22	32.29 ± 0.83	41.6 ± 1.46	21.86 ± 0.37	25.06 ± 0.46	69.63 ± 0.57	74.03 ± 0.21	49.67 ± 0.57	55.33 ± 1.52	3.47 ± 0.01	5.21 ± 0.04
KRL210	3.26 ± 0.38	4.53 ± 0.27	36.24 ± 0.67	47.97 ± 1.79	22.23 ± 0.10	25.16 ± 0.35	67.46 ± 0.76	74.43 ± 0.49	52.00 ± 1.01	56.00 ± 2.64	3.33 ± 0.12	4.92 ± 0.14
HD2380	1.89 ± 0.35	2.44 ± 0.45	26.20 ± 0.35	34.70 ± 2.02	22.55 ± 0.13	25.06 ± 0.47	66.73 ± 0.40	70.03 ± 0.28	45.33 ± 1.69	51.67 ± 1.15	2.83 ± 0.05	3.68 ± 0.05
HD3086	2.65 ± 0.42	4.03 ± 0.5	25.25 ± 0.59	37.15 ± 1.81	19.46 ± 0.11	27.48 ± 1.24	60.2 ± 0.96	65.8 ± 0.4	44.00 ± 1.0	52.67 ± 2.08	3.31 ± 0.08	4.59 ± 0.06
HD2687	2.09 ± 0.43	3.06 ± 0.35	24.83 ± 1.31	32.44 ± 1.04	15.03 ± 0.66	19.36 ± 0.92	59.5 ± 1.13	62.03 ± 0.15	48.33 ± 0.58	58.00 ± 2.01	2.70 ± 0.03	3.83 ± 0.05
LSD$p \leq 0.05$												
Cultivars A	0.487		1.675		0.723		0.788		1.992		0.084	
Treatment B	0.308		1.057		0.467		0.493		1.261		0.054	
Interaction AxB	0.683		2.366		1.03		1.108		2.825		0.114	

**UI, un-inoculated control; I, inoculated treatment.

(32.37%), HD2687 (30.65%), and K65 (28.81%) compared to their respective un-inoculated cultivars. Similarly, the maximum percent increase in shoot length due to inoculation was observed in wheat cultivar KRL210 (10.32%), followed by HD3086 (9.30%), K65 (6.32%), HD2380 (4.94%), and HD2687 (4.25%) over their respective un-inoculated treatments (Table 3). The differences in shoot biomass and shoot height in response to halophilic archaeal inoculation were statistically significant among the wheat cultivars at $p \leq 0.05$. A representative image of the pot experimental study is shown in Figure 2B.

In a similar manner to the shoot parameters, inoculation of *H. pelagica* CDK2 significantly improved root growth in different wheat cultivars compared to their respective un-inoculated treatments (Table 3). The maximum significant increase in root biomass (%) due to inoculation was observed in wheat cultivar HD3086 (52.08%), followed by HD2687 (46.41%), KRL210 (38.96%), K65 (33.66%), and HD2380 (29.10%) compared to their respective un-inoculated treatments (Table 3). The percent increase in root biomass in inoculated HD3086 was significantly higher than the percent increase observed in other wheat cultivars. Similarly, inoculation significantly increased the root length of all wheat cultivars compared to the un-inoculated treatments. The maximum root length due to inoculation was observed in wheat cultivar HD3086 (27.48 cm). Among the inoculated cultivars, KRL210, K65, and HD2380 showed statistically similar root lengths (25.16 cm, 25.06 cm, and 25.06 cm, respectively). The least increase in root length was observed in cultivar HD2687 (19.36 cm). The percent increase in root length due to inoculation was maximum in HD3086 (41.21%), followed by HD2687 (28.81%), K65 (14.63%), KRL210 (13.18%), and HD2380 (11.13%) compared to their respective un-inoculated wheat cultivars (Table 3).

3.3.2. Root architecture at harvest time

The root scanning revealed significant increases in the number of lateral roots, total root surface area, and root volume due to the inoculation of *H. pelagica* CDK2 compared to the un-inoculated control at harvest time (Figure 3). The root surface area in the inoculated wheat treatments at harvest time ranged from 148.34 $\pm$ 6.41 cm^2 to 241.25 $\pm$ 3.91 cm^2, which was significantly higher than their respective un-inoculated control treatments (ranging from 91.67 $\pm$ 1.15 cm^2 to 140 $\pm$ 2.88 cm^2). The overall percent increase in root surface area ranged from 51.34% to 73.75%. The wheat cultivar HD3086 showed the maximum percent increase in root surface area (73.75%), followed by K65 (71.96%), KRL210 (61.82%), HD2687 (56.42%), and HD2380 (51.34%) compared to their respective un-inoculated control (Figure 3A).

The total root volume of the different wheat cultivars significantly increased compared to their respective un-inoculated cultivars. The root volume in the treated wheat cultivars at harvest time ranged from 1.85 $\pm$ 0.061 cm^3 to 2.91 $\pm$ 0.12 cm^3, which was significantly higher than their respective control treatments (ranging from 1.20 $\pm$ 0.018 cm^3 to 2.19 $\pm$ 0.080 cm^3) (Figure 3A). The overall percent increase in root volume ranged from 21.97% to 131.83%. The maximum percent increase in root volume due to inoculation was observed in wheat cultivar HD2687 (131.83%), followed by HD3086 (71.96%). Cultivar HD2380, KRL210, and K65 showed significantly less percent increase due to inoculation (30.14%, 25.11%, and 21.97%, respectively) compared to HD2687 and HD3086. The average root diameter in each of the *H. pelagica* CDK2-treated wheat cultivars (ranging from 0.68 $\pm$ 0.026 mm to 1.76 $\pm$ 0.025 mm) increased significantly compared to their respective non-treated wheat cultivars (ranging from 0.53 $\pm$ 0.02 mm to 1.02 $\pm$ 0.021 mm) (Figure 3B). The average root diameter also varied significantly among inoculated wheat treatments. The maximum root diameter due to inoculation was observed in HD2687 (173.37%), followed by HD3086 (126.87%) and HD2380 (50.06%). In comparison, the salinity-tolerant wheat cultivars, K65 and KRL210, showed significantly less improvement in root diameter upon halophilic archaeal inoculation (20.78% and 12.89%, respectively). The overall effect of halophilic archaeal inoculation seems to be higher in salinity-susceptible wheat varieties compared to tolerant varieties.

3.3.3. Grain yield per spike and per plant

Inoculation with halophilic archaea resulted in a significant increase in both grain yield per spike and grain yield per plant across all wheat cultivars compared to their respective untreated controls (Table 3). The number of grains per spike ranged from 51.67 $\pm$ 1.15 to 58.00 $\pm$ 2.01 in the inoculated wheat cultivars, while it ranged from 44.00 $\pm$ 1.00 to 52.00 $\pm$ 1.01 in the untreated controls. The wheat cultivars HD2687 (20.00%) and HD3086 (19.69%) showed the maximum percentage increase in grain per spike due to inoculation, which was statistically similar to each other. These values were significantly higher than the percentage increase in grain yield per spike observed in HD2380 (13.98%), K65 (11.40%), and KRL210 (7.69%) compared to their respective untreated controls (Table 3).

Similarly, the grain yield per plant also exhibited a significant increase as a result of inoculation with *H. pelagica* CDK2 in various wheat cultivars compared to their respective untreated controls. The grain yield per plant in the inoculated cultivars ranged from 3.68 g to 5.21 g, while it ranged from 2.70 g to 3.47 g in the untreated treatments (Table 3). The increase in grain yield showed significant variation among different wheat cultivars. The wheat cultivar K65 demonstrated the highest percentage increase in grain yield (50.28%), followed by KRL210 (47.91%), HD2687 (41.85%), HD3086 (38.48%), and HD2380 (30.03%). It is worth noting that the salinity-tolerant varieties of wheat displayed a stronger response to inoculation with halophilic archaea in terms of grain yield per plant (Table 3).

3.3.4. Effect of *H. pelagica* CDK2 inoculation on biochemical growth parameters and osmolyte content of wheat cultivars

3.3.4.1. Total shoot protein and leaf chlorophyll content

The inoculation of wheat cultivars with *H. pelagica* CDK2 resulted in a significant increase in wheat shoot protein content across all cultivars compared to their respective untreated controls. Among the different inoculated treatments of wheat cultivars, the total shoot protein content ranged from 201.27 $\pm$ 6.92 to 205.92 $\pm$ 2.39 $\mu g\ mg^{-1}$ fresh weight (FW) (Figure 4A) and was statistically similar. The wheat cultivars HD2687 (44.63%) and HD2380 (43.01%) exhibited the highest percentage increase in

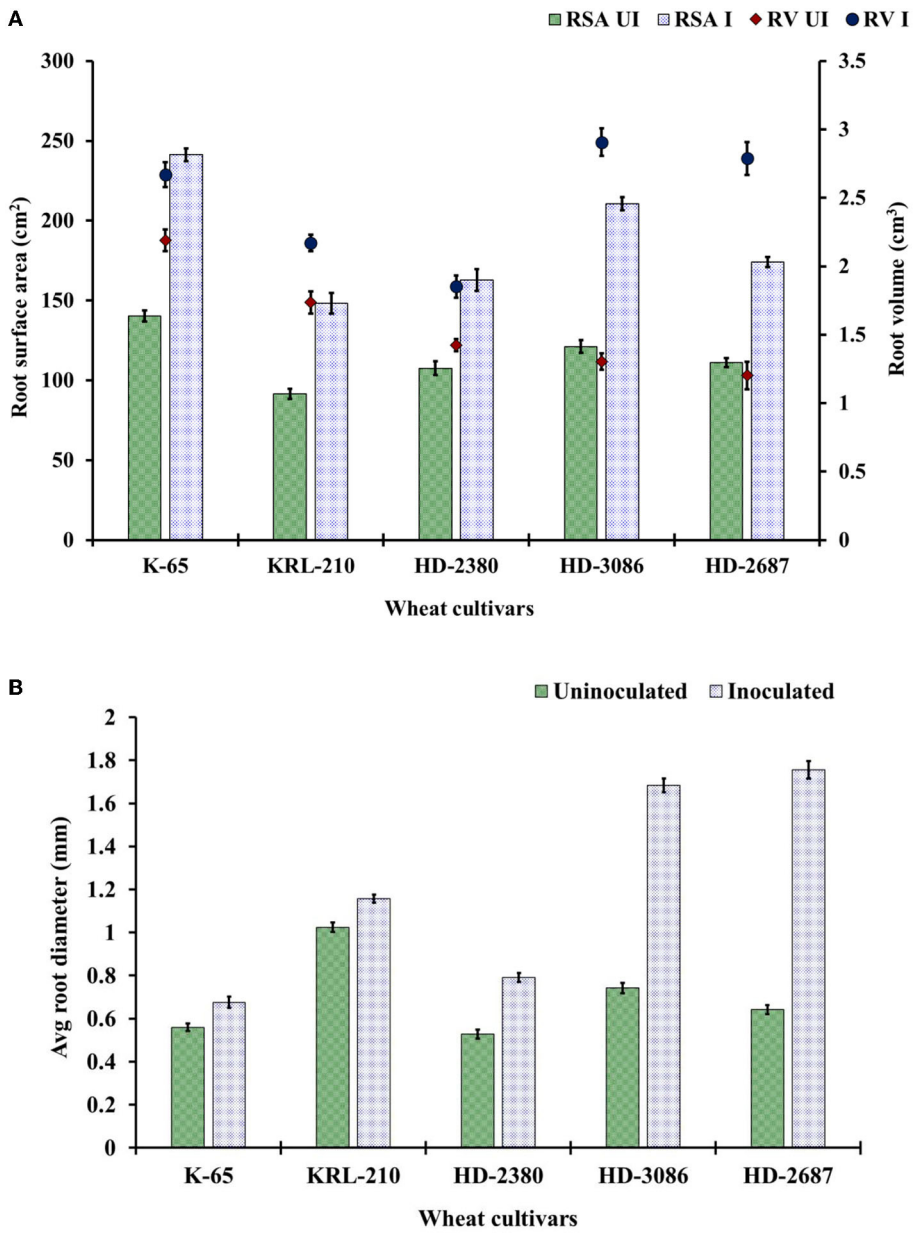


FIGURE 3
Root parameters of wheat cultivars: **(A)** root surface area (RSA) (cm^2) and the total root volume (RV) (cm^3) and **(B)** average root diameter as influenced by the seed inoculation of *H. pelagica* CDK2 in different wheat cultivars (UI: un-inoculated; I: inoculated). (LSD $p \leq 0.05$ for root surface area: Factor A (Cultivars): 5.20, Factor B (Treatments): 3.29, Interaction AxB: 7.36; LSD $p \leq 0.05$ for root volume: Factor A (Cultivars): 0.077, Factor B (Treatments): 0.042, Interaction AxB: 0.107, LSD $p \leq 0.05$ for average root diameter: Factor A (Cultivars): 0.036, Factor B (Treatments): 0.029, Interaction AxB: 0.04; error bar represents standard deviation).

protein content due to inoculation, which was statistically similar to each other. HD3086 showed a significant increase of 29.37% in total shoot protein. However, the salinity-tolerant wheat cultivars, KRL210 and K65, demonstrated significantly lower percentage increases in total shoot protein, with values of 1.86% and 4.26%, respectively (Figure 4A).

In addition, the chlorophyll content in different inoculated wheat cultivars also showed a significant increase compared to the untreated controls (Figure 4B). The overall increase in chlorophyll content ranged from 16.14% to 23.72% due to inoculation with halophilic archaea. The salt-susceptible wheat cultivar HD2687 displayed the maximum response to inoculation, with a 20.12% increase in chlorophyll content. This increase was significantly higher than the increases observed in HD3086 (19.40%), K65 (17.80%), KRL210 (17.61%), and HD2380 (16.14%).

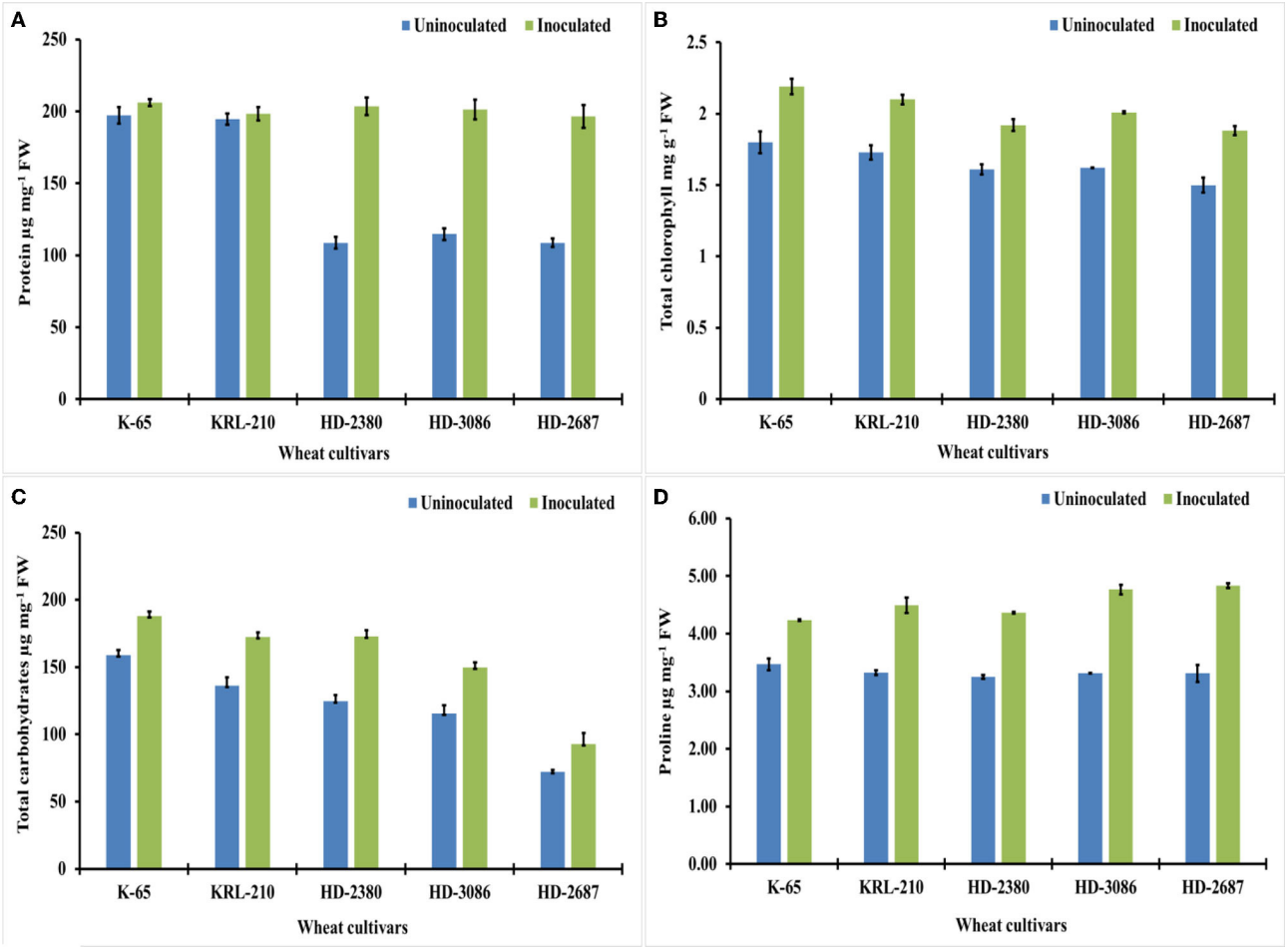


FIGURE 4
Biochemical growth parameters and osmolyte content of the wheat cultivars (pot experiment): **(A)** protein (µg mg-1 FW*), **(B)** chlorophyll (µg g-1 FW) **(C)** total carbohydrates (µg mg-1 FW), and **(D)** proline content of different wheat cultivars as influenced by archaeal inoculation (LSD $p \leq 0.05$ for protein: Factor A (Cultivars): 6.333, Factor B (Treatments): 4.007, Interaction AxB: 8.968; LSD $p \leq 0.05$ for chlorophyll: Factor A (Cultivars): 0.047, Factor B (Treatments): 0.034, Interaction AxB: 0.073, LSD $p \leq 0.05$ for total carbohydrates: Factor A (Cultivars): 6.097, Factor B (Treatments): 3.856, Interaction AxB: 8.613 and LSD $p \leq 0.05$ for proline content: Factor A (Cultivars): 0.085, Factor B (Treatments): 0.056, Interaction AxB: 0.125; error bar represents standard deviation). *FW, fresh weight.

3.3.4.2. Total carbohydrate and proline content

Treatment with *H. pelagica* CDK2 resulted in a significant increase in the total carbohydrate content of all wheat cultivars compared to their respective untreated varieties. The total carbohydrate content ranged from 92.88 ± 8.16 to 188.01 ± 3.46 µg mg^{-1} FW in the treated cultivars, which was significantly higher than the total carbohydrates ranging from 72.23 ± 1.11 to 159.0 ± 3.65 µg mg^{-1} FW in the un-inoculated treatments (Figure 4C). Among the cultivars, HD2380 showed the highest increase in total carbohydrate content (27.85%) after treatment with halophilic archaea, followed by HD3086 (22.85%), which was statistically similar to HD2687 (22.23%). KRL210 and K65 demonstrated increases of 20.93% and 15.42%, respectively. The differences in the percentage increase in total carbohydrates between HD3086, HD2687, and KRL210 were not statistically significant.

Inoculation with *H. pelagica* CDK2 resulted in a significant increase in proline content in different wheat cultivars, ranging from 18.11% to 31.51%. The proline content in un-inoculated wheat cultivars ranged from 3.25 ± 0.032 to 3.47 ± 0.103 µg g^{-1} FW, and a significant increase was observed in the respective inoculated wheat cultivars, ranging from 4.23 ± 0.011 to 4.83 ± 0.043 µg g^{-1} FW (Figure 4D). The highest percentage increase in proline content was observed in HD2687 (31.51%), followed by HD3086 (30.47%), KRL210 (25.97%), and HD2380 (25.49%), and the lowest increase was seen in K65 (18.11%).

3.3.5. Impact of halophilic archaea inoculation on antioxidant enzyme activity

Seed treatment with halophilic archaea resulted in a significant reduction in antioxidant enzyme activity in all wheat cultivars. The inoculated wheat cultivars showed a decrease in ascorbate peroxidase activity ranging from 20.0% to 57.43%, while the reduction in superoxide dismutase activity ranged from 59.22% to 75.99%. The decrease in ascorbate peroxidase activity was statistically similar among the susceptible cultivars HD2687 (57.43%), HD2380 (56.08%), and HD3086 (55.17%) but significantly higher than the reduction observed in the

TABLE 4 Quantification of antioxidant enzymes in different wheat cultivars as influenced by inoculation of *H. pelagica* CDK2.

Cultivars	Ascorbate peroxidase		SOD		Catalase	
	UI	I	UI	I	UI	I
K65	14.01 ± 0.35	8.10 ± 0.33	32.5 ± 1.11	13.2 ± 0.035	10.42 ± 0.018	7.04 ± 0.21
KRL210	12 ± 0.01	9.20 ± 0.17	33.0 ± 0.18	13.1 ± 0.02	10.70 ± 0.04	7.51 ± 0.10
HD2380	17.53 ± 0.69	7.70 ± 0.09	41.2 ± 1.07	12.96 ± 0.53	15.27 ± 0.02	5.93 ± 0.18
HD3086	16.73 ± 0.61	7.50 ± 0.26	43.0 ± 1.17	10.1 ± 0.15	15.03 ± 0.31	7.53 ± 0.04
HD2687	18.17 ± 0.03	7.73 ± 0.25	41.2 ± 0.038	10.0 ± 0.16	16.13 ± 0.45	7.600 ± 0.29
LSD ≤ 0.05						
Cultivars A	0.406		0.734		0.26	
Treatment B	0.258		0.464		0.169	
Interaction (AxB)	0.574	0.1036	0.377			

*Ascorbate peroxidase (mM g^{-1} FW min^{-1}); SOD: superoxide dismutase (U g^{-1} FW min^{-1}); Catalase (U g^{-1} FW min^{-1}); U, unit activity; FW, fresh weight; **UI, un-inoculated control; I, inoculated treatment.

salinity-tolerant wheat cultivars, KRL210 (23.33%) and K65 (20.17%). The highest percentage reduction in SOD activity was observed in wheat cultivars HD3086 (75.99%), followed by HD2687 (75.82%), HD2380 (68.55%), KRL210 (60.16%), and K65 (59.22%) (Table 4). Catalase activity also exhibited a significant reduction in susceptible wheat cultivars (HD2380: 61.14%, HD2687: 52.86%, and HD3086: 49.89%) compared to tolerant ones (K65: 32.50% and KRL210: 29.88%) when compared to their respective un-inoculated treatments (Table 3). The overall impact of halophilic archaeal inoculation was more pronounced in susceptible wheat cultivars than in tolerant ones. This suggests that the inoculation of halophilic archaea *H. pelagica* CDK2 has assisted wheat cultivars in mitigating salinity stress.

4. Discussion

A variety of cultural and metagenomic studies across the world have changed the notion that archaea inhabit only niches with extreme physiological conditions. Furthermore, they have been discovered in normal soil conditions as well as in the rhizospheres of many crops, where they help improve plant growth (Jung et al., 2020) and form an important part of soil microbiomes, phytobiomes, and plant-associated ecosystems (Gubry-Rangin et al., 2010; Yadav et al., 2019; Taffner et al., 2020; Zhang et al., 2020; Wicaksono et al., 2022). Seasonal population dynamics of halophilic archaea inhabiting the rhizosphere of wild vegetation growing in the saline Indian desert were previously reported (Yadav et al., 2019). There is evidence that rhizospheric archaea do play an important role in the growth variety of crops, such as *Zea mays, Oryza sativa, Lycopersicon esculentus*, and *Coffea arabica,* in arid and semi-arid regions (Alori et al., 2020). However, to date, no significant reports are available in the literature indicating the direct role of rhizosphere-dwelling halophilic archaea in alleviating the harmful effects of salinity in crop plants. This study investigated the plant growth-promoting characteristics of 28 different halophilic rhizosphere-dwelling archaea and evaluated the efficacy of selected isolates in promoting the growth of wheat under salinity stress. In their respective HPS, HKS, and HZS modified media, a total of 17, 21, and 6 halophilic archaeal isolates solubilized the insoluble source of P, K, and Zn, respectively, and significantly lowered the pH of medium (up to 3.6) (Figure 1). Our previous study reported that halophilic archaea solubilizing P in different sources (rock phosphate, hydroxyapatite, and tricalcium phosphate) lowered the pH of growth media, and the lowering of pH was attributed to the production of organic acids (gluconic, citric, fumaric, succinic, propionic, formic, and tartaric acid) (Yadav et al., 2015). Hence, it can be stated that the mechanism of P solubilization by halophilic archaea is similar to that of bacteria and is accompanied by a lowering of pH due to the production of organic acids. Because no significant information is available regarding the mechanisms of K and Zn solubilization by archaea, it is possible that the lowering of pH in growing media suggests a similar process. It has been reported that most of the prokaryotes lower the pH of the growth medium by the secretion of various organic acids and/or by proton extrusion (Illmer and Schinner, 1995). In a study, Siles et al. (2022) found that organic P hydrolyzing alkaline phosphatases, *Pho*D and *Pho*X, were expressed in archaea (Euryarchaeota) isolated from arable, forest, and grassland soil, indicating that P hydrolyzes around plants.

Bacteria in the plant rhizosphere produce indole acetic acid (IAA), a key plant growth hormone that regulates cell division, cell expansion, root initiation, and lateral root formation (Goswami et al., 2014; Khatoon et al., 2020). Exogenous production of IAA is not restricted to bacteria as archaea have also been found capable of producing IAA. IAA production was observed in 17 halophilic archaeal isolates, with concentrations ranging from 17.30 to 49.3 μg ml^{-1} IAA (Figure 1C). *Halogeometricum rufum* IARI-WRAK7 produced the significantly highest quantity of IAA (49.3 μg ml^{-1}) as compared to other isolates. The first report on the production of IAA by archaea was reported in *Sulfolobus acidocaldarius* (White, 1987). Later, biosynthesis of IAA was also reported in the hyperthermophilic archaeon *Ferroglobus placidus* during the anaerobic degradation of tryptophan (Aklujkar et al., 2014). A metagenomic study revealed genetic evidence for auxin biosynthesis in archaea associated with bog vegetation, which supports archaea's plant growth-promoting activity (Taffner et al., 2018). IAA production and the solubilization of P, K,

and Zn by rhizosphere-dwelling halophilic archaea indicate their crucial role in ensuring that plant nutrients are available in high-salinity ecosystems. This is an important paradigm shift in how we understand plant–microbiota interactions in hypersaline environments. For further studies, *Halolamina pelagica* CDK2 was selected from 28 halophilic archaea as it produced a significant quantity of IAA and solubilized P, K, and Zn in HRA media with EC 119.8 dSm^{-1}. Most agricultural soils, however, have much lower salinity levels, and halophilic archaea must be able to grow in low-to-moderate salinity levels and be able to withstand hypo-osmotic conditions genetically and biochemically. The halophilic archaea used in this study were isolated from the rhizosphere of wild grasses, non-rhizospheric soil, sediments, and saline water bodies having different salinity levels (EC ranging from 1.19 to 106.7 dSm^{-1}). Our previous study demonstrated that isolates from rhizospheric soil samples with less salinity than bulk soil, sediments, or water samples could grow in a defined medium with a NaCl concentration of 10 to 25% but were not able to produce measurable growth below 10% (Yadav et al., 2019). In the past, several methods have been developed for culturing un-culturable bacteria that mimic the physicochemical conditions of natural habitats (Vartoukian et al., 2010). The concept of using soil extract in the growth medium is one such strategy to culture bacteria (Taylor, 1951). In a study, an intensive soil extract medium was successfully used to isolate previously uncultured bacteria and new taxonomic candidates, which accounted for 49% and 55% of the total isolates examined, respectively (Nguyen et al., 2018). In this study, a modified growth medium (halophilic soil extract medium) (HSE medium) with different levels of electrical conductivity (7.13 to 30.84 dSm^{-1}) was developed using soil extract to test the ability of *H. pelagica* CDK2 to solubilize nutrients (P, K, and Zn) and produce IAA. *H. pelagica* CDK2 grew in the HKS broth over a wider range of ECs (7.13 to 30.84 dSm^{-1}), and its growth (protein $\mu g\ ml^{-1}$) showed an increasing trend as the EC of the HKS broth increased (Table 2). It also produced IAA and solubilized the P, K, and Zn in HSE broth (HSE-1 to HSE-9) and different levels of EC (7.13 to 30.84 dSm^{-1}) (Table 2). The study showed that the selected isolate was capable of growing and exhibiting PGP attributes in HSE broth at low, moderate, and high EC. Oren (2014) reported that halophilic archaea belonging to the class Halobacteria possess wider adaptability to salinity levels for growth (1.5 M NaCl to saturation). In another study, halophilic archaea (*Haloferax* sp. and *Halogeometricum* sp.) were isolated using low salinity (2.5% NaCl) growth media, and it was concluded that they can grow at all salinity levels that are lower than those considered minimum for halophilic archaea (9–10% w/v NaCl) (Purdy et al., 2004). With the ability to grow at a wide range of salinities, *H. pelagica* CDK2 with PGP attributes was evaluated further in plant–microbe interaction studies. To date, no significant findings are available on plant–microbe interaction studies involving archaea and/or halophilic archaea. In the soft agar (EC 8 dsm^{-1}) experiment, the inoculation of the halophilic archaea *H. pelagica* CDK2 significantly reduced the germination time by 2–3 d and improved the initial vegetative growth of all the wheat cultivars as compared to un-inoculated treatment (Figure 2A). Further in a pot experiment (soil with EC 8 dSm^{-1}), inoculation of *H. pelagica* CDK2 in two salt-tolerant (K65 and KRL210), and three susceptible wheat cultivars (HD2380, HD3086, and HD2687) improved the vegetative parameters and grain yield per plant (30 to 50%) of wheat as compared with the un-inoculated treatment. Several researchers have previously reported the improvement in plant growth and yield parameters of plant growth under saline conditions by inoculating with different salt-tolerant bacterial isolates such as *Azospirillum brasilense* (Nabti et al., 2010), *Pseudomonas fluorescence*, *Bacillus pumilus*, and *Exiguobacterium aurantiacum* (Kakar et al., 2016; Sardar et al., 2023). A significant increase in wheat shoot protein content was observed across different salinity-susceptible wheat cultivars compared to salinity-tolerant wheat cultivars (1.86 to 4.26%) and un-inoculated treatments. The protein content ranged from 44.63% to 29.37% (Figure 4A). Treatment of salinity-stressed wheat plants with halotolerant *Bacillus safensis*, *B. pumilus*, and *Zhihengliuella halotolerant* isolated from halophytic range land plants increased leaf crude protein by 30%, water-soluble sugar content by 34%, and metabolic energy by 37% (Amini et al., 2021). Rajput et al. (2018) and Nawaz et al. (2020) both reported a significant improvement in total sugar content, protein, and chlorophyll synthesis due to the inoculation of halotolerant PGPR. After inoculation with *H. pelagica* CDK2, a significant increase in the total carbohydrate content of all wheat cultivars was observed compared to their respective un-inoculated wheat varieties. The total carbohydrate content ranged from 92.88 ± 8.16 to $188.01 \pm 3.46\ \mu g\ mg^{-1}$ FW in treated cultivars (Figure 4). Inoculation of halotolerant plant growth-promoting microbes is known to alleviate salinity stress in plants by modulating membrane integrity, proline accumulation, and reactive oxygen species scavenging and activating antioxidant mechanism (Sandhya et al., 2010; Upadhyay et al., 2012; Yogendra et al., 2015; Etesami and Noori, 2019). In this study, inoculation of halophilic archaea significantly reduced the antioxidant enzyme activity (ascorbate peroxidase, superoxide dismutase, and catalase) and improved the proline accumulation in all the wheat cultivars (Table 3 and Figure 4). Proline protects plant cells from osmotic stress damage and does not interfere with cellular machinery (Iqbal and Nazar, 2015). An increase in proline accumulation in different crops grown under salt stress due to the inoculation of halotolerant plant growth-promoting bacteria has been reported by various workers (Nawaz et al., 2020; Amini et al., 2021). This is the first report of halophilic archaea inoculating plants under salt stress and resulting in a reduction in antioxidant enzyme activity and an improvement in proline accumulation. No significant reports are available in the literature indicating this.

Archaea are still an under-detected and little-studied part of the plant rhizosphere, and their contributions to plants' health remain mostly unknown. Our data provide the first evidence of the importance of halophilic archaea as a functional component of the plant rhizosphere. In a previous study, the presence of certain plant growth-promoting and salinity resistance genes in *H. pelagica* CDK2 was reported through genome sequencing (Gaba et al., 2017); accession number: LGUC00000000) and transcriptome analysis (unpublished report; NCBI Accession number SRX13131461 and SRX13131462). The comprehensive analysis of the genome, genes, and pathways of halophilic archaea *Halolamina pelagica* CDK2 revealed the presence of genes for phosphate uptake and metabolism (polyphosphate kinase, alkaline phosphatase, phosphate ABC transporter, phosphate transport

system regulatory protein, and pyrophosphate kinase), osmolyte biosynthesis (trehalose synthase and trehalose phosphatase), and antioxidant enzymes (superoxide dismutase and catalase peroxidases; Gaba et al., 2022). Through plant–microbe interaction studies, the genomic insights obtained in the previous report were corroborated. Inoculation of halophilic archaeon *H. pelagica* CDK2 showed greater potential in improving the growth and yield of susceptible wheat cultivars as compared to tolerant ones and decreased the activity of antioxidant enzymes. Hence, the inoculation alleviated the harmful effects of salinity on plants, allowing them to grow more efficiently. More efforts are needed to cultivate plant-associated archaea and to learn more about plant-associated archaeal diversity.

5. Conclusion

The potential of halophilic archaea isolated from the rhizosphere of wild vegetation in improving wheat growth by alleviating the effects of high salinity was investigated in this study. This is the first report highlighting the prospects of using rhizosphere-dwelling halophilic archaea in alleviating salinity-associated abiotic stress in wheat. The plant growth-promoting halophilic archaeon *Halolamina pelagica* CDK2 demonstrated tremendous potential not only in improving the vegetative growth and biochemical parameters of different wheat cultivars but also in improving osmolyte levels. The use of *H. pelagica* CDK2 also helped plants in reducing the negative effects of salinity stress by significantly lowering the level of antioxidant enzymes. As a result, this halophilic archaeon can be further evaluated in field trials before being included in various biofertilizer development programs for managing abiotic stress in agriculture.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

RK developed the concept underlying the manuscript and reviewed the manuscript. MN conducted the laboratory experimentation, wrote the soft agar and pot evaluation studies, and compiled the manuscript. BR and MG reviewed the results and helped in data analysis along with the literature review. All authors contributed to the article and approved the submitted version.

Funding

The proposed research study is a part of registered Ph. D. work. The complete research study was carried out using the facilities available in the Division of Microbiology, ICAR-Indian Agricultural Research Institute, New Delhi.

Acknowledgments

The authors would like to thank the Indian Council of Agricultural Research, New Delhi, for financial support and Post Graduate School, Indian Agricultural Research Institute, New Delhi, for providing research facilities.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2023.1212349/full#supplementary-material

References

Ábrahám, C. C., László Erdei, L. S. (2010). Methods for determination of proline in plants. *Methods Mol. Biol.* 2, 1–14. doi: 10.1007/978-1-60761-702-0_20

Aebi, H. (1984). Catalase in Vitro. *Methods Enzymol.* 105, 121–126. doi: 10.1016/S0076-6879(84)05016-3

Akinola, S. A., and Babalola, O. O. (2021). The fungal and archaeal community within plant rhizosphere: a review on their contribution to crop safety. *J. Plant Nutr.* 44, 600–618. doi: 10.1080/01904167.2020.1845376

Aklujkar, M., Risso, C., Smith, J., Beaulieu, D., Dubay, R., Giloteaux, L., et al. (2014). Anaerobic degradation of aromatic amino acids by the hyperthermophilic archaeon Ferroglobus placidus. *Microbiol.* 160, 2694–2709. doi: 10.1099/mic.0.083261-0

Alori, E. T., Emmanuel, O. C., Glick, B. R., and Babalola, O. O. (2020). Plant–archaea relationships: a potential means to improve crop production in arid and semi-arid regions. *World J. Microbiol. Biotechnol.* 36, 1–10. doi: 10.1007/s11274-020-02910-6

Amini, A., Mosleh Arani, A., Ghasemi, S., Rad, M. H., Etesami, H., Shabazi Manshadi, S., et al. (2021). Mining the rhizosphere of halophytic rangeland plants for halotolerant bacteria to improve growth and yield of salinity-stressed wheat. *Plant Physiol. Biochem.* 163, 139–153. doi: 10.1016/j.plaphy.2021.03.059

Banerjee, P., and Prasad, B. (2020). Determination of concentration of total sodium and potassium in surface and ground water using a flame photometer. *Appl. Water Sci.* 10, 1–7. doi: 10.1007/s13201-020-01188-1

Blanke, M. (1992). Determination of chlorophyll using DMSO. *Wein-Wissenschaft* 47, 32–35.

Calanca, P. P. (2017). *Quantification of Climate Variability, Adaptation and Mitigation for Agricultural Sustainability*. Berlin: Springer.

Chaudhary, P., Xu, M., Ahamad, L., Chaudhary, A., Kumar, G., Adeleke, B. S., et al. (2023). Application of synthetic consortia for improvement of soil fertility, pollution remediation, and agricultural productivity: A review. *Agronomy* 13, 643. doi: 10.3390/agronomy13030643

Dhindsa, R. S., Plumb-dhindsa, P., and Thorpe, T. A. (1981). Leaf senescence: Correlated with increased levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide dismutase and catalase. *J. Exp. Bot.* 32, 93–101. doi: 10.1093/jxb/32.1.93

Dubois, M., Gilles, K., Hamilton, J. K., Rebers, P. A., and Smith, F. (1951). A colorimetric method for the determination of sugars. *Nature* 168, 167. doi: 10.1038/168167a0

Etesami, H., and Noori, F. (2019). Soil salinity as a challenge for sustainable agriculture and bacterial-mediated alleviation of salinity stress in crop plants. *Saline Soil-Based Agric. Microoorg.* 2, 1–22. doi: 10.1007/978-981-13-8335-9_1

Filek, M., Zembala, M., Kornaś, A., Walas, S., Mrowiec, H., Hartikainen, H., et al. (2010). The uptake and translocation of macro- and microelements in rape and wheat seedlings as affected by selenium supply level. *Plant Soil* 336, 303–312. doi: 10.1007/s11104-010-0481-4

Gaba, S., Naitam, M. G., Kumari, A., Medema, M. H., and Kaushik, R. (2022). Comprehensive genome analysis of halolamina pelagica CDK2: insights into abiotic stress tolerance genes. *J. Pure Appl. Microbiol.* 16, 460–470. doi: 10.22207/JPAM.16.1.44

Gaba, S., Singh, R. N., Labs, A., and Yadav, A. N. (2017). Draft genome sequence of halolamina pelagica CDK2 isolated from natural salterns from rann of Kutch, Gujarat, India. *Genome Announc.* 5, 2–4. doi: 10.1128/genomeA.01593-16

Gill, S. S., and Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.* 48, 909–930. doi: 10.1016/j.plaphy.2010.08.016

Gorji, T., Yildirim, A., Hamzehpour, N., Tanik, A., and Sertel, E. (2020). Soil salinity analysis of Urmia Lake Basin using Landsat-8 OLI and Sentinel-2A based spectral indices and electrical conductivity measurements. *Ecol. Indic.* 112, 106173. doi: 10.1016/j.ecolind.2020.106173

Goswami, D., Pithwa, S., Dhandhukia, P., and Thakker, J. N. (2014). Delineating *Kocuria turfanensis* 2M4 as a credible PGPR: A novel IAA-producing bacteria isolated from saline desert. *J. Plant Interact.* 9, 566–576. doi: 10.1080/17429145.2013.871650

Gubry-Rangin, C., Nicol, G. W., and Prosser, J. I. (2010). Archaea rather than bacteria control nitrification in two agricultural acidic soils. *FEMS Microbiol. Ecol.* 74, 566–574. doi: 10.1111/j.1574-6941.2010.00971.x

Hagagy, N., Abdel-Mawgoud, M., Akhtar, N., and Selim, S., and AbdElgawad, H. (2023). The new isolated Archaea strain improved grain yield, metabolism and quality of wheat plants under Co stress conditions. *J. Plant Physiol.* 280, 153876. doi: 10.1016/j.jplph.2022.153876

Hu, H., Natarajan, V. P., and Wang, F. (2021). Towards enriching and isolation of uncultivated archaea from marine sediments using a refined combination of conventional microbial cultivation methods. *Mar. Life Sci. Technol.* 3, 231–242. doi: 10.1007/s42995-021-00092-0

Illmer, P., and Schinner, F. (1995). Solubilization of inorganic calcium phosphates-Solubilization mechanisms. *Soil Biol. Biochem.* 27, 257–263. doi: 10.1016/0038-0717(94)00190-C

Iqbal, N., and Nazar, R. (2015). "Proline accumulation in plants: Roles in stress tolerance and plant development," in *Osmolytes and Plants Acclimation to Changing Environment: Emerging Omics Technologies*, eds N. Iqbal, R. Nazar, and N. Khan (New Delhi: Springer), 1–170. doi: 10.1007/978-81-322-2616-1

Jung, J., Kim, J. S., Taffner, J., Berg, G., and Ryu, C. M. (2020). Archaea, tiny helpers of land plants. *Comput. Struct. Biotechnol. J.* 18, 2494–2500. doi: 10.1016/j.csbj.2020.09.005

Kakar, K. U., Ren, X. L., Nawaz, Z., Cui, Z. Q., Li, B., Xie, G. L., et al. (2016). A consortium of rhizobacterial strains and biochemical growth elicitors improve cold and drought stress tolerance in rice (*Oryza sativa* L.). *Plant Biol.* 18, 471–483. doi: 10.1111/plb.12427

Khatoon, Z., Huang, S., Rafique, M., Fakhar, A., Kamran, M. A., Santoyo, G., et al. (2020). Unlocking the potential of plant growth-promoting rhizobacteria on soil health and the sustainability of agricultural systems. *J. Environ. Manage.* 273, 111118. doi: 10.1016/j.jenvman.2020.111118

Kumar, S., Puniya, A. K., Puniya, M., Dagar, S. S., Sirohi, S. K., Singh, K., et al. (2009). Factors affecting rumen methanogens and methane mitigation strategies. *World J. Microbiol. Biotechnol.* 25, 1557–1566. doi: 10.1007/s11274-009-0041-3

Marion, M. B. (1976). A rapid and sensitive method for the quantitation microgram quantities of protein utilizing the principle of protein-dye binding. *Anal. Biochem.* 72, 248–254. doi: 10.1016/0003-2697(76)90527-3

Nabti, E., Sahnoune, M., Ghoul, M., Fischer, D., Hofmann, A., Rothballer, M., et al. (2010). Restoration of growth of durum wheat (Triticum durum var. waha) under saline conditions due to inoculation with the rhizosphere bacterium azospirillum brasilense nh and extracts of the marine alga ulva lactuca. *J. Plant Growth Regul.* 29, 6–22. doi: 10.1007/s00344-009-9107-6

Naitam, M. G., and Kaushik, R. (2021). Archaea: an agro-ecological perspective. *Curr. Microbiol.* 78, 2510–2521. doi: 10.1007/s00284-021-02537-2

Nakano, Y., and Asada, K. (1981). Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. *Plant Cell Physiol.* 22, 867–880.

Nawaz, A., Shahbaz, M., Asadullah, M., Imran, A., Marghoob, M. U., Imtiaz, M., et al. (2020). Potential of salt tolerant PGPR in growth and yield augmentation of wheat (Triticum aestivum L.) under saline conditions. *Front. Microbiol.* 11, 1–12. doi: 10.3389/fmicb.2020.02019

Nguyen, T. M., Seo, C., Ji, M., Paik, M.-. J., Myung, S-, W., Kima, J., et al. (2018). Effective soil extraction method for cultivating previously uncultured soil bacteria. *Appl. Environ. Microbiol.* 84, 1–14. doi: 10.1128/AEM.01145-18

Ondrasek, G., Rathod, S., Manohara, K. K., Gireesh, C., Anantha, M. S., Sakhare, A. S., et al. (2022). Salt stress in plants and mitigation approaches. *Plants* 11, 1–21. doi: 10.3390/plants11060717

Oren, A. (2014). Halophilic archaea on Earth and in space: Growth and survival under extreme conditions. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 372. doi: 10.1098/rsta.2014.0194

Oren, A. (2019). Halophilic archaea. *Encycl. Microbiol.* 4, 495–503. doi: 10.1016/B978-0-12-809633-8.20800-5

Purdy, K. J., Cresswell-Maynard, T. D., Nedwell, D. B., McGenity, T. J., Grant, W. D., Timmis, K. N., et al. (2004). Isolation of haloarchaea that grow at low salinities. *Environ. Microbiol.* 6, 591–595. doi: 10.1111/j.1462-2920.2004.00592.x

Rajput, L., Imran, A., Mubeen, F., Hafeez, F. Y., Road, J., Section, P. P., et al. (2018). Wheat (*Triticum aestivum* L.) growth promotion by halo-tolerant PGPR-consortium Identification of potential halo-tolerant PGPR Physiological and Biochemical Characterization Plant inoculation assays Formulation of PGPR. *Soil Env.* 37, 178–189. doi: 10.25252/SE/18/61522

Rakshit, A., Singh, H. B., Singh, A. K., Singh, U. S., and Fraceto, L. (2020). *New Frontiers in Stress Management for Durable* Agriculture. Cham: Springer.

Sadaty, S. A., and Nazari, N. (2021). Impact of land use change on the effectiveness of traditional arable land systems and environmental in Miandorood, Mazandaran, Iran. *Environ. Challenges* 4, 100165. doi: 10.1016/j.envc.2021.100165

Sandhya, V., Ali, S. Z., Grover, M., Reddy, G., and Venkateswarlu, B. (2010). Effect of plant growth promoting Pseudomonas spp. on compatible solutes, antioxidant status and plant growth of maize under drought stress. *Plant Growth Regul.* 62, 21–30. doi: 10.1007/s10725-010-9479-4

Saravanan, V. S., Subramoniam, S. R., and Raj, S. A. (2004). Assessing in vitro solubilization potential of different zinc solubilizing bacterial (ZSB) isolates. *Brazilian J. Microbiol.* 35, 121–125. doi: 10.1590/S1517-83822004000100020

Sardar, H., Khalid, Z., Ahsan, M., Naz, S., Nawaz, A., Ahmad, R., et al. (2023). Enhancement of salinity stress tolerance in lettuce (*Lactuca sativa* L.) via foliar application of nitric oxide. *Plants* 12, 1–24. doi: 10.3390/plants12051115

Sharma, V., Singh, A., Sharma, D., Sharma, A., Phogat, S., Chakraborty, N., et al. (2021). Stress mitigation strategies of plant growth-promoting rhizobacteria: Plant growth-promoting rhizobacteria mechanisms. *Plant Sci. Today* 8, 25–32. doi: 10.14719/pst.1543

Siles, J. A., Starke, R., Martinovic, T., Parente Fernandes, M. L., Orgiazzi, A., and Bastida, F. (2022). Distribution of phosphorus cycling genes across land uses and microbial taxonomic groups based on metagenome and genome mining. *Soil Biol. Biochem.* 174, 108826. doi: 10.1016/j.soilbio.2022.108826

Širić, I., Eid, E. M., Taher, M. A., El-Morsy, M. H. E., Osman, H. E. M., Kumar, P., et al. (2022). Combined use of spent mushroom substrate biochar and PGPR improves growth, yield, and biochemical response of cauliflower (*Brassica oleracea* var. *botrytis*): A preliminary study on greenhouse cultivation. *J. Hortic.* 8, 830. doi: 10.3390/horticulturae8090830

Suman, A., Govindasamy, V., Ramakrishnan, B., and Aswini, K., SaiPrasad, J., Sharma, P., et al. (2022). Microbial community and function-based synthetic bioinoculants: a perspective for sustainable agriculture. *Front. Microbiol.* 12, 1–19. doi: 10.3389/fmicb.2021.805498

Taffner, J., Bergna, A., Cernava, T., and Berg, G. (2020). Tomato-associated archaea show a cultivar-specific rhizosphere effect but an unspecific transmission by seeds. *Phytobiomes J.* 4, 133–141. doi: 10.1094/PBIOMES-01-20-0017-R

Taffner, J., Erlacher, A., Bragina, A., Berg, C., Moissl-Eichinger, C., Berg, G., et al. (2018). What is the role of archaea in plants? New insights from the vegetation of alpine bogs. *mSphere* 3, 1–14. doi: 10.1128/mSphere.00122-18

Taylor (1951). Nature of the factor in soil-extract responsible for bacterial growth-stimulation. *Nature* 176, 115–116. doi: 10.1038/168115a0

Upadhyay, S. K., Singh, J. S., Saxena, A. K., and Singh, D. P. (2012). Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. *Plant Biol.* 14, 605–611. doi: 10.1111/j.1438-8677.2011.00533.x

Vartoukian, S. R., Palmer, R. M., and Wade, W. G. (2010). Strategies for culture of "unculturable" bacteria. *FEMS Microbiol. Lett.* 309, 1–7. doi: 10.1111/j.1574-6968.2010.02000.x

White, R. H. (1987). Indole-3-acetic acid and 2-(indol-3-ylmethyl)indol-3-yl acetic acid in the thermophilic archaebacterium Sulfolobus acidocaldarius. *J. Bacteriol.* 169, 5859–5860. doi: 10.1128/jb.169.12.5859-5860.1987

Wicaksono, W. A., Egamberdieva, D., Berg, C., Mora, M., and Kusstatscher, P. (2022). Function-based rhizosphere assembly along a gradient of desiccation in the former aral sea. *MSystems* 7, 1–16. doi: 10.1128/msystems.00739-22

Yadav, A., Verma, P., Kaushik, R., Singh Dhaliwal, H., Kumar Saxena, A., Author, C., et al. (2017). Archaea endowed with plant growth promoting attributes. *Attrib. EC Microbiol.* 8, 294–298.

Yadav, A. N., Gulati, S., Sharma, D., Singh, R. N., Rajawat, M. V. S., Kumar, R., et al. (2019). Seasonal variations in culturable archaea and their plant growth promoting attributes to predict their role in establishment of vegetation in Rann of Kutch. *Biologia.* 74, 1031–1043. doi: 10.2478/s11756-019-00259-2

Yadav, A. N., Sharma, D., Gulati, S., Singh, S., Dey, R., Pal, K. K., et al. (2015). Haloarchaea endowed with phosphorus solubilization attribute implicated in phosphorus cycle. *Sci. Rep.* 5, 1–10. doi: 10.1038/srep12293

Yogendra, S. G. U., and A., K. S. (2015). Bacterial mediated amelioration of drought stress in drought tolerant and susceptible cultivars of rice (*Oryza sativa* L.). *African J. Biotechnol.* 14, 764–773. doi: 10.5897/AJB2015.14405

Zhang, M., Liwei, C., Muke, H., Weiqian, J., Jiabao, G., and Yi, H. (2020). Structure, assembly, and co-occurrence of archaeal communities in tree rhizosphere of the qinghai-tibetan plateau. *J. Res.* 5, 1–25. doi: 10.21203/rs.3.rs-34088/v1

frontiers | Frontiers in Environmental Science

TYPE Review
PUBLISHED 31 July 2023
DOI 10.3389/fenvs.2023.1182586

OPEN ACCESS

EDITED BY
Parul Chaudhary,
Graphic Era Hill University, India

REVIEWED BY
Geeta Bhandari,
Swami Rama Himalayan University, India
Raman Kumar,
Maharishi Markandeshwar University, Mullana, India
Viabhav Kumar Upadhayay,
Dr. Rajendra Prasad Central Agricultural University, India

*CORRESPONDENCE
Olubukola O. Babalola,
olubukola.babalola@nwu.ac.za

RECEIVED 09 March 2023
ACCEPTED 07 July 2023
PUBLISHED 31 July 2023

CITATION
Ayilara MS, Adeleke BS, Adebajo MT, Akinola SA, Fayose CA, Adeyemi UT, Gbadegesin LA, Omole RK, Johnson RM, Edhemuino M, Ogundolie FA and Babalola OO (2023), Remediation by enhanced natural attenuation; an environment-friendly remediation approach.
Front. Environ. Sci. 11:1182586.
doi: 10.3389/fenvs.2023.1182586

Remediation by enhanced natural attenuation; an environment-friendly remediation approach

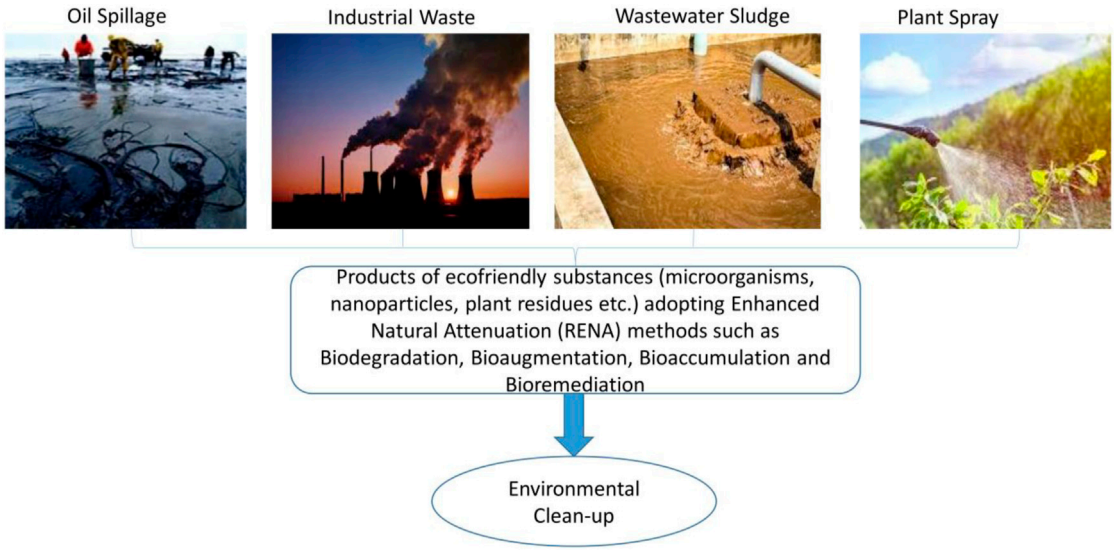
Modupe S. Ayilara[1,2,3], Bartholomew S. Adeleke[1,4], Mosimininuoluwa T. Adebajo[5], Saheed A. Akinola[6], Chris A. Fayose[7], Uswat T. Adeyemi[8], Lanre A. Gbadegesin[9], Richard K. Omole[10,11], Remilekun M. Johnson[10], Mary Edhemuino[12], Frank Abimbola Ogundolie[13] and Olubukola O. Babalola[1]*

[1]Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa, [2]Department of Microbiology, Faculty of Science, Kings University, Odeomu, Osun State, Nigeria, [3]Environmental Pollution Science and Technology (ENPOST), Ido-Ijesha, Ilesha, Nigeria, [4]Department of Biological Sciences, Microbiology Unit, School of Science, Olusegun Agagu University of Science and Technology, Okitipupa, Nigeria, [5]Department of Criminology and Security Studies, Faculty of Humanities, Management and Social Sciences, Kings University, Odeomu, Osun State, Nigeria, [6]Department of Medical Microbiology and Parasitology, School of Medicine and Pharmacy, College of Medicine and Health Sciences, University of Rwanda, Butare, Rwanda, [7]Department of Agricultural Technology, Ekiti State Polytechnic, Isan-Ekiti, Nigeria, [8]Department of Agricultural Economics and Farm Management, Faculty of Agriculture, University of Ilorin, Ilorin, Nigeria, [9]Institute of Mountain Hazards and Environment, University of Chinese Academy of Sciences, Beijing, China, [10]Department of Microbiology, Obafemi Awolowo University, Ile-Ife, Nigeria, [11]Microbiology Unit, Department of Applied Sciences, Osun State College of Technology, Esa-Oke, Nigeria, [12]Pan African University Life and Earth Sciences Institute, University of Ibadan, Ibadan, Nigeria, [13]Department of Biotechnology, Baze University, Abuja, Nigeria

The uncontrolled use of chemicals, urban wastes, nuclear resources, mining, petrochemicals and disposal of sewage sludge only a few anthropogenic activities that have contributed to the rapid industrialization and severe heavy metal contamination of soils and waterways. Both inorganic and organic pollutants, such as heavy metals, pesticides, petroleum hydrocarbons, and polycyclic aromatic hydrocarbons, can impact the composition and functionality of soils. Soils and plants are affected by pollution, thus, pose a dire threat to food security. This directly renders the soil unuseful for agricultural purposes, destroys the beneficial microbes in the soil, reduces the soil organic matter content, causes the imbalance of soil nutrients, affects plant growth and the interaction between the plants and microbes, subsequently affecting the soil and crop productivity. In addition, environmental pollutants affect human health, leading to different illnesses such as headaches, allergies, coughs, depression, chest pain, nausea, diabetes, liver problems, cancers, eye problems, and so on. Remediation (physical, chemical or biological) is therefore necessary to reduce the impacts of these pollutants in the environment. Bioremediations involve using natural products from plants, microbes, and so on, to detoxify the environment and make it useful or productive again. A key type of remediation is the Remediation by Enhanced Natural Attenuation (RENA) which involves the turning of soil to promote microbial proliferation, aeration, nutrient availability, moisture and consequently, the degradation of pollutants. This review discusses the technology of RENA, the associated microbes, the mechanism of its action, challenges associated with its usage and recommendations to advance the use of RENA for a sustainable environment.

KEYWORDS

bioremediation, nanoremediation, phytoremediation, microbial enzymes, bioaugmentation



GRAPHICAL ABSTRACT

1 Introduction

The soil is often polluted by different agents, such as heavy metals from mining, agricultural, petrochemical and other industries, including radiological, nuclear and other anthropogenic pollutants (Li et al., 2019b; Chaudhary et al., 2022) (Table 1). These agents negatively affect the soil, plants, organisms and humans, and have necessitated the need for remediation (Tyagi and Kumar, 2021). Many compounds arising from different pollutants have been reported to be very dangerous to humans. Acetaldehyde causes lesions to the nervous system, benzaldehyde causes irritation to the respiratory system, eyes, and skin and reduces the functioning ability of the brain, while polychlorinated dibenzo-dioxin causes cancers, respiratory system, eye, and skin irritation (Alabi et al., 2019). In animals, plastic wastes have been reported to disrupt the digestive systems of cattle (Evode et al., 2021). Equally, plant growth and root development have been reduced as a result of hydrocarbon pollutants (Hussain et al., 2019). These have called for a need for remediation. Remediation is the removal or reduction of the effects of pollutants in the environment; remediation can be carried out physically, chemically or biologically (Ayangbenro et al., 2018) (Figure 1). The physical and chemical methods involve soil washing, chemical extraction, soil treatment, supercritical fluid oxidation, encapsulation, stream extraction, chemical treatment, thermal treatment and volatilization (Riser-Roberts, 2020). The biological method, referred to as bioremediation, is a process by which wastes and toxic materials are organically removed or rendered less harmful into the environment (Ojuederie and Babalola, 2017; Ayangbenro and Babalola, 2018). This utilizes agents such as plants, microbes and nanoparticles of biological sources (Figure 1), which are more cost-effective compared to the other methods (Tyagi and Kumar, 2021; Chaudhary et al., 2023b; Bhandari et al., 2023). Remediation by enhanced natural attenuation (RENA) is a type of remediation process used to control soil pollutants by turning the soil to promote microbial proliferation, aeration, nutrient, moisture and degradation (Okoye et al., 2019). RENA is mainly used to control pollution caused by crude oil through different microbes such as those belonging to the genera *Achromobacter*, *Azospirillus*, *Ochrobactrum*, *Bacillus*, *Alcaligenes*, *Lysinibacillus*, *Pusillimonas*, and *Proteus* (Chikere et al., 2017). These microbes reduce the environmental pollutants by using them as carbon sources or by immobilizing them, thus making them unavailable for plant uptake (Chikere et al., 2017). Different organic and inorganic substrates are applied to improve the ability of microbes used in RENA (Kumar et al., 2021b; Mafiana et al., 2021; Parveen et al., 2022). Microbes produce different enzymes such as lipase, hydrogenase, laccase, *etc.*, which help to degrade a wide range of pollutants (Bhandari et al., 2021). This is a very important mechanism of pollutants which should be well explored, especially in cases where an environment is polluted with more than one contaminant. The efficiency of RENA bioremediation can be altered by different factors which include the environmental pH, oxygen, temperature, and nutrient (Al-Hawash et al., 2018b). These factors affect the microorganisms directly and in cases where they are unfavorable the microbes that are expected to carry the bioremediation process die. RENA can be applied on both dry and swampy land areas, in cases where bioremediation is carried out in a swampy area, different steps are taken. Firstly, the stumps on the land has to be removed before the baseline studies are carried out (this is to ensure that the proper method of bioremediation is utilized (Orji et al., 2012). These procedures are followed by soil tillage, nutrient application and the monitoring of remediation. In cases

TABLE 1 Different pollutants and their toxicity effects.

Pollutant	Source	Impact	References
Polycyclic aromatic hydrocarbon	Crude oil	They are highly toxic and they have mutagenic and carcinogenic properties	Sakshi et al. (2019)
Pesticides	Agricultural activities	Soil toxicity	El Enshasy et al. (2017)
Heavy metals such as Cd, Cr, V, Cu, As, Zn and Pb	Industrial activities	Reduction in plant biomass, plant transpiration, nutrient uptake, photosynthesis, stomatal size, and ATP enzyme activity, changing	Long et al. (2021)
Chemical fertilizer	Agricultural activities	Renders the soil brittle, reduces soil nutrients, increases soil acidification, reduces the soil microbial population and alters the pH of the soil	Pahalvi et al. (2021)
Pyrites and pyrrhotites	Mining	Renders the soil unfit for agricultural activities	Havugimana et al. (2017), Agboola et al. (2020)
Sulfur dioxide	Burning of gasoline, and natural gas as well as refineries, coal and paper mill industries	It dissolves with water to form acid rain, leading to the destruction of stones, metals and forests	El Enshasy et al. (2017)
Radioactive wastes, accidental oil spillage	Industrial activities	Renders the soil unfit for agricultural activities	Havugimana et al. (2017)
Lead	Acid manufacturing companies	Slow down the rate of plant growth	El Enshasy et al. (2017)
cadmium, chromium, lead, arsenic, selenium	Sanitary wastes	Destroys the balance of the underground soil	Havugimana et al. (2017)

where baseline studies are not carried out on the soil, the extent of pollution might not be known. For instance, in cases of underground water pollution, which leads to an assumption that RENA is not an efficient bioremediation procedure (Adesipo et al., 2020). The aim of this review is to discuss the technology of RENA, the different microbes associated with its usage, its mechanism of action, challenges associated with its application and recommendations to advance its usage to promote a sustainable environment.

2 Environmental pollutants and their negative impacts

There are different types of soil pollutants which have different detrimental effects on the environment.

3 Types of bioremediation

To remove pollutants arising from heavy metals such ascadmium, copper, nickel, mercury, organic pollutants and hydrocarbons from the soil, different plants, microbes, and nanobiomaterials have been utilized (Masowa et al., 2022). Therefore, according to their agents, bioremediation can be classified as a plant, microbial and nanobiomaterial remediation.

3.1 Phytobioremediation

Phytobioremediation (phytoremediation), is a process by which plants and the microbes associated with them (the plants) helps to reduce toxic pollutants in the environment. This mechanism of pollutant reduction is a cost-effective and environment friendly, it stabilizes, immobilizes, degrades and uptake pollutants from the environment (Kafle et al., 2022). Plants are capable of removing antibiotics, heavy metals, pesticides, radionuclides and organic pollutants from the environment (Kafle et al., 2022). Different plants have been reported to be involved in phytoremediation, these include *Parthenium hysterophorus, Melilotus indicus, Cnicus benedictus, Anagallis arvensis, Verbesina encelioides, Dalbergia sissoo, Conyza canadensis, Lathyrus aphaca, Stellaria media, Xanthium strumarium, Chenopodium album, Medicago polymorpha, Amaranthus viridis, Mirabilis jalapa, Chenopodiastrum murale, Prosopis juliflora, Chrozophora tinctoria, C. tinctoria, Cerastium dichotomum* and *Arenaria serpyllifolia* (Naz et al., 2022).

Jiang et al. (2019) and Parsamanesh and Sadeghi (2019) reported that plant species, *Medicago scutellata* and *Mulberry* sp. were able to bioremediate cadmium successfully from the soil. Similarly, other plants have been reported to bioremediate heavy metals; for instance, *Cassia tora* was reported to remediate chromium (Patra et al., 2021), while *Polypogon monspeliensis* and *Rumex dentatus* remediated nickel from the soil (Samreen et al., 2021). The different types of phytoremediation that exist include phytoextraction, phytostabilization, phytofiltration and phytovolatilization (Shen et al., 2022). Phytoextraction is the process by which metalloids are extracted from contaminated soil, with the aid of accumulator plants (Yu et al., 2022). The phytostabilization process, uses plants that are resistant to metals to reduce he availability of pollutants in the environment (Kumar et al., 2023). Phytofiltration is the application of plants and the microbes associated with their roots in the removal of heavy metals from the environment (Akhtar et al., 2019). Phytovolatization is the process by which wastes are taken off the environment through plants and they are transformed into gaseous state, which is released into the atmosphere (Pidlisnyuk et al., 2021). These processes are affected by the bioavailability of heavy metals and biomass of plants (Shen et al., 2022). The efficiency of phytoremediation is affected by stomatal conductance, the species of the microorganism present, intensity of light, plant species

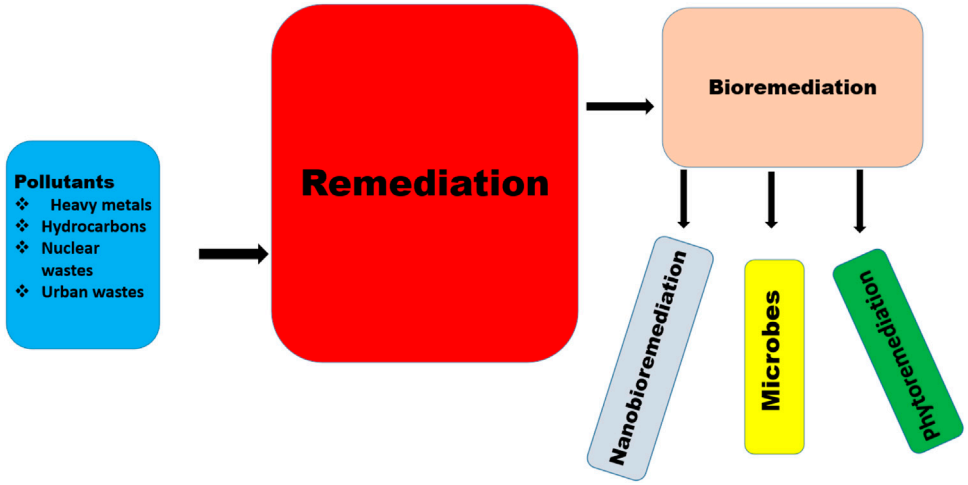


FIGURE 1
Types of bioremediation.

involved (its metabolism, photosynthesis and absorption rate) and temperature (Wei et al., 2021).

3.2 Nanoremediation

Nanoremediation is the application of nanomaterials in the treatment of environmental pollutants, especially on the soil and in water (El-Ramady et al., 2020). The different types of nanoparticles used in bioremediation, they include zinc nanoparticles, iron nanoparticles, aluminum nanoparticles, gold nanoparticles, titanium nanoparticles, carbon nanoparticles, and silver nanoparticles (Alazaiza et al., 2021). Nanoparticles, especially iron nanoparticles, are very active in soil bioremediation. The mechanism of nanoremediation include catalysis, adsorption, photodegradation and filtration (Mukhopadhyay et al., 2022). In a study carried out by Ji et al. (2023), diatomaceous earth nanoparticles were combined with polyethyleneimine nanoparticles to remove copper pollutants arising from acid mine drainages. Equally, nano biosurfactants have been reported to be capable of cleaning up toxic wastes from the soil arising from fertilizers, pesticides, herbicides, insecticides and heavy metals (Boregowda et al., 2022). Research carried out by Cao et al. (2022) showed that iron oxide nanoparticles could bioremediate cadmium and lead. These nanobiomaterials have been proven to be very efficient in the removal of toxic chemicals and heavy metals from the environment, particularly, the soil (Torimiro et al., 2021 (Chaudhary et al., 2023a)). However, a few drawbacks like adverse effects on soil microorganisms and the reduction in the activity of these nanoparticles as they age have been reported (Cecchin et al., 2017). Since the reduction in the efficiency of these nanoparticles with age can impact negatively their shelf life when made into commercial products, it is necessary that more research should be channeled toward strategies to increase their stability and lessen their harmful impacts on beneficial soil microbes to enhance their applicability as agents of bioremediation. The efficiency of nanoparticle as agents of bioremediation can be improved by fortifying them with polymers, zeolites, biochar, activated carbon and clay minerals (Mukhopadhyay et al., 2022).

3.2.1 Microbial bioremediation

Microbial remediation is the use of microbes to reduce the concentration of heavy metal pollutants in the environment (Jin et al., 2018). Microorganisms such as fungi, algae and bacteria have been used to bioremediate polluted soils (Ndeddy Aka and Babalola, 2016; Karthika et al., 2017; Ndeddy Aka and Babalola, 2017; Thesai et al., 2021; Kumar et al., 2022) (Table 2). The efficiency of these organisms is affected by the temperature of the environment, substrate where the microbes are getting their nutrient from and the pH of the environment (Jin et al., 2018). A report by Ghosh et al. (2021) revealed that generally, bacteria species like *Brevibacterium iodinum*, *Pseudomonas aeruginosa, Pseudomonas florescens* and *Alcaligenes faecalis,* as well as the fungi species like *Saccharomyces cerevisiae* are very active in the bioremediation of the soil; the researchers equally reported the effectiveness of *Anaeromyxobacter* sp., *Comamonas* sp., *Saccharibacteria* sp., *Desulfomicrobium* sp., *Acinetobacter* sp., *Zoogloea* sp., *Sphingobiun* sp., *Terrimonas* sp. and *Thiobacillus* sp. in the bioremediation of organic compounds such as pyridine, indole and quinolone. El-Ansary and Ahmed-Farid (2021) as well reported the ability of algae species such as *Scenedesmus obliquus*, *Nostoc muscorum*, *Chlorella vulgaris* and *Anabaena oryza* to degrade oxyl nematicide. These organisms usually use these pollutants as carbon and energy sources and convert them into water, microbial biomass, metabolites and carbon dioxide, which are generally not as toxic as the initial pollutants but could be useful to the soil health and plants alike (Tyagi and Kumar, 2021).

Some microbes utilize pollutants as their energy source during remediation, while some may immobilize or transform them and make them unavailable for plant uptake. RENA has been reported to be effective in the remediation of coal tar; Telesiński and Kiepas-Kokot (2021) reported that there was a decrease in the contents of phenol and naphthalene by 98%–100%, when the RENA technology was used.

TABLE 2 Different microorganisms used in bioremediation.

Organism	Species	Pollutant removed	References
Bacteria	*Achromobacter, Lysinibacillus* sp., *Azospirillus* sp., *Ochrobactrum* sp., *Proteus sp, Bacillus* sp., *Pusillimonas* sp. and *Alcaligenes* sp.,	Hydrocarbons	Chikere et al. (2017)
	Cellulosimicrobium sp	Chromium	Bharagava and Mishra (2018)
	Klebsiella sp.	Lead	Wei et al. (2016)
	Organisms from the genera *Cupriavidus, Burkholderia*, *Paenibacillus* and *Ensifer*	Chromium and Cadmium	Minari et al. (2020)
	Enterobacter asburiae, Stenotrophomonas sp., *Enterobacter cloacae*, *Brevibacillus reuszeri*, *Acinetobacter junii*, and *Enterobacter aerogenes*	Lead, chromium, and nickel	Sarma et al. (2019)
	Staphylococcus pasteuri	Phenanthrene pyrene, and fluoranthene	Anawar (2015)
	Bacillus amyloliquefaciens, Bacillus aerius, *Bacillus subtilis*, *Bacillus cereus, Pseudomonas aeruginosa,* and *Chryseobacterium* sp.	Lead, nickel and cadmium	Su (2016)
	Modicisalibacter sp., *Idiomarina sp* and *Brevibacterium* sp.	Pyrene, benzopyrene, phenanthrene, naphthalene, phenol, hexadecane	Gomes et al. (2018)
	Bacillus megaterium	Cadmium, boron and lead	Esringü et al. (2014)
	Bacillus thurigiensis, *Rhodococcus hoagii* and *Bacillus pumilus*	Petroleum hydrocarbon	Viesser et al. (2020)
	Enterobacter sp.	Cadmium	Mitra et al. (2018)
	Arthrobacter ureafaciens	Simazine	Viesser et al. (2020)
	Pseudomonas aeruginosa	Cadmium	Chellaiah (2018)
	Morganella morganii	Chromium	Princy et al. (2020)
	Cupriavidus sp. strain Cd^{+2}	Cadmium	Li et al. (2019a)
	Rhodopseudomonas sp.	Crude oil and hydrocarbon	Mai et al. (2021)
	Enterobacter asburiae KUNi5	Nickel	Paul and Mukherjee (2016)
	Erythromicrobium ramosum and *Erythromonas ursincola*	Selenite and tellurite	Maltman and Yurkov (2018)
	Bacillus sp. KL1	Nickel	Taran et al. (2019)
	Halomonas sp. and *Marinobacter* sp.	Phenanthrene	Wang et al. (2020)
	Bradyrhizobium sp. and *Rhizobium metallidurans*	Lead and zinc	Sujkowska-Rybkowska and Ważny (2018)
	Lactobacillus plantarum	Lead and cadmium	Ameen et al. (2020)
	B. cereus, *B. licheniformis* and *B. subtilis*	Copper, lead and chromium	Shameer (2016)
	Cupriavidus metallidurans	Chromium	Alviz-Gazitua et al. (2019)
	Shinella sp.	Arsenic and antimony	Nguyen et al. (2021)
	Escherichia coli, *Acinetobacter lwoffii*, *Bacillus thuringiensis, Enterobacter ludwigii*, *Vitreoscilla* sp., *Pseudomonas fluorescens, Klebsiella pneumoniae*, and *Enterobacter asburiae*	Nickel, lead and zinc	Mosharaf et al. (2018)
	Bacillus aryabhattai	Paraquat	Inthama et al. (2021)
	Bacillus subtilis	Nickel and lead	Igiri et al. (2018)
	Staphylococcus sp. and *Pseudomonas* sp.	Phenanthrene	Mnif et al. (2017)
	Pseudomonas sp.	Arsenic	Satyapal et al. (2018)
	Pseudomonas sp.	Nickel, chromium, lead, and copper	Naz et al. (2016)
	Gemella sp. and *Micrococcus* sp.	Lead, chromium and cadmium	Marzan et al. (2017)
	Bacillus cereus and *Pseudomonas aeruginosa*	Lead and cadmium	Nath et al. (2018)
	Arthrobacter aurescens	Trifluralin pesticides	Lara-Moreno et al. (2022)
	Corynebacterium vitarumen, *Bacillus macerans* and *Bacillus megaterium*	Arsenic	Tyagi et al. (2018)

(Continued on following page)

TABLE 2 (*Continued*) Different microorganisms used in bioremediation.

Organism	Species	Pollutant removed	References
	Sphingomonas sp.	Hydrocarbon	Song et al. (2021)
	Bacillus sp.	Chromium	Ramírez et al. (2019)
	Bacillus safensis and *Pseudomonas fluorescens*	Chromium	Kalaimurugan et al. (2020)
	Bacillus subtilis, Bacillus licheniformis, and *Bacillus cereus*	Lead, chromium, and copper	Syed and Chinthala (2015)
	Halomonas sp.	Chromium	Kalola and Desai (2020)
	Sphingomonadales sp	Hydrocarbon	Bastida et al. (2016)
Fungi	*Arthrographis* sp., *Aspergillus* sp., *Mucor* sp., *Trichophyton* sp., *Fusarium* sp., *Rhizomucor* sp.,	Hydrocarbon	Okoye et al. (2019)
	Rhodotorula sp., *Penicillium* sp., *Candida* sp., *Rhizopus* sp., *Acremonium* sp., *Sporothrix* sp. *and Geotricum* sp.		
	Aspergillus sp.	Crude oil	Zhang et al. (2016)
	Ulocladium sp., *Penicillium* sp., *Fusarium oxysporum, Penicillium crysogenum, Ulocladium atrum, Aspergillus terreus, and Aspergillus parasiticus*	Hydrocarbon	Medaura et al. (2021)
	Aspergillus sp.	Crude oil	Al-Hawash et al. (2019)
	C. tropicalis and *T. asahii*	Hydrocarbon	Gargouri et al. (2015)
	Penicillium sp.	Petroleum hydrocarbon	Al-Hawash et al. (2018a)
	Monilinia sp.	Crude oil	Wu et al. (2008)
	Penicillium sp.	Hydrocarbon	Sari et al. (2019)
	C. tropicalis	Engine oil	Mbachu et al. (2016)
	T. versicolor	Toluene and benzene	PM Tavares et al. (2017)
	A. oryzae	Crude oil	Asemoloye et al. (2020)
	Aspergillus flavus	Surfactants and dyes	Ghosh and Ghosh (2018)
	Aspergillus sp. and *Penicillium* sp.	Crude oil	Sari et al. (2019)
Algae	*Scenedesmus quadricauda, Selenastrum capricornutum, Chlorella vulgaris* and *Scenedesmus platydiscus*	Petroleum hydrocarbon	Fu and Secundo (2016)
	Spirulina platensis and *Nostoc punctiforme*	Crude oil	El-Sheekh and Hamouda (2014)
	Gracilariacorticata sp.	Nickel	Raju et al. (2021)
	Chlorella vulgaris	Crude oil	Kalhor et al. (2017)
	Gelidium amansii	Lead	El-Naggar et al. (2018)
	Sargassum filipendula	Nickel, chromium and zinc	Costa et al. (2020)
	Ulva lactuca	Zinc	Senthilkumar et al. (2019)
	Spirulina platensis	Copper	Anastopoulos and Kyzas (2015)
	Synechocystis sp.	Pyrene	Patel et al. (2015)
	Turbinaria ornata	Lead	Al-Dhabi and Arasu (2022)
	Ulva lactuca	Zinc	Senthilkumar et al. (2019)
	Sargassum filipendula	Cadmium	Nishikawa et al. (2018)
	Chlorella vulgaris	Heavy metals	Alhumairi et al. (2021)
	Oscillatoria pranceps, Phormidium mucicola, Westiellopsis prolific, Lyngbya digueti and *Anabaena variabilia*	Hydrocarbon	Al-Hussieny et al. (2020)
	Dunaliella salina, Nannochloropsis oculata, Platymonas subcordiformis and *Phaeocystis globose*	Nonylphenol	Wang et al. (2019)

(Continued on following page)

TABLE 2 (*Continued*) Different microorganisms used in bioremediation.

Organism	Species	Pollutant removed	References
	Osmundea pinnatifida, Fucus vesiculosus, Ulva intestinalis, Fucus spiralis, Gracilaria sp. and *Ulva lactuca*	Mercury	Fabre et al. (2020)
	Caulerpa scalpelliformis	Zinc	Jayakumar et al. (2021)
	Sargassum filipendula	Chromium	Moino et al. (2017)
	Sargassum polycystum	Zinc and cadmium	Jayakumar et al. (2022)
	Cystoseira barbata and *Cystoseira crinite*	Chromium	Yalçın and Özyürek (2018)

3.2.1.1 Bacterial bioremediation

Bacteria are important agents of bioremediation, they are capable of removing polyaromatic, aromatic and aliphatic hydrocarbons (Table 2). The optimum conditions required for bacterial remediation include a temperature ranging between 30°C and 40°C, a carbon/nitrogen and phosphorus ratio of 100; 20; 1, a pH range of between five to eight and an oxygen level of between 10 and 40 percent (Kebede et al., 2021). Bacteria involved in bioremediation can live in a cooperative or competitive relationship, when in a cooperative relationship, the biodegradation process is enhanced; however, when they are in a competitive relationship, the biodegradation process is reduced (Kebede et al., 2021). Resident bacteria are more competitive in hydrocarbon degradation compared to the introduced species, especially in a long term (Kaminsky et al., 2019). Bacteria undergo genetic modifications to maximally remediate hydrocarbons, otherwise, they produce enzymes. Therefore, more research should be carried out to focus on the discovery of more enzymes that can successfully bioremediate complex pollutants.

3.2.2 Fungal bioremediation

Different fungal species have been successfully used as agents of bioremediation (Table 2). Fungi degrade pollutants by intracellular compartmentalization, organic acid precipitation, metal-binding proteins, active transport, metabolite, and inorganic acid precipitation (Li et al., 2020). When different metabolites and compounds are released by fungi, they help to immobilize and mobilize metal pollutants in the soil. In addition, fungi produce melanin and polymers which have oxygen groups which include carbonyl, carboxyl, phenolic hydroxyl, methoxyl, and alcoholic hydroxyl which are used to clean up pollutants in the environment (Li et al., 2020). They are capable of degrading a wide range of substrates such as pesticides and hydrocarbons, due to their ability to tolerate and survive in adverse environments (Mostafa et al., 2022).

3.2.2.1 Algal bioremediation

Algaebioremediation happens majorly through two different mechanisms, the first is adsorption, while the second is adsorption (Dwivedi, 2012). Adsorption involves the adherence of pollutants to the surface of algae, the process takes place very fast and is independent of the cell metabolism. Adsorption is a two-way process, initially, the pollutants get adsorbed to the surface of the cell, and subsequently, they are moved into the cytoplasm, in a process called chemisorption (Liu et al., 2021). Interestingly, algae can bioremediate pollutants both in their living and dead states, but the living cells have the ability to bioremediate pollutants better than the dead ones (Salama et al., 2019). The ability of algae in bioremediation is affected by different factors such as pH, the effect of counter ion, temperature, ionic strength and contact time (Salama et al., 2019). If these factors are optimized, the maximum potentials in the bioremediation process of algae would be tapped into.

4 Mechanism of RENA

RENA is a modern concept of microbial-assisted remediation, and it is gaining more insights because it enhances the function and the ability of the microbes in bioremediation. It is a more affordable method when compared to other remediation methods which include washing of soils and burning and helps to ensure maximum remediation as the microbes involved are able to completely break down pollutants such as hydrocarbons (Kanwal et al., 2022). Pollutants in the soil can be degraded by the RENA technique through different mechanisms, which include biodegradation, biotransformation (bioaugmentation) and bioaccumulation (bioassimilation) (Oghoje et al., 2021) (Figure 2).

4.1 Bioassimilation

Bioassimilation, which is also referred to as bioaccumulation is the process by which microbes accumulate heavy metals in their body, making them unavailable for uptake by the plant; for instance, the sorption of chromium, cadmium and lead by *Panteoa species* and *Pseudomonas koreensis* have been reported (Ayangbenro and Babalola, 2017; Ayangbenro et al., 2019; Oghoje and Ukpebor, 2020) (Table 3). Bioaccumulation is a bioremediation process that consumes energy and also serves as a basis for methylation and redox in microbial remediation (Yin et al., 2022). When bacterial cells are used, bioaccumulation includes transport mediated by carriers, ion pumps, lipid infiltration and endocytosis (Yin et al., 2022). The pollutants removed from the environment through this method is attached to the cellulose derivatives, chitin and polysaccharides active sites of microorganisms through the physical and chemical binding with biofunctional groups (Tarfeen et al., 2022). This method involves forces such as the ion exchange processes, electrostatic attraction, covalent bonding, Van der Waal's forces, and microprecipitation, while the functional groups involved include the sulfhydryl, hydroxyl, phosphonate, carboxyl and amine on the active cell component (Tarfeen et al., 2022).

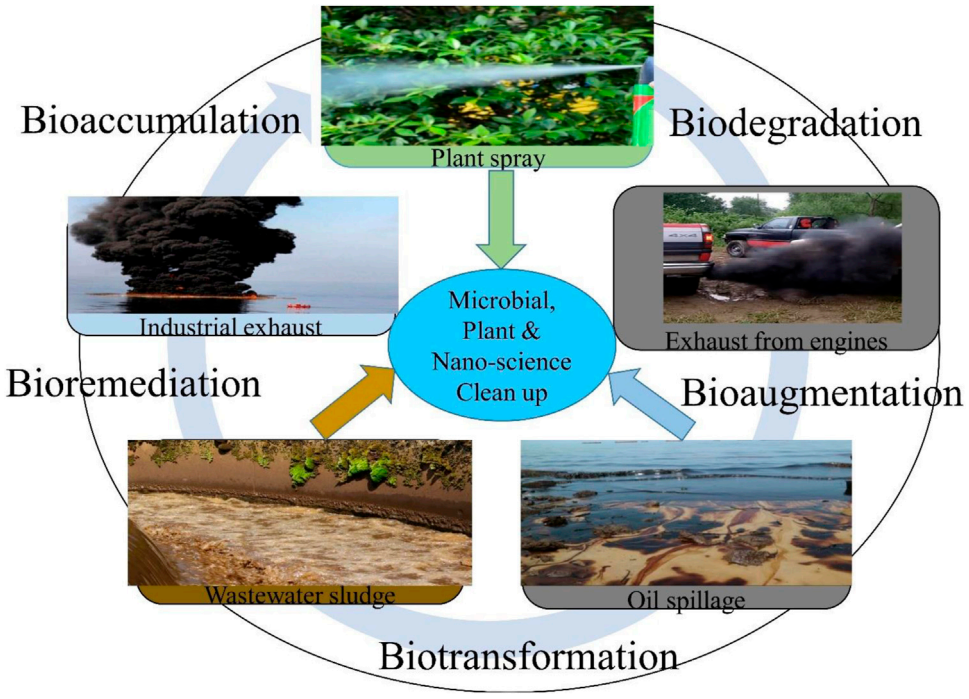


FIGURE 2
Mechanism of RENA.

TABLE 3 Mechanism of microbial bioremediation.

Microbe	Waste remediated	Mechanism	References
Monodictys pelagic and *Aspergillus niger*	Chromium and lead	Bioaccumulation	Sher and Rehman (2019)
Pseudomonas putida IRN22, *Acinetobacter pittii* IRN19, *Micrococcus luteus* IRN20	polyethylene	Biodegradation	Montazer et al. (2019)
Bacillus cereus M116	Nickel	Bioaccumulation	Naskar et al. (2020)
Bacillus cereus	Lead	Bioaccumulation	Utami et al. (2020)
Streptomyces rimosus	Iron and lead	Biosorption	Sahmoune (2018)
Staphylococcus hominis	Lead and cadmium	Biosorption	Rahman et al. (2019)
Cronobacter muytjensii KSCAS2	Different heavy metals	Biosorption	Saranya et al. (2018)
Bacillus sp. and *Paenibacillus* sp	Plastic	Biodegradation	Park and Kim (2019)
Serratia liquefaciens	Kraft lignin	Biotransformation	Singh et al. (2019)
Stenotrophomonas sp	Poly (butylene adipate- co -terephthalate)	Biodegradation	(Jia et al., 2021; Shilpa et al., 2022)
	(PBAT)		

5 Biotransformation

Biotransformation, also called bioaugmentation, is the conversion of a pollutant from one oxidation state to another. In bioaugmentation, microbes that are capable of degrading hydrocarbons but are not residents in the soil are introduced from external sources to supplement the resident organism, mostly bacteria and fungi (Essabri et al., 2019; Sayed et al., 2021) (Table 3). Sulfur-reducing bacteria such as *Sulfolobus* sp., *Acidiphilium cryptum, T. thioparus, A. cryptum, S. acidophilus, Citrobacter* sp., *Thiobacillus denitrificans, Acidithiobacillus ferrooxidans, Sulfobacillus thermosulfidooxidans, At. caldus, Gallionella ferruginea, At. thiooxidans, Ferroplasma acidiphilum, Clostridium* sp.,

Acidianus brierleyi, and *Leptospirillum ferrooxidans* have been reported to be potent in the mobilization and elimination of heavy metals from mines by dissolution, precipitation and retrieving safer metals from them (Schippers et al., 2010; Martins et al., 2011; Anawar, 2015; Ayangbenro et al., 2018). The bioaugmentation procedure is a fast, easy and effective method of RENA using different agents such as bacteria, algae, archaea and fungi (Ghosal et al., 2016; Kong et al., 2018).

6 Biodegradation

Biodegradation is the process by which microbes use the carbon in petroleum pollutants as a source of energy to disintegrate the hydrocarbon compounds into an environment-friendly form, such as carbon dioxide and water, with the aid of genes and enzymes produced by the microbes (Arumugam et al., 2017; Ahmed et al., 2018; Arumugam et al., 2018; Masowa et al., 2018; Karthika et al., 2020; Masowa et al., 2021; Priya et al., 2022) (Table 3). Adlan et al. (2020) reported the biodegradation of crude oil paraffin wax using *Anoxybacillus geothermalis*, *Geobacillus kaustophilus*, *Parageobacillus caldoxylostilyticus*, *Geobacillus jurassicus*, *Geobacillus stearothermophilus* and *Geobacillus thermocatenulatus* where around 70% degradation efficiency was observed in crude oil; the organisms involved in the degradation produced enzymes such as esterase, alkane monooxygenase, lipase and alcohol dehydrogenase.

When microbes use pollutants as carbon sources, they do so through three different techniques, namely, biostimulation, bioaugmentation and bio-facilitation (Azubuike et al., 2016; Oghoje et al., 2021). Bio-facilitation is a process by which the physiochemical content, and oxygen level, among others, in the soil are altered to make the inherent soil microbes more active to access pollutants. An example of this technique is land farming which involves the spread of evacuated soil and the tilling of soils where pollutants are found to increase oxidation (Oghoje et al., 2021). For instance, nutrients from organic wastes, synthetic fertilizers, humic acids, nanomaterials and so on, can be added to enhance microbial growth (Bianco et al., 2020). Bianco et al. (2020) carried out research to assess the ability of fresh organic municipal solid wastes, combined macro and micronutrients and digestate to increase the metabolism of microbes in the remediation of pyrene, anthracene, fluoranthene and phenanthrene. Other agents of biostimulation include blood meal which is a form of fertilizer that releases nutrients slowly. It is highly rich in nutrients such as tryptophan, lysine, histidine, leucine and valine, and can be used in the degradations of dichlorodiphenyltrichloroethane and polycyclic hydrocarbons (Wang et al., 2017). Biostimulation can be carried out using composting; it is cost friendly as it employs agents like manures, activated sludge and maple leaves, which will increase the population of microbes in the soil; compost from green forest debris and sewage sludge was able to reduce polycyclic hydrocarbons pollution (Guo et al., 2020).

7 Enzymes used in RENA

Scanty information is available on the microbial enzymes used in RENA; however, enzymes like laccase, hydrolase, cytochrome P450, protease, dehalogenase, lipase, dehydrogenase and so on, have been reported to be useful (Adlan et al., 2020). Proteases enhance the disintegration of peptide bonds in a protein. Their ability to degrade a wide range of substrates and their unique catalytic mechanism makes them a very effective method of bioremediation (Bhunia and Basak, 2014). Examples of microbes that produce proteinases are *Aspergillus* sp., *Cladosporium* sp., *Trichoderma* sp., *Bacillus* sp. and *Penicillium* sp. (Kumar and Jain, 2020). Cytochrome P450 enzymes are monooxygenases (haem) that can bioremediate pollutant compounds by reducing an atom to water and inserting an atom from molecular oxygen into the substrate (Behrendorff, 2021). White rot fungi have recently been used extensively in degrading pollutants, owing to the cytochrome enzyme produced by them (Lin et al., 2022); cytochrome P450 degrades xenobiotics using chemical transformation techniques such as dehalogenation, epoxidation, dealkylation and aliphatic hydroxylation (Bhandari et al., 2021). Laccases are enzymes that oxidize compounds in pollutants, leading to degradation and bioremediation. They are majorly observed in plants and fungi but lately, researches are emerging about their production by bacteria (because of their ability to survive at high temperatures and in different organic compounds), although their efficiency is determined by their substrate tolerance, selectivity and the center of their catalysis (Zhang et al., 2020). Dai et al. (2020) reported the ability of laccase from bacteria to degrade pollution resulting from heavy oil by 66.5% in 100 days. Remediation using dehydrogenase happens through reductive, oxygenlytic and hydrolytic mechanisms; oxygenlytic mechanism occurs when one or two atoms of oxygen is incorporated into a substrate, hydrolytic mechanism occurs with the water molecule acts as a cofactor when the hydroxyl group replaces the halogen substituent in SN reaction. In contrast, in the reductive mechanism, under aerobic conditions, hydrogen substitutes the halogen using the organohalides as the terminal electron acceptor (Bhandari et al., 2021). Li et al. (2019c) unraveled a novel hydrolase enzyme from *Bacillus amyloliquefaciens* to degrade soil and food polluted by carbendazim. Equally, Ugochukwu et al. (2008) carried out a research and reported that *Bacterium aliphaticum, Candida tropicalis, Bacillus megaterium, Pseudomonas maltiphilia, Bacillus cereus, Botryodiphodia thiobroma, Edwardsiella tarda, Fusarium vertiaculloide, Cryptococcus neofomas, Aspergillus niger* and *Fusiarum oxysporum* can bioremediate crude oil pollution due to the production of lipase.

Six Esterases which are produced by *Bacillus sp*. are useful in degrading polyesters, plastics and polyurethane (Bhatt et al., 2019). Nitrilases were used to remediate cyanide and can be produced by different yeast, bacteria and fungi (Gong et al., 2012; Park et al., 2017). Similarly, peroxidases produced by *Sphingobium sp*. are used to degrade phenols, lignin, methoxybenzenes and manganese oxide (Wang et al., 2009; Sharma et al., 2019). Dehydrogenase which is an active enzyme utilized for respiration by microbes was observed to be very helpful in the measurement of the total oxidation activity during the bioremediation of diesel (Lee et al., 2011). Manganese peroxidase which was sourced from fungi was reported to be positively correlated with the complete biodegradation of petroleum hydrocarbon (Košnář et al., 2019). Out of all the enzymes produced by fungi, oxidoreductases and hydrolases have a broad spectrum, with the ability to degrade a wide variation of pollutants (Kumar et al., 2021a). In their natural

environment, microbes produce enzymes which are very active in the degradation of environment pollutants, however, the further utilization of these microbes has proved to be very challenging (Sharma et al., 2018). Sometimes, compaenzyme production in the lab can be complicated, as microbes tend to act differently in the lab red to the when they are in their natural environment. In situations where they are able to produce the enzymes in the laboratory, technologies such as enzyme immobilization, nanozymes and recombinant technology are used to multiply and/or stabilize the enzymes so that they can be further used on the field (Meng et al., 2019; Kumar et al., 2021a). Practical application of RENA at the field level.

On the field scale, RENA is used to remove pollutants from the soil and water, using methods such as stabilization, chemical transformation, dilution, volatilization dispersion and biodegradation (Naeem and Qazi, 2020). RENA has been used to clean up different oil spillage in groundwater and soil. In Nigeria, RENA was reported to be used in the remediation of oil spillage in Emohua community, Rivers State by adding top soils to the polluted site and frequent aeration (Chikere et al., 2019). A significant reduction was observed in the petroleum hydrocarbon from 8,635.68 mg/kg to 677.2 mg/kg after 56 days on this site. The bacteria involved were *Pseudomonas* sp., *Xenorhabdus* sp., *Bacillus* sp., *Myroides* sp., *Proteus* sp., *Staphylococcus* sp., *Pectobacterium* sp., and *Providencia* sp., while the fungi species which include *Fusarium* sp., *Penicillium* sp., *Meyerozyma* sp., and *Candida* sp. were used. Generally, topsoil contains many bacteria and fungi species and nutrients irrespective of organic and inorganic nutrient amendments. Hence, mixed plowing of nutrient-rich topsoil with contaminated soil can increase soil nutrient parameters necessary for microbial growth (Celestina et al., 2019) Similarly, in the Ikarama community, Bayelsa state, Nigeria RENA was used to clear oil spillage in a period of 60 days, by burning the polluted site's vegetation and plowing with a tractor (Ezekoye et al., 2018). This process utilized different organisms such as *Acremonium* sp., *Phoma* sp., *Candida* sp., *Scopulariosis* sp., *Aspergillus* sp., *Sepedonium* sp., *Cladophialophora carrionii, Gliocladium* sp., *Paecilomyces variotii, Trichophyton tonsurans* and *Geotrichum cardidum* (Ezekoye et al., 2018). The effective usage of RENA on the field has been ascertained; however, the technology might be ineffective when practices such as fertilizer application, tilling and windrow are used, this is as a result of the presence of non-biodegradable residues in the soil beyond where there is aeration. Other challenges with this technology include a delayed response to oil spillage emergencies, which enhances the penetration of oil to a region beyond the soil which can be reached by turning (Mafiana et al., 2021).

Chicken manure digestates have been reported to serve as a source of nutrients when RENA technology is used in the removal of diesel on farmland (Oghoje et al., 2021). When 10% and 20% of the chicken manure digestate were used, about 50% and 58% of the diesel were removed from the environment. Spent mushroom substrate also have been reported to be used to serve as a source nutrients for four different fungal species, namely, *Agaricus bisporus*, *Pleurotus eryngii, Pleurotus ostreatus*, and Lentinula edodes, which were used to remediate petroleum hydrocarbon. The remediation process was evaluated for 40 days and the aliphatic and aromatic hydrocarbon were observed to reduce from C_{10} to C_{35} (Antón-Herrero et al., 2022).

7.1 Molecular mechanism of RENA

Identification of the microbes involved in RENA bioremediation is very necessary as it will help to understand better, the mechanism and enzymes used in the remediation of different heavy metals, organic pollutants, and hydrocarbons and also enhance the remediation process. Different molecular methods are used to study the microbes involved in the bioremediation processes such as RENA, as the methods (proteomics, transcriptomics, metagenomics and metabolomics) help to elucidate non-culturable organism, and also reveals the genes involved in bioremediation process (Rawat and Rangarajan, 2019). Each of these methods have an advantage of others, for instance, in a case where the quantity of the total mRNA is required, transcriptomics is used; however, this method does not reveal other expressed protein as well as their biological activity and expressed protein. Metagenomics is a method used to study the taxonomic and functional structure of different microbes (Pande et al., 2020; Hualpa-Cutipa et al., 2023). Proteomics is the study of the entire protein that are produced or modified by different microorganism (Nascimento et al., 2022). Transcriptomics deals with use of the total set of mRNA and the noncoding RNA transcripts which are produced by microbial cells, it controls the physical expression and acts as a connector between protein and DNA (Bogati and Walczak, 2022). Metabolomics is the study of all the primary and secondary metabolites produced by microbes, and in RENA, it involves microbes that are involved in RENA remediation (Wu et al., 2022). Hence, to have a detailed knowledge of the microbes present during RENA remediation, it would be helpful to combine different omics processes instead of just one approach.

8 Factors affecting the efficiency of RENA

The application of RENA to biodegrade pollutants is hindered by several factors ranging from the availability of microbes capable of degrading the pollutants to pH, temperature, nutrients and oxygen. When the diversity of microbes that can degrade microbes in the soil is limited, the biodegradation process is limited (Al-Hawash et al., 2018b). This is why sometimes nutrients are added to the environment, which will promote the growth and activities of the desired organism.

Bioremediation using RENA can be carried out in the presence and absence of oxygen, while in the presence of oxygen, it is referred to as aerobic condition the lack of oxygen, it is termed anaerobic condition; in the latter, microbes utilizes iron, carbon dioxide, sulfate and nitrate to exchange electron, thereby, forming methane and carbon (Patel et al., 2020). An oxygen percentage of 10%–40% was reported to be optimum for the biodegradation of hydrocarbon because, at this temperature, microbial activity and degradative enzymes are promoted (Kebede et al., 2021).

The mobility of pollutants (e.g., oil) can be affected by the moisture content in the soil, which consequently affects the allocation, existence, movement and activities of microbes in the soil (Al-Hawash et al., 2018b). Some pollutants are more soluble in

aqueous solutions, while some are not, and this affects their remediation (Fu and Secundo, 2016). The chemical constituent of hydrocarbons or waste to be degraded is an important factor to be considered when hydrocarbons are degraded, and specific microorganisms are just capable of degrading a single chemical compound, while some are capable of degrading multiple hydrocarbons or pollutants (Fu and Secundo, 2016).

The pH of the soil is paramount in the survival of microbes in the soil, unfavorable pH can be dangerous to the survival of microbes in the soil. Those that survive in acidic pH are termed acidophiles. Those that live in alkaline pH are called alkaliphiles, while those that survive neutral pH are called neutrophils (Schröder et al., 2020). The optimum pH observed when *A. niger* was used to bioremediate Hg, Cu, Co., Zn, and Ag was between 4–5.5 (Acosta-Rodríguez et al., 2018). On the other hand, Pawar (2015) reported that a pH of 7.5 was optimum for the degradation of hydrocarbons when *Penicillium freii* and *A. niger* were used.

Microbes required for the degradation of toxic heavy metals can die in the absence of optimum nutrients. Hence the presence of desired nutrients is needed for them to metabolize and remediate pollutants effectively. For example, *Aspergillus sydowii* bioremediated heavy metals and pesticides when mineral salt was used as the medium, as the nutrient was optimum for the growth and metabolism of the fungi (Zhang et al., 2019).

Some organisms are capable of surviving in extreme conditions; some organisms which live in extreme temperatures are termed extremophiles; those capable of living in cold regions are termed psychrophiles, and those who live in high temperatures are termed thermophiles (Malakootian et al., 2018). Research carried out by Acosta-Rodríguez et al. (2018) where *A. niger* was used to remove heavy metal pollutants in the environment revealed that the optimum remediation process occurred at a temperature of 28°C (Acosta-Rodríguez et al., 2018). Hence, it is important to carry out more research to understand the different pH levels, temperature, nutrient and oxygen requirements which will enable the survival of other microbes that can degrade various pollutants in the environment.

9 Challenges associated with the adoption of RENA

RENA, as technology has proven useful in the degradation of pollutants in the soil, and in ensuring the effective bioremediation of soil, but, the RENA process comes with some challenges which will be highlighted in this section. First, the RENA technology cannot degrade all waste. For example, RENA is highly specific in nature, hence, if there is the presence of more than one waste on the site, different microbes must be recruited, which probably might not be compatible to survive together (Sharma, 2020). Second, the biodegradation process of RENA sometimes brings about new products that may be more toxic compared to the initial pollutant, and the process is often time-consuming (Sharma, 2020). Third, the introduction of external nutrients or the turning of the normal soil structure of the soil during RENA to enhance the activity of microbes from another perspective can be seen as a negative move, as the normal eco-balance of the soil could shift and the soil structure can be destroyed by the movement of the soil (Chikere et al., 2017). Still, the addition of nutrients, especially from synthetic sources can lead to air and water pollution during rainy seasons (Chikere et al., 2017). Turning of the soil during RENA can as well promote the leaching of soil pollutants, as the pollutants which were at the surface are moved downwards, leading to underground water pollution (Chikere et al., 2017). Fourth, when the environment is altered, such as in the case of RENA, the expression of the gene by microbes might be altered (Smith et al., 2018). This may eventually affect the activity of the microbes either positively or negatively. It would not be appropriate to leave this to a game of chance, more research should be done to optimize the alteration in gene expression to be favorable to the microbes.

Lastly, the inhabitants of many communities do not trust the RENA technology, owing to the fact that in cases of severe pollution, a rapid method is always preferred. Since RENA is most times slow, it is assumed that it is not effective (Council, 2000). As a buttress, in some cases where a soil sample is taken from the environment to the laboratory or greenhouse to demonstrate the RENA technology, a false positive result might emerge because other factors might favor the technique in the greenhouse and might be otherwise on the field, resulting in lack of trust from the populace (O'Brien et al., 2021).

10 Conclusion and future prospects

RENA is an adequate, sustainable, non-toxic, cost-effective process which can be carried out at the site of pollution without posing any major health threat to the land, microbes and humans. This method removes the pollutants permanently, and not just transfer them to another environment (Sharma, 2020; Nuhu et al., 2022). Methods of RENA, such as the introduction of aeration and moisture to the soil which does not involve the movement of the soil, should be encouraged. Also, in cases where external nutrients would be added to the soil, organic nutrients in optimum quantity should be added as they are non-toxic to the environment, and if applied in optimum quantity, they will help to reduce the risk of eutrophication in water bodies.

RENA technology has proven to be effective and has successfully bioremediated some wastes, it comes with some drawbacks. This includes the inability to degrade some pollutants and the fact that RENA occurs mainly at the topsoil (0–5 m). Hence pollutants that go beyond this depth are leached into underground water (Ebuehi et al., 2005; Orji et al., 2012; Bolade et al., 2021)); therefore, it is recommended that research should be intensified to unravel organisms with strong abilities to bioremediate complex wastes. Also anaerobic microorganisms can be utilized through a deep injection technique to give microbes' access to wastes that are beyond 5 m where microbes used in RENA cannot access. Alternatively, RENA should be combined with other safe bioremediation techniques such as phytoremediation and nanoremediation to ensure a safe and more sustainable environment.

Since remediation using RENA has come with some challenges, it is therefore advised to carry out more research to beat the challenges associated with it to improve the utilization of the technology. For instance, when using RENA, the microbes used are highly specific, that

is, they remove one compound at a time from the environment which makes the process complicated in a situation where different compounds pollute a particular environment. Hence, it is recommended that more studies should be carried out to discover different microbes that have no antagonistic effects on each other and are capable of remediating different organic compounds and pollutants in a favourable manner. In addition, more studies should be conducted to recruit more microbes, especially from untapped resources such as the endophytes, rhizosphere and rhizoplane of underutilized legumes, since the underutilized legumes can survive in extreme conditions and the microbes capable of surviving in such environments could possess the same ability as well. Furthermore, not much work has been done on the different microbial enzymes and their ability to produce enzymes in different environments. An insight on this could help develop these enzymes into stable products for commercial purposes, which could be applied directly on the soil for bioremediation. To promote the use and acceptability of RENA, it has become important that more attention should be paid to local communities. Informal and formal education in secondary schools on the benefits of a sustainable environment should be conducted. Hesitancy and other cultural quirks that could slow the adoption of RENA technology should be broken through proper enlightenment. This will in turn, help to foster homegrown technological expertise, researchers, stake holders, investors, and grant donors, thereby, further reducing the cost of bioremediation in the long run.

Experiments which have been tested in the laboratory or greenhouse should be well tested on the field in different environments to ascertain their functionality and effectiveness across diverse soil conditions, to earn the trust of the populace. Governmental policies could also be amended to promote the use of bioremediation techniques like RENA, compared to the physical and chemical methods, which are more disadvantageous and environmentally unsustainable. Finally, it is necessary to understand the mechanism of RENA when combined with other bioremediation methods, as this would help to improve these two technologies and make them more sustainable.

Author contributions

MA and OB conceived the idea, wrote and revised the manuscript. BA, MA, SA, CF, FO, UA, LG, RO, RJ, and ME contributed to the writing of the manuscript and the final version of the work was approved by all authors for publication and production. All authors contributed to the article and approved the submitted version.

Funding

This study was funded through research grants from the National Research Foundation, South Africa (UID: 123634).

Acknowledgments

This OB appreciates the research grants from the National Research Foundation, South Africa.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Acosta-Rodríguez, I., Cárdenas-González, J. F., Rodríguez Pérez, A. S., Oviedo, J. T., and Martínez-Juárez, V. M. (2018). *Bioremoval of different heavy metals by the resistant fungal strain Aspergillus Niger*. Bioinorganic Chemistry Applications.

Adesipo, A. A., Freese, D., and Nwadinigwe, A. O. (2020). Prospects of *in-situ* remediation of crude oil contaminated lands in Nigeria. *Sci. Afr.* 8, e00403. doi:10.1016/j.sciaf.2020.e00403

Adlan, N. A., Sabri, S., Masomian, M., Ali, M. S. M., and Rahman, R. N. Z. R. A. (2020). Microbial biodegradation of paraffin wax in Malaysian crude oil mediated by degradative enzymes. *Front. Microbiol.* 11, 565608. doi:10.3389/fmicb.2020.565608

Agboola, O., Babatunde, D. E., Fayomi, O. S. I., Sadiku, E. R., Popoola, P., Moropeng, L., et al. (2020). A review on the impact of mining operation: Monitoring, assessment and management. *Results Eng.* 8, 100181. doi:10.1016/j.rineng.2020.100181

Ahmed, A. A. Q., Babalola, O. O., and Mckay, T. (2018). Cellulase-and xylanase-producing bacterial isolates with the ability to saccharify wheat straw and their potential use in the production of pharmaceuticals and chemicals from lignocellulosic materials. *Waste biomass valorization* 9, 765–775. doi:10.1007/s12649-017-9849-5

Akhtar, M., Oki, Y., Bich, B., and Nakashima, Y. (2019). Estimation of phytofiltration potential for Cu and Zn and relative growth response of Azolla japonica and Azolla pinnata. *J. Agric. Sci. Technol.* 21, 895–909.

Al-Dhabi, N. A., and Arasu, M. V. (2022). Biosorption of hazardous waste from the municipal wastewater by marine algal biomass. *Environ. Res.* 204, 112115. doi:10.1016/j.envres.2021.112115

Al-Hawash, A. B., Alkooranee, J. T., Abbood, H. A., Zhang, J., Sun, J., Zhang, X., et al. (2018a). Isolation and characterization of two crude oil-degrading fungi strains from Rumaila oil field, Iraq. *Biotechnol. Rep.* 17, 104–109. doi:10.1016/j.btre.2017.12.006

Al-Hawash, A. B., Dragh, M. A., Li, S., Alhujaily, A., Abbood, H. A., Zhang, X., et al. (2018b). Principles of microbial degradation of petroleum hydrocarbons in the environment. *Egypt. J. Aquatic Res.* 44, 71–76. doi:10.1016/j.ejar.2018.06.001

Al-Hussieny, A. A., Imran, S. G., and Jabur, Z. A. (2020). The use of local blue-green algae in the bioremediation of hydrocarbon pollutants in wastewater from oil refineries. *Plant Arch.* 20, 797–802.

Alabi, O. A., Ologbonjaye, K. I., Awosolu, O., and Alalade, O. E. (2019). Public and environmental health effects of plastic wastes disposal: A review. *J. Toxicol. Risk Assess.* 5, 1–13.

Alazaiza, M. Y., Albahnasawi, A., Ali, G. A., Bashir, M. J., Copty, N. K., Amr, S. S. A., et al. (2021). Recent advances of nanoremediation technologies for soil and groundwater remediation: A review. *Water* 13, 2186. doi:10.3390/w13162186

Alhumairi, A. M., Hamouda, R. A., and Saddiq, A. A. (2021). Bio-remediation of most contaminated sites by heavy metals and hydrocarbons in dhiba port kingdom of Saudi arabia using Chlorella vulgaris. *Res. Square* 1, 1–17.

Alviz-Gazitua, P., Fuentes-Alburquenque, S., Rojas, L. A., Turner, R. J., Guiliani, N., and Seeger, M. (2019). The response of Cupriavidus metallidurans CH34 to cadmium involves inhibition of the initiation of biofilm formation, decrease in intracellular c-di-GMP levels, and a novel metal regulated phosphodiesterase. *Front. Microbiol.* 10, 1499. doi:10.3389/fmicb.2019.01499

Al-Hawash, A. B., Zhang, X., and Ma, F. (2019). Removal and biodegradation of different petroleum hydrocarbons using the filamentous fungus Aspergillus sp. RFC-1. *Microbiologyopen* 8, e00619. doi:10.1002/mbo3.619

Ameen, F. A., Hamdan, A. M., and El-Naggar, M. Y. (2020). Assessment of the heavy metal bioremediation efficiency of the novel marine lactic acid bacterium, Lactobacillus plantarum MF042018. *Sci. Rep.* 10, 314–411. doi:10.1038/s41598-019-57210-3

Anastopoulos, I., and Kyzas, G. Z. J. J. O. M. L. (2015). Progress in batch biosorption of heavy metals onto algae. *J. Mol. Liq.* 209, 77–86. doi:10.1016/j.molliq.2015.05.023

Anawar, H. M. (2015). Sustainable rehabilitation of mining waste and acid mine drainage using geochemistry, mine type, mineralogy, texture, ore extraction and climate knowledge. *J. Environ. Manag.* 158, 111–121. doi:10.1016/j.jenvman.2015.04.045

Antón-Herrero, R., García-Delgado, C., Baena, N., Mayans, B., Delgado-Moreno, L., and Eymar, E. (2022). Assessment of different spent mushroom substrates to bioremediate soils contaminated with petroleum hydrocarbons. *Appl. Sci.* 12, 7720. doi:10.3390/app12157720

Arumugam, K., Renganathan, S., Babalola, O. O., and Muthunarayanan, V. (2018). Investigation on paper cup waste degradation by bacterial consortium and *Eudrillus eugeinea* through vermicomposting. *Waste Manag.* 74, 185–193. doi:10.1016/j.wasman.2017.11.009

Arumugam, K., Seenivasagan, R., Kasimani, R., Sharma, N., and Babalola, O. (2017). Enhancing the post consumer waste management through vermicomposting along with bioinoculumn. *Int. J. Eng. Trends Technol.* 44, 179–182. doi:10.14445/22315381/ijett-v44p235

Asemoloye, M. D., Tosi, S., Daccò, C., Wang, X., Xu, S., Marchisio, M. A., et al. (2020). Hydrocarbon degradation and enzyme activities of Aspergillus oryzae and Mucor irregularis isolated from nigerian crude oil-polluted sites. *Microorganisms* 8, 1912. doi:10.3390/microorganisms8121912

Ayangbenro, A. S., and Babalola, O. O. (2017). A new strategy for heavy metal polluted environments: A review of microbial biosorbents. *Int. J. Environ. Res. public health* 14, 94–16. doi:10.3390/ijerph14010094

Ayangbenro, A. S., Babalola, O. O., and Aremu, O. S. (2019). Bioflocculant production and heavy metal sorption by metal resistant bacterial isolates from gold mining soil. *Chemosphere* 231, 113–120. doi:10.1016/j.chemosphere.2019.05.092

Ayangbenro, A. S., and Babalola, O. O. (2018). Metal(loid) bioremediation: Strategies employed by microbial polymers. *Sustainability* 10, 3028. doi:10.3390/su10093028

Ayangbenro, A. S., Olanrewaju, O. S., and Babalola, O. O. (2018). Sulfate-reducing bacteria as an effective tool for sustainable acid mine bioremediation. *Front. Microbiol.* 1, 1986. doi:10.3389/fmicb.2018.01986

Azubuike, C. C., Chikere, C. B., and Okpokwasili, G. C. (2016). Bioremediation techniques–classification based on site of application: Principles, advantages, limitations and prospects. *World J. Microbiol. Biotechnol.* 32, 180–218. doi:10.1007/s11274-016-2137-x

Bastida, F., Jehmlich, N., Lima, K., Morris, B., Richnow, H., Hernández, T., et al. (2016). The ecological and physiological responses of the microbial community from a semiarid soil to hydrocarbon contamination and its bioremediation using compost amendment. *J. Proteomics* 135, 162–169. doi:10.1016/j.jprot.2015.07.023

Behrendorff, J. B. (2021). Reductive cytochrome P450 reactions and their potential role in bioremediation. *Front. Microbiol.* 12, 649273. doi:10.3389/fmicb.2021.649273

Bhandari, G., Dhasmana, A., Chaudhary, P., Gupta, S., Gangola, S., Gupta, A., et al. (2023). A perspective review on green nanotechnology in agro-ecosystems: Opportunities for sustainable agricultural practices and environmental remediation. *Agriculture* 13, 668. doi:10.3390/agriculture13030668

Bhandari, S., Poudel, D. K., Marahatha, R., Dawadi, S., Khadayat, K., Phuyal, S., et al. (2021). Microbial enzymes used in bioremediation. *J. Chem.* 2021, 1–17. doi:10.1155/2021/8849512

Bharagava, R. N., and Mishra, S. (2018). Hexavalent chromium reduction potential of Cellulosimicrobium sp. isolated from common effluent treatment plant of tannery industries. *Ecotoxicol. Environ. Saf.* 147, 102–109. doi:10.1016/j.ecoenv.2017.08.040

Bhatt, P., Gangola, S., Chaudhary, P., Khati, P., Kumar, G., Sharma, A., et al. (2019). Pesticide induced up-regulation of esterase and aldehyde dehydrogenase in indigenous Bacillus spp. *Bioremediation J.* 23, 42–52. doi:10.1080/10889868.2019.1569586

Bhunia, B., and Basak, B. (2014). A review on application of microbial protease in bioremediation. *Industrial Environ. Biotechnol.* 1, 217–228.

Bianco, F., Race, M., Papirio, S., and Esposito, G. (2020). Removal of polycyclic aromatic hydrocarbons during anaerobic biostimulation of marine sediments. *Sci. Total Environ.* 709, 136141. doi:10.1016/j.scitotenv.2019.136141

Bogati, K., and Walczak, M. (2022). The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy* 12, 189. doi:10.3390/agronomy12010189

Bolade, O. P., Akinsiku, A. A., Oluwafemi, O. S., Williams, A. B., and Benson, N. U. (2021). Biogenic iron oxide nanoparticles and activated sodium persulphate for hydrocarbon remediation in contaminated soil. *Environ. Technol. Innov.* 23, 101719. doi:10.1016/j.eti.2021.101719

Boregowda, N., Jogigowda, S. C., Bhavya, G., Sunilkumar, C. R., Geetha, N., Udikeri, S. S., et al. (2022). Recent advances in nanoremediation: Carving sustainable solution to clean-up polluted agriculture soils. *Environ. Pollut.* 297, 118728. doi:10.1016/j.envpol.2021.118728

Cao, X., Xu, L., Chen, Y. P., Decho, A. W., Cui, Z., and Lead, J. R. A. (2022). Contribution, composition, and structure of eps by *in vivo* exposure to elucidate the mechanisms of nanoparticle-enhanced bioremediation to metals. *Environ. Sci. Technol.* 56, 896–906. doi:10.1021/acs.est.1c05326

Cecchin, I., Reddy, K. R., Thomé, A., Tessaro, E. F., and Schnaid, F. (2017). Nanobioremediation: Integration of nanoparticles and bioremediation for sustainable remediation of chlorinated organic contaminants in soils. *Int. Biodeterior. Biodegrad.* 119, 419–428. doi:10.1016/j.ibiod.2016.09.027

Celestina, C., Wood, J. L., Manson, J. B., Wang, X., Sale, P. W., Tang, C., et al. (2019). Microbial communities in top-and subsoil of repacked soil columns respond differently to amendments but their diversity is negatively correlated with plant productivity. *Scientific Reports* 9 (1), 8890.

Chaudhary, P., Ahamad, L., Chaudhary, A., Kumar, G., Chen, W.-J., and Chen, S. (2023a). Nanoparticle-mediated bioremediation as a powerful weapon in the removal of environmental pollutants. *J. Environ. Chem. Eng.* 11, 109591. doi:10.1016/j.jece.2023.109591

Chaudhary, P., Singh, S., Chaudhary, A., Agri, U., and Bhandari, G. (2022). Agrochemicals and their effects on soil microbial population. *Plant Prot. Chem. Biol.* 1, 45.

Chaudhary, P., Xu, M., Ahamad, L., Chaudhary, A., Kumar, G., Adeleke, B. S., et al. (2023b). Application of synthetic consortia for improvement of soil fertility, pollution remediation, and agricultural productivity: A review. *Agronomy* 13, 643. doi:10.3390/agronomy13030643

Chellaiah, E. R. (2018). Cadmium (heavy metals) bioremediation by *Pseudomonas aeruginosa*: A minireview. *Appl. water Sci.* 8, 154–210. doi:10.1007/s13201-018-0796-5

Chikere, C. B., Azubuike, C. C., and Fubara, E. M. (2017). Shift in microbial group during remediation by enhanced natural attenuation (RENA) of a crude oil-impacted soil: A case study of Ikarama community, Bayelsa, Nigeria. *Biotech* 7, 152–211. doi:10.1007/s13205-017-0782-x

Chikere, C. B., Tekere, M., and Adeleke, R. (2019). Enhanced microbial hydrocarbon biodegradation as stimulated during field-scale landfarming of crude oil-impacted soil. *Sustain. Chem. Pharm.* 14, 100177. doi:10.1016/j.scp.2019.100177

Costa, C. S. D., Bertagnolli, C., Boos, A., Da Silva, M. G. C., and Vieira, M. G. A. (2020). Application of a dealginated seaweed derivative for the simultaneous metal ions removal from real and synthetic effluents. *J. Water Process Eng.* 37, 101546. doi:10.1016/j.jwpe.2020.101546

Council, N. R. (2000). *Natural attenuation for groundwater remediation*.

Dai, X., Lv, J., Yan, G., Chen, C., Guo, S., and Fu, P. (2020). Bioremediation of intertidal zones polluted by heavy oil spilling using immobilized laccase-bacteria consortium. *Bioresour. Technol.* 309, 123305. doi:10.1016/j.biortech.2020.123305

Dwivedi, S. (2012). Bioremediation of heavy metal by algae: Current and future perspective. *J. Adv. Lab. Res. Biol.* 3, 195–199.

Ebuehi, O., Abibo, I., Shekwolo, P., Sigismund, K., Adoki, A., and Okoro, I. (2005). Remediation of crude oil contaminated soil by enhanced natural attenuation technique. *Jasem* 9, 103–106.

El Enshasy, H. A., Hanapi, S. Z., Abdelgalil, S. A., Malek, R. A., and Pareek, A. (2017). Mycoremediation: Decolourization potential of fungal ligninolytic enzymes. *Mycoremediation Environ. Sustain.* 1 (1), 69–104.

El-Ansary, M. S. M., and Ahmed-Farid, O. A. (2021). Bioremediation of oxyl compounds by algae: Description and traits of root-knot nematode control. *Waste Biomass Valorization* 12, 251–261. doi:10.1007/s12649-020-00950-5

El-Naggar, N. E.-A., Hamouda, R. A., Mousa, I. E., Abdel-Hamid, M. S., and Rabei, N. H. (2018). Biosorption optimization, characterization, immobilization and application of Gelidium amansii biomass for complete Pb2+ removal from aqueous solutions. *Sci. Rep.* 8, 13456–13519. doi:10.1038/s41598-018-31660-7

El-Ramady, H., El-Henawy, A., Amer, M., Omara, A. E.-D., Elsakhawy, T., Salama, A.-M., et al. (2020). Agro-pollutants and their nano-remediation from soil and water: A mini-review. *Environ. Biodivers. Soil Secur.* 4, 0–375. doi:10.21608/jenvbs.2020.47751.1111

El-Sheekh, M., and Hamouda, R. (2014). Biodegradation of crude oil by some cyanobacteria under heterotrophic conditions. *Desalination Water Treat.* 52, 1448–1454. doi:10.1080/19443994.2013.794008

Esringü, A., Turan, M., Güneş, A., and Karaman, M. R. (2014). Roles of Bacillus megaterium in remediation of boron, lead, and cadmium from contaminated soil. *Commun. soil Sci. plant analysis* 45, 1741–1759. doi:10.1080/00103624.2013.875194

Essabri, A., Aydinlik, N. P., and Williams, N. E. (2019). Bioaugmentation and biostimulation of total petroleum hydrocarbon degradation in a petroleum-contaminated soil with fungi isolated from olive oil effluent. *Water, Air, Soil Pollut.* 230, 76–16. doi:10.1007/s11270-019-4127-8

Evode, N., Qamar, S. A., Bilal, M., Barceló, D., and Iqbal, H. M. (2021). Plastic waste and its management strategies for environmental sustainability. *Case Stud. Chem. Environ. Eng.* 4, 100142. doi:10.1016/j.cscee.2021.100142

Ezekoye, C., Chikere, C., and Okpokwasili, G. (2018). Fungal diversity associated with crude oil-impacted soil undergoing *in-situ* bioremediation. *Sustain. Chem. Pharm.* 10, 148–152. doi:10.1016/j.scp.2018.11.003

Fabre, E., Dias, M., Costa, M., Henriques, B., Vale, C., Lopes, C. B., et al. (2020). Negligible effect of potentially toxic elements and rare Earth elements on mercury removal from contaminated waters by green, Brown and red living marine macroalgae. *Sci. Total Environ.* 724, 138133. doi:10.1016/j.scitotenv.2020.138133

Fu, P., and Secundo, F. (2016). Algae and their bacterial consortia for soil bioremediation. *Chem. Eng. Trans.* 49, 427–432.

Gargouri, B., Mhiri, N., Karray, F., Aloui, F., and Sayadi, S. (2015). Isolation and characterization of hydrocarbon-degrading yeast strains from petroleum contaminated industrial wastewater. *BioMed Res. Int.* 2015, 1–11. doi:10.1155/2015/929424

Ghosal, D., Ghosh, S., Dutta, T. K., and Ahn, Y. (2016). Current state of knowledge in microbial degradation of polycyclic aromatic hydrocarbons (PAHs): A review. *Front. Microbiol.* 7, 1369. doi:10.3389/fmicb.2016.01369

Ghosh, P., and Ghosh, U. (2018). *Bioconversion of agro-waste to value-added product through solid-state fermentation by a potent fungal strain Aspergillus flavus PUF5. Utilization and Management of Bioresources*. Springer.

Ghosh, S., Sharma, I., Nath, S., and Webster, T. J. (2021). *Bioremediation—the natural solution. Microbial ecology of wastewater treatment plants*. Elsevier.

Gomes, M., Gonzales-Limache, E., Sousa, S., Dellagnezze, B., Sartoratto, A., Silva, L., et al. (2018). Exploring the potential of halophilic bacteria from oil terminal environments for biosurfactant production and hydrocarbon degradation under high-salinity conditions. *Int. Biodeterior. Biodegrad.* 126, 231–242. doi:10.1016/j.ibiod.2016.08.014

Gong, J.-S., Lu, Z.-M., Li, H., Shi, J.-S., Zhou, Z.-M., and Xu, Z.-H. (2012). Nitrilases in nitrile biocatalysis: Recent progress and forthcoming research. *Microb. Cell factories* 11, 142–218. doi:10.1186/1475-2859-11-142

Guo, Y., Rene, E. R., Wang, J., and Ma, W. (2020). Biodegradation of polyaromatic hydrocarbons and the influence of environmental factors during the co-composting of sewage sludge and green forest waste. *Bioresour. Technol.* 297, 122434. doi:10.1016/j.biortech.2019.122434

Havugimana, E., Bhople, B. S., Kumar, A., Byiringiro, E., Mugabo, J. P., and Kumar, A. (2017). Soil pollution–major sources and types of soil pollutants. *Environ. Sci. Eng.* 11, 53–86.

Hualpa-Cutipa, E., Acosta, R. A. S., Cariga, O. J. M., Espinoza-Medina, M. A., Chavez-Rojas, D. C., Medina-Cerna, D., et al. (2023). *Metagenomic approach role of psychrotrophic and psychrophilic microbes in bioremediation. Metagenomics to Bioremediation*. Elsevier.

Hussain, I., Puschenreiter, M., Gerhard, S., Sani, S. G. A. S., Khan, W.-U.-D., and Reichenauer, T. G. (2019). Differentiation between physical and chemical effects of oil presence in freshly spiked soil during rhizoremediation trial. *Environ. Sci. Pollut. Res.* 26, 18451–18464. doi:10.1007/s11356-019-04819-6

Igiri, B. E., Okoduwa, S. I., Idoko, G. O., Akabuogu, E. P., Adeyi, A. O., and Ejiogu, I. K. (2018). Toxicity and bioremediation of heavy metals contaminated ecosystem from tannery wastewater: A review. *J. Toxicol.*, 2018, 1–16. doi:10.1155/2018/2568038

Inthama, P., Pumas, P., Pekkoh, J., Pathom-Aree, W., and Pumas, C. (2021). Plant growth and drought tolerance-promoting bacterium for bioremediation of paraquat pesticide residues in agriculture soils. *Front. Microbiol.* 12, 604662. doi:10.3389/fmicb.2021.604662

Jayakumar, V., Govindaradjane, S., Rajamohan, N., and Rajasimman, M. (2022). Biosorption potential of Brown algae, Sargassum polycystum, for the removal of toxic metals, cadmium and zinc. *Environ. Sci. Pollut. Res.* 29, 41909–41922. doi:10.1007/s11356-021-15185-7

Jayakumar, V., Govindaradjane, S., and Rajasimman (2021). Efficient adsorptive removal of Zinc by green marine macro alga Caulerpa scalpelliformis–characterization, optimization, modeling, isotherm, kinetic, thermodynamic, desorption and regeneration studies. *Surfaces Interfaces* 22, 100798. doi:10.1016/j.surfin.2020.100798

Ji, M., Li, B., Majdi, A., Alkhalifah, T., Alturise, F., and Ali, H. E. (2023). Application of nano remediation of mine polluted in acid mine drainage water using machine learning model. *Chemosphere* 311, 136926. doi:10.1016/j.chemosphere.2022.136926

Jia, H., Zhang, M., Weng, Y., Zhao, Y., Li, C., and Kanwal, A. (2021). Degradation of poly (butylene adipate-co-terephthalate) by Stenotrophomonas sp. YCJ1 isolated from farmland soil. *J. Environ. Sci.* 103, 50–58. doi:10.1016/j.jes.2020.10.001

Jiang, Y., Jiang, S., Li, Z., Yan, X., Qin, Z., and Huang, R. (2019). Field scale remediation of Cd and Pb contaminated paddy soil using three mulberry (Morus alba L) cultivars. *Ecol. Eng.* 129, 38–44. doi:10.1016/j.ecoleng.2019.01.009

Jin, Y., Luan, Y., Ning, Y., and Wang, L. (2018). Effects and mechanisms of microbial remediation of heavy metals in soil: A critical review. *Appl. Sci.* 8, 1336. doi:10.3390/app8081336

Kafle, A., Timilsina, A., Gautam, A., Adhikari, K., Bhattarai, A., and Aryal, N. (2022). Phytoremediation: Mechanisms, plant selection and enhancement by natural and synthetic agents. *Environ. Adv.* 8, 100203. doi:10.1016/j.envadv.2022.100203

Kalaimurugan, D., Balamuralikrishnan, B., Durairaj, K., Vasudhevan, P., Shivakumar, M., Kaul, T., et al. (2020). Isolation and characterization of heavy-metal-resistant bacteria and their applications in environmental bioremediation. *Int. J. Environ. Sci. Technol.* 17, 1455–1462. doi:10.1007/s13762-019-02563-5

Kalhor, A. X., Movafeghi, A., Mohammadi-Nassab, A. D., Abedi, E., and Bahrami, A. (2017). Potential of the green alga Chlorella vulgaris for biodegradation of crude oil hydrocarbons. *Mar. Pollut. Bull.* 123, 286–290. doi:10.1016/j.marpolbul.2017.08.045

Kalola, V., and Desai, C. (2020). Biosorption of Cr (VI) by Halomonas sp. DK4, a halotolerant bacterium isolated from chrome electroplating sludge. *Environ. Sci. Pollut. Res.* 27, 27330–27344. doi:10.1007/s11356-019-05942-0

Kaminsky, L. M., Trexler, R. V., Malik, R. J., Hockett, K. L., and Bell, T. H. (2019). The inherent conflicts in developing soil microbial inoculants. *Trends Biotechnol.* 37, 140–151. doi:10.1016/j.tibtech.2018.11.011

Kanwal, M., Ullah, H., Gulzar, A., Sadiq, T., Gul, Z., Ullah, M., et al. (2022). Biodegradation of petroleum hydrocarbons and the factors effecting rate of biodegradation. *Am. J. Biomed. Sci. Res.* 16, 6–15. doi:10.34297/ajbsr.2022.16.002182

Karthika, A., Seenivasagan, R., Kasimani, R., Babalola, O. O., and Vasanthy, M. (2017). The role of Eudrillus eugenia in the degradation of paper cup waste and the morphological, physiological and histological changes in the organism. *Bioremediation Sustain. Technol. Clean. Environ.* 1, 65–76.

Karthika, A., Seenivasagan, R., Kasimani, R., Babalola, O., and Vasanthy, M. (2020). Cellulolytic bacteria isolation, screening and optimization of enzyme production from vermicompost of paper cup waste. *Waste Manag.* 116, 58–65. doi:10.1016/j.wasman.2020.06.036

Kebede, G., Tafese, T., Abda, E. M., Kamaraj, M., and Assefa, F. (2021). Factors influencing the bacterial bioremediation of hydrocarbon contaminants in the soil: Mechanisms and impacts. *J. Chem.* 2021, 1–17. doi:10.1155/2021/9823362

Kong, F.-X., Sun, G.-D., and Liu, Z.-P. (2018). Degradation of polycyclic aromatic hydrocarbons in soil mesocosms by microbial/plant bioaugmentation: Performance and mechanism. *Chemosphere* 198, 83–91. doi:10.1016/j.chemosphere.2018.01.097

Košnář, Z., Částková, T., Wiesnerová, L., Praus, L., Jablonský, I., Koudela, M., et al. (2019). Comparing the removal of polycyclic aromatic hydrocarbons in soil after different bioremediation approaches in relationto the extracellular enzyme activities. *J. Environ. Sci.* 76, 249–258. doi:10.1016/j.jes.2018.05.007

Kumar, A., Das, S. K., Nainegali, L., and Reddy, K. R. (2023). Phytostabilization of coalmine overburden waste rock dump slopes: Current status, challenges, and perspectives. *Bull. Eng. Geol. Environ.* 82, 130. doi:10.1007/s10064-023-03159-7

Kumar, A., Yadav, A. N., Mondal, R., Kour, D., Subrahmanyam, G., Shabnam, A. A., et al. (2021a). Myco-remediation: A mechanistic understanding of contaminants alleviation from natural environment and future prospect. *Chemosphere* 284, 131325. doi:10.1016/j.chemosphere.2021.131325

Kumar, G., Lal, S., Maurya, S. K., Bhattacherjee, A., Chaudhary, P., Gangola, S., et al. (2021b). Exploration of *Klebsiella pneumoniae* M6 for paclobutrazol degradation, plant growth attributes, and biocontrol action under subtropical ecosystem. *Plos one* 16, e0261338. doi:10.1371/journal.pone.0261338

Kumar, G., Lal, S., Soni, S. K., Maurya, S. K., Shukla, P. K., Chaudhary, P., et al. (2022). Mechanism and kinetics of chlorpyrifos co-metabolism by using environment restoring microbes isolated from rhizosphere of horticultural crops under subtropics. *Front. Microbiol.* 13, 891870. doi:10.3389/fmicb.2022.891870

Kumar, L., and Jain, S. K. (2020). Role of proteases in bioremediation of temple protein-containing waste with special reference to mangalnath, ujjain (MP)–India. *Indian J. Pure Appl. Biosci.* 8, 602–607. doi:10.18782/2582-2845.8178

Lara-Moreno, A., Morillo, E., Merchán, F., Madrid, F., and Villaverde, J. (2022). Bioremediation of a trifluralin contaminated soil using bioaugmentation with novel isolated bacterial strains and cyclodextrin. *Sci. Total Environ.* 840, 156695. doi:10.1016/j.scitotenv.2022.156695

Lee, E.-H., Kang, Y.-S., and Cho, K.-S. (2011). Bioremediation of diesel-contaminated soils by natural attenuation, biostimulation and bioaugmentation employing Rhodococcus sp. EH831. *Microbiol. Biotechnol. Lett.* 39, 86–92.

Li, F., Zheng, Y., Tian, J., Ge, F., Liu, X., Tang, Y., et al. (2019a). Cupriavidus sp. strain Cd02-mediated pH increase favoring bioprecipitation of Cd2+ in medium and reduction of cadmium bioavailability in paddy soil. *Ecotoxicol. Environ. Saf.* 184, 109655. doi:10.1016/j.ecoenv.2019.109655

Li, Q., Liu, J., and Gadd, G. M. (2020). Fungal bioremediation of soil co-contaminated with petroleum hydrocarbons and toxic metals. *Appl. Microbiol. Biotechnol.* 104, 8999–9008. doi:10.1007/s00253-020-10854-y

Li, T., Liu, Y., Lin, S., Liu, Y., and Xie, Y. (2019b). Soil pollution management in China: A brief introduction. *Sustainability* 11, 556–615. doi:10.3390/su11030556

Li, Y., Chi, M., and Ge, X. (2019c). Identification of a novel hydrolase encoded by hy-1 from Bacillus amyloliquefaciens for bioremediation of carbendazim contaminated soil and food. *Int. J. Agric. Biol. Eng.* 12, 218–224. doi:10.25165/j.ijabe.20191202.4190

Lin, S., Wei, J., Yang, B., Zhang, M., and Zhuo, R. (2022). Bioremediation of organic pollutants by white rot fungal cytochrome P450: The role and mechanism of CYP450 in biodegradation. *Chemosphere* 301, 134776. doi:10.1016/j.chemosphere.2022.134776

Liu, P., Rao, D., Zou, L., Teng, Y., and Yu, H. (2021). Capacity and potential mechanisms of Cd (II) adsorption from aqueous solution by blue algae-derived biochars. *Sci. Total Environ.* 767, 145447. doi:10.1016/j.scitotenv.2021.145447

Long, Z., Huang, Y., Zhang, W., Shi, Z., Yu, D., Chen, Y., et al. (2021). Effect of different industrial activities on soil heavy metal pollution, ecological risk, and health risk. *Environ. Monit. Assess.* 193, 20–12. doi:10.1007/s10661-020-08807-z

Mafiana, M. O., Bashiru, M. D., Erhunmwunsee, F., Dirisu, C. G., and Li, S.-W. (2021). An insight into the current oil spills and on-site bioremediation approaches to contaminated sites in Nigeria. *Environ. Sci. Pollut. Res.* 28, 4073–4094. doi:10.1007/s11356-020-11533-1

Mai, C. T. N., Linh, N. V., Lich, N. Q., Ha, H. P., Van Quyen, D., Tang, D. Y. Y., et al. (2021). Advanced materials for immobilization of purple phototrophic bacteria in bioremediation of oil-polluted wastewater. *Chemosphere* 278, 130464. doi:10.1016/j.chemosphere.2021.130464

Malakootian, M., Mahdizadeh, H., Nasiri, A., Mirzaienia, F., Hajhoseini, M., and Amirmahani, N. (2018). Investigation of the efficiency of microbial desalination cell in removal of arsenic from aqueous solutions. *Desalination* 438, 19–23. doi:10.1016/j.desal.2018.03.025

Maltman, C., and Yurkov, V. (2018). Bioremediation potential of bacteria able to reduce high levels of selenium and tellurium oxyanions. *Archives Microbiol.* 200, 1411–1417. doi:10.1007/s00203-018-1555-6

Martins, M., Santos, E. S., Faleiro, M. L., Chaves, S., Tenreiro, R., Barros, R. J., et al. (2011). Performance and bacterial community shifts during bioremediation of acid mine drainage from two Portuguese mines. *Int. Biodeterior. Biodegrad.* 65, 972–981. doi:10.1016/j.ibiod.2011.07.006

Marzan, L. W., Hossain, M., Mina, S. A., Akter, Y., and Chowdhury, A. M. A. (2017). Isolation and biochemical characterization of heavy-metal resistant bacteria from tannery effluent in Chittagong city, Bangladesh: Bioremediation viewpoint. *Egypt. J. Aquatic Res.* 43, 65–74. doi:10.1016/j.ejar.2016.11.002

Masowa, M., Kutu, F., Babalola, O., and Mulidzi, A. (2022). Optimizing application rate of winery solid waste compost for improving the performance of maize (zea mays L) grown on luvisol and cambisol. *Appl. Ecol. Environ. Res.* 20, 815–828. doi:10.15666/aeer/2001_815828

Masowa, M., Kutu, F., Babalola, O., and Mulidzi, A. (2018). Physico-chemical properties and phyto-toxicity assessment of co-composted winery solid wastes with and without effective microorganism inoculation. *Res. Crops* 19, 549–559.

Masowa, M. M., Kutu, F. R., Babalola, O. O., Mulidzi, A. R., and Dlamini, P. (2021). Effects of complementary and sole applications of inorganic fertilizers and winery solid waste compost on maize yield and soil health indices. *Emir. J. Food Agric.* 1, 565–574. doi:10.9755/ejfa.2021.v33.i7.2721

Mbachu, A., Chukwura, E., and Mbachu, N. (2016). Isolation and characterization of hydrocarbon degrading fungi from used (spent) engine oil polluted soil and their use for polycyclic aromatic hydrocarbons (PAHs) degradation. *Univers. J. Microbiol. Res.* 4, 31–37. doi:10.13189/ujmr.2016.040105

Medaura, M. C., Guivernau, M., Moreno-Ventas, X., Prenafeta-Boldú, F. X., and Viñas, M. (2021). Bioaugmentation of native fungi, an efficient strategy for the bioremediation of an aged industrially polluted soil with heavy hydrocarbons. *Front. Microbiol.* 12, 626436. doi:10.3389/fmicb.2021.626436

Meng, X., Fan, K., and Yan, X. (2019). Nanozymes: An emerging field bridging nanotechnology and enzymology. *Sci. China Life Sci.* 62, 1543–1546. doi:10.1007/s11427-019-1557-8

Minari, G. D., Saran, L. M., Constancio, M. T. L., Da Silva, R. C., Rosalen, D. L., De Melo, W. J., et al. (2020). Bioremediation potential of new cadmium, chromium, and nickel-resistant bacteria isolated from tropical agricultural soil. *Ecotoxicol. Environ. Saf.* 204, 111038. doi:10.1016/j.ecoenv.2020.111038

Mitra, S., Pramanik, K., Sarkar, A., Ghosh, P. K., Soren, T., and Maiti, T. K. (2018). Bioaccumulation of cadmium by Enterobacter sp. and enhancement of rice seedling growth under cadmium stress. *Ecotoxicol. Environ. Saf.* 156, 183–196. doi:10.1016/j.ecoenv.2018.03.001

Mnif, S., Chebbi, A., Mhiri, N., Sayadi, S., and Chamkha, M. (2017). Biodegradation of phenanthrene by a bacterial consortium enriched from Sercina oilfield. *Process Saf. Environ. Prot.* 107, 44–53. doi:10.1016/j.psep.2017.01.023

Moino, B. P., Costa, C. S., Da Silva, M. G., and Vieira, M. G. (2017). Removal of nickel ions on residue of alginate extraction from *Sargassum <scp>f</scp>ilipendula* seaweed in packed bed. *Can. J. Chem. Eng.* 95, 2120–2128. doi:10.1002/cjce.22859

Montazer, Z., Habibi Najafi, M. B., and Levin, D. B. (2019). Microbial degradation of low-density polyethylene and synthesis of polyhydroxyalkanoate polymers. *Can. J. Microbiol.* 65, 224–234. doi:10.1139/cjm-2018-0335

Mosharaf, M., Tanvir, M., Haque, M., Haque, M., Khan, M., Molla, A. H., et al. (2018). Metal-adapted bacteria isolated from wastewaters produce biofilms by expressing proteinaceous curli fimbriae and cellulose nanofibers. *Front. Microbiol.* 9, 1334. doi:10.3389/fmicb.2018.01334

Mostafa, A. A.-F., Yassin, M. T., Dawoud, T. M., Al-Otibi, F. O., and Sayed, S. R. (2022). Mycodegradation of diazinon pesticide utilizing fungal strains isolated from polluted soil. *Environ. Res.* 212, 113421. doi:10.1016/j.envres.2022.113421

Mukhopadhyay, R., Sarkar, B., Khan, E., Alessi, D. S., Biswas, J. K., Manjaiah, K., et al. (2022). Nanomaterials for sustainable remediation of chemical contaminants in water and soil. *Crit. Rev. Environ. Sci. Technol.* 52, 2611–2660. doi:10.1080/10643389.2021.1886891

Naeem, U., and Qazi, M. A. (2020). Leading edges in bioremediation technologies for removal of petroleum hydrocarbons. *Environ. Sci. Pollut. Res.* 27, 27370–27382. doi:10.1007/s11356-019-06124-8

Nascimento, S. V. D., Costa, P. H. D. O., Herrera, H., Caldeira, C. F., Gastauer, M., Ramos, S. J., et al. (2022). Proteomic profiling and rhizosphere-associated microbial communities reveal adaptive mechanisms of dioclea apurensis kunth in eastern amazon's rehabilitating minelands. *Plants* 11, 712. doi:10.3390/plants11050712

Naskar, A., Majumder, R., and Goswami, M. (2020). Bioaccumulation of Ni (II) on growing cells of Bacillus sp.: Response surface modeling and mechanistic insight. *Environ. Technol. Innovation* 20, 101057. doi:10.1016/j.eti.2020.101057

Nath, S., Deb, B., and Sharma, I. (2018). Isolation of toxic metal-tolerant bacteria from soil and examination of their bioaugmentation potentiality by pot studies in cadmium- and lead-contaminated soil. *Int. Microbiol.* 21, 35–45. doi:10.1007/s10123-018-0003-4

Naz, R., Khan, M., Hafeez, A., Fazil, M., Khan, M., Ali, B., et al. (2022). Assessment of phytoremediation potential of native plant species naturally growing in a heavy metal-polluted industrial soils. *Braz. J. Biol.* 84, e264473. doi:10.1590/1519-6984.264473

Naz, T., Khan, M. D., Ahmed, I., Rehman, S. U., Rha, E. S., Malook, I., et al. (2016). Biosorption of heavy metals by Pseudomonas species isolated from sugar industry. *Toxicol. Ind. health* 32, 1619–1627. doi:10.1177/0748233715569900

Ndeddy Aka, R. J., and Babalola, O. O. (2016). Effect of bacterial inoculation of strains of *Pseudomonas aeruginosa*, Alcaligenes feacalis and Bacillus subtilis on germination, growth and heavy metal (Cd, Cr, and Ni) uptake of Brassica juncea. *Int. J. Phytoremediation* 18, 200–209. doi:10.1080/15226514.2015.1073671

Ndeddy Aka, R. J., and Babalola, O. O. (2017). Identification and characterization of Cr-Cd-and Ni-tolerant bacteria isolated from mine tailings. *Bioremediation J.* 21, 1–19. doi:10.1080/10889868.2017.1282933

Nguyen, D. D., Ha, M.-G., and Kang, H. Y. (2021). Potential of versatile bacteria isolated from activated sludge for the bioremediation of arsenic and antimony. *J. Water Process Eng.* 39, 101890. doi:10.1016/j.jwpe.2020.101890

Nishikawa, E., Da Silva, M. G. C., and Vieira, M. G. A. (2018). Cadmium biosorption by alginate extraction waste and process overview in life cycle assessment context. *J. Clean. Prod.* 178, 166–175. doi:10.1016/j.jclepro.2018.01.025

Nuhu, M. M., Rene, E. R., and Ishaq, A. (2022). Remediation of crude oil spill sites in Nigeria: Problems, technologies, and future prospects. *Environ. Qual. Manag.* 31, 165–175.

O'Brien, R. M., Phelan, T. J., Smith, N. M., and Smits, K. M. (2021). Remediation in developing countries: A review of previously implemented projects and analysis of stakeholder participation efforts. *Crit. Rev. Environ. Sci. Technol.* 51, 1259–1280. doi:10.1080/10643389.2020.1755203

Oghoje, S., and Ukpebor, J. (2020). The effects and efficacy of chicken manure digestates on bioremediation of petroleum hydrocarbons polluted soils. *Niger. Res. J. Chem. Sci.* 8, 311–328.

Oghoje, S., Ukpebor, J., and Ukpebor, E. (2021). The effects of chicken manure digestates on the removal of diesel range organics from petroleum products polluted soils. *Bulg. J. Soil Sci.* 6, 78–95. doi:10.5281/zenodo.4887779

Ojuederie, O. B., and Babalola, O. O. (2017). Microbial and plant-assisted bioremediation of heavy metal polluted environments: A review. *Int. J. Environ. Res. public health* 14, 1504. doi:10.3390/ijerph14121504

Okoye, A., Chikere, C., and Okpokwasili, G. (2019). Fungal population dynamics associated with active-phase of hydrocarbon degradation in oil-polluted soil. *J. Adv. Microbiol.* 19, 1–12. doi:10.9734/jamb/2019/v19i230190

Orji, F., Ibiene, A., and Ugbogu, O. (2012). Petroleum hydrocarbon pollution of mangrove swamps: The promises of remediation by enhanced natural attenuation. *Am. J. Agric. Biol. Sci.* 7, 207–216. doi:10.3844/ajabssp.2012.207.216

Pahalvi, H. N., Rafiya, L., Rashid, S., Nisar, B., and Kamili, A. N. (2021). Chemical fertilizers and their impact on soil health. *Microbiota Biofertilizers Ecofriendly Tools Reclam. Degraded Soil Environs* 2, 1–20.

Pande, V., Pandey, S. C., Sati, D., Pande, V., and Samant, M. (2020). Bioremediation: An emerging effective approach towards environment restoration. *Environ. Sustain.* 3, 91–103. doi:10.1007/s42398-020-00099-w

Park, J. M., Trevor Sewell, B., and Benedik, M. J. (2017). Cyanide bioremediation: The potential of engineered nitrilases. *Appl. Microbiol.* 101, 3029–3042. doi:10.1007/s00253-017-8204-x

Park, S. Y., and Kim, C. G. (2019). Biodegradation of micro-polyethylene particles by bacterial colonization of a mixed microbial consortium isolated from a landfill site. *Chemosphere* 222, 527–533. doi:10.1016/j.chemosphere.2019.01.159

Parsamanesh, S., and Sadeghi, H. (2019). The phytoremediation effect of Medicago scutellata (L) mill. On soils under Cd–water stress: A good choice for contaminated dry lands. *Environ. Sci. Pollut. Res.* 26, 29065–29073. doi:10.1007/s11356-019-05989-z

Parveen, H., Chaudhary, A., Chaudhary, P., Sultana, R., Kumar, G., Khati, P., et al. (2022). *Omics approaches for the production of the microbial enzymes and applications.* Industrial Applications of microbial enzymes. CRC Press.

Patel, A. B., Shaikh, S., Jain, K. R., Desai, C., and Madamwar, D. (2020). Polycyclic aromatic hydrocarbons: Sources, toxicity, and remediation approaches. *Front. Microbiol.* 11, 562813. doi:10.3389/fmicb.2020.562813

Patel, J. G., Nirmal Kumar, J., Kumar, R. N., and Khan, S. R. (2015). Enhancement of pyrene degradation efficacy of Synechocystis sp., by construction of an artificial microalgal-bacterial consortium. *Cogent Chem.* 1, 1064193. doi:10.1080/23312009.2015.1064193

Patra, D. K., Grahacharya, A., Pradhan, C., and Patra, H. K. (2021). Phytoremediation potential of coffee pod (Cassia tora): An *in situ* approach for attenuation of chromium from overburden soil of sukinda chromite mine, India. *Environ. Prog. Sustain. Energy* 40, e13510.

Paul, A., and Mukherjee, S. K. (2016). Enterobacter asburiae KUNi5, a nickel resistant bacterium for possible bioremediation of nickel contaminated sites. *Pol. J. Microbiol.* 65, 115–118. doi:10.5604/17331331.1197284

Pawar, R. (2015). The effect of soil pH on bioremediation of polycyclic aromatic hydrocarbons (PAHS). *Bioremediat Biodegr.* 2015, 291–304. doi:10.4172/2155-6199.1000291

Pidlisnyuk, V., Hettiarachchi, G. M., Zgorelec, Z., Prelac, M., Bilandžija, N., Davis, L. C., et al. (2021). *Phytotechnologies for site remediation. Phytotechnology with biomass production*. CRC Press.

Pm Tavares, A., R Pereira, S., and Mrb Xavier, A. (2017). Biotechnological applications of *Trametes versicolor* and their enzymes. *Curr. Biotechnol.* 6, 78–88. doi:10.2174/2211550105666160510113212

Princy, S., Sathish, S. S., Cibichakravarthy, B., and Prabagaran, S. R. (2020). Hexavalent chromium reduction by *Morganella morganii* (1Ab1) isolated from tannery effluent contaminated sites of Tamil Nadu, India. *Biocatal. Agric. Biotechnol.* 23, 101469. doi:10.1016/j.bcab.2019.101469

Priya, A., Dutta, K., and Daverey, A. (2022). A comprehensive biotechnological and molecular insight into plastic degradation by microbial community. *J. Chem. Technol. Biotechnol.* 97, 381–390. doi:10.1002/jctb.6675

Rahman, Z., Thomas, L., and Singh, V. P. (2019). Biosorption of heavy metals by a lead (Pb) resistant bacterium, Staphylococcus hominis strain AMB-2. *J. basic Microbiol.* 59, 477–486. doi:10.1002/jobm.201900024

Raju, C. A., Anitha, J., Kalyani, R. M., Satyanandam, K., and Jagadeesh, P. (2021). Sorption of cobalt using marine macro seaweed graciliariacorticatared algae powder. *Mater. Today Proc.* 44, 1816–1827. doi:10.1016/j.matpr.2020.12.009

Ramírez, V., Baez, A., López, P., Bustillos, R., Villalobos, M. Á., Carreño, R., et al. (2019). Chromium hyper-tolerant Bacillus sp. MH778713 assists phytoremediation of heavy metals by mesquite trees (Prosopis laevigata). *Front. Microbiol.* 10, 1833. doi:10.3389/fmicb.2019.01833

Rawat, M., and Rangarajan, S. (2019). *Omics approaches for elucidating molecular mechanisms of microbial bioremediation. Smart bioremediation technologies*. Elsevier.

Riser-Roberts, E. (2020). *Remediation of petroleum contaminated soils: Biological, physical, and chemical processes*. Boca Raton, Florida, United State: CRC Press.

Sahmoune, M. N. (2018). Performance of Streptomyces rimosus biomass in biosorption of heavy metals from aqueous solutions. *Microchem. J.* 141, 87–95. doi:10.1016/j.microc.2018.05.009

Salama, E.-S., Roh, H.-S., Dev, S., Khan, M. A., Abou-Shanab, R. A., Chang, S. W., et al. (2019). Algae as a green technology for heavy metals removal from various wastewater. *World J. Microbiol. Biotechnol.* 35, 75–19. doi:10.1007/s11274-019-2648-3

Samreen, S., Khan, A. A., Khan, M. R., Ansari, S. A., and Khan, A. (2021). Assessment of phytoremediation potential of seven weed plants growing in chromium-and nickel-contaminated soil. *Water, Air, Soil Pollut.* 232, 209–218. doi:10.1007/s11270-021-05124-0

Saranya, K., Sundaramanickam, A., Shekhar, S., Meena, M., Sathishkumar, R. S., and Balasubramanian, T. (2018). Biosorption of multi-heavy metals by coral associated phosphate solubilising bacteria Cronobacter muytjensii KSCAS2. *J. Environ. Manag.* 222, 396–401. doi:10.1016/j.jenvman.2018.05.083

Sari, E. M., Novianty, R., Awaluddin, A., and Pratiwi, N. W. (2019). Effectiveness of crude oil degrading fungi isolated from petroleum hydrocarbon contaminated soil in Siak, Riau. *Acta Biochim. Indones.* 2, 15–22. doi:10.32889/actabioina.v2i1.35

Sarma, H., Sonowal, S., and Prasad, M. (2019). Plant-microbiome assisted and biochar-amended remediation of heavy metals and polyaromatic compounds─a microcosmic study. *Ecotoxicol. Environ. Saf.* 176, 288–299. doi:10.1016/j.ecoenv.2019.03.081

Satyapal, G. K., Mishra, S. K., Srivastava, A., Ranjan, R. K., Prakash, K., Haque, R., et al. (2018). Possible bioremediation of arsenic toxicity by isolating indigenous bacteria from the middle Gangetic plain of Bihar, India. *Biotechnol. Rep.* 17, 117–125. doi:10.1016/j.btre.2018.02.002

Sayed, K., Baloo, L., and Sharma, N. K. (2021). Bioremediation of total petroleum hydrocarbons (TPH) by bioaugmentation and biostimulation in water with floating oil spill containment booms as bioreactor basin. *Int. J. Environ. Res. Public Health* 18, 2226. doi:10.3390/ijerph18052226

Schippers, A., Breuker, A., Blazejak, A., Bosecker, K., Kock, D., and Wright, T. (2010). The biogeochemistry and microbiology of sulfidic mine waste and bioleaching dumps and heaps, and novel Fe (II)-oxidizing bacteria. *Hydrometallurgy* 104, 342–350. doi:10.1016/j.hydromet.2010.01.012

Schröder, C., Burkhardt, C., and Antranikian, G. (2020). What we learn from extremophiles. *ChemTexts* 6, 8–6. doi:10.1007/s40828-020-0103-6

Senthilkumar, R., Prasad, D. R., Govindarajan, L., Saravanakumar, K., and Prasad, B. N. J. E. T. (2019). Green alga-mediated treatment process for removal of zinc from synthetic solution and industrial effluent. *Environ. Technol.* 40, 1262–1270. doi:10.1080/09593330.2017.1420696

Shameer, S. (2016). Biosorption of lead, copper and cadmium using the extracellular polysaccharides (EPS) of Bacillus sp., from solar salterns. *Biotech* 6, 194–210. doi:10.1007/s13205-016-0498-3

Sharma, A., Sharma, T., Sharma, T., Sharma, S., and Kanwar, S. S. (2019). Role of microbial hydrolases in bioremediation. *Microbes Enzym. Soil Health Bioremediation J.* 16, 149–164.

Sharma, B., Dangi, A. K., and Shukla, P. (2018). Contemporary enzyme based technologies for bioremediation: A review. *J. Environ. Manag.* 210, 10–22. doi:10.1016/j.jenvman.2017.12.075

Sharma, I. (2020). "Bioremediation techniques for polluted environment: Concept, advantages, limitations, and prospects," in *Trace metals in the environment-new approaches and recent advances*. Editors M. A. MURILLO-TOVAR, H. SALDARRIAGA-NORENA, and A. SAEID (London: IntechOpen).

Shen, X., Dai, M., Yang, J., Sun, L., Tan, X., Peng, C., et al. (2022). A critical review on the phytoremediation of heavy metals from environment: Performance and challenges. *Chemosphere* 291, 132979. doi:10.1016/j.chemosphere.2021.132979

Sher, S., and Rehman, A. (2019). Use of heavy metals resistant bacteria—A strategy for arsenic bioremediation. *Appl. Microbiol. Biotechnol.* 103, 6007–6021. doi:10.1007/s00253-019-09933-6

ShilpaBasak, N., and Meena, S. S. (2022). Microbial biodegradation of plastics: Challenges, opportunities, and a critical perspective. *Front. Environ. Sci. Eng.* 16, 161. doi:10.1007/s11783-022-1596-6

Singh, A. K., Yadav, P., Bharagava, R. N., Saratale, G. D., and Raj, A. (2019). Biotransformation and cytotoxicity evaluation of kraft lignin degraded by ligninolytic *Serratia liquefaciens*. *Front. Microbiol.* 10, 2364. doi:10.3389/fmicb.2019.02364

SAKSHISingh, S., and Haritash, A. (2019). Polycyclic aromatic hydrocarbons: Soil pollution and remediation. *Int. J. Environ. Sci. Technol.* 16, 6489–6512. doi:10.1007/s13762-019-02414-3

Smith, A., Kaczmar, A., Bamford, R. A., Smith, C., Frustaci, S., Kovacs-Simon, A., et al. (2018). The culture environment influences both gene regulation and phenotypic heterogeneity in *Escherichia coli*. *Front. Microbiol.* 9, 1739. doi:10.3389/fmicb.2018.01739

Song, L., Niu, X., Zhang, N., and Li, T. J. C. (2021). Effect of biochar-immobilized Sphingomonas sp. PJ2 on bioremediation of PAHs and bacterial community composition in saline soil. *Chemosphere* 279, 130427. doi:10.1016/j.chemosphere.2021.130427

Su, L. S. (2016). Isolation and identification of heavy metal-tolerant bacteria from an industrial site as a possible source for bioremediation of cadmium, lead, and nickel. *Adv. Environ. Biol.* 10, 10–15.

Sujkowska-Rybkowska, M., and Ważny, R. (2018). Metal resistant rhizobia and ultrastructure of Anthyllis vulneraria nodules from zinc and lead contaminated tailing in Poland. *Int. J. phytoremediation* 20, 709–720. doi:10.1080/15226514.2017.1413336

Syed, S., and Chinthala, P. (2015). Heavy metal detoxification by different Bacillus species isolated from solar salterns. *Scientifica* 2015, 1–8. doi:10.1155/2015/319760

Taran, M., Fateh, R., Rezaei, S., and Gholi, M. K. (2019). Isolation of arsenic accumulating bacteria from garbage leachates for possible application in bioremediation. *Iran. J. Microbiol.* 11, 60–66. doi:10.18502/ijm.v11i1.707

Tarfeen, N., Nisa, K. U., Hamid, B., Bashir, Z., Yatoo, A. M., Dar, M. A., et al. (2022). Microbial remediation: A promising tool for reclamation of contaminated sites with special emphasis on heavy metal and pesticide pollution: A review. *Processes* 10, 1358. doi:10.3390/pr10071358

Telesiński, A., and Kiepas-Kokot, A. (2021). Five-year enhanced natural attenuation of historically coal-tar-contaminated soil: Analysis of polycyclic aromatic hydrocarbon and phenol contents. *Int. J. Environ. Res. Public Health* 18, 2265. doi:10.3390/ijerph18052265

Thesai, A. S., Nagarajan, G., Rajakumar, S., Pugazhendhi, A., and Ayyasamy, P. M. (2021). Bioaccumulation of fluoride from aqueous system and genotoxicity study on Allium cepa using Bacillus licheniformis. *J. Hazard. Mater.* 407, 124367. doi:10.1016/j.jhazmat.2020.124367

Tyagi, B., and Kumar, N. (2021). *Bioremediation: Principles and applications in environmental management*. Bioremediation for environmental sustainability. Elsevier.

Tyagi, D., Tyagi, S., and Narayan, R. (2018). Bacterial bioremediation of arsenic from contaminated groundwater and soil. *Eur. J. Biotechnol. Biosci.* 6, 45–51.

Ugochukwu, K. C., Agha, N., and Ogbulie, J. (2008). Lipase activities of microbial isolates from soil contaminated with crude oil after bioremediation. *Afr. J. Biotechnol.* 7.

Utami, U., Harianie, L., and Dunyana, N.ROMAIDI (2020). Lead-resistant bacteria isolated from oil wastewater sample for bioremediation of lead. *Water Sci. Technol.* 81, 2244–2249. doi:10.2166/wst.2020.281

Viesser, J. A., Sugai-Guerios, M. H., Malucelli, L. C., Pincerati, M. R., Karp, S. G., and Maranho, L. T. (2020). Petroleum-tolerant rhizospheric bacteria: Isolation,

characterization and bioremediation potential. *Sci. Rep.* 10, 2060–2111. doi:10.1038/s41598-020-59029-9

Wang, B.-Z., Guo, P., Hang, B.-J., Li, L., He, J., and Li, S.-P. (2009). Cloning of a novel pyrethroid-hydrolyzing carboxylesterase gene from Sphingobium sp. strain JZ-1 and characterization of the gene product. *Appl. Environ. Microbiol.* 75, 5496–5500. doi:10.1128/aem.01298-09

Wang, C., Huang, Y., Zhang, Z., Hao, H., and Wang, H. (2020). Absence of the nahG-like gene caused the syntrophic interaction between Marinobacter and other microbes in PAH-degrading process. *J. Hazard. Mater.* 384, 121387. doi:10.1016/j.jhazmat.2019.121387

Wang, H., Wang, X., Liu, C., Wang, Y., Rong, L., Sun, L., et al. (2017). *In-situ* bioremediation of DDTs and PAH contaminated aging farmland soil using blood meal. *Soil Sediment Contam. Int. J.* 26, 623–635. doi:10.1080/15320383.2017.1385593

Wang, L., Xiao, H., He, N., Sun, D., and Duan, S. (2019). Biosorption and biodegradation of the environmental hormone nonylphenol by four marine microalgae. *Sci. Rep.* 9, 5277–5311. doi:10.1038/s41598-019-41808-8

Wei, W., Wang, Q., Li, A., Yang, J., Ma, F., Pi, S., et al. (2016). Biosorption of Pb (II) from aqueous solution by extracellular polymeric substances extracted from Klebsiella sp. J1: Adsorption behavior and mechanism assessment. *J. Sci. Rep.* 6, 31575–31610. doi:10.1038/srep31575

Wei, Z., Van Le, Q., Peng, W., Yang, Y., Yang, H., Gu, H., et al. (2021). A review on phytoremediation of contaminants in air, water and soil. *J. Hazard. Mater.* 403, 123658. doi:10.1016/j.jhazmat.2020.123658

Wu, C., Ma, Y., Wang, D., Shan, Y., Song, X., Hu, H., et al. (2022). Integrated microbiology and metabolomics analysis reveal plastic mulch film residue affects soil microorganisms and their metabolic functions. *J. Hazard. Mater.* 423, 127258. doi:10.1016/j.jhazmat.2021.127258

Wu, Y., Luo, Y., Zou, D., Ni, J., Liu, W., Teng, Y., et al. (2008). Bioremediation of polycyclic aromatic hydrocarbons contaminated soil with monilinia sp.: Degradation and microbial community analysis. *Biodegradation* 19, 247–257. doi:10.1007/s10532-007-9131-9

YalçıN, S., and Özyürek, M. (2018). Biosorption potential of two Brown seaweeds in the removal of chromium. *Water Sci. Technol.* 78, 2564–2576. doi:10.2166/wst.2019.007

Yin, S., Zhang, X., Yin, H., and Zhang, X. (2022). Current knowledge on molecular mechanisms of microorganism-mediated bioremediation for arsenic contamination: A review. *Microbiol. Res.* 258, 126990. doi:10.1016/j.micres.2022.126990

Yu, F., Tang, S., Shi, X., Liang, X., Liu, K., Huang, Y., et al. (2022). Phytoextraction of metal(loid)s from contaminated soils by six plant species: A field study. *Sci. Total Environ.* 804, 150282. doi:10.1016/j.scitotenv.2021.150282

Zhang, C., Tao, Y., Li, S., Tian, J., Ke, T., Wei, S., et al. (2019). Simultaneous degradation of trichlorfon and removal of Cd (II) by Aspergillus sydowii strain PA F-2. *Environ. Sci. Pollut. Res.* 26, 26844–26854. doi:10.1007/s11356-019-05811-w

Zhang, J. H., Xue, Q. H., Gao, H., Ma, X., and Wang, P. (2016). Degradation of crude oil by fungal enzyme preparations from Aspergillus spp. for potential use in enhanced oil recovery. *J. Chem. Technol. Biotechnol.* 91, 865–875. doi:10.1002/jctb.4650

Zhang, Y., Lin, D.-F., Hao, J., Zhao, Z.-H., and Zhang, Y.-J. (2020). The crucial role of bacterial laccases in the bioremediation of petroleum hydrocarbons. *World J. Microbiol. Biotechnol.* 36, 116–210. doi:10.1007/s11274-020-02888-1

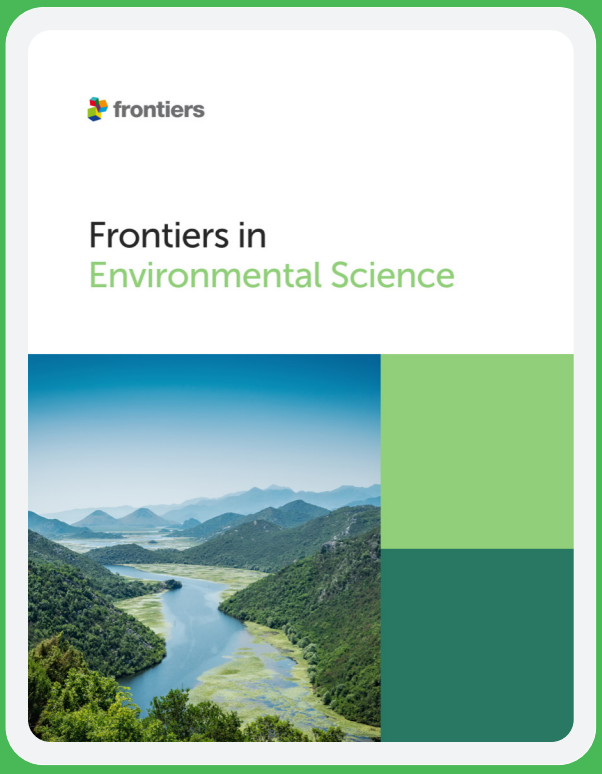
Frontiers in Environmental Science

Explores the anthropogenic impact on our natural world

An innovative journal that advances knowledge of the natural world and its intersections with human society. It supports the formulation of policies that lead to a more inhabitable and sustainable world.

Discover the latest Research Topics

See more →



Frontiers

Avenue du Tribunal-Fédéral 34
1005 Lausanne, Switzerland
frontiersin.org

Contact us

+41 (0)21 510 17 00
frontiersin.org/about/contact