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# Overview of biofertilizers in crop production and stress management for sustainable agriculture

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With the increase in world population, the demography of humans is estimated to be exceeded and it has become a major challenge to provide an adequate amount of food, feed, and agricultural products majorly in developing countries. The use of chemical fertilizers causes the plant to grow efficiently and rapidly to meet the food demand. The drawbacks of using a higher quantity of chemical or synthetic fertilizers are environmental pollution, persistent changes in the soil ecology, physiochemical composition, decreasing agricultural productivity and cause several health hazards. Climatic factors are responsible for enhancing abiotic stress on crops, resulting in reduced agricultural productivity. There are various types of abiotic and biotic stress factors like soil salinity, drought, wind, improper temperature, heavy metals, waterlogging, and different weeds and phytopathogens like bacteria, viruses, fungi, and nematodes which attack plants, reducing crop productivity and quality. There is a shift toward the use of biofertilizers due to all these facts, which provide nutrition through natural processes like zinc, potassium and phosphorus solubilization, nitrogen fixation, production of hormones, siderophore, various hydrolytic enzymes and protect the plant from different plant pathogens and stress conditions. They provide the nutrition in adequate amount that is sufficient for healthy crop development to fulfill the demand of the increasing population worldwide, eco-friendly and economically convenient. This review will focus on biofertilizers and their mechanisms of action, role in crop productivity and in biotic/abiotic stress tolerance.

## KEYWORDS

abiotic stress, biotic stress, biofertilizers, crop productivity, plant-root interaction

## Introduction

The world population will reach 9 billion by 2050 in accordance with Food and Agricultural Organization; as a result, there should be an enhancement in crop yield to meet the food demand. Soil is an important source of food production in human lifespan. In the last decades, due to the increase in agricultural practices

such as pesticides and chemical fertilizers it has been degraded at a universal scale and causes lower fertility due to loss in biodiversity, water retention, and disturbance in biogeochemical cycles. Soil health and plant productivity are severely influenced by numerous interactions among plant, soil, and microorganisms (Harman et al., 2020). Soil microbes cooperate with one another and also with plant roots in numerous means providing a wide variety of essential acts which are valuable for sustaining the ecological balance in soil (Kumar et al., 2021c). Plant microbial interactions are positive if they improve plant survival, nutritional status, and crop productivity and they are negative if they reduce plant growth. Soil fertility is inextricably linked to the balance of microorganisms and plants (Vishwakarma et al., 2020). The application of biofertilizers can be a probable approach to improve soil microbial status that stimulates the natural soil microbiota therefore influencing nutrient accessibility and decomposition of organic matter (Chaudhary et al., 2021). It was observed that the supply of biofertilizers in apricot modifies the microbial composition and degradation process which could be efficient in nutrient cycles in soil under field conditions (Agri et al., 2021; Baldi et al., 2021). The capability of biofertilizers to form a high-level microbial diversity in soil may outcome better crop productivity for sustainable agriculture (Agri et al., 2022). Recently, many studies reported the positive impact of beneficial soil microbes on crop productivity, but the role of consortium in agriculture is not entirely unstated. Usage of consortium has positive impact on nutrient uptake efficiency by plants, protection from pathogens, and stress conditions (Aguilar-Paredes et al., 2020). This review provided information on effective approaches such as biofertilizers which help in the restoration of agricultural soil thus improving crop health for sustainable agriculture. This can permit agriculturalists to enhance farming and reach a high standard of soil quality and subsequently lead to raised plant development.

Nutrients are required by every living creature in this world. A total of 17 essential plant nutrients are mandatory for the proper development of plants (Kumar et al., 2021a). These 17 nutrients are divided into three classes based on the amount required such as major nutrients (carbon, hydrogen, oxygen, nitrogen, phosphorus, and potassium), minor nutrients such as sulfur, calcium, and magnesium, and micronutrients (nickel, zinc, molybdenum, manganese, iron, copper, chlorine, and boron). The plant takes up oxygen, hydrogen, and carbon from air and water, but the other nutrients are taken from soils in inorganic forms (Gong et al., 2020). Biofertilizer or biological fertilizer is a material that contains living or dormant microorganisms that colonize the rhizosphere or present inside the plants and directly or indirectly promotes the growth of plants by supplying nutrition (Malusa and Vassilev, 2014; Fasusi et al., 2021). Microorganisms present in soil used as biofertilizers can mobilize the nutrient from soil and convert them into a usable form from unusable form through biological

processes like nitrogen fixation, phosphorus solubilization, zinc solubilization, siderophores production, and producing plant growth-promoting substances (Bhattacharjee and Dey, 2014; Mazid and Khan, 2015). Biofertilizers are applied to seed, root, soil, or by the foliar spray to enhance the microbial activity through their multiplication which then mobilizes the nutrients to target plants which remarkably improved the soil fertility and sooner increases the crop health and production (Pandey and Singh, 2012; Ismail et al., 2013).

Biotic stress is responsible to damage plants by pathogenic organisms like bacteria, fungi, viruses, parasites, and insects and by other harmful plants. They lead to declining the crop productivity by causing diseases such as vascular wilts, leaf spots, cankers, nutrient deficiency, systematic damage, chlorosis, stunting and reduce plant vigor, ultimately causing the death of the plants (Iqbal et al., 2021). Plant protects themselves to biotic stress *via* direct mechanisms like synthesis of secondary metabolite, hormones, cell-wall-degrading enzymes, and antioxidants (Kaur et al., 2022). The indirect mechanisms include the induction of acquired systematic resistance, plant pathogen molecular patterns (PAMPs) which in turn trigger the immunity and plant resistance proteins (Yu et al., 2022). Microorganisms solubilize the phosphorus and zinc, fixing the nitrogen and other macro- and micronutrients which promote the growth of the plants under biotic stress condition by providing nutrition (Singh et al., 2022a). They also enhance the stress resistance in plants by expressing the gene of phytohormones and stress-related metabolite. Some microorganisms also produce the volatile organic compounds (VOCs) such as melatonin to protect the plant from pathogens (Moustafa-Farag et al., 2019). When pathogen attacks, the plant produces various compounds within the tissues that lead to the activation of defense mechanisms inside the plants such as induced systematic resistance, peroxidases, phenylalanine ammonia-lyase, polyphenol oxidase, and hypersensitivity (Kaur et al., 2022).

Climatic change is one of the major factors for enhancing abiotic stress on crops which results in reduced crop productivity (Liu et al., 2017a). Climatic-related abiotic stresses included drought, waterlogging, excessive heat, and soil-related abiotic stresses are fertility, heavy metals, and salinity; all these are responsible for the poor yields of crops around the whole globe (Upadhyay et al., 2019). There is less water available to plants during drought conditions, and biofertilizers have the potential to produce cytokinin, gibberellins, abscisic acid, and IAA, which cause the plant to increase its growth, root length, total surface area, and the formation of root hairs and lateral roots, which increases water absorption from water-deficient soil (Kenneth et al., 2019; Raza et al., 2019). Pollutants released from industry without any further operation if released in the environment then they cause the accumulation of heavy metals such as copper, lead, nickel, zinc, etc., which have detrimental effects on the plants and animals (Popp et al., 2013). These heavy metals are

removed from the environment by micro- and macro-nutrient solubilizing and mineralizing microorganisms (Bhojiya et al., 2021). Heat stress causes cellular changes like production of reactive oxygen species, reduction in cell turgidity, reduction in water uptake, reduction in growth of plants, ultimately leading to death of plant by showing initial symptoms like leaf senescence, damages to chloroplast, wilting of plant, and chlorosis (Ahluwalia et al., 2021), whereas low temperature causes the inactivation of protein and reduces the cell membrane fluidity leading to increases in photosynthesis, imbalance of water transport (Odoh et al., 2020). All these temperature-related stresses coped up by plants after the accumulation of the hydrophilic and osmolytes protein. Huang et al. (2015) reported that due to high salt concentration there is increased toxicity to cell due to accumulations of sodium and chloride ions inside the cell which in turn disturb the photosynthetic processes, stomatal opening and closing, shrinkage of cell within plant tissue. Various studies showed that bacteria and arbuscular mycorrhizae fungi help in surviving the plants under salinity stress condition by enhancing the plant growth and development. In this review, we will discuss about the biofertilizers and its mechanism for crop production and biotic/abiotic tolerance for sustainable agriculture.

## Biofertilizers

In India, biofertilizer refers to the use of microorganisms to meet nutritional needs, whereas in other countries, the term microbial bioinoculant is used (Mitter et al., 2021). Biofertilizers are bio-based organic fertilizers that either could be from plant or animal sources or from living or dormant microbial cells that have the potential to improve the bioavailability and bioaccessibility of nutrient uptake in plants (Lee et al., 2018; Abbey et al., 2019). Bhardwaj et al. (2014) reported that live microbial mass is a major ingredient of biofertilizers. So biofertilizers are properly defined as “the preparations containing live microbes that help in enhancing soil fertility by fixing atmospheric nitrogen, solubilizing phosphorus or decomposing organic wastes or by elevating plant growth through the production of growth hormones with their biological activities” (Okur, 2018). Biofertilizers are generally applied in solid or dry forms, which are prepared after packing on suitable carriers such as clay minerals, rice bran, peat, lignite, wheat bran, humus, and wood charcoal. Carriers increase the shelf life and enable the easy handling of microbial inoculants (Bhattacharjee and Dey, 2014). The benefits of biofertilizers include low cost, enhanced nutrient availability, improved soil fertility, protect plants from soil-borne pathogens, sustainable agricultural production, enhanced biotic and abiotic stress tolerance, promote phytohormone production, improve soil health, causing less environmental pollution, and its continued use improves the fertility of soil considerably (Chaudhary

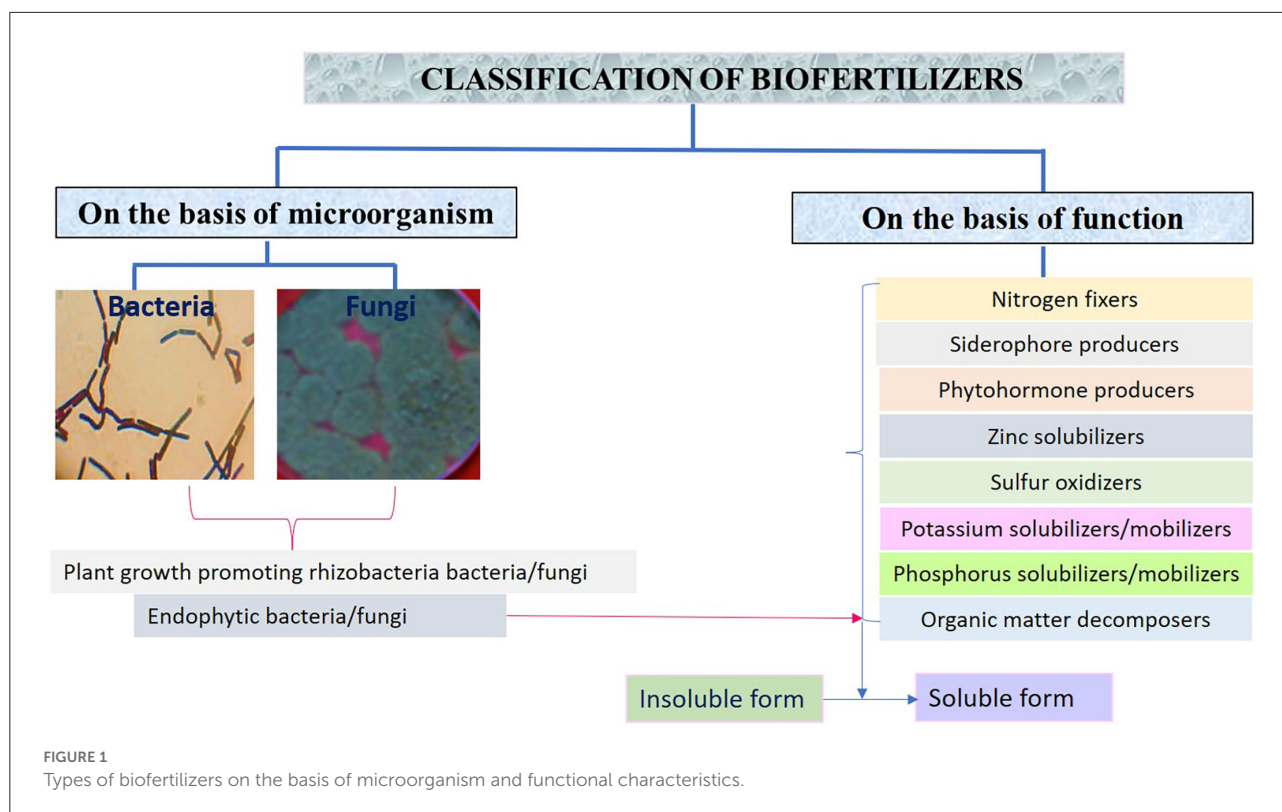
et al., 2021, 2022a). Based on the source and raw material, global biofertilizer is marketed under two major categories like organic residue-based biofertilizer and microorganisms-based biofertilizer. Green manure, crop residues, treated sewage sludge, and farmyard manure are generally organic-based biofertilizers. While on the contrary, microorganism-based biofertilizers contain beneficial microorganisms like bacteria, fungi, and algae. Directly or indirectly, these biofertilizers mediate the performance of plant growth (Figure 1). Direct mechanisms that act upon plants directly include nitrogen fixation, phosphate solubilization, micronutrient solubilization, and the production of phytohormones (Chaudhary et al., 2021). The indirect mechanism generally protects the plant from the deleterious effect of the pathogens by releasing lytic enzymes, antibiotics, siderophores, and cyanide production (Mahmud et al., 2021).

## Types of biofertilizers and their role in crop production and soil health maintenance

Various types of biofertilizers are classified based on microorganisms such as bacteria and fungi and function of the biofertilizers as shown in Figure 1.

### Nitrogen-fixing biofertilizers

Nitrogen is the vital macro-nutrient essential by plants because it improves the growth of the shoot system, helps in reproduction, is a constituent of chlorophyll responsible for the deep green color, and also increases the size of the grains (Sandhu et al., 2021). Although the nitrogen content in the atmosphere is 78% by a mass fraction, dinitrogen contains triple bonds and is an unavailable form of nitrogen present in the air for the plants. Dinitrogen should be first converted into soluble non-toxic form ammonia by the diazotrophs through the biological process of nitrogen fixations (Abbey et al., 2019). This ammonia is then converted to the nitrite and nitrate by the ammonia-oxidizing bacteria and by nitrifying bacteria, respectively (Roy et al., 2020). The unused nitrate is converted to the atmospheric nitrogen in the deeper soil horizons through the process of denitrification which will then escape to the atmosphere as dinitrogen gas. This is the typical path of the nitrogen cycle (Mahanty et al., 2017). *Azotobacter* and *Bacillus* sp. are involved in N fixation, growth promotion of maize plants, and forest crops (Etesami et al., 2014; Azeem et al., 2022). Inoculation of *Bradyrhizobium japonicum* in soybean plants improved plant biomass, nodulation, and N fixation (Htwe et al., 2019). *Azotobacter chroococcum* improved the plant height and chlorophyll content in maize plants (Jain et al., 2021). *Bradyrhizobium* sp. showed nitrogen fixation, IAA,



and siderophores production and improved the yield of mung bean (Alkurtany et al., 2018). Nitrogen-fixing microbes are considered as symbiotic, free-living, and associative nitrogen-fixing bacteria (Aasfar et al., 2021). Jing et al. (2020) reported that the application of *Pseudomonas protegens* promoted plant growth in nitrogen-deficient conditions.

## Symbiotic nitrogen-fixing microbes

In the process of symbiosis, macro-symbiont is the plant and microsymbionts are the prokaryotic bacteria. *Rhizobium* and legume symbiosis is one of the most studied mutualistic relationships between plant root nodules and nitrogen-fixing microorganisms. Mutualistic relationships are initiated when the plant began to secrete the flavonoids and iso-flavonoids in its rhizosphere, where it is recognized by *Rhizobium* (Hawkins and Oresnik, 2022). It started to do infection by differentiating root hairs, developing infection thread up to the root hair cell where infectious thread releases all its bacteria in the cytoplasmic region. Then, bacterial cell are terminally differentiated into the bacteroides, and the further development of bacteroides leads to the formation of symbiosome which is the site of nitrogen fixation (Cissoko et al., 2018; Jimenez-Jimenez et al., 2019; Suzaki et al., 2019). This atmospheric nitrogen fixation inside the nodule is carried out

by the nitrogenase enzyme (Brahmaprakash and Sahu, 2012). Examples include *Rhizobium* associated with leguminous plants, *Frankia* (actinomycetes) associated with non-leguminous plants (*Alnus*, *Casuarina*), *Azolla* and the blue-green alga *Anabaena azollae*, and association of cyanobacteria with gymnosperms (Ghodhbane-Gtari et al., 2021). Fixation of N helps to improve the soil fertility and crop productivity. Mondal et al. (2020) reported that *Rhizobium meliloti* involved in N<sub>2</sub> fixation produced chitinase enzyme and improved the yield of peanut plants. The alfalfa-Rhizobium symbiotic system can stimulate plant N fixation, increase phytohormone production, and promote plant growth (Fang et al., 2020).

## Free-living nitrogen-fixing bacteria

Mostly *Azotobacter* is studied because it is a free-living, non-symbiotic, and phototropic bacterium. *Azotobacter chroococcum* can be used as a biofertilizer because it has the potential to fix 10 mgN/g of carbon source supplied *in-vitro* (Mukherjee et al., 2022). Plant hormones such as indole acetic acids, gibberellic acids, naphthalene acetic acid, and vitamin B complex are produced by *Azotobacter*. It inhibits the root pathogens while promoting root growth, helps in mineral uptake, and improves soil fertility (Sumbul et al., 2020). Examples include *Azotobacter*, *Bacillus*, *Clostridium*, and *Azospirillum*. Application of *Bacillus*

sp. significantly enhanced the growth of *Arachis hypogea* plant, protects plants from stress, and exhibits the production of ammonia and IAA (Gohil et al., 2022). *Azospirillum brasilense* reduces N fertilization, improves plant nutrition, and increases plant biomass and wheat grain yield as reported by Galindo et al. (2022).

## Associative nitrogen-fixing bacteria

The *Spirillum lipoferum* was firstly isolated by M.W. Beijerinck in 1925. *Spirillum* was found associated with the roots of the grain which were also capable of fixing nitrogen (Soumare et al., 2020). *Azospirillum* is gram-negative, non-nodulating, aerobic-associative nitrogen-fixing bacteria with plants having a C4 dicarboxylic pathway of photosynthesis, such as sugarcane, maize, sorghum, bajra, and cereals like wheat, rice, barley (Yasuda et al., 2022). They also produce cytokinin, gibberellins, and indole acetic acid, which aid in the uptake of N, P, and K and promote the growth of roots. Examples such as *Gluconobacter*, *Acetobacter*, *Herbaspirillum*, and *Azoarcus*.

## Phosphorus-solubilizing biofertilizers

Phosphorus is the second macro-nutrient that is responsible for limiting the growth of plants (Bechtaoui et al., 2021). It is an important constituent of organic and nucleic acids and is responsible for the synthesis of ATP and several amino acids. P helps in the nodulation process, amino acid synthesis, and proteins in leguminous plants (Wang et al., 2020). Soluble form of phosphorus is phosphate anion (orthophosphate), and their uptake is facilitated by rhizospheric microbes which help in plant nutrition. There are different microbes which can solubilize the remaining unavailable form of P into available form via organic acid production by bacteria which lowers the pH of the soil, leads to the dissolution of the phosphate compounds, and makes them available for the plant's nutrition (Mahanty et al., 2017). Examples of phosphate-solubilizing bacteria and fungi (PSB and PSF) are *Bacillus*, *Rhizobium*, *Aerobacter*, *Burkholderia*, *Aspergillus*, and *Penicillium*. Inoculation of *Alcaligenes* sp. improved plant growth parameters via P solubilization and IAA production (Abdallah et al., 2016). *Rhizobium leguminosarum* and *Pseudomonas moraviensis* enhanced the yield and growth of wheat plants and showed IAA and solubilization (Igiehon et al., 2019; Fahsi et al., 2021). Application of Arbuscular fungi can make greater availability of P in plants and protects them from stress condition as reported by Nacoon et al. (2020). *Bacillus subtilis* is also known as PSB which improved safflower growth and protects plants from salinity stress as reported by Zhang et al. (2019). NanoPhos containing phosphate-solubilizing bacteria enhanced the maize production via increasing the

soil enzymes and bacteria population under field conditions (Chaudhary et al., 2021).

## Phosphorus-mobilizing biofertilizers

They are beneficial bacteria that effectively mobilize the soluble phosphorus and mineralization of the organic phosphorus compound, both are unavailable form of phosphorus. *Bacillus*, *Pseudomonas*, and *Rhizobium* are representative phosphorus-mobilizing microorganisms (PMB) (Kirui et al., 2022). Three different mechanisms have been reported for this process. First, PMB is releasing the phosphatases enzyme. Second, PMB is producing organic acids. The last one added PMB may interact symbiotically with the other fungal mycorrhiza which mobilizes the soluble phosphorus from distant places where plant roots cannot reach by absorbing soluble phosphate by hyphae (Nassal et al., 2018; Etesami et al., 2021). One of the major advantages of Arbuscular mycorrhiza is transporting both inorganic and organic forms of phosphorus to plants. Examples of arbuscular mycorrhiza fungi (AMF) include *Acaulospora* sp., *Glomus* sp., *Entrophospora*, and *Paraglomus* sp. and ectomycorrhiza include *Amanita*, *Laccaria*, and *Boletus* spp. Fungal endophyte (*Serendipita*) increased the K content in maize and protects plants from salinity stress (Haro and Benito, 2019).

## Potassium-solubilizing biofertilizers

Subsequently, potassium (K) is the third major constituent of the macro-nutrients required by plants. It is mainly intricate in the regulation of stomatal closing and opening, nutrient uptake, protein synthesis improving the quality of products and provides resistance against stress environment (Santosh et al., 2022). K is present in different forms in soil depending upon the type of the soil composition like water-soluble, available form, and non-available form of the K (Basak et al., 2022). K is present in immobilized forms in silicate minerals like illite, orthoclase, biotite, illite, feldspar, etc. K solubilization occurs by both bacteria and fungi, and the major mechanism for solubilization of the unavailable form of K is acidification (means release of organic acids) (Varga et al., 2020). There are mechanisms also for solubilization of the K, namely, siderophores production, exchange reaction, and complexation (Sattar et al., 2019). Examples of potassium-solubilizing bacteria include *Bacillus mucilaginosus*, *B. edaphicus*, *B. circulans*, *Acidithiobacillus ferrooxidans*, *Frateruria aurantia*, *Herbaspirillum* spp., and *Clostridium* spp., and potassium-solubilizing fungi include *Aspergillus* spp. and some arbuscular mycorrhiza fungi. *Bacillus cereus* showed K solubilization and improved potato plant health parameters and yield (Ali et al., 2021). Dal et al. (2020) reported that the combination

of *Rhizophagus irregularis* and *A. vinelandii* improved soil enzyme activities and plant growth of wheat plants via P and K solubilization.

## Potassium-mobilizing biofertilizers

The potassium-mobilizing microorganisms (PMMs) effectively release the unavailable potassium through the solubilization process (Patel et al., 2021). PMM is also recognized as potassium-dissolving bacteria or potassium-solubilizing bacteria. Ghaffari et al. (2018) observed that *Frateuria* and *B. megaterium* are efficient K-mobilizing bacteria used for crop farming purposes. *Azotobacter* showed K mobilization and solubilization in wheat plant and improved growth and soil microbial activities as reported by Game et al. (2020). *Enterococcus* and *Pseudomonas aeruginosa* also showed P and K solubilization and improved the maize height, yield, and nutrient acquisition (Kumar et al., 2021b). *Bacillus aryabhatai* showed K solubilization, protects plants from stress, and improves their growth via the expression of K-solubilizing genes (Chen et al., 2022).

## Sulfur-solubilizing biofertilizers

Sulfur helps in chlorophyll formation, activation of a certain enzyme, amino acid formation, vitamin formation and promotes nodulation, vital for the development of all plants (Wang et al., 2019). Sulfur solubilizers are also known as sulfur-oxidizing bacteria because they are transforming the most insoluble form of sulfur that is hydrogen sulfide (H<sub>2</sub>S) into an available form of sulfur known as sulfate (SO<sub>4</sub><sup>2-</sup>), and the reverse of this process is known assimilatory sulfate reduction which is mediated by sulfate-reducing bacteria (Wang et al., 2019). Sulfur transformation in the soil is primarily due to the microbial activity through the processes of mineralization, immobilization, oxidation, and reduction (Malik et al., 2021). Examples of aerobic sulfur-oxidizing bacteria include *Bacillus*, *Beggiatoa*, *Aquifer*, *Paracoccus*, *Sulfolobus*, *Thiobacillus*, *Thermithiobacillus*, *Xanthobacter*; phototropic anaerobic sulfur-oxidizing bacteria include *Allochroamatium*, *Chlorobium*, *Rhodobacter*, *Rhodospseudomonas*; non-phototrophic obligate anaerobes include *Wolinella succinogenes*; and aerobic sulfur-oxidizing archaea include *Sulfolobales* members (Kusale et al., 2021). *Thiobacillus thiooxidans* and *Bradyrhizobium japonicum* are sulfur-oxidizing biofertilizers which showed better effect on cereal crops, medicinal plants, and forage crops (Zhang et al., 2018). *Halothiobacillus* bacteria tolerated the high salt concentration and improved crop production in saline soils (Boroujeni et al., 2021).

## Zinc-solubilizing biofertilizers

Zinc is required during protein synthesis, DNA-protein interaction, growth hormone production, seed development, production of chlorophyll and protects plants from stress conditions (Umair Hassan et al., 2020). Insoluble forms of zinc are mostly ZnO, Zn<sub>3</sub>(PO<sub>4</sub>)<sub>2</sub>, ZnCO<sub>3</sub>, and metallic Zn. The usable form of zinc by the plant is divalent cations (Ayoub et al., 2022). Zinc-solubilizing fertilizers contain the zinc solubilization bacteria which produce the organic acids to solubilize the insoluble zinc to Zn<sup>+2</sup>, thereby enhancing zinc uptake in plants (Nitu et al., 2020). Examples of zinc-solubilizing bacteria and fungi are *Bacillus subtilis*, *Pseudomonas striata*, *Serratia*, *Burkholderia cenocepacia*, *Aspergillus niger*, *A. nomius*, and *A. oryza* which improved the soil enzyme activities and availability of Zn in crop plants (Batool et al., 2021). *Leclercia adecarboxylata* solubilizes Zn and produced siderophores which enhanced the Zn uptake in the roots of cucumber plants (Kang et al., 2021). *Bacillus* spp. and *Pseudomonas taiwanensis* showed a positive impact on the growth and chlorophyll content of maize plants (Chaudhary and Sharma, 2019; Hussain et al., 2020). Inoculation of *Trichoderma longibrachiatum* and *Bacillus megaterium* improved the seed germination of soybean plants in the pot experiment (Bakhshandeh et al., 2020). The application of PSB along with fertilizers improved the growth of faba bean in sandy soils (Ding et al., 2021).

## Phytohormone-producing biofertilizers

Plant hormone or phytohormone plays a substantial role in plant development, secreted by both plants and microorganisms (Usman et al., 2022). Plant hormone production is an important feature of the beneficial microbes which is producing the indole-3-acetic acids, gibberellins, cytokinin, etc. (Eichmann et al., 2021). Auxin helped in the differentiation and division of plant cells. Cytokinin prevents the premature leaf senescence of plants (Wu et al., 2021a). Abscisic acid is also identified as hormone which is produced by plants during stress conditions. Gibberellins are involved in seed germination, shoot elongation, flowering, and fruiting (Binenbaum et al., 2018). These hormones are generally secreted by microorganisms under environmental stress conditions to protect the plants by modulating the phytohormone level inside the host plants (Lopes et al., 2021). *Bacillus thuringiensis* has the genes required for IAA production which improved the growth of tomato plants (Batista et al., 2021). *B. licheniformis* is known for the production of IAA, ABA, and gibberellin which improved the growth of grapevine and protects plants from stress conditions (Salomon et al., 2014).

## Siderophores producing biofertilizers

Iron (Fe) is a micronutrient that performs various functions like photosynthesis, respiration, chlorophyll, and many of the enzymatic reactions in plants (Gao et al., 2022). The unavailable form of iron in nature present under aerobic environment predominately is  $\text{Fe}^{+3}$  and is more probable form of insoluble oxyhydroxides and hydroxides complex. So, bacteria are producing the low-molecular weight iron-binding protein molecules called siderophores (Lurthy et al., 2020). Siderophores are water-soluble molecules that exist in two forms, namely, extracellular and intracellular. After capturing  $\text{Fe}^{+3}$  by siderophore inside bacteria,  $\text{Fe}^{+3}$  is reduced to the  $\text{Fe}^{+2}$  inside the cytoplasmic membrane which is then transported inside the cytoplasm by gating mechanisms (Gu et al., 2020). This available form of iron is given by the bacteria to the host plant for its development (Mahanty et al., 2017). Plant assimilates the iron with the help of siderophores by releasing the chelating agent via bacteria. Examples include *Pseudomonas fluorescens* C7, *Pseudomonas aeruginosa* RSP5, and *Pseudomonas aeruginosa* RSP8. Application of siderophore-producing *Bacillus* sp. improves the growth of groundnut (Sarwar et al., 2020). *Pseudomonas koreensis* inoculation in maize plants inhibited the growth of plant pathogens via the production of siderophore and antioxidant enzymes (Ghazy and El-Nahrawy, 2021).

## Organic matter decomposer biofertilizers

Soil organic matter is a mixture of living organisms consisting of bacteria, fungi, and insects, and the non-living part which includes fresh organic residues or waste, the dead and decaying matter of living organisms is generally known as humus (Lou et al., 2022). In organic matter generally, cellulose, lignin, hemicellulose, chitin, and lipids are present which are degraded by microbes such as bacteria, actinomycetes, and fungi. The organic-matter-degrading organisms break down the SOM into simpler or inorganic from which they derive energy and carbon for their growth. Examples of bacteria include *Bacillus subtilis* and *Pseudomonas fluorescens* and of fungi include ectomycorrhizal fungi. *Trichoderma* spp. involved in the degradation of litter at a faster rate releases antimicrobial compounds, improves the physicochemical properties of soil, and improves microbial diversity (Baldi et al., 2021). *Bacillus subtilis* and *B. hisashii* are involved in lignocellulose biodegradation by secreting the microbial enzymes as reported by Niu and Li (2022).

## Endophytic bacteria as biofertilizers

Mutualistic microorganisms that employ the whole or part of their life cycle inside the plant tissues are known as

endophytes (Fadiji and Babalola, 2020). Endophytes are of interest because they improve the nutritional requirements of the non-leguminous and leguminous plants by nitrogen fixation, phosphate solubilization, or by siderophores production (Janati et al., 2021). These bacteria have the potential to suppress pathogenic effects by activating the plant defense system (Dicko et al., 2021). Examples of endophytic bacteria include *Klebsiella* spp., *Pseudomonas* spp., *Serratia* spp., *Bacillus* spp., *Burkholderia* spp., *Citrobacter* spp. and endophytic fungi include *Colletotrichum*, *Fusarium*, *Alternaria*, and *Aspergillus*. *Penicillium* and *Aspergillus* isolated from roots of *Taxus wallichiana* solubilized P and produced phosphatase and phytase enzymes (Adhikari and Pandey, 2019). Kang et al. (2014a) observed that *Bacillus megaterium* regulates the content of amino acids and carbohydrates to promote the growth of mustard plant. Endophytes isolated from rice such as *Bradyrhizobium* sp., *Paraburkholderia* sp., showed acetylene reduction properties and high sugar content contributing to high nitrogen-fixing ability. High content of sugar in different crops such as sweet potato, pineapple, and sugar has known to assist endophytic N-fixing activity among non-leguminous plants (Okamoto et al., 2021).

## Plant growth-promoting rhizobacteria

PGPR is used as biofertilizers; it represents the variation of soil bacteria that live in association with the rhizosphere, rhizoplane associated to root surface, and endophytes present inside the intercellular places (Vandana et al., 2021). PGPRs are soil bacteria which increase the growth and enhance the tolerance of plants toward stress conditions (Ghosh et al., 2019). There are diverse mechanisms shown by PGPR which support the plant growth such as  $\text{N}_2$  fixation, macro- and micronutrient mineralization, secretion of exopolysaccharides, phytohormone production, siderophore, hydrogen cyanide to prevent the growth of phytopathogens, antibiotics, etc. (Gouda et al., 2018; Numan et al., 2018). *Rhizobium lupini* increased alfalfa growth and enhanced nutrient uptake efficiency (Duan et al., 2022). Application of biofertilizers such as *Pseudomonas taiwanensis*, *Bacillus* spp., and *Pantoea agglomerans* improved the maize growth, yield, and soil health parameters (Khatri et al., 2018; Chaudhary et al., 2022b). Application of *Bacillus* spp. improved the plant/soil health parameters and maize productivity as reported by Chaudhary et al. (2021). Kukreti et al. (2020) reported that *Pseudomonas taiwanensis* improved maize plant health and soil enzyme activities in the pot experiment.

## Role of biofertilizers in biotic stress management

The outbreak of plant diseases in nature necessitates sustainable agriculture with minimum use of agrochemicals. For

a long time, the use of chemicals has posed a significant risk to the environment and the agricultural sector (Akanmu et al., 2021). Long-term use of pesticides, on the other hand, harms both plant/soil health and eventually leads to significant crop loss. Thus, effective and eco-friendly phytopathogen control strategies such as biofertilizers are required. The exploitation of potential biofertilizers as endophytes could be useful to improve crop plants from various bacterial and fungal diseases (Collinge et al., 2022). Biological control of plant diseases occurs via destruction of pathogens via beneficial microbes such as *Bacillus* spp., *Pseudomonas* spp., *Streptomyces*, *Pantoea* spp., and several fungal spp. (Köhl et al., 2019; Chaudhary et al., 2021). Such endosymbiont group of biocontrol agents being friendly, they not only colonize internal plant tissue but also protect host plant throughout its life cycle without causing any apparent damage (Lahlali et al., 2022). The use of *Bacillus* sp. for crop growth promotion and biocontrol has a long history (Zhu et al., 2021). *Bacillus thuringiensis* (Bt), a producer of endotoxins that can be used as biopesticide and a source of genes for the creation of transgenic plants that are resistant to insects, is currently the most effective biopesticide on the market (Sujayanand et al., 2021).

Biofertilizers in the form of potential biocontrol agents represent a safe alternative to harmful chemicals like fertilizers, herbicides, pesticides, and insecticides (Hernández-Fernández et al., 2021). Consequently, the use of biofertilizers is receiving special attention for the management of phytopathogens that are comprised of bacteria, fungi, virus, aphids, and nematodes (Table 1). Their ubiquitous nature and the ability to reside within plant tissues make them unique, showing multidimensional interactions within the host plant (Khare et al., 2018). The biodiversity of endophytes is hyperdiverse in almost every other plant species ranging from small non-vascular plants to large conifers like *Pinus radiata* (Liu et al., 2017b). Some of the known endophytes are *Burkholderia*, *Stenotrophomonas*, *Rhizobium*, *Microbacterium*, and *Bacillus* spp. (Kandel et al., 2017).

There are several enzymes which protect the plants from stress conditions such as antioxidant enzymes like peroxidase (POD), polyphenol oxidase, phenylalanine ammonia-lyase (PAL), lipoxygenase, and chitinase (Cataldo et al., 2022). Lipoxygenase enzymes have its place to non-heme iron comprising dioxygenases which contribute to stress response via lipid oxidation. Also, it is found to act as signals for communication with the plant host, with associated endophytes and pathogens (Singh et al., 2022b). In response to pathogen attack, endophytes boost plant immunity by priming induced systemic resistance (ISR) and systemic acquired resistance (SAR) via several phytohormones (Romera et al., 2019; Oukala et al., 2021). Pathogenesis-related proteins with antimicrobial properties are produced and accumulated by several endophytes symbiotically living with their host plants. Many endosymbionts have the capability to complement the inefficient antioxidative system of plants by different mechanisms (Shukla et al., 2022). In

some strains, production of lipopeptides, surfactin, plipastatin, and mycosubtilin differentially activated the plant innate immune response (Kumar et al., 2021c). Production of surfactin may have an important role in the suppression of *Fusarium* infestation on germinating seeds (Eid et al., 2021). *Bacillus* strains inhibited the verticillium wilt caused due to *Verticillium dahliae* by the production of secondary metabolites such as surfactin, fengycin, and bacillibactin, as well as expressing defense-related genes such as SOD and PAL (Hasan et al., 2020). *Bacillus atrophaeus* inhibits *Meloidogyne incognita* growth by producing volatile dimethyl disulfide and antioxidant enzymes (Ayaz et al., 2021). According to Nie et al. (2019), *Bacillus cereus* inhibits the growth of *Pseudomonas syringae* by producing antioxidant enzymes. *Pseudomonas fluorescent* controls the iron uptake genes and protects plants from phytopathogens as reported by Desrut et al. (2020). *Acrophialophora jodhpurensis* defends tomato plants from *Rhizoctonia solani* which causes crown root disease via the production of peroxidase enzyme, chitinase, and phenylalanine (Daroodi and Taheri, 2021). Plants are protected from *Botrytis cinerea* by *Trichoderma atroviride* via the production of glutamate and glyoxylate aminotransferase (González-López et al., 2021).

Secondary metabolites play the foremost role in defense mechanism toward pathogens, pests, and herbivores. Many plants microbiome especially endosymbionts regulate defense mechanisms through secreting various metabolites (Divekar et al., 2022). Secondary plant metabolites belonging to the family of steroids, alkaloids, phenolics, flavonoids, and terpenoids function in innate immunity and defense response signaling (Pang et al., 2021). Volatile compounds from endophytes modulate plant microbiome and possess antimicrobial properties. A variety of fungi, including *Ascomycetes* and *Deuteromycetes*, are inhibited by a mixture of VOCs produced by the fungal endophyte *Phomopsis* sp. (Hummadi et al., 2022). Three VOCs, including caryophyllene, 2-methoxy-4-vinylphenol, and 3,4-dimethoxystyrol, produced by endophytic fungi *Sarocladium bravhiariae* HND5 have been found to have antifungal activity against *Fusarium oxysporum* (Yang et al., 2021). Alkaloid produced by *Epichloe* sp. in a variety of grass species is one of the well-known secondary metabolites produced by endophytic fungi. Hennessy et al. (2022) reported *Epichloe festucae* colonized agricultural forage grasses and offered the plant defense against herbivorous insects. *Streptomyces hydrogenans* metabolites can be used as safe biocontrol agents against *Meloidogyne incognita* and plant growth promoters for *Solanum lycopersicum* (Sharma et al., 2020). *Bacillus velezensis* is a potential pesticide due to its strong biocontrol activity and ability to strengthen host defense against *Magnaporthe oryzae* fungi, which cause rice blast disease in plants (Chen et al., 2021). An isolate of *Trichoderma asperellum* increased the resistance in tomato seedling to the disease *A. alternata* leaf spot (Yu et al., 2021). *Trichoderma asperellum* also produces mycolytic enzymes such as chitinase and 1,3, glucanase



TABLE 1 Role of biofertilizers in biotic stress tolerance.

Biofertilizers	Host plant	Pathogen	Response	References
<i>Bacillus subtilis</i>	<i>Atractylodes macrocephala</i>	<i>Ceratobasidium</i> sp.	Inhibit growth of pathogen and promote plant growth	You et al., 2018
<i>Bacillus cereus</i>	<i>Arabidopsis</i>	<i>Botrytis cinerea</i>	Regulates signaling pathway such as JA and MAPK	Nie et al., 2019
<i>Bacillus velezensis</i>	<i>Arabidopsis</i>	<i>Myzus persicae</i>	Protects host plant from pathogen via systemic resistance response	Rashid et al., 2017
<i>Bacillus safensis</i>	<i>Vaccinium</i>	<i>Botrytis cinerea</i>	Enhanced the chitinase, hydrolytic, protease production and protects plants from pathogen	Hassan et al., 2021
<i>Pseudomonas aeruginosa</i>	<i>Cruciferous vegetables</i>	<i>Xanthomonas campestris</i>	Protects plants from pathogen via chitinase production	Mishra and Arora, 2012
<i>Gluconacetobacter diazotrophicus</i>	<i>Arabidopsis thaliana</i>	<i>Ralstonia solanacearum</i>	Protects from pathogen and activates defense response in plants	Rodriguez et al., 2019
<i>Streptomyces</i> spp.	<i>Oryzae sativa</i>	<i>Xanthomonas oryzae</i>	Provides immunity to plants and protect from disease via increasing antioxidant enzymes	Hata et al., 2021
<i>Paenibacillus polymyxa</i>	<i>Brassica napus</i>	<i>Verticillium</i> spp.	Increased production of volatile fatty acids and antibiotics	Rybakova et al., 2017
<i>Bacillus subtilis</i>	<i>Solanum lycopersicum</i>	<i>Fusarium oxysporum</i>	Increased expression of auxin-related genes and improved plant growth	Samaras et al., 2021
<i>Trichoderma koningii</i>	<i>Nicotiana tabacum</i>	<i>Tobacco Mosaic Virus</i>	Enhanced proline content and pathogen-related enzymes and inhibit the growth of pathogens	Taha et al., 2021
<i>Aureobasidium pullulans</i>	Olive trees	<i>Colletotrichum acutatum</i>	Increased production of volatile fatty acids and improves seed germination	Sdiri et al., 2022
<i>Trichoderma harzianum</i>	<i>Zea mays</i>	<i>Curvularia lunata</i>	Provides protection to plants from pathogen via JA signaling and platelet-activating factor	Yu et al., 2015
<i>Bacillus amyloliquefaciens</i>	<i>Solanum lycopersicum</i>	Viruses	Induced SA and JA signaling and protects plants from disease	Beris et al., 2018
<i>Bacillus endophyticus</i> , <i>Pseudomonas aeruginosa</i>	<i>Solanum lycopersicum</i>	<i>Spodoptera litura</i>	Increased secondary metabolite, phytohormone production and improved plant growth	Kousar et al., 2020
<i>Bacillus subtilis</i>	<i>Solanum lycopersicum</i>	<i>Fusarium oxysporum</i>	Increased plant growth and suppress the growth of pathogens	Sundaramoorthy and Balabaskar, 2013
<i>Bacillus</i> sp.	Common bean	<i>Rhizoctonia solani</i>	Inhibit growth of pathogens via production of cyanogens and lytic enzymes	Kumar et al., 2012
<i>Pseudomonas</i> spp.	<i>Gossypium</i>	<i>Fusarium</i> spp.	Inhibit pathogens via production of HCN and enzymes	Zain et al., 2019
<i>Bacillus halotolerans</i> , <i>Agrobacterium fabrum</i> <i>P.putida</i>	Common bean	<i>Alternaria</i> sp.	Improved plant growth and increased chitinase, siderophore, and IAA production	Sendi et al., 2020
<i>Aureobasidium pullulans</i>	<i>Solanum tuberosum</i>	<i>Phytophthora infestans</i>	Increased production of HCN against pathogens	Anand et al., 2020
	Crops	<i>Botrytis cinerea</i> , <i>Alternaria alternata</i>	Increased production of volatile organic acids and inhibit pathogen growth	Don et al., 2020

which may be capable of destroying phytopathogens cell walls (Win et al., 2021). *Trichoderma* spp. also have biocontrol potential against *V. dahliae*, which causes olive tree wilting, and inhibit the pathogenic fungus mycelial growth (Reghmit et al., 2021). *Trichoderma* sp. has been shown successfully to suppress *Sclerospora graminicola*, the cause of pearl millet downy mildew disease, and develop systemic resistance (Nandini et al., 2021).

Some endophytes can also regulate stress management through SAR mediated by salicylic acid. SAR offers long-lasting stress management and broad-spectrum effectiveness against a variety of pathogens (Xia et al., 2022). It frequently involves the accumulation of chitinase and pathogenesis-related proteins (PR). In a study by Samain et al. (2019), *Paenibacillus* strain (PB2) used to control *Mycosphaerella graminicola* induced pathogenesis-related proteins (PR1) which is considered as marker of SAR. Application of *Bacillus aryabhatai* activated a durable defense response against pathogens facilitated through salicylic acid/ethylene pathways (Portieles et al., 2021). *Trichoderma harzianum* helps to improve plant immediate resistance against *Nezara viridula* feeding invasion via enhancing JA marker gene transcript levels (Alınç et al., 2021). *Bacillus subtilis* and *Pseudomonas fluorescens* mediated systemic alleviated the biotic stress in *Solanum lycopersicum* against *Sclerotium rolfsii*. Heat-killed endophytic strain *B. aryabhatai* (HKEB) induced defense-related genes protein (PR1) and phytoalexin-deficient 3 in *A. thaliana*. PR1 gene expression was found to be 20-fold higher in treated plants than control, and other genes found in the study were associated with jasmonic and salicylic acid pathways (Portieles et al., 2021). Endophytes exhibit different gene upregulation and a distinct signaling pathway in response to distinct colonization strategies (Morelli et al., 2020). *Trichoderma* spp. demonstrated antagonistic activity against phytopathogens such as *B. cinerea*, *Fusarium solani*, and *Rhizoctonia solani* used as biocontrol agent in greenhouse experiment (Sánchez-Montesinos et al., 2021).

## Role of biofertilizers in abiotic stress management

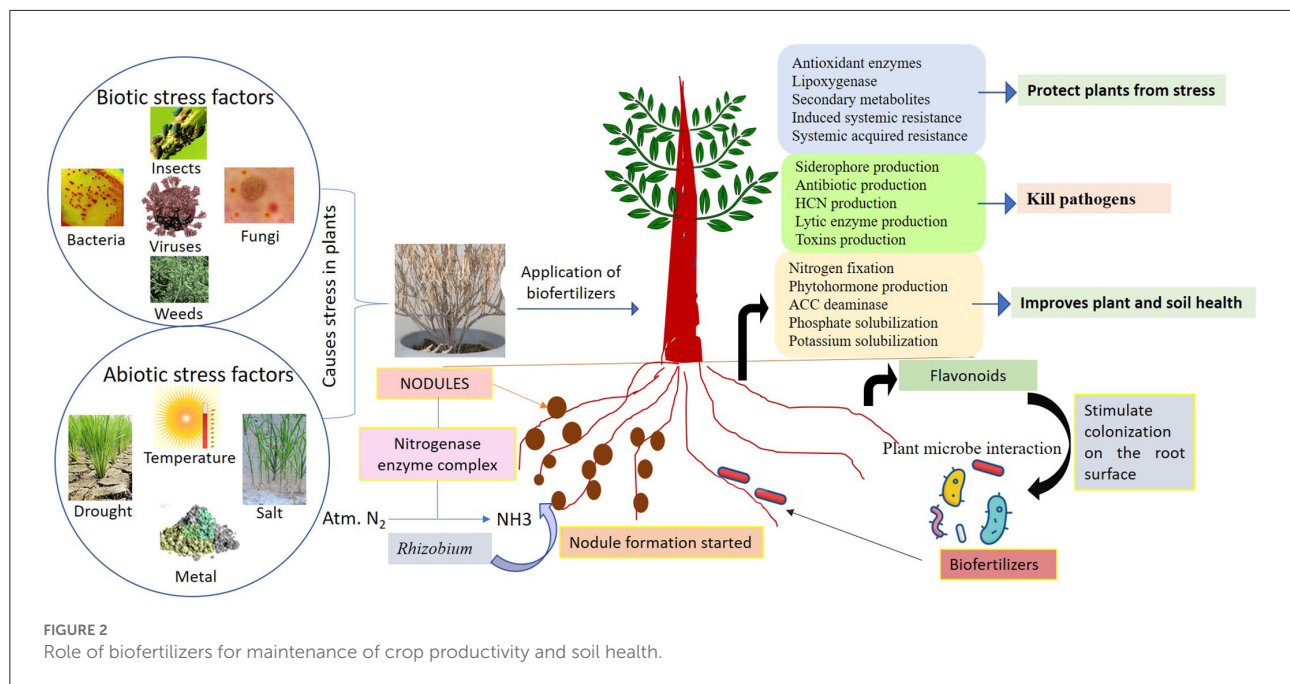
Climate change is one of the major reasons for the increasing abiotic stresses on the crops, which results in reducing the world's agriculture productivity. Abiotic stresses like drought, salinity, waterlogging, and excessive heat are responsible for the poor yield of crops (He et al., 2018). In recent years, the abiotic stress has increased so fast, because of the fluctuation of climates or climate change, and it has caused an unusual rise in the weather conditions and incidents, which is responsible for the substantial losses of crops around the globe. These abiotic stresses induce several physiological, biochemical, and morphological changes in plant that finally affect the economic yield of crop plants, and it was reported that the yield loss from

abiotic stress is about 51–82%, which if continues will affect the goal of sustainable food production (dos Santos et al., 2022).

The use of beneficial microbes such as endophytes capable of producing growth hormones, like IAA, ACC deaminase, augmented the K uptake in plant tissues but decreased the ethylene level which helps in tolerance of stress in diverse plants (Figure 2). Biofertilizers as endophytes are found to have diverse associations with its host plant such as symbiotic, parasitic, and mutualistic and colonize plant tissues without causing any disease, thus benefiting for plants (Chaudhary et al., 2022c). Endophytes may benefit from mutualistic associations as they obtain nutrients from the hosts, and they spread by host seed transmission. They are also able to enhance the nutrients uptake like nitrogen, magnesium, zinc, and phosphorus from soil and provide to the host plant for better growth and survival (Bamisile et al., 2018). It is well-identified that plant biofertilizers play a significant role in supporting the growth of crops under different abiotic stresses (Table 2). Actinobacteria are well-known for plant growth via metabolite production and antibiotics under stress conditions (Yadav et al., 2018). Abd El-Daim et al. (2014) observed that the application of *Pseudomonas* sp. improved plant growth under heat stress via HSPs and ROS reduction. *Paenibacillus* sp. improved *Phaseolus vulgaris* growth via facilitating the siderophore, IAA and HCN production under salinity stress conditions (Gupta and Pandey, 2019). *Trichoderma harzianum* inoculation in rice plants improved root growth and protects from drought stress as reported by Shukla et al. (2012). Mukhtar et al. (2020a) reported that *Bacillus cereus* enhanced the production of ACC deaminase and exopolysaccharide which protects *Solanum lycopersicum* plants from heat stress.

## Drought stress

Drought stress is one of the main abiotic stresses which causes water scarcity to meet the plant necessity and causes economic fatalities in agriculture production. The normal progress of plants is hindered due to decrease in water shortage in their cells. Drought stress decreased the rate of photosynthesis, germination in plants, and loss in crop productivity (Lata et al., 2018). Inoculation of beneficial biofertilizers (rhizospheric and endophytic microbes) improved plant growth and development via different direct/indirect mechanisms under stress situations. Stress can be overcome via using biofertilizers which produced growth hormones such as IAA and cytokinins and improved plant development (Fasusi et al., 2021). Inoculation of *Pseudomonas putida* boosted the flavonoids, salicylic, and abscisic acid production which protects soybean plants from drought stress (Kang et al., 2014b). Inoculation of *Pseudomonas* spp. protects maize plants and improved biomass and sugar content in treated plants from drought stress via upregulation of dehydrin proteins and



proline content (Sandhya et al., 2010). Khan et al. (2018) found that *Bacillus thuringiensis* improved chickpea growth under drought conditions via production of volatile organic compounds. Application of *Microbacterium* sp. improved maize plant growth, root length, photosynthetic rate, and yield under drought stress (Romera et al., 2019). Usage of *Phoma* improved the drought tolerance in *Pinus tabulaeformis* plants and increased seedling growth by improving the mechanism of water uptake, proline, and SOD (Zhou et al., 2021). Sheteiwy et al. (2021) reported that *Bradyrhizobium japonicum* and AMF improved the yield of soybean bacterial count and enzyme activities of soil via improving the nutrient accessibility in soil under drought stress. AMF and *Rhizobium* inoculation improved the *Glycyrrhiza* plant growth and phosphorus content in roots in drought stress (Hao et al., 2019). Combined inoculation of arbuscular fungi and bioinoculants improved plant biomass and chlorophyll content in date palm (*Phoenix dactylifera*) under water-deficit conditions via enhanced antioxidant enzyme activities, soluble sugars, and proteins (Anli et al., 2020). Inoculation of *Glomus mosseae* and *Bacillus amyloliquefaciens* in *Phaseolus vulgaris* significantly improved the photosynthetic rate and yield under water stress conditions (Salem and Al-Amri, 2021).

## Salinity stress

Accumulation of salt in agricultural soil will have a negative impact on plants including its physiological, morphological, and molecular aspects. This affects plants via creating osmotic stress,

ion toxicity and reducing the photosynthesis, CO<sub>2</sub> fixation, and transpiration rate in plants. Availability of nutrients and microbial diversity are also affected due to the salinity stress (Luo et al., 2021). Usage of bioinoculants is enormously supportive in countering the lethal properties of soil salinity via improving the soil physicochemical properties and thus improved crop production (Jiménez-Mejía et al., 2022). Interaction between microbes and plants can overcome stress problem. Gond et al. (2015) reported that inoculation of *Pantoea agglomerans* in tropical corn under salt stress (0–100 mM) improves tolerance and growth of plants due to the upregulation of aquaporins. *Bacillus megaterium* also regulates the aquaporin genes during salt stress in maize plants and improved root growth and leaf water content (Marulanda et al., 2010). Waqas et al. (2012) reported that *Penicillium* and *Phoma glomerata* improved the rice plant growth under salinity stress via increased production of CAT, POD, and IAA. Checchio et al. (2021) observed that *Azospirillum brasilense* improved resistance in corn plants via enhancing the production of antioxidant enzymes and glycine betaine. Application of *Pseudomonas* sp. improves *Arabidopsis thaliana* germination and growth via upregulation of lipoxygenase genes which are involved in tolerance mechanism via jasmonic pathway (Chu et al., 2019). The *Arthrobacter nitroguajacolicus* improved wheat growth under salt stress via upregulation of IAA, ACC, flavonoid, stilbenoid, terpenoids, and cytochrome P450 genes (Safdarian et al., 2019). Inoculation of *Planococcus rifietoensis* protects *Cicer arietinum* plants from salt stress (200 mM) via EPS and biofilm production (Qurashi and Sabri, 2012). Gupta and Pandey (2019) observed that inoculation of *Paenibacillus* sp.

TABLE 2 Role of biofertilizers in abiotic stress tolerance.

Biofertilizers	Host plant	Stress	Response	References
<i>Bacillus aryabhatai</i>	<i>Oryza sativa</i>	Salinity, heavy metals	Improved salt tolerance ability <i>via</i> exopolysaccharide production	Sultana et al., 2020
<i>Bacillus amyloliquefaciens</i>	<i>Arabidopsis</i>	Salt	Improved plant growth <i>via</i> regulation of JA pathway and antioxidant enzymes	Liu et al., 2020
<i>Bacillus licheniformis</i>	<i>Chrysanthemum</i>	Salt	Improved salt tolerance ability in stressed plants <i>via</i> production of antioxidant enzymes and Fe attainment	Zhou et al., 2017
<i>Bacillus HL3RS14</i>	<i>Zea mays</i>	Salt	Increased weight of roots and shoots <i>via</i> production of IAA, proline, and glycine betaine	Mukhtar et al., 2020b
<i>Bacillus subtilis</i> , <i>Pseudomonas</i> sp.	<i>Solanum melongena</i>	Salt	Increase chlorophyll content and protects plants from stress	Mokabel et al., 2022
<i>Bacillus</i> sp.	<i>Pisum sativum</i>	Salt	Improved plant growth and photosynthesis <i>via</i> antioxidant enzyme and AAC and siderophore production	Gupta et al., 2021
<i>Gluconacetobacter diazotrophicus</i>	<i>Zea mays</i>	Drought and nitrogen	Increase plant biomass and chlorophyll content	Tufail et al., 2021
<i>Pseudomonas pseudoalcaligenes</i>	<i>Glycine max</i>	Salt	Improved plant health parameters <i>via</i> production antioxidant enzyme, proline contents in shoots and roots	Yasmin et al., 2020
<i>Alternaria alternata</i>	<i>Triticum aestivum</i>	Drought	Improved photosynthesis <i>via</i> increasing antioxidant enzymes	Qiang et al., 2019
<i>Aspergillus flavus</i>	<i>Glycine max</i>	Salt	Increased antioxidant enzyme activity and chlorophyll content	Asaf et al., 2018
<i>Aspergillus violaceofucus</i>	<i>Helianthus annuus</i>	Heat	Improved plant height, biomass, and chlorophyll content	Ismail et al., 2020
<i>Funneliformis mosseae</i>	<i>Trifoliate orange</i>	Drought	Improved phenols, terpenoids and soil protein and enzyme activities	Cheng et al., 2021
<i>Glomus lomus</i>	<i>Date palm</i>	Salt	Improved shoot weight and growth	Meddich et al., 2018
<i>Piriformospora indica</i>	<i>Triticum aestivum</i>	Nutrient	Improved Zn uptake and root and shoot biomass	Abadi et al., 2021
<i>Piriformospora indica</i>	<i>Arabidopsis</i>	Cold	Increased proline content and cold stress tolerance genes	Jiang et al., 2020
<i>Trichoderma atroviridae</i>	<i>Arabidopsis</i>	Cold	Improved auxin production and cold-related gene expression	González-Pérez et al., 2018
<i>Rhizophagus intraradices</i>	C3 plants	Salt	Improved chlorophyll content in plants	Chandrasekaran et al., 2019
AMF and <i>Bradyrhizobium japonicum</i>	<i>Glycine max</i>	Drought	Increased yield and protects from stress <i>via</i> upregulation of CAT and POD activity	Sheteiwiy et al., 2021
AMF and <i>Rhizobium</i> spp.	<i>Glycine max</i>	Drought	Improved plant health and microbial diversity in soil Triggered CAT, proline, and IAA production	Igichon et al., 2021
<i>Serratia marcescens</i>	<i>Lactuca sativa</i>	Salinity		Fortt et al., 2022

protects and improved *Phaseolus vulgaris* plant growth under salinity stress *via* the production of IAA and ACC deaminase. Meena et al. (2020) reported that *Nocardioides* sp. improved

seedling growth of *Triticum aestivum* under salt stress (0–100 mM) *via* increasing the CAT and POD genes. Inoculation of *Penicillium* and *Ampelomyces* spp. improved drought and

salinity stress tolerance in tomato plants *via* the production of osmolytes, stress-responsive genes, and antioxidant enzymes (Morsy et al., 2020). Inoculation of *Piriformospora indica* highly enhanced plant development and attenuated NaCl-induced lipid peroxidation which helps to build tolerance during salinity stress (Ghaffari et al., 2018). Studies show that the inoculation of *Trichoderma longibrachiatum* T6 in wheat increased the levels of antioxidant enzymes (SOD, POD, and CAT) which helped to improve the stress tolerance in plants during salt stress (Zhang et al., 2016). *Agrobacterium* and *Raoultella* showed production of IAA, HCN, and ACC under salt stress and improved growth of *Tetragonia tetragonoides* plants (Egamberdieva et al., 2022). Fortt et al. (2022) reported that the application of PGPR improved the growth of lettuce under salt stress *via* the production of IAA and antioxidant enzymes which provide protection to plants.

## Temperature stress

Global warming is a serious risk to all living creatures and is becoming a worldwide concern. Temperature stress such as heat and cold greatly limits the growth and development of plants (Yadav et al., 2018). Heat stress causes modification in homeostasis, degradation of proteins, which have lethal effects on physiology of plants as it delays the seed germination, damages to seeds and affects agricultural production (Imran et al., 2021). Cold stress causes dehydration due to ice formation which is responsible for protein denaturation. It also causes plant leaves lesions, yellowing of leaves, and rotting. It also affects the seed germination and yield of crops (Wu et al., 2021b). The application of several microbes alleviated the damaging effects of heat stress in various plants such as wheat, tomato, and sorghum *via* producing phytohormones, biofilm formation, and enhancing heat shock proteins (Issa et al., 2018; Sarkar et al., 2018). *Bacillus cereus* inoculation in tomato plants increased the production of HSPs, IAA, essential amino acids, and organic acids and protects plants from stress conditions (Khan et al., 2020). Inoculation of *Azospirillum* and *B. amyloliquefaciens* improved the heat tolerance *via* reducing oxidative damage in wheat seedling (Abd El-Daim et al., 2014). Duc et al. (2018) reported that *Glomus* sp. tolerates heat stress and protects tomato plants *via* scavenging ROS generation. *Bacillus velezensis* improved wheat plant survival under cold stress *via* increase in cold stress-related proteins as reported by Abd El-Daim et al. (2019). Zulfikar et al. (2011) reported that *Pseudomonas putida* also improved the growth of wheat plants under heat stress *via* enhanced production of proline, sugars, and antioxidant enzymes. *R. irregularis* and *F. mosseae* increased plant height, transpiration rate in maize, and nutrient composition in roots of *triticum aestivum* during heat stress (Cabral et al., 2016). *Paraburkholderia phytofirmans* having ACC deaminase-producing efficiency helps

in normal growth of tomato plants under heat stress as reported by Esmael et al. (2018). Bacterial inoculants such as *Rhodococcus* and *Burkholderia* protect the medicinal plant *Atractylodes lancea* from heat stress and improved their growth *via* enriched root-associated microbes (Wang et al., 2022a).

## Heavy metal stress

Extreme usage of inorganic chemical fertilizers in agriculture system causes the accumulation of toxic metals such as nickel, manganese, cadmium, iron, and zinc in soil (Ghori et al., 2019). These metals are beneficial for plants at low level, but if their concentration increases cause stress *via* decrease in plant growth due to the decrease in photosynthesis, deprived nutrients, membrane integrity, and enzyme activities. It causes oxidative stress *via* ROS and H<sub>2</sub>O<sub>2</sub> generation and reduces plant growth and crop productivity (Ahmad et al., 2019; Gong et al., 2020). ROS generation occurs both under favorable and unfavorable circumstances, and it has a negative impact on vital macromolecules (Köhl et al., 2019). *Rhizobium* inoculation at nickel-contaminated site improves the chlorophyll content and increased lentil plant growth (Wani and Khan, 2013). *Bradyrhizobium* increased IAA production and siderophore production and improved the shoot weight of *Lolium multiflorum* at cadmium-contaminated site (Guo and Chi, 2014). *Candida parapsilosis* and *B. cereus* protect *Trifolium repens* plants from heavy metal stress conditions as reported by Azcón et al. (2010). Toxicity of arsenic in *Brassica juncea* is reduced by *Staphylococcus arlettae* *via* enhanced production of dehydrogenase and phosphatase enzyme in soil (Srivastava et al., 2013). Inoculation of *Talaromyces pinophilus* in *Triticum aestivum* plants stimulates plant growth *via* the production of gibberellic acid under heavy metal stress (El-Shahir et al., 2021). Paredes-Páliz et al. (2018) reported that inoculation of metal-resistant bacteria such as *B. aryabhattai* and *Pantoea agglomerans* brings production of phenylalanine ammonia-lyase enzyme and SOD which protects plants from metal stress. The addition of bioinoculants like *P. aeruginosa* and *Burkholderia gladioli* reduced Cd toxicity in *Solanum lycopersicum* by producing phenols, organic acids, and osmoprotectants (Khanna et al., 2019). Application of *Serratia marcescens* and *E. bugandensis* improved spinach (*Ipomoea aquatica*) growth *via* the production of polyamine under Pb and Cd toxicity (Wang et al., 2022b). *Citrobacter* and *Enterobacter cloacae* mitigate the Cd and Pb toxicity, improve the wheat plant health parameters, and protect from stress *via* the generation of antioxidant enzymes (Ajmal et al., 2022). Oubohssaine et al. (2022) reported that *Pseudarthrobacter oxydans* improved *Sulla spinosissima* growth and can be used as biofertilizer at heavy metal-contaminated sites. Cadmium tolerance bacteria such as *Curtobacterium ocnosedimentum* having P-solubilizing,

IAA, and siderophore-producing possessors improved chili growth and increased shoot/root length (Patel et al., 2022). Inoculation of *Pseudoarthrobacter* and *Vibrio neocaledonicus* improved the *Salicornia ramosissima* growth at As- and Cu-polluted sites (Mesa-Marín et al., 2020). *Rhizobium* inoculation can promote soil nutrient cycling by increasing enzyme activity in metal-contaminated soil, thereby providing more N and P for microbial activity and growth of plants (Ma et al., 2021; Duan et al., 2022). Heavy metal toxicity is a growing problem in the world; therefore, finding appropriate microbes proficient to depollution of the metals can benefit to improve the crop efficiency. Application of biofertilizers for sustainable food crop production and boosting various stress tolerance of plants are gaining popularity. Still, further studies are crucial to unravel the potential role of biofertilizers in responding to the impact of different stresses at molecular level.

## Conclusion

Agriculture systems have to face the task of food production, stress management, and dependency on agrochemicals. The presence of pest and pathogen in crops causes decrease in crop yield and heavy crop losses every year. The occurrence of abiotic stresses due to the change in climatic conditions leads to difficult challenge to crop production worldwide. Different effective approaches should be employed to reduce crop output loss and control diseases. Hence, the necessity to implement the eco-friendly approaches such as biofertilizers is of great importance for sustainable agriculture. The application of biofertilizers not only improves plant health parameters but also enhances the crop productivity, soil health and protects from stress environment.

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## Author contributions

PC: conceptualization and wrote the manuscript. SS, AC, AS, and GK: editing the manuscript. All authors contributed to the article and approved the submitted version.

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## 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.

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