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Physiological and molecular insight of microbial biostimulants for sustainable agriculture

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Increased food production to cater the need of growing population is one of the major global challenges. Currently, agro-productivity is under threat due to shrinking arable land, increased anthropogenic activities and changes in the climate leading to frequent flash floods, prolonged droughts and sudden fluctuation of temperature. Further, warm climatic conditions increase disease and pest incidences, ultimately reducing crop yield. Hence, collaborated global efforts are required to adopt environmentally safe and sustainable agro practices to boost crop growth and productivity. Biostimulants appear as a promising means to improve growth of plants even under stressful conditions. Among various categories of biostimulants, microbial biostimulants are composed of microorganisms such as plant growth-promoting rhizobacteria (PGPR) and/or microbes which stimulate nutrient uptake, produce secondary metabolites, siderophores, hormones and organic acids, participate in nitrogen fixation, imparts stress tolerance, enhance crop quality and yield when applied to the plants. Though numerous studies convincingly elucidate the positive effects of PGPR-based biostimulants on plants, yet information is meagre regarding the mechanism of action and the key signaling pathways (plant hormone modulations, expression of pathogenesis-related proteins, antioxidants, osmolytes etc.) triggered by these biostimulants in plants. Hence, the present review focuses on the molecular pathways activated by PGPR based biostimulants in plants facing abiotic and biotic challenges. The review also analyses the common mechanisms modulated by these biostimulants in plants to combat abiotic and biotic stresses. Further, the review highlights the traits that have been modified through transgenic approach leading to physiological responses akin to the application of PGPR in the target plants.

KEYWORDS

PGPR, biostimulant, antioxidants, phytohormones, signaling, stress tolerance, crop productivity, systemic resistance

Introduction

Agriculture is presently facing several challenges due to shortage of cultivable land, fluctuating weather conditions, increased incidence of pests and pathogens and rising weed infestations. To increase crop productivity, chemical fertilizers are used indiscriminately (Rouphael and Colla, 2020; Hendriksen, 2022). However, extreme usage of chemicals causes detrimental effects on the soil microorganisms, human and the environment leading to decreased water holding capacity, loss of soil fertility, imbalances in soil nutrients, and increased salinity levels (Wan et al., 2021; Jin et al., 2022). To meet the rising demand for food, boosting crop productivity is imperative. Hence there is a need for a green, efficient, sustainable and economically productive system to improve agronomic traits of crops (Drobek et al., 2019; Cataldo et al., 2022). Currently, biostimulants have emerged as one of the most potent and promising tools for enhancing the growth and productivity of crops naturally, simultaneously addressing the issues related to chemical fertilizers. Biostimulants/bioeffectors/bioprotectors or biobased products are different classes of organic or inorganic compounds which consists of bioactive substances or microorganisms and when applied on target plants promote its growth and productivity (Shahrajabian et al., 2021; Franzoni et al., 2022; Monteiro et al., 2022). Over the time, various researchers have classified biostimulants into nine broad categories including seaweeds and plant extracts, complex organic materials (obtained from sewage sludge extracts, composts, manure urban and agro-industrial waste products), humic substances, antitranspirants (kaolin and polyacrylamide), chitin and chitosan derivatives, elements (Al, Co, Se, Na, and Si), hydrolyzed proteins, nitrogen-containing compounds and microbial inoculants (Colla and Rouphael, 2020; Teklić et al., 2021; Franzoni et al., 2022; Monteiro et al., 2022). Out of this wide category, microbial-based biostimulants including plant growth-promoting bacteria (*Bacillus*, *Serratia*, *Arthrobacter*, *Pseudomonas*, *Rhodococcus*, *Enterobacter*, *Ochrobactrum*, *Acinetobacter*, *Azospirillum*, *Rhizobium*, *Streptomyces* and *Stenotrophomonas*) have surfaced as highly valuable and inexpensive agricultural input for improving plant yield (Orozco-Mosqueda et al., 2020; Baltazar et al., 2021; Miceli et al., 2021; Ayed et al., 2022; Fadji et al., 2022). These microbiome based biostimulants trigger plant growth through solubilization of minerals (Zn, P and K), nitrogen fixation, production of phytohormones like indole-3-acetic acid (IAA), abscisic acid (ABA), ethylene (ET), cytokinin (CK), jasmonic acid (JA), secondary metabolites (siderophores, N-acyl homoserine lactone, lipopeptides, rhamnolipids, cyclic lipopeptides), enzymes (chitinases, cellulose, protease, glucanase etc.), volatile organic compounds (VOCs) (fatty acids and derivatives, hydrocarbons (alkanes, alkenes and alkynes), carbohydrates, (acids, alcohols, lactones, aldehydes, benzenoids, etc.) terpenoids, nitrogen (metalloid, amides, amines and imines), volatile inorganic compounds (HCN, H₂S, NH₃, CO₂, CO, and NO) and lipopolysaccharides (Caulier et al., 2019; Lephatsi et al., 2021). These components modulate root morphology including biomass of roots, its surface area and newly formed lateral roots, shoot length, leaf area, soil structure (nutrient, water holding capacity, porosity and water filtration), improve nutrient and mineral acquisition (N, P, Fe, Zn, Mn etc.) and photosynthetic capacity of a plant. Further, they also

enhance biotic and abiotic stress tolerance by activating genes responsible for antioxidant defense system, production of phenolics, enzymes, amino acids and organic acids (Backer et al., 2018; Rouphael and Colla, 2018; Hamid et al., 2021; Aremu et al., 2022; Lin and Jones, 2022; Vociante et al., 2022), but the exact functionality at cellular and biomolecular mechanisms are yet to be deciphered (Lephatsi et al., 2021; Othibeng et al., 2022). To elucidate the mechanism of action of biostimulants on plants, combined potential of molecular tools, proteomics, transcriptomics and metabolomics have been harnessed by several researchers (Franzoni et al., 2022). Although progress has been made in understanding the physiological and biochemical aspect of plant-microbe interactions under stress, but the core mechanism and elucidation of molecular interactions are still in infancy. Thus, the present review comprehends the physiological and biochemical modulations along with the signaling components of PGPR based biostimulants in imparting abiotic (major detrimental stresses like temperature, drought and salinity) and biotic stress tolerance in plants. An in-depth understanding of the biochemical and molecular mechanisms triggered by the microbial biostimulants particularly PGPR based will aid in designing and developing novel bioformulations for sustainable agriculture.

Role of PGPR-based biostimulants in combating abiotic stress

Drought and heat stress

About 60% of the world's region falls under arid and semi-arid areas and depends mainly on irrigated agriculture (Swain et al., 2017). With climate change, it is expected that there will be a decrease in rainfall, a rise in temperature, an increase in atmospheric CO₂ and severe alternations in weather conditions leading to frequent floods and droughts (Torres and Henry, 2018). In upcoming years, agriculture will be increasingly challenged by water scarcity, and plants will experience drought and heat stress leading to compromised productivity. Drought stress occurs under low humidity levels in soil, air and high ambient temperature (Lipiec et al., 2013; Kaya et al., 2020; Kosar et al., 2021; Mansoor et al., 2021), while heat stress can be described as an increase in temperature beyond a threshold measure hampering the normal development of a plant. It is observed that the combined action of both stresses restrict the physiological (photosynthesis, respiration, etc.), biochemical and cellular metabolism of plants such as cell membrane fluidity, integrity, elasticity, water potential, stomatal conductance, the structure of amino acids, proteins, nucleic acids, enzymes etc. (Rana et al., 2021; Mitra et al., 2021; Murali et al., 2021a; Noor et al., 2022; Shaffique et al., 2022). In order to adapt under environmental stress plants regulate their diverse molecular signaling pathways such as phytohormones, stress responsive proteins, antioxidants machinery, and osmolytes (Kosar et al., 2021). While understanding the physiological response of plants, it is crucial that both drought and heat stresses must be considered together as the physiological responses are closely interlinked and dependent (Dreesen et al., 2012). Numerous studies have elucidated the positive impact of PGPR functioning as a biostimulant on plants challenged by heat

and drought (Rashid et al., 2022; Yasmin et al., 2022). Basically, drought and thermotolerance is a complex mechanism, however, microbial metabolites including organic acids, sugars, trehalose, choline, amino acids, proline, glycine betaine, polyamines, exopolysaccharides (EPS), production of heat shock proteins (HSPs), dehydrins, VOCs, ACC-deaminase, phytohormones etc. play a vital role in imparting drought and heat tolerance [Figures 1A, B; (Ahluwalia et al., 2021; Ansari et al., 2021; Yasmin et al., 2021a; Notununu et al., 2022; Kour and Yadav, 2022; Shaffique et al., 2022)].

1-Amino Cyclopropane-1-Carboxylate (ACC) deaminase produced by several PGPRs help in combating drought stress experienced by its host plant by interfering with the ethylene biosynthesis pathway leading to lowering of ethylene concentration thereby counteracting stress signals. In one of the studies, the application of *B. licheniformis* K11 capable of producing auxin and ACC deaminase reduced the negative impact of drought in pepper without the use of agrochemicals (Lim and Kim, 2013). Similarly, improved growth was noticed in pea and maize under drought conditions on treating with ACC deaminase producing strain

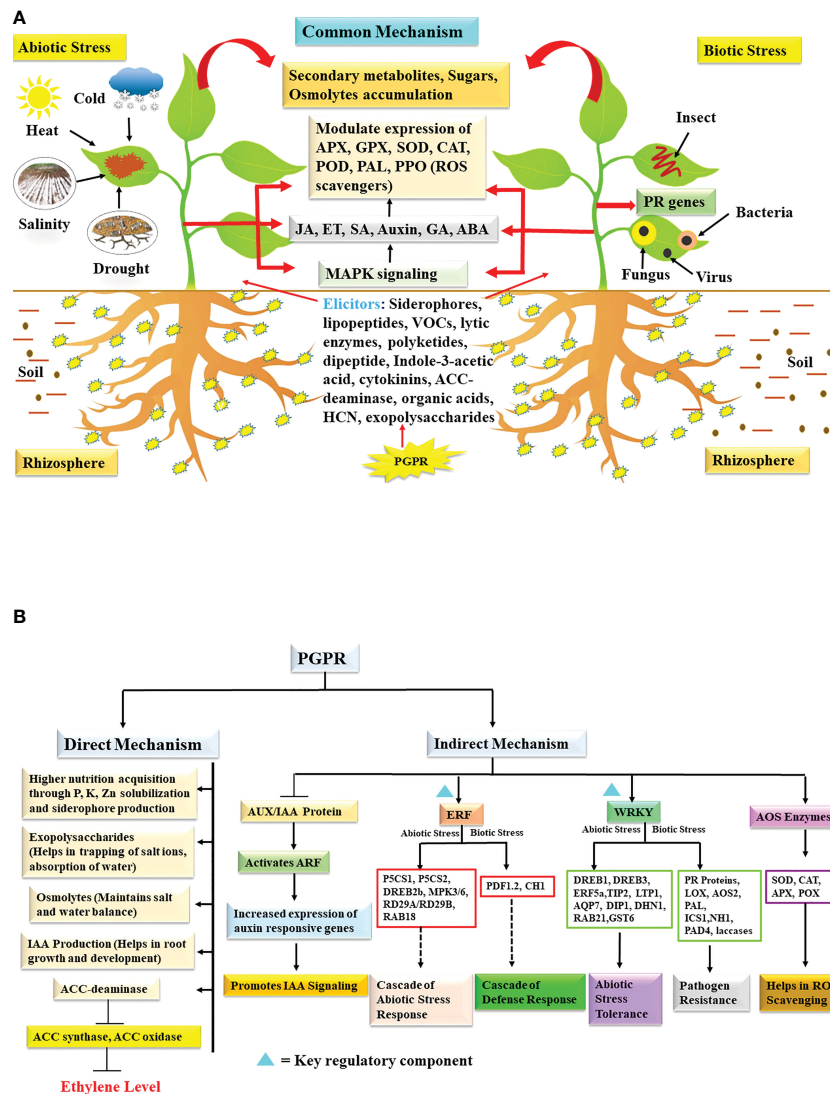


FIGURE 1

(A) Schematic representation of PGPR induced stress tolerance mechanism in plant challenged by abiotic and biotic stresses. Different elicitors released by PGPRs modulates endogenous phytohormones which in turn influences secondary metabolites, osmolytes production, activity of antioxidant enzymes and PR proteins. These combined metabolic pathways imparts stress tolerance and promotes plant growth under stressed environment. (B) PGPR-based direct and indirect mechanism involved in activating cascade of abiotic and biotic stress signaling in plants. The activation events are represented by arrows, inhibition process is represented by bar while dashed arrows represent signaling cascade. IAA, indole-3-acetic acid; ACC, 1-Amino Cyclopropane-1-Carboxylate; AUX/IAA, auxin/indole-3-acetic acid; ARF, auxin response factor; ERF, ethylene response factor; P5CS1, Δ^1 -pyrroline-5-carboxylate synthase1; P5CS2, Δ^1 -pyrroline-5-carboxylate synthase 2; DREB2b/DREB1/DREB3, drought-responsive element binding protein 2b, drought-responsive element binding protein 1, drought-responsive element binding protein 3; MPK3/MPK6, mitogen-activated protein kinase 3, mitogen-activated protein kinase 6; RD29A/RD29B, response-to-desiccation 29A, response-to-desiccation 29B; PDF1.2, protodermal factor 1.2; CH1, chitinase; WRKY, W-box domain binding transcription factor; TIP2, tonoplast intrinsic protein 2; LTP1, lipid transfer protein 1; AQP7, aquaporin 7; GST6, glutathione S-transferase; DIP1, dehydration stress-inducible protein 1; DHN1, dehydrin 1; RAB21, responsive to ABA protein 21; PR, pathogenesis related proteins; LOX, lipoxygenase; AOS2, allene oxide synthase 2; PAL, phenylalanine ammonia lyase; ICS1, isochorismate synthase 1; NH1, *Arabidopsis* NPR1 homolog 1; PAD4, p hytoalexin-deficient 4; AOS, antioxidant scavenging; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; POX, peroxidases; ROS, reactive oxygen species.

Pseudomonas spp., *Enterobacter cloacae*, *Achromobacter xylosoxidans* and *Leclercia adecarboxylata* primarily due to reduced ethylene accumulation as compared to untreated plants (Arshad et al., 2008; Danish et al., 2020). Additionally, these bacteria are capable of supplying nitrogen by sequestering and degrading ACC to α -ketobutyrate using ACC deaminase (Gupta and Pandey, 2019) thereby promoting better vegetative growth of plants.

Production of reactive oxygen species (ROS) is a common phenomenon observed under drought conditions causing damage to cells (Cruz de Carvalho, 2008) and antioxidant enzymes such as catalase (CAT), peroxidase (POD) and polyphenol oxidase (PPO) scavenge ROS preventing stress related injury thereby imparting stress tolerance [Figures 1A, B; (Zandalinas et al., 2018)]. These antioxidants also promote faster recovery from water limitation and dehydration compared to the control plants (Laxa et al., 2019). Hence, the potential of PGPR in enhancing the production of antioxidants is a desirable attribute. Several studies illustrate the beneficial trend of antioxidant enzymes under severe drought, as was noticed in mentha (Chiappero et al., 2019; Asghari et al., 2020) and in tomato (Mekureyaw et al., 2022). Noticeably, seeds of Pearl millet treated with *Bacillus amyloliquefaciens* (MMR04) enhanced expression of ascorbate peroxidase (APX) and superoxide dismutase (SOD) genes leading to the enhanced concentration of SOD and APX and decreased level of malondialdehyde (MDA) compared to the untreated lot (Murali et al., 2021b).

Accumulation of proline is one of the common mechanisms involved in imparting drought tolerance. Proline helps to maintain protein structure and activity thereby supporting membrane integrity (Kishor et al., 2005). Also, proline has multiple roles as it can act as a chelator of metals, a signaling molecule, and a defense molecule triggering the production of a series of antioxidants (Hayat et al., 2012). It has been observed that *Bacillus subtilis* (HAS31), *Pseudomonas* strains apart from increasing antioxidants (SOD, CAT and POD) activity also significantly enhanced the total soluble sugars and proline in potato and sweet corn (Batool et al., 2020; Zarei et al., 2020).

PGPRs have an inherent capability to produce plant growth hormones like auxin, gibberellins (GA), JA, salicylic acid (SA) and ABA. These hormones may be directly responsible for triggering a series of responses in the host (plant) to combat stress conditions. The role of SA in imparting drought stress has been illustrated to alter nitrogen metabolism, triggering the production of antioxidants and accumulation of glycine betaine thus conferring protection against stress (Khan et al., 2022). An interesting research showed that under heat-stress conditions inoculation of *Bacillus tequilensis* SSB07 strain in soybean enhanced the endogenous level of JA, SA, and reduced the level of ABA content (Kang et al., 2019a). All the treated plants had better biomass and photosynthetic pigment compared to the control. Two PGPR strains *Bacillus* sp. WM13-24 and *Pseudomonas* sp. M30-35, promoted the growth of ryegrass subjected to drought stress by modulating auxin distribution and ABA content in the plant (He et al., 2021).

Several scientific investigations illustrated that microbial applications induce the expression of specific genes related to drought response. Treating *Arabidopsis* and soybean with *Paenibacillus polymyxa* CR1 upregulated dehydration-responsive genes (*RD29A* and *RD29B*), which equipped the plants to face

drought conditions (Liu et al., 2020). Similarly, application of *Bacillus subtilis* strain GOT9 triggered up-regulation of numerous drought stress related genes particularly *Response-to-desiccation 29B*, *20* (*RD29B*, *RD20*), *RAB18* (encodes dehydrin protein), *9-cis-epoxycarotenoid dioxygenase* (*NCED3*) in *Arabidopsis* and *BrDREB1D*, *BrWRKY7* and *BraCSD3* in *Brassica* thereby minimizing the physiological damage. Enhanced expression of ABA inducible genes clearly showed that GOT9 increased ABA accumulation in plant and hence provided drought tolerance (Woo et al., 2020). Inoculation of *Pseudomonas putida* GAP-P45 in *Arabidopsis* modulated several important polyamine biosynthetic genes (*arginine decarboxylase* (*ADC*), *agmatine iminohydrolase* (*AIH*), *N-carbamoyl putrescine amidohydrolase* (*CPA*), *spermidine synthase* (*SPDS*), *spermine synthase* (*SPMS*) and *S-adenosylmethionine decarboxylase* (*SAMDC*) thereby impacting cellular polyamine levels. The increased level of free cellular spermidine and putrescine positively correlated with water stress (Sen et al., 2018). In transgenic *Arabidopsis* overexpressing *ABA stress ripening 6* (*OsASR6*) (auxin activated) gene increased the expression of auxin-responsive genes, *small auxin up-regulated family* (*SAUR32*), Ser/Thr protein kinase (*PINOID*), and *auxin response factor 5* (*ARF5*) auxin transcription factor leading to greater root density and biomass. These effects of *OsASR6* expression were found to mimic the beneficial effects of PGPRs in rice (Agarwal et al., 2019). PGPR strain *Streptomyces* mitigated drought stress in tomato and regulated the expression of transcription factors *ethylene response factor 1* (*ERF1*) and *WRKY70* [Figure 1B; (Abbasi et al., 2020)]. In another study, expression of ABA independent genes, i.e. *drought-responsive element binding protein* (*DREB2* and *DREB1-2*) significantly enhanced due to PGPR (*Bacillus* sp.) inoculation in *Brassica* under water scarcity indicating *Bacillus*-mediated priming for drought tolerance (Bandeppa et al., 2019). Pepper treated with *B. licheniformis* K11 upregulated genes *Cadhn*, *VA*, *sHSP* and *CaPR10* leading to higher production of dehydrin-like protein, vacuolar H⁺-ATPase, small heat shock protein and pathogenesis-related protein which helped in survival of plants under severe drought conditions (Lim and Kim, 2013). An interesting study was carried out wherein it was elucidated that *Pseudomonas putida* modulates the expression of important stress-responsive miRNAs in response to drought and salt stresses (Jatan et al., 2019).

All these studies illustrate that PGPRs influence expression of heat/drought related genes there by triggering production of series of antioxidants, osmolytes, proline and several key biomolecules which may contribute in mitigating heat and drought stress. Also, several hormones produced by PGPRs as illustrated in Figure 1A trigger cascade of biochemical reaction in host which enable plants to tie over drought stress.

Cold stress

Low temperatures limit agriculture productivity in temperate ecosystems. In these areas, the plants constantly face chilling stress that leads to 51-82% annual yield loss (Hwarari et al., 2022). It generally affects the critical processes of plants such as ROS homeostasis, energy metabolism (electron transport chain), photosynthesis efficiency, cell wall structure, fluidity, root hydraulic

conductance and structure of biomolecules (enzymes, proteins and nucleic acids) (Kazemi-Shahandashti and Maali-Amiri, 2018; Tiryaki et al., 2018; Zhou et al., 2021). In order to survive under prolonged low temperatures, the plants exhibit altered gene and transcription factor expression, leading to changes in membrane lipids, proteins, osmolytes levels, phytohormones, phenolic content and reactive oxygen scavenging enzymes (Brüggemann et al., 1999; Saltveit, 2000; Ait Barka et al., 2006; Amini et al., 2021; Guo et al., 2021; Ritonga et al., 2021; Saleem et al., 2021a; Eom et al., 2022; Hwarari et al., 2022; Wei et al., 2022).

The application of PGPR to improve crop productivity is a sustainable and safer means compared to chemical inputs. It has been found that treatment of *Burkholderia phytofirmans* strain *PsJN* (*Bp PsJN*) on *Arabidopsis thaliana* subjected to cold stress prevented disruption of plasmalemma, exhibited cell wall strengthening of mesophyll cells (Su et al., 2015). Inoculation of *Vitis vinifera* with PGPR strain *PsJN* exhibited better CO₂ fixation, increased content of phenolics, proline and starch (Ait Barka et al., 2006). In another study, *PsJN* improved cold tolerance in *Vitis vinifera* wherein higher accumulation of proline, MDA and aldehydes (ALD) were observed along with higher expression of phenylalanine ammonia lyase (PAL) and stilbene synthase (STS) genes in primed plants compared to non-treated plants (Theocharis et al., 2012). Similarly, another finding revealed that under chilling stress treatment of tomato plants with psychrotolerant *Pseudomonas Vancouverensis* (OB155) and *P. frederiksborgensis* (OS261) microbes minimized the stress effect by increasing the level of proline, antioxidant enzymes [(SOD, APX and glutathione (GSH)] (Subramanian et al., 2016). Further, *Pseudomonas fragi*, *P. chloropaphis*, *P. fluorescens* and *Brevibacterium frigoritolerans* inoculants also improved the growth of beans by regulating the activities of SOD, CAT, POX, APX and GR during low temperature stress [Figure 1A; (Tiryaki et al., 2018)]. Subsequently, further research reflected the key role of *Bacillus* spp. in wheat under cold stress. Under cold stress, the bacterial treatment significantly reduced the level of ABA, ET, MDA by directly targeting the ABA- response element (ABARE), Ethylene response factor (ERF) and 4-Hydroxy-2-nonenal (4-HNE; encodes α , β -unsaturated aldehyde during lipid peroxidation) genes, but at the same time the expression of Δ^1 -pyrroline-5-carboxylate synthase (P5CS), expansin (*expA1*), cytokinin (*CKX2*) and auxin (*ARF*) increased (Zubair et al., 2019). Another study evaluated the role of *Rhizobium* inoculation (RI) in legumes model plant i.e. *Medicago truncatula* against cold stress. Compared to the control plant, the treated plant showed a significant increase in the SOD, CAT, APX, ascorbate, reduced glutathione, proline, soluble sugars and glycine betaine, whereas POD, lipoxygenase (*LOX*) activity and nitro-oxidative damage was notably reduced. Moreover, RI also stimulated the nitrogen (N) uptake in cold stress seedlings by enhancing the activity of nitrate reductase (NR) enzyme (Irshad et al., 2021). In addition, *Streptomyces* sp. 506 (TOR3209) played a distinct function in boosting tolerance to cold stress in tomato. Expression profile of TOR3209 treated stressed plants showed an increased level of HY5 (bZIP) mediated ABA signaling genes [(zeaxanthin epoxidase (*ZEP1*), 9-cis-epoxycarotenoid dioxygenase (*NCED1*), carotenoid dioxygenase and carotene beta-hydroxylase), *dehydrin* (*TASI4*) (that triggers accumulation of soluble sugars, proline). Besides this, TOR3209 also reduced the photosynthetic damage by modulating the activities of RUBISCO (Ribulose 1, 5-

bisphosphate carboxylase/oxygenase), NAD-MDH and NADP-MDH (malate dehydrogenases) enzymes suggesting that main mechanism of imparting cold tolerance is by ABA pathway (Ma et al., 2022). Over and above, other finding highlights the role of cold active PGPR in rice growth and development. It was observed that strains of *Pseudomonas*, *Enterobacter*, *Stenotrophomonas* genera inoculation ameliorated the effect of cold in rice by increasing the accumulation of metabolites (proline and soluble sugars), protein content, nutrients (N, P and K), antioxidants (SOD, POD and CAT) (Expósito et al., 2022).

These studies illustrate that most of the cold tolerance by PGPRs are due to cross-interlinkage of antioxidants, soluble sugars, proteins, proline, phenolics, phytohormones etc. Further scientific investigations will provide better insight into PGPR mediated cold tolerance in plants but nevertheless, there are credential evidences which indicate that the right microbial strains can boost productivity in the temperate ecosystem.

Salinity stress

High salt concentration leads to osmotic stress that interferes with physiology, biochemical functioning (photosynthesis, stomatal conductance, enzyme activities, water and nutrient uptake), growth and yield of crops (Yasmin et al., 2021b; Choudhary et al., 2022). Microbial application triggers various mechanisms for improving plant growth under salinity stress (Sarkar et al., 2018). It generally includes the production of ACC-deaminase, EPS, phytohormones (auxin, CK and SA), antioxidant enzymes, VOCs, synthesis of osmoprotectant metabolites (proline, trehalose, alanine, glycine, glutamic acid, serine, threonine, aspartate, choline, betaine and organic acids), regulation of ion affinity transporters that in turn maintains ionic, osmotic, water homeostasis, thus resulting in improved plant growth under salt stress [Figure 1A; (Tewari and Arora, 2018; Abbas et al., 2019; Kumar et al., 2019; Bhat et al., 2020; Sunita et al., 2020; Choudhary et al., 2022; Gamalero and Glick, 2022; Kumawat et al., 2022)].

PGPR based compounds modulate the phytohormones, antioxidants and osmolytes levels in plants for their growth under stress conditions (Choudhary et al., 2022). A study demonstrated that under salt stress *Rhodopseudomonas palustris* G5 treated cucumber seedlings showed higher expression of SOD, POD, PPO and soluble sugars (Ge and Zhang, 2019) compared to untreated plants. Another ACC- deaminase producing endophytic strain *Pseudomonas* spp. OFT5 confers salt tolerance to tomato by reducing ethylene production (Win et al., 2018). Inoculating paddy with halotolerant *Curtobacterium albidum* strain SRV4 improved plant growth under various salinity levels by significantly increasing SOD, CAT, POX, APX expression, and by maintaining Na⁺/K⁺ homeostasis. This study showed that EPS production by strain reduced sodium ions availability to the plant and hence overcome effect of salinity stress (Vimal et al., 2019). Furthermore, *Planomicrobium* sp. MSSA-10 regulated antioxidants, phenolics and nutrients mobilization pathways in pea and promoted its growth in saline conditions. It was observed that bio-inoculant treatment increased total phenolics, POD, CAT and nutrients (N, P and K) uptake for reducing negative effects of salt [Figure 1B; (Shahid et al., 2018)]. Additionally, it was observed that salt tolerant *Bacillus pumilus* FAB10 significantly

decreased antioxidant enzymes like SOD, CAT, glutathione reductase (GR) activities, proline and MDA content in wheat at different salt concentrations (Ansari et al., 2019). Furthermore, endophytic bacteria *Curtobacterium* sp. SAK1 treatment reduced the effect of salt stress in soybean by lowering endogenous ABA, JA, ROS, PPO and POD levels, whereas glutathione (cellular antioxidant) concentrations were found to be higher (Khan et al., 2019c). Another research team observed that inoculation of soybean with five halotolerant strains i.e. *Arthrobacter woluwensis* (AK1), *Microbacterium oxydans* (AK2), *Arthrobacter aurescens* (AK3), *Bacillus megaterium* (AK4) and *Bacillus aryabhatai* (AK5) conferred salt tolerance by elevating the expression of SOD, glutathione synthase (GSH) and enhancing K⁺ uptake. Besides the antioxidants, microbial inoculation significantly reduced Na⁺ ion concentration, ABA level, but increased the expression of IAA related gene i.e. *auxin resistant 1* (*GmLAX3*) and salt tolerant gene (*Soybean salt tolerance 1*) (*GmST1*) (Khan et al., 2019b). In addition to this, it was found that halotolerant bacteria *Leclercia adecarboxylata* MO1 improved tomato growth under salt stress by significantly increasing sugars (sucrose, glucose and fructose), organic acids (citric acid and malic acid), amino acids (serine, glycine, methionine and proline) and simultaneously decreasing endogenous ABA level (Kang et al., 2019b). Similarly, PGPR *Pseudomonas* PS01 imparted salt tolerance in *Arabidopsis* by modulating the expression of stress related genes. Results illustrate that PS01 inoculation in salt stressed plants increased expression of *lipoxygenase* (*LOX2*) (related to JA synthesis), while decreased *APX2*, *GLY17* (ROS scavenging and detoxification). No significant change was observed in the expression of *RD29A* and *RD29B* (ABA signaling genes) (Chu et al., 2019). One more study figured out that in rice inoculation with halotolerant *Glutamicibacter* sp. YD01 increased the expression of antioxidants such as *OsPOX1*, *OsFeSOD*, *OsGR2*, abiotic stress related genes (*OsWRKY1*, *OsDREB2*), *OsHKT1* (related to ionic balance) and downregulated *OsERF1* (related to ethylene production), thus enhancing their tolerance to salt stress (Ji et al., 2020). In a different fascinating research it was found that *Pseudomonas pseudoalcaligenes* (SR16) and *Bacillus subtilis* (SR3) also provide salt stress tolerance to hydroponically grown soybean seedlings. The strain SR16 effectively reduced 100mM NaCl stress by increasing the total protein, proline content, and activities of various antioxidants (SOD, CAT, APX, POD, PAL and PPO) (Yasmin et al., 2020). Recent findings suggest that soil application of *Kosakonia sacchari* improved mung bean performance by reducing the level of oxidative stress markers such as proline, MDA, H₂O₂ content, antioxidants like APX, CAT, SOD and GR. In contrast, the level of antioxidant metabolites i.e. ascorbic acid and glutathione increases in the foliage of treated plants which in turn reduced the toxicity of NaCl (Shahid et al., 2021). Moreover, inoculation of salt-tolerant PGPR *Acinetobacter johnsonii* provided tolerance to maize by downregulating SOD, CAT, proline and MDA content. It was observed that rhizobacterial inoculation improved dehydrogenase, alkaline phosphatase, acid phosphatase, urease and enzyme activity in the soil. Improved microbes mediated soil enzyme activities plays an important role in balancing nutrient profile, plant growth under salt stress (Shabaan et al., 2022). Additional evidence demonstrates role of halotolerant *Bacillus* strains (NMCN-1 and LLCG23) in mitigating 200mM salinity stress in wheat. Application of both inoculants

significantly downregulated the expression of ABA- response element (*ABARE*), *4-Hydroxy-2-nonenal* (*4-HNE*), whereas the *P5CS* gene was found to be upregulated. This clearly illustrates that these halophilic microbes regulate key stress signaling pathways (ABA synthesis, MDA and proline production) that subsequently lowered the effect of stress (Ayaz et al., 2022). From the cited literature (Table 1), it is evident that PGPR could alleviate salt stress by improving soil health, nutrient uptake, hormone production, antioxidant activity, and stress- responsive genes.

From the above studies it is clear that bacterial production of ACC deaminase (lowers ethylene concentration), enhanced production of a range of antioxidants (scavenges ROS) and higher production of proline (signaling molecule) in stress affected plants are some of the common mechanisms operate in PGPR treated plants to enable them combat temperature, drought and salinity stress. Hence, application of PGPR based biostimulants with proven PGP traits could be an ecofriendly sustainable means to boost crop productivity under single or combined abiotic stress.

Role of PGPR-based biostimulants in imparting tolerance against disease (biotic stress)

Plant resistance against pathogens is generally based upon two mechanisms i.e. induced systemic resistance (ISR) and systemic acquired resistance (SAR). ISR is mainly mediated by beneficial microorganisms through root colonization, root immunity modulation and production of certain elicitors like siderophores, polysaccharides, VOCs, plant hormones, enzymes etc. whereas SAR is defined as the plant's acquired or adaptive resistance (Olowe et al., 2020; Hamid et al., 2021). Both ISR and SAR resistance mechanism is effective against wide group of pests and pathogens (Vlot et al., 2021; Meena et al., 2022; Yu et al., 2022). Though numerous studies reported that PGPR modulates various physiological, biochemical and molecular processes in plants and helps their survival under pathogens attack (Olowe et al., 2020; Castiglione et al., 2021; Yu et al., 2022), but the core mechanism of action is not fully understood. The results obtained through systematic studies indicate that induction of resistance against multiple pathogens including virus, fungi, bacteria rely on combined mechanisms that may work simultaneously (Yu et al., 2022). It includes induction of specific defense response genes/enzymes like ROS scavengers/antioxidants such as (CAT, APX, guaiacol peroxidase (GPX), GR, POD and SOD), accumulation of phytohormones (JA, ET, SA, GA and auxin), glucanases, chitinases, sugars, osmolytes, pathogenesis related proteins (PR) and secondary metabolites which in turn are directly involved in controlling growth and proliferation of pathogen [Figures 1A, B; (Baxter et al., 2014; Pieterse et al., 2014; Conrath et al., 2015; Camejo et al., 2016; Li et al., 2016; Guo et al., 2019; Ebrahimi et al., 2020; Olowe et al., 2020; da Silva et al., 2021; Luo et al., 2022)].

From the wide group of PGPR, *Bacillus* sp. has been considered as an excellent agent for controlling pathogens attack in various plants such as tomato, banana, tobacco, rice, wheat, cucumber, watermelon, cotton (Saechow et al., 2018; Gamez et al., 2019; Wu et al., 2019; Fu et al., 2020; Jiao et al., 2020; Dimopoulou et al., 2021; Kazerooni et al.,

TABLE 1 PGPRs along with their mode of action in combating abiotic stress.

PGPR Strain	Host Plant	Stress	Mechanism of action	References
<i>Pseudomonas aeruginosa</i>	Sorghum	Heat	Increased proline, chlorophyll, sugar, amino acids, and protein content	Ali et al. (2009)
<i>Rhizobium, Pseudomonas</i>	Maize	Salinity	Decreased electrolyte leakage and increased proline, relative water content	Bano and Fatima (2009)
<i>Pseudomonas putida</i>	Wheat	Heat	Reduced membrane injury and the level of antioxidant enzymes such as SOD, APX and CAT	Ali et al. (2011)
<i>Pseudomonas fluorescens, Bacillus subtilis</i>	Green Gram	Water	Enhanced activity of CAT1 and POD	Saravanakumar et al. (2011)
<i>Pseudomonas chlororaphis</i>	<i>Arabidopsis thaliana</i>	Drought	Up-regulation of genes such as <i>NIT1</i> (associated with plant growth regulators), <i>Atcor15a</i> (associated with ABA), <i>RD21a</i> , KIC (calcium binding protein)	Cho et al. (2011)
<i>Pseudomonas koreensis, Pseudomonas fluorescens, Pseudomonas jessenii</i>	Wheat	Cold	Increased relative water content, anthocyanin, proline, total phenolics, starch and reduced electrolyte leakage	Mishra et al. (2011)
<i>Bacillus licheniformis</i>	Pepper	Drought	Increased content of stress proteins i.e. <i>Cadhm</i> , <i>VA</i> , <i>sHSP</i> and <i>CaPR-10</i>	Lim and Kim (2013)
<i>Bacillus pumilus, Bacillus firmus</i>	Potato	Salinity/ Drought	Enhanced mRNA expression related to ROS scavenging enzymes (SOD, GR, CAT, DHAR and APX) and proline level	Gururani et al. (2013)
<i>Bacillus megaterium, Bacillus subtilis</i>	Wheat/ Barley	Cold	Significant reduction in the level of ROS and antioxidant enzyme (SOD, POD and CAT)	Turan et al. (2013)
<i>Pseudomonas aeruginosa</i>	Mung bean	Drought	Increased expression of CAT, POX, SOD and drought responsive genes (<i>DREB2A</i> , <i>CAT1</i> and <i>DHN</i>)	Sarma and Saikia (2014)
<i>Bacillus amyloliquefaciens, Azospirillum brasilense</i>	Wheat	Heat	Increased level of DHAR (Dehydroascorbate reductase), MDHAR (Mono-dehydroascorbate reductase) and GR whereas decreased APX and modulated expression of <i>SAMS1</i> , <i>HSP17.8</i>	Abd El-Daim et al. (2014)
<i>Enterobacter</i> sp.	<i>Arabidopsis</i>	Salinity	Up-regulated expression of salt stress responsive genes such as <i>DREB2b</i> , <i>RD29A</i> , <i>RD29B</i> , and <i>RAB18</i> , proline biosynthesis genes (<i>P5CS1</i> and <i>P5CS2</i>), MPK signaling genes (<i>MPK3</i> and <i>MPK6</i>)	Kim et al. (2014)
	Tomato		Enhanced expression of APX	
<i>Proteus penneri, Pseudomonas aeruginosa, Alcaligenes faecalis</i>	Maize	Drought	Increased relative water content, sugar, decreased proline, antioxidant enzymes (SOD, POD and CAT)	Naseem and Bano (2014)
<i>Burkholderia phytofirmans</i>	<i>Arabidopsis thaliana</i>	Salinity	Enhancement of the proline and transcript level of ABA signaling genes (<i>RD29</i> , <i>RD29B</i>), <i>APX2</i> (antioxidant related), <i>GYL17</i> (glyoxylate pathway), decreased expression of <i>LOX2</i> (related to JA)	Pinedo et al. (2015)
<i>Bacillus megaterium, Enterobacter</i> sp.	Okra	Salinity	Increased ROS scavenging enzymes (CAT, SOD, APX, GR and DHAR)	Habib et al. (2016)
<i>Bacillus pumilus</i>	Rice	Salinity	Augmented activity of antioxidants such as (SOD, POD and CAT)	Khan et al. (2016)
<i>Dietzia natronolimnaea</i>	Wheat	Salinity	Enhanced expression of salt stress tolerant (<i>TaST</i>), Salt Overly Sensitive (SOS) related genes (<i>SOS1</i> and <i>SOS4</i>), antioxidant enzymes genes (<i>APX</i> , <i>MnSOD</i> , <i>CAT</i> , <i>POD</i> , <i>GPX</i> and <i>GR</i>) and ABA signaling (<i>TaABARE</i> and <i>TaOPR1</i>)	Bharti et al. (2016)
<i>Pseudomonas frederiksbergensis, Flavobacterium glaciei, Pseudomonas vancouverensis</i>	Tomato	Cold	Increased proline content and, enhanced antioxidant enzymes such as SOD, APX and GSH	Subramanian et al. (2016)
<i>Bacillus aryabhatai</i>	Soybean	Heat	Enhanced levels of phytohormones IAA, JA, GA, ABA, antioxidants (CAT and SOD), but CK decreased	Park et al. (2017)
<i>Bacillus megaterium</i>	<i>Arabidopsis</i>	Salinity	Enhanced level of <i>CYP94B3</i> (responsible of JA-Ile catabolism), MDHAR and ATP synthase	Erice et al. (2017)
<i>Bacillus subtilis</i>	Wheat	Salinity	Decreased proline, MDA content whereas SA and water storage capacity enhanced	Lastochkina et al. (2017)
<i>Bacillus amyloliquefaciens</i>	<i>Arabidopsis thaliana</i>	Salinity	Up-regulation of genes such as <i>GST</i> and <i>POX</i> (antioxidant responsive), <i>ACS7</i> , <i>ACS2</i> , <i>ACS8</i> , and <i>ACS11</i> (ET signaling), <i>LOX</i> (JA signaling) downregulated <i>NCED3</i> , <i>NCED4</i> , <i>ABI1</i> and <i>MARD1</i> (ABA signaling)	Liu et al. (2017)

(Continued)

TABLE 1 Continued

PGPR Strain	Host Plant	Stress	Mechanism of action	References
<i>Pseudomonas chlororaphis</i> , <i>Pseudomonas extremorientalis</i>	Tomato	Salinity	Decreased H ₂ O ₂ , APX, GR level with simultaneous increase in SOD and CAT activity	Egamberdieva et al. (2017)
<i>Azospirillum brasilense</i> , <i>Herbaspirillum seropedicae</i>	Maize	Drought	Decreased expression of <i>ZmVP14</i> (involved in the biosynthesis of ABA), proline, ET content but MDA level increased	Curá et al. (2017)
<i>Pseudomonas putida</i>	Finger Millet	Drought	Increased activities of SOD, CAT, APX and GPX antioxidants	Chandra et al. (2018)
<i>Paraburkholderia phytofirmans</i>	Tomato	Heat	Augmented chlorophyll content, gas exchange, expression of <i>APX2</i> and <i>CAT1</i> . No significant change was observed in SOD, <i>CHI3</i> , <i>TIV1</i> , <i>Frk2</i> , <i>Hxk1</i> , <i>Hxk2</i> , <i>RbcL</i> and <i>RbcS</i> level	Issa et al. (2018)
<i>Ochrobactrum pseudogrignonense</i> , <i>Pseudomonas</i> sp., <i>Bacillus subtilis</i>	Black gram/ Pea	Drought	Downregulated expression of <i>ACO</i> , increased proline content and, antioxidant enzymes (CAT and POD)	Saikia et al. (2018)
<i>Pseudomonas fragi</i> , <i>Pseudomonas chlororaphis</i> , <i>Pseudomonas fluorescens</i> , <i>Brevibacterium frigoritolerans</i>	Bean	Cold	Decreased MDA, ROS (O ₂ and H ₂ O ₂) and POX level whereas SOD, CAT, APX and GR activity increased	Tiryaki et al. (2018)
<i>Arthrobacter woluwensis</i>	Soybean	Salinity	Upregulated expression of salt stress response genes such as <i>GmLAXs</i> and <i>GmST</i> , Low level of ABA and JA. Significant change in the activities of PPO and POD was also observed	Khan et al. (2019a)
<i>Ochrobactrum pseudogrignonense</i>	Wheat	Salinity	Increased activity of APOX, GR, SOD and germin-like proteins, whereas no significant change in the level of POX and CAT	Chakraborty et al. (2019)
<i>Bacillus pumilus</i>	Wheat	Salinity	Reduced antioxidant enzyme (CAT, SOD, GR) activities, proline and MDA content	Ansari et al. (2019)
<i>Bacillus velezensis</i>	Wheat	Heat/ Cold/ Drought	Modulated various stress related proteins, antioxidant activity, amino acids metabolic pathways and accumulation of γ -aminobutyric acid (GABA)	Abd El-Daim et al. (2019)
<i>Pseudomonas fluorescens</i> , <i>Bacillus amyloliquefaciens</i>	Peppermint	Drought	Increased total phenolic content, antioxidant enzymes (SOD and POX), reduced proline and MDA content	Chiappero et al. (2019)
<i>Bacillus</i> sp.	Guinea grass	Drought	Reduced proline accumulation GR activity and increased APX level	Moreno-Galván et al. (2020)
<i>Cupriavidus necator</i> , <i>Pseudomonas fluorescens</i>	Maize	Drought	Increased nitrogen and phosphorous use efficiency	Pereira et al. (2020)
<i>Azotobacter chroococcum</i> , <i>Azospirillum brasilense</i>	Peppermint	Drought	Augmented ABA, SOD, proteins, soluble sugars, phenolic, flavonoid and oxygenated monoterpenes, but other antioxidant enzymes GPX and CAT activity decreased	Ashgari et al. (2020)
<i>Kocuria rhizophila</i>	Maize	Salinity	Increased antioxidant enzyme (APX, GPX and GR), proline and expression of <i>ZmGR1</i> , <i>ZmAPX</i> (encoding antioxidants), <i>ZmNHX1</i> , <i>ZmNHX2</i> , <i>ZmNHX3</i> , <i>ZmWRKY58</i> and <i>ZmDREB2A</i> (salt tolerance genes), whereas decreased MDA	Li et al. (2020)
<i>Bacillus cereus</i>	Soybean	Heat	Increased APX, SOD, GSH, proline, expression of <i>GmLAX3</i> , <i>GmAKT2</i> (genes involved in the regulation of the ABA). Decreased MDA content and expression of <i>GmHSP</i> (heat shock protein)	Khan et al. (2020)
<i>Bacillus cereus</i>	Tomato	Heat	Increased proline content, and antioxidant enzymes (SOD, POD and CAT)	Mukhtar et al. (2020)
<i>Bacillus cereus</i> , <i>Serratia marcescens</i> , <i>Pseudomonas aeruginosa</i>	Wheat	Salinity	Decreased antioxidant enzymes (SOD, CAT and POX), non-enzymatic antioxidants (GSH, AsA, and α -TOC)	Desoky et al. (2020)
<i>Bacillus</i> sp.	Rye grass	Drought	Increased proline, antioxidant enzymes (CAT and POD), decreased MDA, relative membrane permeability and H ₂ O ₂ accumulation	He et al. (2021)
<i>Bacillus sonorensis</i> , <i>Bacillus cereus</i> , <i>Bacillus subtilis</i> , <i>Bacillus safensis</i> , <i>Bacillus paramycoides</i> , <i>Bacillus tequilensis</i> , <i>Brevibacillus</i> sp.	Cotton	Salinity	Increased absorption of K ⁺ , while decreased absorption of Na ⁺ and, maintenance of the proline content, Chlorophyll Content Index (CCI), Relative Water Content (RWC) and Relative Electrolyte Leakage (EL)	Saleem et al. (2021b)
<i>Pseudomonas putida</i> , <i>Alcaligenes</i> sp., <i>Klebsiella</i> sp., <i>Pseudomonas cedrina</i>	Alfalfa	Salinity	Reduced proline, MDA and H ₂ O ₂ level	Tirry et al. (2021)

(Continued)

TABLE 1 Continued

PGPR Strain	Host Plant	Stress	Mechanism of action	References
<i>Bacillus megaterium</i> , <i>Bacillus licheniformis</i>	Wheat	Drought	Increased proline, and antioxidant enzymes (SOD, CAT, APX, POD and GR)	Rashid et al. (2022)
<i>Bacillus subtilis</i> , <i>Bacillus pumilus</i>	Cotton	Salinity	Modulated the ascorbate, aldarate, glyoxylate, dicarboxylate metabolism pathways, and pentose, glucuronate interconversions pathway	Akbar et al. (2022)
<i>Bacillus subtilis</i> , <i>Pseudomonas</i> sp.	Brinjal	Salinity	Increased level of free polyamines (spermine, spermidine, putrescine), expression of <i>psbD</i> , GR, GST and Protease I/II whereas lipases level decreased	Mokabel et al. (2022)
<i>Bacillus thuringiensis</i> PM25	Maize	Salinity	Increased antioxidants (APX, POD, SOD, AsA), total soluble sugars, proteins, flavonoids, osmolytes (free amino acids, glycine betaine and proline)	Ali et al. (2022)
<i>Bacillus butanolivorans</i>	Pepper	Drought	Increased expression of <i>P5CS</i> , <i>P5CR</i> (proline synthesis genes), <i>Cadhm</i> , <i>sHSP</i> (drought-sensitive gene), <i>bZIP1</i> (ABA-related genes), <i>LOX</i> , <i>COI1</i> (JA-related genes), POX, glutathione, but decreased CAT and SOD	Kim et al. (2022)

2021; Luo et al., 2022). *Bacillus amyloliquefaciens* (SN13) is a bio-protective agent against *Rhizoctonia solani* (causative agent of sheath blight disease), which enhances defense response in the rice plants. The colonized plants showed alteration in phytohormone content (increased level of SA, ABA and GA), and MAPKinases (increased level of phospholipase D and serine-threonine protein kinases) signaling pathways that helped in controlling disease proliferation. Apart from these, SN13 treatment also modulated the production of secondary metabolites (quinazoline) and ROS regulators (arabitol, proline and mannitol, sugars like β -D-glucopyranose, fructopyranose, and myoinositol, ferric reductase glutathione S-transferase and peroxidase precursor) (Srivastava et al., 2016). Moreover, cotton (*Gossypium hirsutum*) plants treated with blend of *Bacillus* spp. enhanced secretion of gossypol (allelochemical) and JA (defense related phytohormone) which in turn reduced larval feeding of *Spodoptera exigua* (beet armyworm). In addition, treated cotton plants exhibited increased expression of genes involved in synthesis of allelochemicals i.e. (+)- δ -*cadinene synthase* (*CAD1* gene family, including *Cad1-C1*, *Cad1-A*, *Cad1-C14* and *Cdn-C3*) and jasmonates (*allene oxide synthase*) (*GhAOS*), *13-lipoxygenase* (*GhLOX1*) and *12-oxo-phytodienoic acid reductase 3* (*GhOPR3* [Figure 1A; (Zebelo et al., 2016)]. Another rhizobacterium strain *Bacillus amyloliquefaciens* SQRT3 strongly inhibited tomato bacterial wilt disease (caused by *Ralstonia solanacearum*). The application of SQRT3 increased the expression of POD, PPO, stress marker genes like *proteinase inhibitor 2* (*PIN2*) (related to JA pathway) and *pathogenesis related protein-1a* (*PR-1a*) (related to SA pathway) and *Omsotin-like* (related to ET pathway) (Chunyu et al., 2017). Likewise, *Bacillus velezensis* enhanced resistance of pepper plants against *Botrytis cinerea* BC1301 (causative agent of gray mold disease) by triggering antioxidants SOD, CAT, POD and SA-mediated defense signaling genes namely *non-expressor of pathogenesis-related genes 1* (*NPR1*), *pathogenesis related protein-1* (*PR1*) and *peroxidase*. However, no effect was observed in the expression of *proteinase inhibitor 2* (*PIN2*) and (*TIN1*) genes (Jiang et al., 2018). In another study, anti-pathogenic role of *Bacillus amyloliquefaciens* Ba13 against tomato yellow leaf curl virus (TYLCV) was observed. It was found that inoculation of this beneficial microbe improved tomato growth by elevating the expression of systemic resistance related genes including *pathogenesis related protein-1, 2, 3* (*PR1*, *PR2* and *PR3*), chitinase, PAL, POD, PPO, and β -1,3-glucanase (Guo et al., 2019).

Furthermore, an interesting work underline the effectiveness of *Bacillus amyloliquefaciens* YN201732 against tobacco powdery mildew disease (caused by *Erysiphe cichoracearum*). Results highlight that bacterial treatment inhibited pathogenic fungi growth over tobacco cultivar by increasing the expression of disease-related genes like *non-expressor of pathogenesis-related genes 1* (*NPR1*), *plant defensin 1.2* (*PDF1.2*), *chitinase* (*chit*) and PPO, whereas, no significant change was observed in POD and PAL activity (Jiao et al., 2020). Also, *Enterobacter asburiae* BQ9 imparted tolerance against tomato yellow leaf curl virus by enhancing the expression of antioxidant enzymes such as POD, CAT, PAL and SOD; defense-related genes i.e. *pathogenesis related protein-1a, 1b* (*PR1a* and *PR1b*) (Li et al., 2016). These findings illustrate that treatment with PGPR may activate biochemical and molecular changes to restrict pathogenic invasions in plants. Additionally, in *Nicotiana tabacum* cv. plants *Peanibacillus lentimorbus* B-30488 inoculation reduced cucumber mosaic virus (CMV) RNA accumulation by ~12 fold (91%). This ISR was linked with an increase in expression of stress related genes *Brassinosteroid signaling kinase 1* (*BR-SK1*), *RNA dependent RNA polymerase 2* (*RdRP2*), *zinc finger – homeodomain* (*ZF-HD*), *pathogenesis related protein 1* (*PR1*), β -1,3-glucanase (*Gluc*), *asparagine synthetase* (*AsSyn*), *tetrahydrocannabinolic acid synthase* (*TCAS*) and antioxidant enzyme (APX, GPX, SOD and CAT) (Kumar et al., 2016). Similarly, *Peanibacillus lentimorbus* B-30488 also provides resistance against southern blight (caused by *Scelerotium rolfsii*) disease in tomato. The treated plants showed alteration of the ET pathway by significantly suppressing *1-aminocyclopropane-1-carboxylate synthase* (*ACC synthase*) and *oxidase* (*ACO*) enzymes, and antioxidant enzyme activities (APX, GPX and SOD); whereas systemic tolerance was associated with expression of *pathogenesis – related protein -1, 2A, 4, 7* (*PR1*, *PR2A*, *PR4* and *PR7*), CAT, *chitinase* (*CHI3* and *CHI9*), β -1, 3- *glucanase* (*GLU*), calmodulin and PPO (Dixit et al., 2016). Another report elucidates the role of *Pseudomonas aeruginosa* in controlling fungus (*Botrytis cinerea*) infection in *Brassica napus* by inducing the expression of transcription factor (*BnWRKY33*), *mitogen-activated protein kinase 3, 4* (*BnMPK3* and *BnMPK4*) and *pathogenesis related protein-1 and 4* (*BnPR1* and *BnPR4*) (Monnier et al., 2018).

Apart from this, some PGPRs also impart resistance against pathogens by secreting anti-microbial compounds (Hamid et al., 2021; Ji et al., 2021). For example, different *Bacillus* strains such as

Bacillus velezensis QST713, *Bacillus velezensis* (C2), *Bacillus velezensis* OEE1, *Bacillus subtilis* release antifungal compounds such as lipopeptides (fengycin, bacillomycin and surfactin), polyketides (bacillaene, macrolactin and difficidin), dipeptide bacilysin, antifungal VOCs (phenylethyl alcohol, benzenoacetic acid, benzaldehyde, 1-decene, tetradecane) and lytic enzymes (chitinase, protease and β -glucanase), 3-indolylacetonitrile and suppresses green mold (caused by *Trichoderma aggressivum* f. *europaeum*), Verticillium wilt disease (caused by *Verticillium dahliae*), Septoria tritici blotch (caused by *Zymoseptoria tritici*), in button mushroom, tomato, olive, wheat (Mejri et al., 2018; Pandin et al., 2018; Dhoub et al., 2019; Azabou et al., 2020). Moreover, a research illustrated that application of *Herbaspirillum seropedicae* (BAC) suppressed *Xanthomonas euvesicatoria* (Xe), a causative agent of bacterial spot disease in 'Micro-Tom' *Solanum lycopersicum* L by downscaling the concentration of various organic acids such as oxalic acid, succinic acid, citric acid that enhances pathogens virulence (da Silva et al., 2021). The compiled studies (Table 2) clearly illustrate that PGPRs help in imparting tolerance against pathogen by activating pathway(s) that leads to production of array of defense related metabolites in plants.

Developing stress resilient crops

To full fill the goal of providing nutritious food for an increasing population, it is critical to develop resilient crops which can withstand the pressure of climate change. Scientists are strategizing, investigating, and discovering key genes which can aid in developing new transgenic crops tolerant to biotic and abiotic stresses without compromising on productivity. Wheat and rice are major staple crops grown across different regions of the world. Hence a lot of efforts are being made to develop better varieties through the classical breeding approach and newer biotechnological tools. The transgenic approach is one of the common techniques for inserting a gene of interest to achieve the desired trait. Among the transgenic approach, one of the studies illustrated that mutated transcription factor (*HaHB4*) from sunflower belonging to homeodomain-leucine zipper family (*HD-Zip*) improved water use efficiency and productivity of wheat (González et al., 2019). In another study introduction of beta gene-encoding choline dehydrogenase enhanced the glycine betaine content making the transformed wheat tolerant to drought (He et al., 2011). Similarly, in rice introduction of transcription factor *PeSNAC-1* lead to increased production of proline, thereby making the plant tolerant to salinity and drought (Hou et al., 2020). Also, insertion of gene *MYB49* lead to increased POD, SOD activity, chlorophyll content offering better resistance to drought, salinity and pathogen *Phytophthora infestans* in tomato (Cui et al., 2018). The transcription factor, *SIDREB3* increased membrane stability and prevented ROS from imparting tolerance to chilling (Wang et al., 2019). The above studies clearly suggest that modifications at the genetic level either by inserting specific genes; altering transcription factor families like *WRKY*, *DREB*, *MYB*, *NAC* and *ERF* and modifying signal transduction genes significantly enhances the tolerance of plants to various stresses (Khan et al., 2019d). Similar physiological changes can be introduced in target plants by applying appropriate PGPRs

(Tables 1, 2 and Figure 2). In wheat, over expression of *TaWRKY2* (drought stress tolerance gene) improved drought tolerance by withholding water for 8-10 days before re-watering and enhancing proline content compared to wild type plant (Gao et al., 2018). Similarly, application of *Azospirillum lipoferum* significantly augmented the proline content in wheat seedling resulting in higher drought tolerance by withholding water for 10 days before watering (Kanwal et al., 2017). Engineering of *E. coli* cold shock protein (*CspA* and *CspB*) genes to convert it into plant-preferred codon namely *SeCspA* and *SeCspB* resulted in better stress tolerance potential by lowering MDA content, preventing water loss, reduced Na^+ level and higher levels of chlorophyll, proline content under drought and salt stresses (200 mM NaCl) compared to the control wheat plants (Yu et al., 2017), similar response was evoked by endophytic strain *Bacillus subtilis* in wheat wherein lower MDA level was observed in plants grown under (340 mM NaCl) compared to control counter parts (Lastochkina et al., 2017). Cloning of *Arabidopsis WRKY30* (*AtWRKY30*) transcription factor followed by its over-expression in wheat seedling subjected to drought stress by with-holding water for 12 days exhibited enhanced activities of antioxidant enzymes CAT, SOD, POX and APX (El-Esawi et al., 2019). Similar observation was made by (Akhtar et al., 2021) wherein antioxidant enzyme namely SOD, CAT and POX increased upon treating wheat with *Bacillus* sp., *Azospirillum lipoferum* and *Azospirillum brasilense* and subjected to drought stress by withholding water to 40% field capacity. Overexpression of *TaFER-5B* improved multiple stress including heat stress tolerance in wheat induced by keeping 10 days old seedling under 40°C, the protective mechanism was attributed to ROS scavenging activity (Zang et al., 2017). Similarly, modulation in expression of heat shock proteins (HSPs) was noticed in wheat seeds primed with *Bacillus safensis*. The treated plants tolerated heat shock (40°C) without generation of excessive ROS (Sarkar et al., 2021). Introduction of *HVA1* (ABA-responsive barley gene) in wheat improved water use efficiency subjected to drought stress in wheat (Sivamani et al., 2000). Similarly, application of bacteria based bioformulation improved relative water content and range of antioxidants of wheat seedlings experiencing drought stress (40% the field capacity) (Akhtar et al., 2021). Several scientific studies conclusively indicate that applications of PGPRs could lead to development of resilient plants tolerant to sudden fluctuations in the weather, rise in temperature, salinity, drought, disease and insect attack. The association between plant and rhizospheric soil microbes is a functionally dynamic association and changes in the environment are perceived even at miniscule level triggering a cascade of appropriate stress-related responses making the plant tolerant to perceived challenges. In spite of beneficial attribute of transgenic crops, their acceptability for human consumption is still an issue of concern. Hence, knowledge-based application of the right PGPR could be a sustainable and ecofriendly approach to develop stress resilient crops.

Conclusion

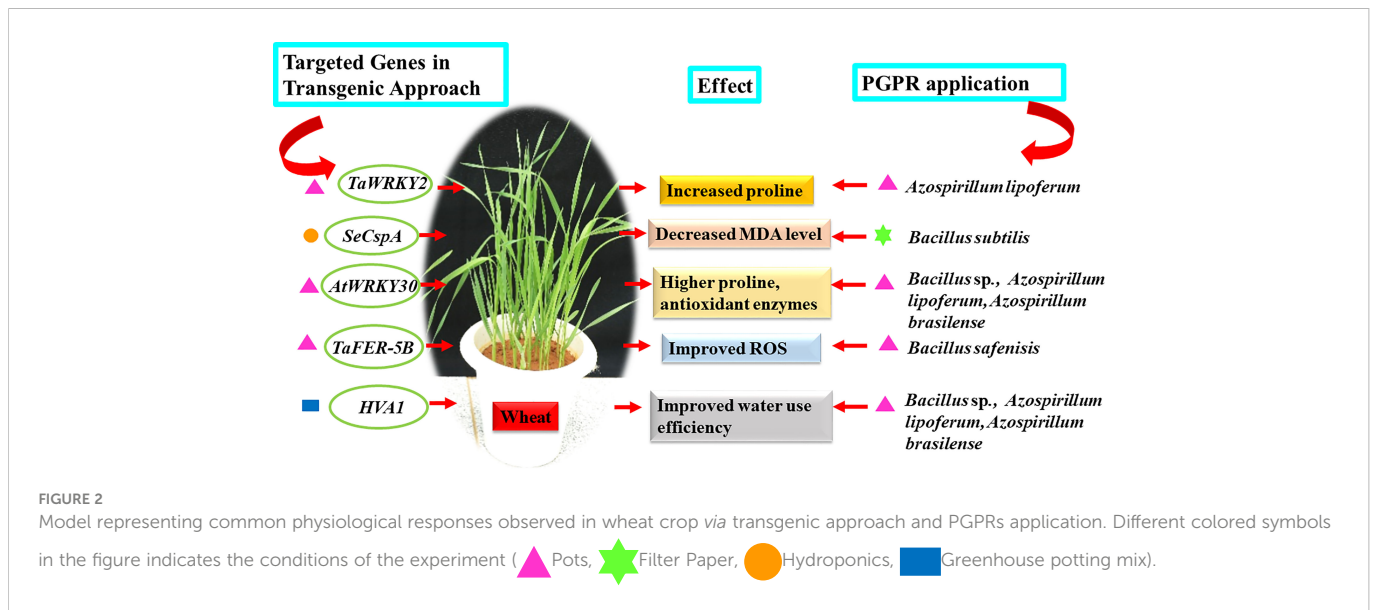
A sustainable agriculture system strives to protect the environment, without compromising crop yield to provide sufficient

TABLE 2 PGPRs along with their mode of action in combating biotic stress.

PGPR Strain	Host Plant	Pathogen	Disease	Mechanism of action	Benefits	References
<i>Bacillus amyloliquefaciens</i> (SN13)	Rice	<i>Rhizoctonia solani</i>	Sheath blight	Target phytohormones (SA, ABA, GA), MAPK, ROS signaling. Increased secondary metabolite production	Reduces fungal dry mass, number, size, length and diameter of spot lesions	Srivastava et al. (2016)
<i>Bacillus</i> sp.	Cotton	<i>Spodoptera exigua</i>	–	Increased gossypol and JA production	Significant reduction in larvae mortality rate	Zebelo et al. (2016)
<i>Enterobacter asburiae</i> BQ9	Tomato	<i>Tomato yellow leaf curl virus</i>	–	Enhanced expression of <i>PR1a</i> , <i>PR1b</i> , POD, CAT, POL and SOD	Milder disease symptoms (stunting, yellowing, curling of leaves)	Li et al. (2016)
<i>Peanibacillus lentimorbus</i> B-30488	Tobacco cv.	<i>Cucumber mosaic virus</i>	–	Targets PR genes and antioxidant enzymes	Reduces CMV RNA accumulation with 20-75% viral elimination rate	Kumar et al. (2016)
<i>Peanibacillus lentimorbus</i> B-30488	Tomato	<i>Scelerotium rolfsii</i>	Southern blight	Increased expression of PR genes but down-regulation of antioxidant enzymes and ethylene signaling	Reduces fungal dry biomass, mycelia growth	Dixit et al. (2016)
<i>Bacillus amyloliquefaciens</i> SQR3	Tomato	<i>Ralstonia solanacearum</i>	Bacterial wilt	Modulates JA/ET/SA hormonal signaling and POD, PPO expression	Suppresses disease incidence with 84.1% biocontrol efficacy	Chunyu et al. (2017)
<i>Bacillus subtilis</i>	Wheat	<i>Zymoseptoria tritici</i>	Septoria tritici blotch	Produces lipopeptides such as mycosubtilin, surfactin, fengycin	Reduces mycelia growth	Mejri et al. (2018)
<i>Bacillus velezensis</i>	Pepper	<i>Botrytis cinerea</i>	Gray mold	Stimulates SA signaling genes and antioxidants (SOD, CAT and POD)	Suppresses sporulation, mycelia growth	Jiang et al. (2018)
<i>Pseudomonas aeruginosa</i>	Rapeseed	<i>Botrytis cinerea</i>	Gray mold	Activates MAPK and PR genes	Reduces pathogenic lesions size, mycelium development	Monnier et al. (2018)
<i>Bacillus velezensis</i> QST713	Button mushroom	<i>Trichoderma aggressivum</i> f. <i>europaeum</i>	Green mold	Produces antifungal secondary metabolites (macrolactin, bacillaene, bacillomycin D, fengycin, surfactin, bacilysin, subtilin-like/ericin, difficidin and bacillibactin (siderophore))	Inhibits fungus sporulation, mycelium growth	Pandin et al. (2018)
<i>Bacillus amyloliquefaciens</i> Ba13	Tomato	<i>Tomato yellow leaf curl virus</i>	–	Induces expression of resistance related genes and defense enzymes	Milder disease symptoms (stunting, yellowing, curling of leaves) with decrease in virus load in leaves	Guo et al. (2019)
<i>Bacillus velezensis</i> OEE1	Olive	<i>Verticillium dahliae</i>	Verticillium wilt	Produces antifungal secondary metabolites/lipopeptides (surfactin A, iturin C and D, bacillomycin C, fengycin A, B and D, plipastatin, macrolactin, bacillaene, difficidin and bacilysin)	Inhibits conidia, microsclerotia germination (92% inhibition)	Azabou et al. (2020)
<i>Bacillus velezensis</i> (C2)	Tomato	<i>Verticillium dahliae</i>	Verticillium wilt	Production of metabolites, lipopeptides and lytic enzymes	Significant reduction in disease incidence (70.43 ± 7.08%)	Dhouib et al. (2019)
<i>Bacillus amyloliquefaciens</i> YN201732	Tobacco	<i>Erysiphe cichoracearum</i>	Tobacco powdery mildew	Promotes the expression of PPO and chitinases, also triggers JA/ET signaling	Inhibits conidia germination (86.11%)	Jiao et al. (2020)
<i>Herbaspirillum seropedicae</i>	Micro-Tom Tomato	<i>Xanthomonas euvesicatoria</i>	Bacterial spot	Reduces the concentration of organic acids	50% reduction in disease severity	da Silva et al. (2021)

food for the growing population. In order to provide adequate food for all, approaches like conventional breeding and genetic engineering have been extensively used for crop improvement. But these processes are costly, tedious, labor intensive and raise safety issues. Further, to improve crop productivity, heavy doses of chemical fertilizers, pesticides, and fungicides have been rampantly used which lead to large scale deterioration of the environment and soil health ultimately

impacting human health. Hence, ecofriendly sustainable means are being explored to increase plant productivity and in this respect application of microbial based biostimulants in agriculture is one of the promising means. PGPR modulates physiological responses in crops and equips them to survive under abiotic and biotic stresses. The majority of these responses are common to both biotic and abiotic challenges implying that the impact of PGPR in plant systems



is broad-based, interaction is multifarious and beneficial in more than one way. Further studies are necessary to unravel the underlying mechanism of plant-microbe interactions and to understand the signal transduction network in an integrated perspective. Holistic information about plant-PGPR functionality will pave the way for developing novel microbial based biostimulants for boosting crop yield for future generations in a sustainable manner.

Author contributions

PK designed, drafted, revised, finalized the original manuscript and prepared the figures; NA drafted and revised the manuscript. Structuring, reviewing, and editing were done by SS. Conceptualization and input in hormonal interaction component was done by PP. Conceptualization, reviewing and editing was done by AP. 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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