Chapter

Bioinoculants in Technological Alleviation of Climatic Stress in Plants

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Abstract

Global climate change is leading to a series of frequent onset of environmental stresses such as prolonged drought periods, dynamic precipitation patterns, heat stress, and cold stress on plants and commercial crops. The increasing severity of such stresses is not only making agriculture and related economic sector vulnerable but also negatively influences plant diversity patterns. The global temperature of planet Earth has risen to 1.1°C since the last 19th century. An increase in surface temperature leads to an increase in soil temperature which ultimately reduces water content in the soil, thereby, reducing crop growth and yield. Moreover, this situation is becoming more intense for agricultural practices in arid and semi-arid regions. To overcome climatically induced stresses, acclimatization of plant species via bioinoculation with Plant Growth Promoting Rhizobacteria (PGPR) is becoming an effective approach. The PGPR are capable of colonizing rhizosphere (exophytes) as well as plant organs (endophytes), where they trigger an accumulation of osmolytes for osmoregulation or improving gene expression of heat or cold stress proteins, or by signaling the synthesis of phytohormones, metabolites, proteins, and antioxidants to scavenge reactive oxygen species. Thus, PGPR exhibiting multiple plant growth-promoting traits can be employed via bioinoculants to improve the plant's tolerance against unfavorable stress conditions.

Keywords: Plant growth promoting rhizobacteria, plant growth-regulating hormones, ACC deaminase, osmoregulation, psychrotrophic microbes

1. Introduction

The agriculture sector has been considered as the main channel through which irreparable climatic change will influence the global economy [1]. The commercial plantation of crops has been severely influenced by various environmental factors mainly being drought, salinity, and intense temperature variation. These factors have become more adverse with continuing fluctuation in climate change. Globally, only 10% of arable land is reported to be free from environmental stress [2]. In arable land, more than 50% is vulnerable to drought and salinization which is expected to inflict an almost 10% rise in global water consumption by 2050. Moreover, the consistent rise in the global population will be succeeded by an increase in food demand double fold in 2050 [3].

Plants adapt and develop their own mechanism to cope the environmental stress. The most effective means of combating environmental stress is the release and accumulation of plant growth-regulating hormones such as abscisic acid (ABA) and salicylic acid (SA). ABA, commonly known as stress hormone is released at the root tip in response to lower water potential, followed by its translocation to leaves where it alters osmotic pressure of the stomatal guard cells, leading to the closure of stomata openings to conserve moisture, thereby, preventing water loss via transpiration. Moreover, accumulated carbohydrates and amino acids being low molecular weight compounds play an active role in osmoregulation. SA, on the other hand, protects the plant against pathogenic attack [4].

PGPR/Treated Plant	Climatic stress	Alleviation of climatic stress
Bacillus cereu/Solanum lycopersicum	Heat stress	Increased production of exo-polysaccharide, cleavage of ACC-deaminase [9]
Bacillus amyloliquefaciens, Agrobacterium fabrum/Triticum aestivum	Water stress	Increase in biomass and grain yield [10]
Aneurinibacillus aneurinilyticus, *Paenibacillus sp./Phaseolus vulgaris*	Salinity stress	Facilitating ACC-deaminase activity, increased production of IAA, hydrogen cyanide and siderophore [11]
Stenostrophomonas maltophilia/Triticum aestivum	Salinity stress	Improved growth and yield, elevated antioxidative enzymatic activity, increased K^+ uptake [12]
Paenibacillus polymyxa/Brassica napus	Soil temperature	Production of antimicrobial and plant growth promoting volatile organic compounds (VOCs) [13]
Bacillus subtilis, *Bacillus thuringiensis*, *Bacillus megaterium/Cicer arietinum*	Climatically induced salinity stress	Regularized photosynthesis via assimilation of soluble sugars, chlorophyll and proline [14]

Table 1.
Alleviation of climatic stress via bioinoculants.

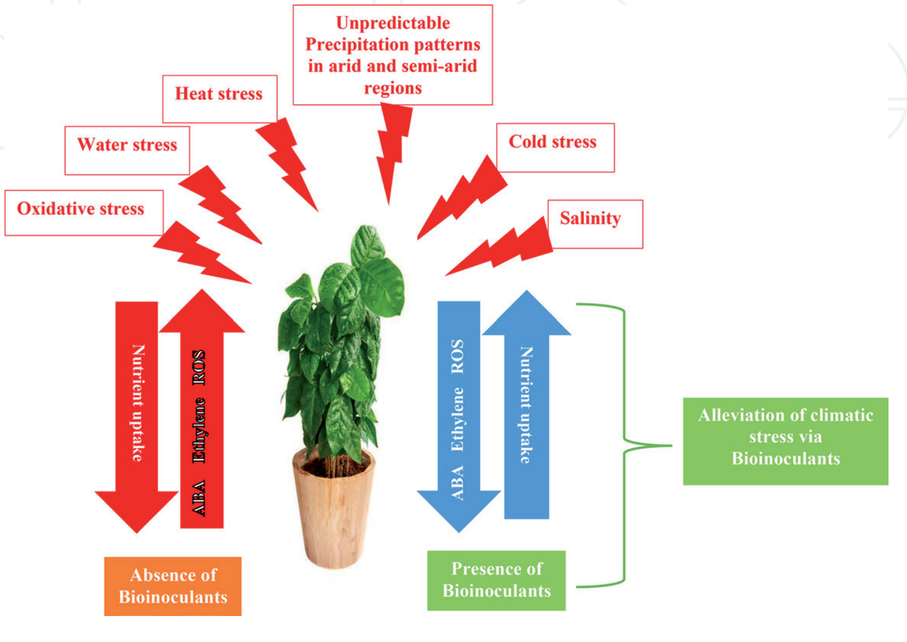

Figure 1.
Plant's responses to various stresses in presence and absence of bioinoculants.

Along with plant internal defense mechanism, the supportive role of PGPR has been widely acknowledged as an effective tool for sustaining plant growth and yield [5–7]. The plant root system serves as a habitat for numerous microorganisms that also interact with soil, thereby developing a complex ecosystem [8]. Certain PGPR inhabiting the rhizosphere penetrates roots and migrates through plant tissues; thereby impact the physiological and biochemical traits of plant cells (**Table 1**). This ecological aspect of the microbial community can be employed to strengthen the stress tolerance in plants, hence increasing their adaptation towards invincible climatic changes (**Figure 1**) [15].

The escalating demand and supply of chemical fertilizers and pesticides along with the persistence of their residual particles has posed an ultimate threat to humans as well as to the ecosystem. As an alternative, the acceptability of bio-fertilizers bearing bioinoculants has been increasing day by day. These bioinoculants act as a potential source of phytohormones which can rectify the climatic stress faced by plants. This chapter will explore various aspects of the utilization of bioinoculants for combating the climatic stress faced by plants.

2. Amelioration of heat stress via thermotolerant microbes

The major climatic stress faced by plants due to the rise in global temperature is heat stress which leads to water stress with counter effect on photosynthetic rate and flowering and fruiting in both tropical and sub-tropical crop systems [16]. The steady increase in surface temperatures is followed by an increase in soil temperature which can influence the root elongation process. Although, root elongation requires optimum soil temperature (specific to each plant), beyond which root elongation is stopped resulting in a stunted root system. Moreover, the activity of rhizobacteria is also relying on optimum soil temperature. In the forest ecosystem, N being a macronutrient acts as a growth-limiting factor. The flow of N cycling is deliberately subjected to temperature variation. The relatively increased temperature triggers N mineralization by microbes and thereby, prompting N uptake by plants as nitrates. However, in this process, the net nitrification is decreased [17]. The inoculation of PGPR is found to be more convenient than hsfs (heat stress transcription factors) genes, transgenic varieties, and breeding of heat-tolerant cultivators [18, 19].

Thermotolerance of certain PGPR has been evaluated to decrease the effect of heat stress on plants. The soybean plants inoculated with *Bacillus cereus* strain SA1 were exposed to heat stress for 5–10 days. The inoculated plants exhibited improved physiological (biomass) and biochemical (chlorophyll content and chlorophyll fluorescence) characteristics. Moreover, SA1 inoculation reduced the synthesis of abscisic acid and increased salicylic acid (a phenolic phytohormone involved in signaling and defense against pathogens) along with remarkable production of antioxidants (ascorbic acid peroxidase, superoxide dismutase, and glutathione) for sequestration of reactive oxygen species (ROS). A continuous increase in the synthesis and assimilation of Heat Shock Protein (HSP) was also claimed throughout the stress period of 5 to10 days, mainly due to the perpetual onset of GmHSP gene expression. Also, over gene expression of GmLAX3 and GmAKT2 were associated with enhanced potassium gradient and altered auxin and ABA stimuli (Aaqil et al. 2020). The bacterial strain *Bacillus cereus* capable of producing ACC-deaminase (0.76–C0.9 μM/mg protein/h) can cleavage ACC to α-ketobutyrate and ammonia to increase heat tolerance in tomato (*Solanum lycopersicum L.)*. Moreover, increase in synthesis of exopolysaccharide (0.66–C0.91 mg/mL) showed promising plant growth in tomato [9] (**Table 2**). Moreover, the presence of enzymatic antioxidants

Treated Plant/PGPR	Stress Alleviation Effect
Potato/*Paraburkholderia phytofirmans*	ACC deaminase production [20]
Tomato/Mycorrhizae	Reduction in lipid peroxidation and H_2O_2, higher ROS scavenging activity [21]
Bacillus amyloliquefaciens, Azospirillum brasilense Pantoea dispersa, *Serratia marcescens*, *Pseudomonas* spp.	ROS reduction, pre-activation of heat shock proteins [22]
	ACC deaminase production [23]
Apple and pear/*Ps. fluorescens*	Competition with INA+ bacteria [24]
Grapevine/*Paraburkholderia phytofirmans*	ACC deaminase production [25]
Soy/*Bacillus aryabhatthai*	ABA production [26]

Table 2.
Alleviation of heat stress via bioinoculants.

such as superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT), and accumulation of metabolites such as amino acids and proline had boosted the scavenging activity against ROS under heat stress.

Among different agro-ecological zones, the arid and semi-arid regions are highly vulnerable to climatic changes mainly due to dynamical precipitation patterns. Being a staple cereal crop, the wheat and its associated endophytic and epiphytic bacterial diversity was investigated for thermotolerance at a temperature range of 30–40°C, pH 3–11, and 3–20% NaCl concentration [27]. Among 32 bacterial strains of 15 genera, 10 strains were reported to exhibit six different plant growth-promoting traits under heat stress. *Arthrobacter sp.* (66.0 ± 0.7 mg L^{-1}) possessed high solubilization of phosphorus followed by *Pseudomonas japonica* (64.6 ± 0.9 mgL^{-1}). Whereas, the potassium solubilization was highest for *Methylobacterium mesophilicum*. *Pseudomonas putida* exhibited the highest IAA production (70.8 ± 1.5 μg mg^{-1} protein day^{-1}) followed by *Rhodobacter capsulatus* (69.1 ± 0.5 μg mg^{-1} protein day^{-1}). The highest production of siderophore had been shown by *Alcaligenes faecalis* (4.9 ± 0.1 mm). Being thermotolerant, *Alcaligenes faecalis* and *Pseudomonas poae* were also characterized as alkali tolerant with 5% NaCl and 10% NaCl tolerance respectively. Besides the production of IAA, siderophore, and ammonia, these bacterial strains were also involved in the solubilization of phosphorus and zinc under heat stress. The chief bacterial groups characterized for nitrogen fixation at high temperatures were *Acromobacter*, *Alcaligenes*, *Bacillus*, *Delftia*, *Providencia*, *Pseudomonas*, *Rhodobacter*, and *Salmonella*.

Similarly, Sorghum being native to arid habitat was inoculated with a thermotolerant bacterial strain of *Psuedomonas aeruginosa* AKM-P6 which was isolated from the rhizosphere of Pigeon Pea plant grown under semi-arid conditions [28]. The inoculated Sorghum seedlings survived the temperature range of 47–50°C up to 15 days. The thermotolerance was imparted by the biosynthesis of high molecular weight proteins in leaves which protected cellular membranes from injury and improved metabolite production mainly proline, chlorophyll, sugars, amino acids, and proteins along with plant biomass. Another strain of *Pseudomonas sp.* PsJN was used to evaluate the heat-stress tolerance level in 18 clones of potatoes via both *in vitro* and *ex-vitro* inoculation [29]. The inoculated potato nodal cuttings were exposed to the temperature range of 20/15°C or 33/15°C day and night for six weeks. The increase in temperature had drastically affected the root system and tuber number and tuber fresh weight. An average root to shoot ratio decreased from 3.7 at 20/15°C to 1.7 at 33/15°C in non-inoculated plantlets and respectively, from 4.3

to 1.5 for inoculated ones. ABA deficient plantlets lack the tuber formation whereas tuberization in inoculated plantlets was significant at 33/15°C. As compared to in vitro, the ex-vitro performance of potato clones (LT-7) exhibited the effectiveness of rhizobacteria in colonizing certain potato clones under heat stress. Hence, the thermotolerant bacterial strains may serve as inoculants and bio-control agents for improving crop productivity with accelerating climatic temperature stress.

3. Amelioration of water stress via 1-aminocyclopropane-1-carboxylate deaminase/exopolysaccharide production

Due to the changes in minimum and maximum temperature, high water requirement and reduction in yield was observed in plants. Although the production of 'Ethylene' as plant stress hormone occurs in response to climatic stress encountered by plants; its accumulation in high amounts could be deleterious. The accumulation occurs under the influence of ACC oxidase that prompts exudation of ACC, a precursor to ethylene synthesis. The PGPR capable of producing ACC deaminase degrades ACC into its intermediates i.e., ammonia and α-ketobutyrate, thereby, declining ethylene level and restoring plant development [30]. The inoculation of *Mucuna pruriens L.* (velvet bean), a well-adapted plant to arid and semi-arid regions with *Bacillus spp.* and *Enterobacter spp.* had shown significantly reduced ACC accumulation by 41% and 21% in leaves respectively, and in the roots by 46% and 15%, respectively. Thereby, the ethylene synthesis was reduced by 45% with *Bacillus spp.* (G9) and 65% with *Enterobacter spp.* (HS9) [29].

In addition to ACC deaminase activity, certain bacterial strains were found to be efficient in plant growth. For instance, *Achromobacter piechaudii* ARV8, a bacterial strain isolated from the arid region, experiencing frequent episodes of water stress was found to be better plant growth promoter as compared to *Pseudomonas putida* GR12–2, a bacterial strain inhabiting area with surplus water supply [31]. The bioinoculation of tomato (*Lycopersicum esculentum* Mill) and pepper (*Capsicum annuum L.*) seedlings with *A. piechaudii* strain improved relative water content (RWC) which subsequently succored plants in maintaining their fresh weight in water stress conditions. The maintenance of the fresh weight in bioinoculated seedling can be justified by the declined production of ethylene to 6.1 nlh^{-1} as compared to stressed seedling with the rise in ethylene level up to 23 nlh^{-1}. Overall, the plant biomass was enhanced four times as compared to uninoculated controls. Similarly bacterial strains mainly *Variovorax paradoxus, Pseudomonas spp. Achromobacter spp.* and *Ochrobactrum anthropi* islolated from rain-fed agricultural soil were reported to possess growth-promoting traits such as N_2 fixation, siderophore, and phosphate solubilization along with sufficient production of ACC deaminase. These bacterial strains both as single inoculation and consortium imparted significant growth, foliar concentration, and antioxidant activity to the wheat (*Triticum aestivum L.*) production [32].

The exopolysaccharide (EPS) released by PGPR tends to form rhizosheath or biofilms around the surface of the roots containing sufficient moisture content, thereby, protect them from prolonged desiccation. Moreover, plants inoculated with EPS are capable of accumulating sugars, amino acids, and proline. The survival of PGPR in dried sandy soils with low moisture content is conceivable due to EPS, which may serve as a biological tool to combat climatic water stress and ultimately providing a path towards global food security [33]. The coalition of ACC deaminase and EPS has been shown to have an affirmative effect on carotenoid pigments in certain plants. The inoculation of *Capsicum annuum* plants with *Bulkhorderia cepacia* (ACC deaminase activity 12.8 ± 0.44, mM αKB mg^{-1} min^{-1} and

EPS 4.89 ± 0.06 mg/mg protein) resulted in increased chlorophyll a and b content (chlorophyll a 5.7 gm L^{-1} and chlorophyll b 3.4 gm L^{-1}, respectively) as compared to control (chlorophyll a 3.2 gm L^{-1}, chlorophyll b 1.9 gm L^{-1}). Moreover, the plant biomass has also increased (fresh weight of 9 g and dry weight of 3.6 g) as compared to control (fresh weight 6 g, and dry weight 1.6 g) [34].

The co-application of PGPR producing ACC deminase with biochar has been utilized as an effective mechanism against prevalent water stress conditions. Timber-waste biochar was co-applied with *Bacillus amyloliquefaciens* strain to increase the productivity of wheat under simulated water stress conditions. Along with high productivity (59% of 100-grain weight), the grain composition (58% N, 18% P, and 23% K), carotenoid (114% chlorophyll a and 123% chlorophyll b), photosynthetic rate (118%), and transpiration rate (73%) in wheat were also reinforced [10]. To understand the PGPR potential for genetic improvement in plants, the physiology and biochemical characteristics of PGPR isolated from chickpea rhizosphere were implored. The seeds of chickpea were grown in the cultures of *Bacillus subtilis, Bacillus thuringiensis,* and *Bacillus megaterium*. The 25-day old chickpea seedlings were sprayed with plant growth regulators/plant growth retardants (PGRs) i.e., salicylic acid (SA) and putrescine (Put) at the rate of 150 mgL^{-1}. The consortium of PGPR and PGRs significantly improved carotenoid, sugar, and protein contents as compared to irrigated and non-irrigated conditions [14].

The inhibitory effect of water stress in two maize species was mitigated by inoculation with two endophytic bacterial species i.e., *Burkholderia phytofirmans* PsJN and *Enterobacter* sp. FD17 [35]. Maize seedlings were exposed to water stress after the 45th day of vegetative growth. The inoculated bacterial seedlings exhibited 30% relative water content in leaves along with the significant increase in root and shoot biomass, leaf area, chlorophyll content, and photochemical efficiency of PSII (Photosystem II). However, the *Paraburkholderia phytofirmans* PsJN was found to be more effective as compared to *Enterobacter* sp. FD17. The remedial potential of PGPR against water stress conditions can be used as a tool for sustainable agriculture practices (**Table 3**).

Treated Plant/PGPR	**Stress Alleviation Effect**
Maize/*Azospirillum lipoferum, Bacillus* Spp.	Increase accumulation of soluble sugar, free amino acids, proline and decrease electrolyte leakage; reduced activity of antioxidant enzyme [36, 37]
Soybean/*Pseudomonas putida* H-2–3	Lower the level of abscisic acid and salicylic acid and a higher level of jasmonic acid content; declined superoxide dismutase, flavonoids and radical scavenging activity [38]
Wheat/*Bacillus amyloliquefaciens*, *Azospirillum brasilense*, *Rhizobium leguminosarum*, *Mesorhizobium cicero*, *Rhizobium phaseoli*	Improved homeostasis; catalase, exo-polysaccharides and IAA production [39, 40]
Chickpea/*Pseudomonas putida*	Osmolyte accumulation, ROS scavenging ability and stress-responsive gene expressions [41]
Lettuce/*Azospirillum* sp.	Promote chlorophyll, ascorbic acid content and antioxidant capacity [42]
Rice/*Trichoderma harzianum*	Promote root growth independent of water status and delay drought response [43]

Table 3.
Alleviation of water stress via bioinoculants.

4. Amelioration of salinity via bioinoculants

The soil salinity is naturally occurring phenomena in arid and semi-arid regions. Besides, extensive use of chemical fertilizers and irregular irrigation practices, the continuously changing precipitation pattern is contributing 1–2% salinity to arable lands every year [44]. The plants growing under salinity conditions tend to have high levels of ethylene, stress hormone released in response to both biotic and abiotic stress. As mentioned earlier, PGPR possessing ACC deaminase enzyme can reduce ethylene level by disintegrating ACC (precursor to ethylene) into α-ketobutyrate and ammonia, thereby suppressing the formation of ethylene and ultimately sustaining the plant growth. In doing so, the strains of *Aneurinibacillus aneurinilyticus* and *Paenibacillus sp.* isolated from Garlic (*Allium sativum*) rhizosphere were used for seed bacterization of French bean (*Phaseolus vulgaris*) and evaluated for their ACC deaminase activity [11]. These strains produced more than ~1500 nmol of α-ketobutyrate mg protein^{-1} h^{-1} and more than ~30 μg/ml Indole Acetic Acid (IAA) under saline and nonsalinity stress conditions. Moreover, the seed bacterization in the form of consortia led to a ~ 60% decline in stress stimulated ethylene levels.

Under saline conditions, water uptake is restricted by ionic stress which develops between Na^+ and K^+ due to Na^+ accumulation in aerial parts of plants. Singh and Jha [12] successfully employed inoculation of *Stenostrophomonas maltophilia* SBP-9 on wheat (*Triticum aestivum)* and increased K^+ uptake by 20–28%. The plant-endophytic relationship has been explored by co-inoculation of *Cicer arietinum* (Chickpea) with *Bacillus subtilis* NUU4 and *Mesorhizobium ciceri* IC53 to alleviate salt stress. These bacterial strains increased proline accumulation which in turn sequestered hydrogen peroxide to strengthen the tolerance level against saline conditions. Besides, coinoculation of endophytes also reduced root rot infection caused by *F. Solani* [45]. The PGPR and their relationship with plants proved to be effective in dealing salt stress simultaneous to other biotic and abiotic stress in given global climatic conditions (**Table 4**).

5. Amelioration of oxidative stress via osmoregulation

Global climate change is amplifying the intensity of environmental factors, causing a profound disturbance in the plant's biological processes mainly via intractable generation of ROS. A condition called 'oxidative stress' develops when the available concentration of antioxidants within plant cells become insufficient to neutralize an unrestrained number of reactive species (OH^-, O^- and $H_2O_2^-$) which leads to disruption of cellular components (lipids, protein, nucleic acids, and metabolites). As a defense mechanism, plants and related rhizobacteria synthesize and release osmolytes when required. Osmolytes are low molecular organic compounds (proline: amino acids, sugars, polyols, methylamines, methylsulfonium compunds, and urea) mainly aiming at neutralization of the osmotic pressure of cells under stress conditions. These plants and PGPR synthesized osmolytes synergistically act to capture ROS. The prominent PGPR strains such as *Azospirillum brasilense* SP-7 and *Herbaspirillum seropedicae* Z-152 managed to retain relatively higher water content in vegetal tissues of inoculated/non-irrigated maize plants as compared to non-inoculated/irrigated maize plants. The plants inoculated with *H. seropedicae* had a higher proline accumulation rate (fourfold) as compared to those inoculated with *A. brasilense* (two-fold), thus indicating better osmoregulation under drought conditions. However, the amount of proline in inoculated plants

Treated Plant/PGPR	Stress Alleviation Effect
Groundnut/*Brachybacterium saurashtrense*, *Brevibacterium casei*, *Haererohalobacter*	Higher K^+/Na^+ ratio and higher Ca^{2+}, phosphorus, and nitrogen content, higher Shoot and root concentration of auxin [43, 46]
Mung bean/*Rhizobium*, *Pseudomonas*	ACC-deaminase activity [47]
Wheat/*Azospirillum* Sp., *Pseudomonas* Sp. *Serratia* Sp.	Osmotic adjustments via proline and soluble sugars [48]
	ACC deaminase activity, reduced ethylene level [49]
Maize/*Pseudomonas*, *Enterobacter*	More N, P, K uptake and high K^+–Na^+ ratios [50]
Rice/*Pseudomonas pseudoalcaligenes*, *Bacillus pumilus, Bacillus amyloliquefaciens*	Reduced reactive oxygen species, lipid peroxidation and superoxide dismutase activity, modulating differential transcription in at least 14 genes [51, 52]
Lettuce/*Azospirillum*	Promoted ascorbic acid content antioxidant capacity [42]

Table 4.
Alleviation of salinity stress via bioinoculants.

was relatively lower than control plants in both water-stressed and well-watered conditions. This decreased concentration of proline in inoculated plants may be attributed to a balanced amount of osmolytes to the available ROS leading to better osmoregulation in water-stressed conditions. Also, inoculated plants have lower ethylene content than that of control plants. However, the gene expression of ZmVP14 responsible for the biosynthesis of abscisic acid was suppressed in inoculated plants [53], allowing stomata to remain open for better CO_2 assimilation even in drought conditions also supported by other researchers [35].

Inoculation of chickpea varieties with *Pseudomonas putida,* also indicated reduced proline concentration with a reduced level of 114% in BG-362 and 214% in BG-1003 on the seventh day of water stress [41, 53]. However, in *Capsicum annum* inoculated with *Burkholderia cepacia*, the accumulation of proline content was higher (0.143 mmoles gm^{-1}) as compared to *the* control plant (0.065 mmoles gm^{-1}). Co-inoculation of *Azotobacter chroococcum* and *Azospirillum brasilense* significantly improved accumulation of proline and other osmolytes along with physic-chemical characteristics of *Mentha pulegium L.* [54]. Other than proline, some soluble sugars play a vital role in maintaining photosynthesis in leaves under water stress, therefore, also termed 'osmoprotectant'. However, the reduced level of soluble sugar can become deleterious to the cellular membranes of plants. The co-inoculation of PGPR (*Bacillus subtilis*, *Bacillus thuringiensis*, and *Bacillus megaterium*) with PGRs (SA & Put) in chickpea seedlings prompt the accumulation of soluble sugar along with chlorophyll and protein content (majorly proline), thus, regularizing photosynthesis under water stress [14]. The accumulated soluble sugar also acts as a signaling molecule, where it triggers the activation and gene expression of certain genes relevant to photosynthesis in plants. Hence, osmolytes being 'abiotic stress busters' are pivotal in maintaining homeostatic equilibrium at the molecular and cellular level to enhance stress tolerance in plants [55].

6. Amelioration of cold stress via psychrotrophic microbes

Due to global warming, extreme environmental conditions are occurring more frequently including cold stress. In northern parts of the world, the cold weather is unexpectedly intensifying specifically due to the Polar vortex bringing cold Arctic air towards southern parts of the planet, bringing more intense winters in some parts of the world. The biomes of extreme environments serve as excellent habitats for archaea, bacteria, and fungi. Agro-ecosystems at high altitudes are vulnerable to low productivity due to low surface temperature resulting in low soil temperature and in turn low soil fertility [56]. High altitude soils comprised diverse microbes that are capable of surviving cold environments mainly due to synthesis and assimilation of cryoprotective compounds such as metabolites (proline), anthocyanin (secondary metabolite), and carbohydrates (trehalose). The induction of such stress-resistance against abiotic stress is also coined with a term called 'Induced Systematic Resistance' (ISR). An in vitro inoculation of *Vitis vinifera L.* (grapevine) explants with *Burkholderia phytofirmans* strain PsJN successfully developed chilling resistance mainly via accumulation of increased level of sugars, proline, and phenolics as compared to non-inoculated plantlets [57].

Several biotechnological and microbiological attempts have been ongoing for the last two decades to utilize the cold-tolerant (psychrotrophic) or cold-loving (psychrophilic) microbes to improve the agricultural practices in chilling mountainous environments. Psychrophilic microbes inhabiting cold environments majorly belong to phyla *Verrucomicrobia*, *Thaumarchaeota*, *Spirochaetes*, *Proteobacteria*, *Planctomycetes*, *Nitrospirae*, *Mucoromycota*, *Gemmatimonadetes*, *Firmicutes*, *Euryar chaeota*, *Cyanobacteria*, *Chloroflexi*, *Chlamydiae*, *Basidiomycota*, *Bacteroidetes*, *Ascomycota*, and *Actinobacteria.* Like thermotolerant PGPR, the psychrotrophic PGPR explicit various attributes like ACC deaminase activity, solubilization of micronutrients (phosphorus, potassium, and zinc), biological N_2 fixation, and production of ammonia, hydrogen cyanide, indole-3-acetic acid, and Fe-chelating compounds (**Figure 2**). The alleviation of cold stress on the production of cereal crops such as wheat was investigated by inoculation with *Bacillus spp.* CJCL2 and RJGP41 strains isolated from Qinghai-Tibetan plateau [58]. The psychrophilic activity of this strain was also compared to temperate *B. velezensis* FZB42 at a temperature range of 14°C, 10°C, and 4°C after 4 h post-inoculation. The cold-tolerant strain CJCL2 produced the finest biofilm structure as compared to RJGP41 which produced slight biofilms at 96 h post-inoculation at 4°C, whereas FZB42 failed to develop any biofilm at 4°C. The basic mechanism against cold stress was based on the regulation of abscisic acid, lipid peroxidation and proline accumulation, and a lower level of ROS. Moreover, genetic expression for ACC deaminse, glucose dehydrogenase encoding phosphate solubilization, and phytohormones was quite effective and led to the improvement in plant growth under cold stress. The cold-tolerant *Bacillus* spp. maintained osmotic balance in a plant cell by synthesizing glycine betaine, a major osmoprotectant and produced due to OpuAC gene expression. All in all linear four-fivefold increase in the gene expression of cold shock proteins (CspB, CspC, and CspD) observed in CJCL2 and RJGP41 inoculated wheat

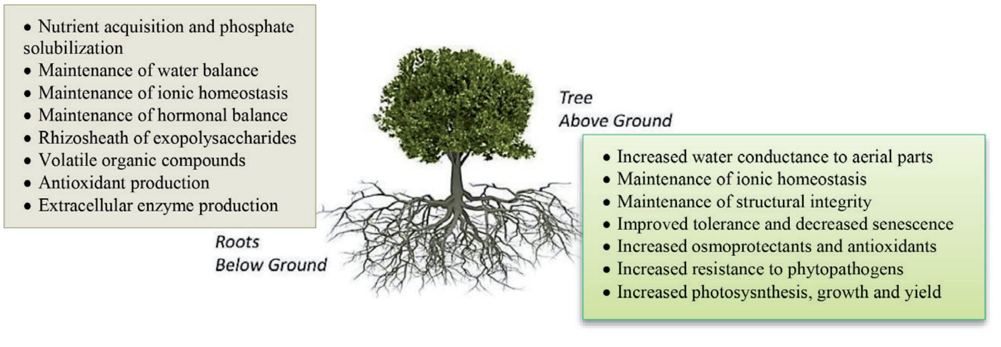

Figure 2.
Key mechanisms targeted by plant growth promoting rhizobacteria.

plants may trigger the modifications in RNA. Also, these proteins may stabilize the secondary structure of nucleotides leading to improved cellular components.

6.1 Plant growth promoting rhizobacteria and root-nodule symbiosis

The PGPR possessing root-nodule symbiosis has also been reported to exhibit psycrotolerant traits at 5°C [59]. These PGPRs were isolated from the root nodule of *Pisum sativum L.* (Pea), cultivated in the Northern Indian plains. Out of nineteen tested strains, four exhibited cold tolerance mainly by producing phytohormone IAA in the range of 62.7–198.1 μg/ml. The inoculation of edible crops growing under adverse climatic conditions with PGPR producing phytohormones showed promising results [60]. The *Serratia nematodiphila* PEJ1011 strain was inoculated to *Capsicum annuum L.* (pepper) at a low temperature of 5°C. The inoculated plants exhibited higher endogenous GA_4 content grown both at normal and low temperatures. Moreover, PGPR increased abscisic acid (phytohormone) level and reduced jasmonic acid and salicylic acid (phytohormones) contents to regulate plant adaptation and growth at low temperature (**Figure 3**).

6.2 Plant growth promoting rhizobacteria and chlorophyll pigments

Chloroplasts containing chlorophyll pigments for photosynthesis are the main organelles affected by the cold. Low temperature also led to stomatal closure in many cold-tolerant plants like *Arabidopsin thliana*. Although the stomatal closure prevents leaf dehydration, CO_2 uptake is inhibited which eventually reduces photosynthesis. The inoculation of *A. thliana* with endophytic *Burkholderia phytofirmans* strain PsJN (Bp PsJN) prevented disruption of the plasma membrane at 0°C, −1°C, and − 3°C and induced cell wall strengthening in leaf cells [62]. Moreover, after night stress, the bacteria led to better photosynthetic pigment content. Similarly, *Vitis vinifera L.* (grapevine) cultivated in temperate and cool climates contains CBF4 gene which is a homolog to *A. thliana* CBF1 accumulates carbohydrates and proline on exposure to low temperature [63]. The *V. vinifera* plantlets were inoculated with endophytic *B. phytofirmans* strain PsJN at 4°C. As expected, the bacterial strain had induced cold resistance principally by enhancing gene expression of CBF (specifically CBF4) genes, along with an accumulation of anti-freeze proteins (PR proteins) and metabolite level. The bacterial strain was found to be highly effective in inhibiting hydrogen peroxide (H_2O_2). However, the inoculated plantlets indicated high H_2O_2 accumulation

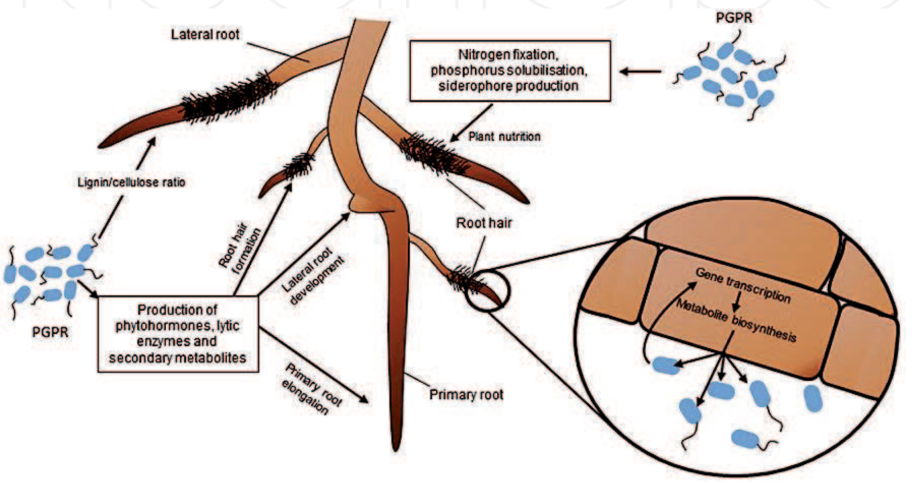

Figure 3.
Impact of plant growth promoting rhizobacteria on nutrient acquisition [61].

in the first three days of cold stress followed by H_2O_2 elimination after a week, further evidenced by a reduction in the level of metabolites after 1 week indicating inhibition of ROS via scavenging process carried out by endophytic PsJN strain.

6.3 Plant growth promoting rhizobacteria and sugar deposition

Certain bacteria, fungi, vascular plants, and invertebrate animals synthesize trehalose or mycose for energy consumption and to tolerate cold and water stress. Trehalose is a disaccharide sugar consisting of two glucose molecules mainly synthesized via phosphorylated intermediate trehalose 6-phosphate (T6P). Being capable of inducing cryoprotective compounds, *B. phytofirmans* strain PsJN was inoculated in grapevine to observe its impact on the accumulation of T6P and trehalose at 4°C. After 120 h of cold exposure, the level of T6P was increased in roots (>0.4 nmol. g^{-1} FW) stems (>0.7 nmol. g^{-1} FW), and leaves (>1.7 nmol. g^{-1} FW) of inoculated plantlets. T6P acts as a signal metabolite in plants responding in particular to changes in sucrose level, thereby a strong correlation had been observed between T6P and sucrose content in all plant organs in both chilled and non-chilled plants. The authors were uncertain about the role of trehalose against chilling because the overall accumulation of trehalose was only found in leaves in low amounts i.e., <15 nmol. g^{-1}. Localized trehalose accumulation might have protected cell membranes against cold-induced dehydration [64, 65]. However, the organ-specific accumulation may indicate trehalose acted as an osmolyte [66]. Previous studies related to drought stress indicated overexpression of genes for the synthesis of trehalose which under water-stress inhibited dehydration [67]. Although psychrotolerant PGPRs are proved to be effective in inducing tolerance against cold stress, the quest of mechanism underlying is still being investigated by the researchers.

7. Conclusions

Despite awareness and efforts being planned or carried out, global temperature, a dynamic entity itself is hard to reverse to its previous levels in 1990. Instead, plant species have to acclimatize themselves to prevailing temperature variations. A natural symbiotic relationship between PGPR and plant growth is known for decades, has been widely considered and accepted as the most convenient and reliable approach to deal with climate-based environmental stresses. This chapter, therefore, quoted and discussed several research studies utilizing PGPR to alter physiological and biochemical processes occurring at inter and intracellular levels to boost the plant's defense mechanism. However, the complexity of the mechanism underlying is still in focus to fully harness the potential of PGPR for sustainable agricultural practices and for sustaining natural plant diversity.

Conflict of interest

The authors declare no conflict of interest.

Abbreviations

PGPR	Plant Growth Promoting Rhizobacteria
1-Aminocyclopropane-1-carboxylate Deaminase	ACC deaminase

ABA	Abscisic Acid
SA	Salicylic Acid
IAA	Indole-3-Acetic Acid
VOCs	Volatile Organic Compounds
ABA	Abscisic Acid (ABA)
HSP	Heat Shock Protein
SOD	Superoxide Dismutase
POD	Peroxidase
CAT	Catalase
ROS	Reactive Oxygen Species
RWC	Relative Water Content
EPS	Exopolysaccharide
PGRs	Plant Growth Retardants (PGRs)
Put	Putrescine
ISR	Induced Systematic Resistance

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