CHAPTER

14

Microbe-mediated amelioration of cold stress in plants: Mechanisms and challenges

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1. Introduction

Agricultural sustainability is often threatened by abiotic pressures such as cold stress (CS). It is established that below-freezing temperatures annually affect about two-thirds of the global terrestrial area, while the temperature of three-quarters of the biosphere of the earth is below 5°C (Awasthi et al., 2019; Baldi et al., 2011). CS impacts crop several biological processes in crop plants including increases in membrane degradation and decreases in the efficiency of the photosynthetic system. However, the primary change in plant systems is caused by cellular alterations brought on by cold stress in plants, disruption of cellular homeostasis, and rapid synthesis of reactive oxygen species (ROS) (Eremina et al., 2016) (Fig. 14.1). Plant tissues and cells are destroyed by ROS, such as hydrogen peroxide molecules, which also degrades large biomacromolecules such as DNA and lipids (Fadiji et al., 2022; Saed-Moucheshi et al., 2014).

The introduction of traits for cold tolerance into crops is not effectively accomplished by genetic modifications or traditional plant breeding techniques (Chen et al., 2019). Cold tolerance is not regulated by a single gene but rather by numerous complex mechanisms that act in unison to protect the plant cells from cold stress despite the fact that some plants can produce cold protective antifreeze proteins (Fowler & Thomashow, 2002). To enhance plant resistance to chilling stress, cold-tolerant microorganisms

Beneficial Microbes for Sustainable Agriculture under Stress Conditions
https://doi.org/10.1016/B978-0-443-13193-6.00014-2

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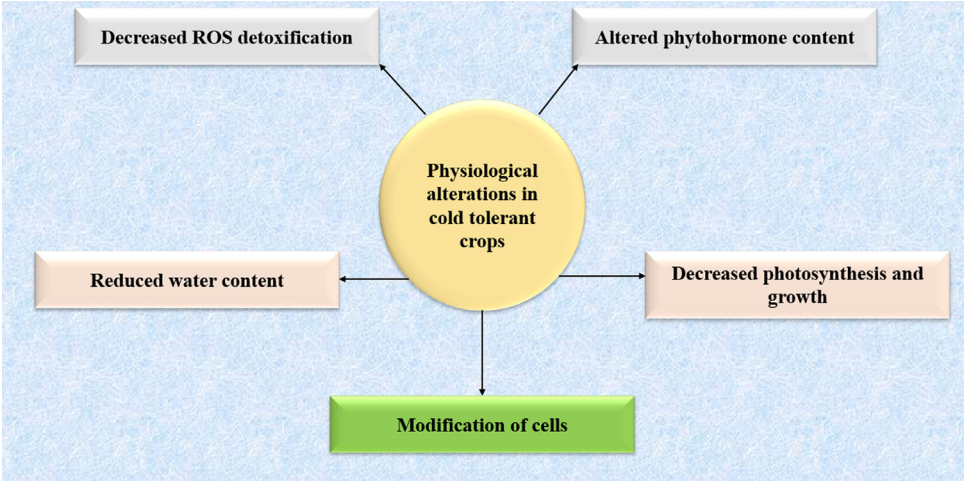

FIGURE 14.1 Physiological alterations often associated with cold tolerance crops. Changes in plant physiology associated with adaptation and tolerance of crops to cold stress.

(CTMs) such as psychrotrophs and psychrophiles may be crucial, making them a viable and promising option for cold-stress injuries in high-altitude agriculture. Psychrophiles grow at a maximum temperature of 15°C while psychrotrophs grow best at this temperature (Srivastava et al., 2019). For example, the growth of wheat seedlings was observed to increase significantly by inoculation with *Pseudomonas* sp., a cold-tolerant strain obtained from the *Amaranth* rhizosphere (Mishra et al., 2009). In another study, low temperature significantly increases the nitrogen fixation and nodulation potentials of soybean crops after inoculation of the plants with *Bradyrhizobium japonicum* (Zhang et al., 2003). Another cold-tolerant strain, *Burkholderia phytofirmans* was reported to increase cold stress tolerance by reducing electrolyte leakage when inoculated into grapevine seedlings (Ait Barka et al., 2006). Also, *Raoultella terrigena*, *Azospirillum brasiliense*, *Bacillus subtilis*, and *B. megaterium* are examples of plant growth–promoting bacteria inoculated into wheat and barley to lessen the adverse effects of cold-stress injury by regulating antioxidant enzyme activity and freezing injury (Turan et al., 2013).

Several research findings have revealed that there are potential mechanisms through which CTMs can be of advantage to crops. This includes mineralization and solubilization of nutrients, activation of antioxidant enzymes, phytohormone production, the release of small and high-affinity iron-chelating compounds, improved efficiency of biological nitrogen fixation, and synthesis of the enzyme ACC enzyme deaminase to reduce ethylene production triggered by cold stress (Subramanian, Krishnamoorthy, et al., 2015). Efforts have been made to understand the current trends in cold-stress management. Attempts are also being made to examine the prognosis for microbiological research, which will provide additional predictions about the effects of CTMs on high-altitude agriculture.

2. Impact of cold stress on crop growth and yield

High-altitude agriculture is faced with the issue of cold stress, and it frequently has a major impact on plant development and metabolism

(Rawat et al., 2020) (Table 14.1). The cellular processes of plants grown in low temperatures are affected by cold stress. Studies have shown the detrimental effects of CS on the growth and development of common crops such as rice and potato (Patni et al., 2018; Rihan et al., 2017), and this often leads to a significant loss in crop yield (Wang, Zhang, et al., 2016). Also, CS delays the cell cycle with reduced synthesis, increased plant susceptibility to diseases, increased wilting, and increased levels of foliar necrosis (Rymen et al., 2007). Also, at the reproductive stage of chickpea plants, cold stress causes skimpy rod settings and flower abortion (Nayyar et al., 2005). It is shown statistically that CS results in panicle distortion, low spikelet fertility, and spikelet degradation in temperate regions, which contributes to a 30%–40% reduction in rice yield (Andaya & Mackill, 2003). In another study, pollen sterility, tube deformation, ovule abortion, meager fruit set, grain yield reduction, and flower abscission were the observed impacts of CS during the reproductive stage of cereal crops (Muryoi et al., 2004; Thakur et al., 2010). In another study, it was reported that root nodulation was drastically hindered by cooler rhizospheric temperatures leading to a major reduction in nodule number, size, and formation (Van der Ent et al., 2009). Also, the negative impact of cold stress on stem elongation and jointing stages of wheat often leads to spikelet death. This also results in a reduction in the total grain yield and biomass, alongside causing a severe decline in the number of productive wheat tillers in each plant (Li et al., 2015; Whaley et al., 2004).

Similarly, the photosynthetic system of plants is compromised by cold stress, which causes a sharp decline in the levels of carbon dioxide in the stomata, chlorophyll, photosystem quantum yield, and net photosynthesis (Karabudak et al., 2014). As a result, plant robustness may deteriorate, and nutrient absorption from the soil may become less effective. Reduction in growth and photosynthetic rate of grapevine plantlets was observed by Fernandez, Theocharis, et al. (2012) after the plantlets were exposed to low temperatures. Membrane fluidity, nutrient and water uptake, protein structures, and genetic materials may be impaired, altering the transcriptome of plants. Also, cold stress alters gene expression and slows the rate of

TABLE 14.1 Alterations in plant development and growth induced by cold stress.

Plant	Growth stage	Temperature	Cold-induced alteration	References
Wheat	Stem elongation		Substantial reduction in grain yieldLimits internode extension, denatures spikelets, reduces assimilate transport, restricts dry matter accumulation, reduces grain yield	(Valluru et al., 2012; Whaley et al., 2004)
Lupine angustifolius	Seedling	7°C	Higher activity of α-amylase, higher level of gibberellins, IAA, and kinetin, low development rate and yield	(Płażek et al., 2018)
Tung tree seedling	Seedling	8°C	Reduction in the net photosynthetic rate (P_n), maximum fluorescence (F_m), stomatal conductance (G_s), actual photochemical, quantum efficiency (Φ_{PSII}), and maximum photochemical efficiency (F_v/F_m)	(Zhang et al., 2020)
Soybean	Root	10°C	Inhibition of soybean roots elongation, alterations in the amount of phenolic contents	(Janas et al., 2000)
Capsicum annum	Pollen grains	10–15°C	Decreased pollen viability and seed number per fruit	(Mercado et al., 1997)

biochemical reactions, which impacts plants' cellular metabolism. In another study, the hardness and stiffness of plant cell membranes in cold-sensitive plants alter membrane-related functions including the opening of ion channels and membrane-related electron transfer pathways (Uemura & Steponkus, 1999). In addition, photosynthetic pigment production is influenced by low temperatures, thereby leading to leaf etiolation (Erdal et al., 2015). Cold stress has been studied in various plants, causing calcium (Ca^{2+}) ion influx from extracellular compartments, which alters cell signaling and gene expression (Mahajan & Tuteja, 2005). Exposure to low temperatures can also alter the cellular homeostasis condition of plants resulting in the accumulation of ROS as the main by-product of cellular changes caused by CS. The disintegration of biological macromolecules (e.g., DNA) by ROS such as singlet oxygen and hydrogen peroxide eventually leads to programmed cell death (Xu et al., 2014).

3. Diversity of psychrotrophs that promote plant growth and health

The regions of the world dominated by low temperatures provide a wide range of cold-tolerant microorganisms that can grow at low temperatures and display cold-adaptive plant growth–promoting properties. These organisms include strains of *Bacillus*, *Pseudomonas*, *Pseudoalteromonas*, *Micrococcus*, *Vibrio*, *Arthrobacter*, *Polaribacter*, *Psychrobacter*, *Halorubrum*, *Methanococcoides*, *Methanogenium*, *Cryptococcus*, *Candida*, *Cladosporium*, and *Penicillium* (Feller & Gerday, 2003) with the majority of these strains being bacteria. *Trichoderma* species that exhibit biocontrol efficacy against various pathogens at temperatures between 4 and 10°C were reported by McBeath and McBeath (2009). In addition, *T. koningii*, *T. harzianum*, and *T. viride* from the Himalayan glacial regions were also found to exhibit biocontrol activity at low temperatures (Ghildiyal & Pandey, 2008). Other cold-tolerant plant growth–promoting organisms are listed in Table 14.2.

4. Mechanisms employed by psychrotrophs in promoting plant growth and health

Microbes can also improve a plant's resistance to cold stress. In numerous crops, the advantages of CTMs in determining individual plant tolerance to cold injury have been reported. Despite poorly understood processes, physiological alterations in plants have often been linked to microbial inoculation (Lorv et al., 2014; Omae & Tsuda, 2022). According to Sun et al. (1995), an important mechanism of cold-adapted microbes under cold stress involves the production of antifreeze proteins and their significant affinity for promoting the growth of plant roots (Fig. 14.2).

For example, *Burkholderia phytofirmans* inoculation increased carbon fixation, carbohydrate, phenolic, and proline accumulation while promoting grapevine cold tolerance (Ait Barka et al., 2006; Fernandez, Theocharis, et al., 2012). This indicates that under low nonfreezing temperatures, a cold-adaptive *B. phytofirmans* could enhance a plant's resistance to low temperatures by decreasing the leakage of electrolytes in the plant seedlings (Ait Barka et al., 2006).

Arbuscular mycorrhizal fungi (AMF) also enhance a plant's response to cold stress (Abdel Latef & Chaoxing, 2011; Caradonia et al., 2019). For instance, under normal and cold-stress environments, the inoculation of tomatoes with the AM *Glomus mosseae* improved the plant's growth, antioxidative enzyme activities, and chlorophyll content. In this case, malondialdehyde build-up due to cold stress was reduced by *G. mosseae* inoculation, indicating that *G. mosseae* enhances the reduction in lipid oxidative damage as a result of cold stress (Abdel Latef & Chaoxing, 2011). According to Zhu et al. (2010), during cold stress, maize seedlings

TABLE 14.2 Cold-adapted plant growth–promoting microorganisms.

Origin	Microorganism(s)	Growth temperature	Function	References
Melville Peninsula, Canadian Arctic	*Rhizobium leguminosarum* and *Mesorhizobium* sp.	0°C	Nitrogen fixation	(Prévost et al., 2003)
Canadian Arctic	*Pseudomonas putida* GR12-2	0–35°C	IAA, siderophore, and ACC deaminase synthesis	(Sun et al., 1995; Xu et al., 1998)
Sub-alpine, Indian Central Himalaya	*Pseudomonas putida*	0–35°C	Biocontrol activity and phosphate solubilization	(Pandey et al., 2006)
Sub-alpine, Almora District, Indian Himalaya	*Pantoea dispersa*	4–42°C	Phosphate solubilization, IAA, siderophore, and HCN production	(Selvakumar, Kundu, et al., 2008; Selvakumar, Mohan, et al., 2008)
Soils from Greenwich Island, South Shetland Islands, Antartica	*Pseudomonas* sp.	4–30°C	Phosphate solubilization, IAA, siderophore, and HCN synthesis, biocontrol activity	(Yarzábal et al., 2018)
Antarctic	*Pseudomonas* sp.	4–20°C	Phosphate solubilization, EPS and IAA production	(Berríos et al., 2013)
	Serratia marcescens	4–15°C	Phosphate solubilization, HCN and siderophore production	(Selvakumar, Kundu, et al., 2008; Selvakumar, Mohan, et al., 2008)
Indian Himalayan region	*Rhodococcus erythropolis*	10–15°C	ACC deaminase, IAA and siderophore production, chromium resistance	(Trivedi et al., 2007)
Cold desert of Lahaul and Spiti, Indian trans-Himalayas	*Acinetobacter rhizosphaerae*		Phosphate solubilization, ACC deaminase, IAA, ammonia, and siderophore production	(Gulati et al., 2009)
Admiralty Bay, King George Island, Antarctica	*Pseudomonas frederiksbergensis*	4–18°C	Biocontrol activity	(Melo et al., 2016)
Cold desert area, Mana, Garhwal Himalaya, India	*Paecilomyces hepiali*	4–35°C	Phosphate solubilization	(Rinu & Pandey, 2011)
Pindari glacier region in Indian Himalaya	*Streptomyces griseobrunneus*, *S. griseoluteus*, *S. aurantiacus*, and *S. sampsonii*		Biocontrol activity	(Malviya et al., 2009)
Karaulnaya-2 cave, Karaulensky karstic district, Eastern Sayan Mountain area, Russia.	*Pseudochrobactrum kiredjianiae*	4–35°C	Siderophore, IAA, and ACC deaminase production, biocontrol activity	(Qin et al., 2017)
Rong Tong, Lahaul and Spiti, Indian trans-Himalayan	*Rahnella* sp.	10–37°C	Phosphate solubilization, ACC deaminase, and ammonia production	(Vyas et al., 2010)

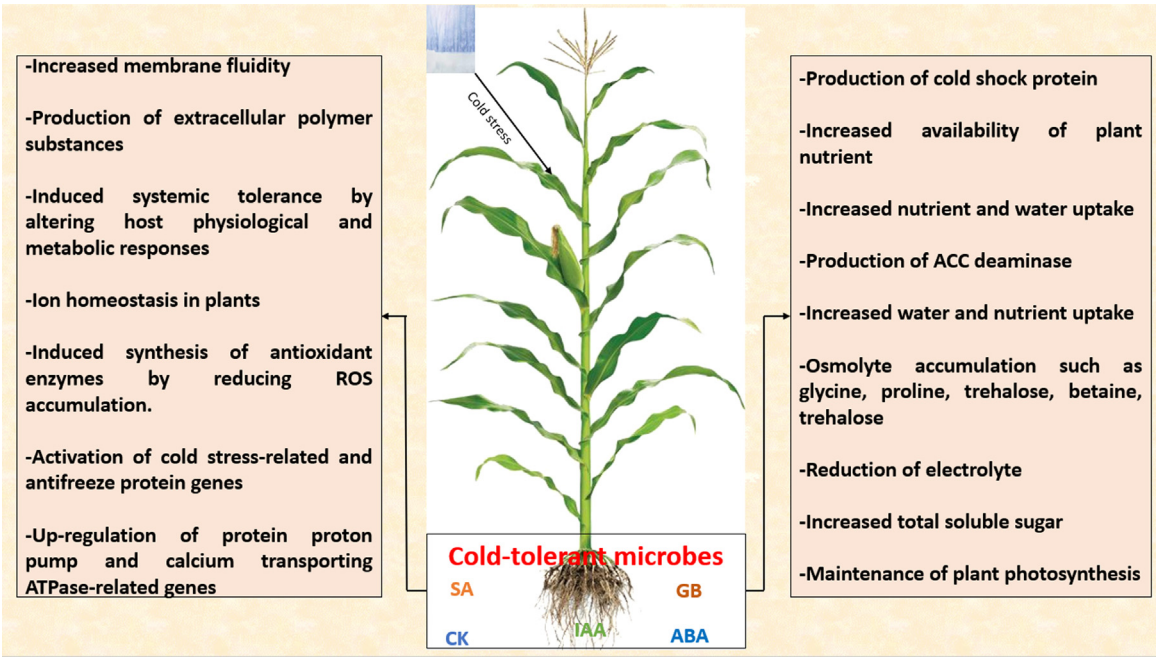

FIGURE 14.2 Diagrammatic representation of different mechanisms used by CTMs for cold mitigation. *ABA*, abscisic acid; *CK*, cytokinin; *GB*, gibberellin; *SA*, salicylic acid.

injected with arbuscular mycorrhizae displayed increased activities of catalase and superoxide dismutase than uninoculated seedlings. Similarly, another study observed an increase in peroxidase and superoxide dismutase enzyme activities in AM fungi colonized seedlings of *T. grandis* (teak plants) subjected to cold stress (Zhou et al., 2012). According to Liu, Chen, et al. (2014), AM fungal colonization under cold stress promotes the activities of plasma membrane ATPase and the build-up of ATP in *Cucumis sativus*, which are responsible for controlling intracellular pH and the generation of electrochemical gradients for active ion transport. At the symbiotic interface near the arbuscule, the plasma membrane H^+-ATPase is active in AM fungi and supplies enough energy for the interactions between the plant and microbe (Gianinazzi-Pearson et al., 1995).

Chen et al. (2013) discovered that flavonoids, phenolics, and lignin rapidly accumulated in cucumber plants after AM inoculation. Additionally, they discovered that AM-inoculated cucumber plants had significantly higher levels of the ROS-inhibiting enzymes caffeic acid peroxidase, cinnamyl alcohol dehydrogenase, glucose-6-phosphate dehydrogenase, guaiacol peroxidase, phenylalanine ammonia-lyase, polyphenol oxidase, shikimate dehydrogenase, and chlorogenic acid peroxidase activity than uninoculated plants exposed to cold stress. Other studies have reported increased sucrose phosphate synthase activities in AM fungus-inoculated rice and maize plants (Liu et al., 2013; Zhu et al., 2015). This suggests that AM symbiosis improves a plant's ability to tolerate cold stress. Liu, Ma, et al. (2014) showed a higher accumulation of trehalose (a disaccharide with a

1,1-glycosidic bond between two α-glucose units) in AM fungus colonized rice exposed to cold stress; this was accompanied by increased expression of trehalose phosphate phosphatase and trehalose phosphate synthase-related genes.

Through an antioxidant scavenging process, *B. phytofirmans*-coated seedlings of grape plants improved plant adaptability and tolerance to cold tolerance (Theocharis et al., 2012). In addition, *B. phytofirmans*-inoculated grapevine plantlets displayed decreased glucose metabolism, which reduced cold-stress sensitivity (Fernandez, Theocharis, et al., 2012). Other physiological alterations in grapevine plantlets inoculated with psychrotolerant bacteria include activation of the genetic machinery linked to the C-repeat binding factor, modifications to the sucrose metabolism pathway, maintenance of the plant's ability to photosynthesize, and a considerable increase in the phenolic contents of the plant (Ait Barka et al., 2006; Fernandez, Theocharis, et al., 2012; Xu et al., 1998). The inoculation of pepper plants with the bacterium *Serratia nematodiphila* at low temperatures improves pepper growth by maintaining high production levels of gibberellic and abscisic acid alongside low production levels of jasmonic and salicylic acid (Kang et al., 2015). This ensures pepper can survive at low temperatures.

According to Chu et al. (2016), AM fungi inoculation increases the tolerance of seedlings of the perennial grass plant *Elymus nutans* to cold by altering the plant's redox balance and activating its reactive oxygen species scavenging system and other stress-associated defense mechanisms. These findings were later confirmed by Pedranzani et al. (2016), who found that inoculating *Digitaria eriantha* plants inoculated with AM fungi exposed to cold conditions led to improvements in the plant's photosynthetic efficiency, shoot dry mass, and activities of ROS-inhibiting enzymes such as ascorbate peroxidase, catalase, and superoxide dismutase, as well as a decrease in hydrogen peroxide and malondialdehyde contents. A summary of other mechanisms is presented in Table 14.3.

5. Microbe-mediated management of cold stress in crops

The relevance of cold-tolerant microbes in agriculture has been expressed through their varying beneficial effects, such as plant growth–promoting potentials, an attribute that is especially important in supporting crops grown under cold-stressed environments (Verma et al., 2017). The effects of these microbes have been explored on different crops, and the potential of cold-tolerant microorganisms in creating an enabling environment to produce cereal crops has been investigated. Some earlier studies have reported that the application of *Pantoea agglomerans, P. fluorescens*, and *Mycobacterium* sp. isolated from soil enhances the growth of winter-grown wheat crops and increases the nutrient uptake efficiency of nitrogen, phosphorous, and potassium at 16°C, although the increase in nutrient uptake is less effective at 26°C (Yadav et al., 2017). Similarly, Kaushik et al. (2002) showed that *Azospirillum brasilense* inoculation could enhance wheat development at suboptimal temperatures. However, effective nutrient absorption facilitation was demonstrated by the impact of *Mycobacterium phlei* strains under both poor and nutrient-rich soils at 38°C and 16°C, respectively.

In a similar study, the enzyme ACC deaminase has been reported to play an active role in decreasing the production of ethylene at low temperatures (around freezing) and thereby aiding the promotion of plant growth and development (Koza et al., 2022). For example, *Serratia marcescens* SRM is a promising cold-tolerant strain that facilitates wheat growth at low temperatures especially in mountainous areas (Yarzábal, 2014). This *S. marcescens* strain promoted plant development at 4°C, stimulating

TABLE 14.3 Summary of microbe-mediated tolerance mechanisms to cold stress in plants.

Microorganism(s)	Plant(s) involved	Growth methods	Mechanisms of actions	References
Pseudomonas sp. NARs9	Wheat	Glasshouse	Phosphate solubilization and IAA production	(Mishra et al., 2009)
Exiguobacterium acetylicum 1P	Wheat	Pot experiments using a glass house	HCN, IAA, and siderophore production; phosphate solubilization	(Selvakumar et al., 2010)
G. mosseae	Tomato	Growth chamber in a controlled environment	Reduction of membrane lipid peroxidation; increase in compounds used for osmotic adjustment, photosynthesis, and activity of antioxidant enzymes	(Abdel Latef & Chaoxing, 2011)
P. lurida M2RH3	Wheat	Pot experiments using a glass house	Production of HCN, siderophores, and IAA and solubilization of phosphate. Increase in nutrient uptake including iron and nitrogen.	(Selvakumar et al., 2011)
Pseudomonas sp.	*Deschampsia antarctica*	Petri dishes	Phosphate solubilization	(Berríos et al., 2013)
Pseudomonas sp.	Lentil	Pot experiment using a greenhouse	–	(Bisht et al., 2013)
P. jesenii MP1	*Vignamungo* (L.), *Cicer arietinum* (L.), *Cajanus cajan* (L.), and *Vignaradiata* (L.)	Pot experiment	Increase in the content of chlorophyll, phosphorous, and the activity of nitrate reductase	(Saurabh et al., 2014)
Trichoderma gamsii NFCCI 2177	Wheat, soybean, lentil and maize	Greenhouse experiment	Solubilization of phosphate, increased chitinase activity, salicylic acid, and ammonia production	(Rinu et al., 2014)
P. frederiksbergensis OS211 and *Flavobacterium* sp. OR306	Tomato	Growth chamber in a controlled environment	Ethylene reduction, increased expression of cold-induced LeCBF3 and LeCBF1 genes as well as reduction in the level of ACO and ethylene-responsive expression transcription factor 13 (ETF-13)	(Subramanian, Mageswari, et al., 2015)
P. frederiksbergensis OS211, *F. glaciei* OB146, *P. frederiksbergensis* OS261, and *P. vancouverensis* OB155	Tomato	Controlled plant growth chamber	Reduced membrane damage, increased synthesis of proline, and antioxidant enzymes	(Subramanian et al., 2016)
Dyadobacter sp.	Chickpea, green gram, black gram, finger millet, and pigeon pea.	Pot trials	Increase in the content of chlorophyll and activity of leaf nitrate reductase	(Kumar et al., 2018)

TABLE 14.3 Summary of microbe-mediated tolerance mechanisms to cold stress in plants.—cont'd

Microorganism(s)	Plant(s) involved	Growth methods	Mechanisms of actions	References
P. fluorescens, *P. fragi*, *P. chlororaphis*, *B. frigoritolerans*, and *P. proteolytica*	Bean	Controlled plant growth chamber	Decreased lipid peroxidation content, freezing injury, lipid peroxidation, and ice nucleating activity alongside a reduction in the level of reactive oxygen species, and an increase in antioxidant enzyme activity	(Tiryaki et al., 2019)

phosphorus solubilization, as well as HCN, siderophore, and indole acetic acid production at 15°C. Furthermore, seed treatment with this strain of *S. marcescens* showed increased nutrient absorption and enhanced wheat biomass under a low-temperature regime. Similarly, some strains of *Pseudomonas* have demonstrated excellent cold tolerance and plant growth (canola and wheat) promotion qualities at 5−10°C temperature under greenhouse and growth chamber conditions, thereby showing potential as seed bioinoculants (Katiyar & Goel, 2003). Thus, seed bacterization considerably increased plant biomass and produced better results than untreated seedlings. The reason for this has been ascribed to the *Pseudomonas* primed plant seedling leading to an increase in the total chlorophyll content, free proline, anthocyanin, starch, and total phenolics, with a drastic reduction in the K^+/Na^+ ratio and the electrolyte leakage (Kumar et al., 2022). Strain *Pseudomonas putida* GR12-2 used by Sun et al. (1995) produces ACC deaminase, IAA, and siderophores and contributes to a low level of nitrogen fixation in addition to producing antifreeze protein.

In a study conducted by Selvakumar et al. (2011), *P. lurida* M2RH3 was identified as a possible psychrotolerant growth−promoting bacterium that can enhance wheat growth. This strain produces siderophores, IAA, and hydrogen cyanide while solubilizing phosphate. This is in addition to the considerable increase in the chlorophyll A concentration and plant biomass recorded when the wheat (cv. HS507) seeds were inoculated with *B. amyloliquefaciens* (IARI-HHS2-30). In addition, the discovery of *Pseudochrobactrum kiredjianiae* strain A4, a cold-tolerant bacterium with broad-spectrum growth-promoting action and biocontrol potential (Fu et al., 2017). The strain that boosted the activities of defense enzymes in wheat plants was also found to improve the physiological characteristics of the plants for efficient suppression of the mycelia growth of the fungal pathogen *Rhizoctonia cerealis*. Hence, cold-adapted microbes offer a promising means of sustaining crop health and growth in cold environments.

Aside from cereal crops, the cold-tolerant activities of microbes have also been reported in legumes. An earlier investigation conducted with clover plants at 10°C showed increased nitrogenase activities, fast nodulation and enhanced growth following treatment with *Rhizobium trifolii* strains obtained from subarctic areas of Scandinavia (Lipsanen & Lindström, 1986). Similarly, the symbiotic relationship of rhizobia isolates with the forage legume *Onobrychis viciifolia* obtained from arctic environments was demonstrated and this results in higher activities of nitrogenase at cold temperatures compared to isolates of rhizobia from the temperate regions (Maróti & Kondorosi, 2014). Interestingly, no discernible variations in nitrogenase activity were recorded across strains from the two areas at higher temperatures (20°C). In addition, the inoculation of soybeans with *B. japonicum* strain

was found to increase soybean yields in a study conducted in Guelph, Ontario, Canada (Hume & Shelp, 1990). Psychrotolerant strains of *Bradyrhizobium japonicum* have been reported to be beneficial in enhancing the nitrogen-fixing capacity and nodulation in soybean plants grown at low chilling temperatures (Kushwaha et al., 2020, pp. 269–292). Strain *R. leguminosarum*-PR1 and *Pseudomonas* spp. strains, which are cold-tolerant, protect lentil plants against cold stress and improve iron absorption, uptake of nutrients, and plant development (Mishra et al., 2011). In another study, a mutant strain of *P. fluoresens* ATCC13525 with a significantly increased level of siderophore production facilitated the development of *Vigna radiata* (mung bean) with improved rhizosphere competitiveness (Rani & Goel, 2012). Moreover, in a study of the psychrotrophic actinobacterium *Rhodococcus erythropolis*, a toxic chromium (Cr^{6+}) ion concentration was transformed to less harmful chromium (Cr^{3+}) ions, thereby supporting the growth of pea plants (Subramanian et al., 2011).

The improved resistance of *Proteus vulgaris* to salt, drought, and cold stress was demonstrated with the plant's symbiotic association with arbuscular mycorrhiza, where the arbuscular mycorrhiza manages the hydraulic properties of the root, which is closely linked with phosphorylation state and the regulation of the level of the PIP2 protein (Pedranzani et al., 2016). The IAA-producing bacterium *Acinetobacter rhizosphaerae* can promote the growth of the leguminous plant *Hippophae rhamnoides*, which is mostly found in the cold Himalayan deserts (Subramanian et al., 2011). Soybean plants treated with *Trichoderma gamsii* NFCCI 2177 recorded growth increases even under cold temperatures (Rinu et al., 2014). In addition, the psychrotolerant strain *Pseudomonas jesenii* MP1 has been reported to promote the growth of *Cajanus cajan* (pigeon pea), *V. radiata* (mung bean), *V. mungo* (black gram), and *Cicer arietinum* (chickpea) (Saurabh et al., 2014).

The ability of psychrotolerant *Dyadobacter* sp. to promote plant development in four legumes (chickpea, green gram, pigeon pea, and black gram) and finger millet was reported by Kumar et al. (2018). They showed that the bacterium could thrive on nitrogen-deficient media at both 10°C and 28°C and obtained positive *nifH* amplification results that support the psychrotolerant bacterium's diazotrophic nature. Furthermore, a pot trial-based investigation revealed that *Dyadobacter* sp. from the cold western Indian Himalayan region possessed the ability to boost pulse and finger millet development through N_2 fixation (Puranik et al., 2021, pp. 379–411). Plants treated with this bacterium also showed an increase in chlorophyll content and nitrate reductase activity, alongside phosphorous content. Thus, psychrotolerant microorganisms may be used to boost plant development in cold-climate agriculture due to their capacity to promote plant growth.

Other crops of agricultural importance in which microbes have been utilized in ameliorating cold stress include grapevine, where *Burkholderia phytofirmans* strain PsJN inoculated grapevine plantlets were resistant to cold (Ait Barka et al., 2006). Furthermore, plantlets treated with *B. phytofirmans* PsJN were observed to possess higher amounts of cold-stress-related metabolites and gene transcripts than their untreated counterparts (Wang, Wang, et al., 2016). *Burkholderia phytofirmans*-induced cold tolerance in grapevines was found to function through trehalose metabolism (Fernandez, Vandesteene, et al., 2012). This investigation revealed an association between the capacity of inoculated grapevine plantlets to overcome cold stress and the presence of proline, phenolics, and starch. Similarly, the growth of canola crops was also significantly enhanced by *P. putida* GR12-2 and UW4 at low temperatures (Siddikee et al., 2015). Whereas, coating of *G. norvegicum* seeds with the fungus *Glomus claroideum* (Kushwaha et al., 2020, pp. 269–292) showed a significant increase in

arbuscular mycorrhiza colonization, plant biomass, percentage of seed germination, and shoot nitrogen content at 8°C, as opposed to the results obtained at 15°C. Abdel Latef and Chaoxing (2011) conducted additional research into the arbuscular mycorrhizal *G. mosseae* and showed the potential of the fungus to improve cold tolerance in tomato plants. The organism also promotes plant growth and increases the host biomass through the prompt secretion of osmotic regulation compounds. The secretion also helps in controlling antioxidant and lipid peroxidation of the membrane, as well as increases the production of photosynthetic pigments. Other investigations have presented the possible use of psychrotolerant bacteria (*F. glaciei* OB146, *P. frederiksbergensis* OS211, *P. frederiksbergensis* OS261, and *P. vancouverensis* OB155) in cold tolerance in tomatoes at low nonfreezing temperatures (Subramanian et al., 2016), while similar experiments by Matsubara et al. (2009) showed the usefulness of AMF inoculation of various species in promoting the development of strawberry plants. More specifically, AMF inoculation increases the cold-stress tolerance level of *Eucalyptus nutans* seedling by ROS scavenging, modifying the redox balance, and activating stress-related defense systems (Chu et al., 2016).

6. Major constraints and future outlook

Cold-tolerant microbes are especially of importance in managing low-temperature stress in agricultural practices in cold-weather regions. Although the application of microorganisms as biological intervention is not new in agriculture, it provides a unique tool for attaining food sufficiency in adverse conditions such as a cold-stress environment (Zubair et al., 2019). There are several factors that need to be addressed to take full advantage of this essential property in ensuring the efficient management of crops in adverse situations. This includes the development of efficient laboratory techniques to enable the mass production of cold-tolerant microbial inoculants, possibly including processes of solid-state fermentation and bioencapsulation. Increasing the economic value, ecological relevance, and social significance of these microbes requires scientific solutions for improved crop production in cold environments. It is imperative that the molecular and genetic interactions between plants, soil, and cold-tolerant microorganisms, as well as their complexity, be thoroughly investigated through laboratory and field experiments. In addition, genomic data on cold-tolerant microorganisms will ease the identification of the experimentally validated novel secondary metabolites that are involved in adaptation to cold ecological niches and the enhancement of beneficial traits for robust cold-temperature agriculture. Hence, it is important to identify and assess various microbial strains for their ability to withstand cold stress to create efficient microbial consortia to address the challenges posed by this environment.

Under the present climate change scenario, the psychrophilic bacteria, which can thrive in both cold environments and at normal ambient temperature (i.e., up to ~35°C), can significantly impact agriculture. Considering this, it is crucial that we evaluate and ensure potential cold-tolerant microbe-based technologies that are effective in field deployment. Meanwhile, another highly effective tactical tool for increasing crop yields in cold climates is the exploration of efficient microbial consortia of various types of compatible cold-tolerant microbes that exhibit synergistic associations with symbionts as well as stable plant growth-promoting characteristics. Furthermore, other potential techniques in cold-tolerant agriculture include the use of microbial elicitors to improve plant resistance to cold stress and the insertion of microbial genes into cold-stressed plants.

7. Conclusions

Cold-tolerant microorganisms contribute to various advantageous processes that can improve the CS tolerance level in different crops globally and throughout the agroecosystem. Thus far, the main aim of the research has been to classify and identify specific fungal, AM, and bacterial species that can facilitate plant growth at cold temperatures. Therefore, to understand the mechanism of plant–CTM interactions, concentrated and targeted research endeavors are needed, paying special attention to the peculiarities of high-altitude agriculture. Identifying and functional cataloging of CTMs can minimize the toxicity and harmful effects of heavy metals of agro-waste, respectively, on plants. These are two exciting promising areas where microbiological research may help to develop biodegradative processes that function in cold environments.

Author contributions

AEF and OOB conceived the ideas. AEF, OMO, AOA, and ASA developed the manuscript. BRG and OOB provided professional input, proofread, and reviewed the work. All authors approved the submitted version.

Funding

This work was supported by the National Research Foundation of South Africa grants (UID132595).

Acknowledgments

AEF, OMO, AOA, and ASA gratefully acknowledged the North-West University for a Postdoctoral fellowship. OOB appreciates the National Research Foundation, South Africa, for the grant (UID132595) that has been supporting her research.

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