14 Microbes for Cold Stress Resistance in Plants: Mechanism, Opportunities, and Challenges

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Abstract

Cold stress (CS) is one of the major hindrances for quality crop production and global food security. Under cold environment, different kinds of alterations in the biochemical, physiological, and molecular processes of plants have been observed. Hence, it becomes mandatory to develop eco-compatible, sustainable, and economically sound options for ensuring quality food grain production of high mountainous regions. The use of cold-tolerant microbes (CTM) enhances growth of agricultural crops under low temperature environment. Additionally, it provides an economically captivating and environment-friendly means for protecting agricultural crops from cold stress injuries. They can also trigger crop growth by improving nutrition acquisition, regulating release of plant hormone and siderophores in addition to the activation of antioxidant system under low temperature conditions. As a result, this plant–CTM interaction under cold environment is vital and CTMs may act as a principal cold stress engineer to answer global agricultural tribulations of high altitude. In this chapter, attempts have been made to explore about CTM and their mechanism of action to boost agricultural production in sustainable manner under low temperature environment.

Keywords

Agriculture · Cold · Microbes · Stress · Sustainability · Temperature

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14.1 Introduction

Cold stress (CS), one of the most commonly occurring abiotic stresses, frequently threatens the sustainability of agriculture through wide range of impacts on plant growth and production. It is well known fact that about two third of the world's cumulative terrestrial area is annually affected by below freezing point temperatures and three fourth portion of the Earth's biosphere's temperature is below 5 °C (Awasthi et al. 2019; Margesin and Collins 2019; Larcher 2001; Baldi et al. 2011). In agricultural crops, CS affects several biological processes, including membrane damage and alterations in photosynthetic apparatus and starch metabolism of plant cells (Zhuang et al. 2019). Suzuki and Mittler (2006) observed cold stress-induced cellular changes in plants and mentioned rapid synthesis of reactive oxygen species (ROS) and disruption in cellular homeostasis as major alterations in plant system. ROS include singlet oxygen (O_2^-), hydrogen radical ($HO^·$), and hydrogen peroxide (H_2O_2) molecules that break large biomacromolecules (e.g., DNA, proteins, carbohydrates, and lipids) and responsible for complete death of plant tissue and cells (Gill and Tuteja 2010). Under such circumstances, traditional plant breeding tactics or genetic transformations are not observed as ideal options for improving agricultural crops by incorporating traits for frost hardiness (Kasuga et al. 1999). Fowler and Thomashow (2002) mentioned that property of cold resistance is not controlled by a single major gene, but involves multifaceted and convoluted mechanisms working simultaneously to guard plant cells from cold stress injury (Fowler and Thomashow 2002). Therefore, CTM (=psychrophiles and psychrotrophs) can play prominent role in enhancing plant resistance to chilling stress (Subramanian 2011). The maximum temperature for growth of psychrophiles lies at ≤15 °C, while psychrotrophic microbes showed their optimum growth at ≥15 °C (Srivastava et al. 2013; Moyer and Morita 2007). Utilizing such CTM can assuage cold stress in various crop plants, therefore emerging as a prospective and a sustainable option for solving chilling problem of high altitude agriculture. For instance, Mishra et al. (2009) inoculated cold-tolerant strain of *Pseudomonas* sp. derived from the rhizosphere of *Amaranthus* sp. and observed significant increments in the growth of wheat seedlings as a result of microbial inoculation (Mishra et al. 2009). Significant rise in nodulation and nitrogen fixation capabilities of soybean crop under low temperatures have been observed after plant inoculations with cold-tolerant strains of *Bradyrhizobium japonicum* (Zhang et al. 2003). Similarly, *Burkholderia phytofirmans* inoculated to grapevine seedlings have been reported to improve CS tolerance capacity by plummeting electrolyte leakage (Ait Barka et al. 2006). Additionally, plant inoculations with different types of plant growth-promoting rhizobacteria including *Azospirillum brasilense, Bacillus megaterium*, *B. subtilis,* and *Raoultella terrigena* have been reported as potential alleviator for minimizing the deleterious effects of chilling injury in barley and wheat seedlings by regulating freezing injury and antioxidant enzymes activity (Turan et al. 2013). Based on the available research findings, it seems that the possible mechanisms by which CTM could be advantageous to agricultural crops involve: (1) rapid synthesis of

1-aminocyclopropane-1-carboxylate deaminase (ACC) enzyme for minimizing cold stress triggered ethylene production (Shi et al. 2012; Subramanian et al. 2015); (2) enhanced efficiency of biological nitrogen fixation processes for ensuring sufficient available nitrogen (N_2) for plant under cold stress; (3) production of phytohormones [e.g., abscisic acid (ABA), gibberellic acid (GA), indole-3-acetic acid (IAA)]; (4) release of small and high affinity iron-chelating compounds by CTM; (5) activation of antioxidant enzymes machinery; and (6) solubilization and mineralization of nutrients, etc. Based on the existing research knowledge base on microbial mediated cold stress management, an effort is made to comprehend the current understanding of cold stress management of plants using microbes in this chapter. Additionally, attempts has been made to present a synthesis of budding trends in the field of crop stress microbiology and discuss plausible directions for future microbiological exploration that will offer more sound and erudite predictions regarding the role of cold-tolerant microbes in sustaining agriculture of high altitudes.

14.2 Cold Stress and Its Impact on Crop Growth and Yield

Cold stress (CS) is one of the biggest challenges of high altitude agriculture and resulted in significant hampering of plant growth and metabolism (Kashyap et al. 2018). Practically, CS influences entire cellular functions of the plants grown under low temperature. It has been well documented that CS negatively prejudices the normal crop growth and development (Patni et al. 2018; Rihan et al. 2017; Yadav 2010). Earlier published reports clearly highlighted the negative impacts of CS on quality growth of various agricultural crops including rice, cotton, tomato, potato, muskmelons, and sugarcane (Hussain et al. 2018; Ghadirnezhad and Fallah 2014; Zhu et al. 2013; Zhao et al. 2012; Thakur et al. 2010; van der Ploeg and Heuvelink 2005). Generally, low temperature stress severely affects the seedling vigor, lowers the seed germination rate, delays plant growth, and results in severe yield loss (Wang et al. 2016a, b; Ruelland et al. 2009; Oliver et al. 2007; Cruz and Milach 2004; Kang and Saltveit 2002). It also causes foliar necrosis, hinder leaf growth, protract cell cycle with diminishing cell production, wilting, and enhance susceptible level of plants against different kinds of pathogens and diseases (Rymen et al. 2007; Korkmaz and Dufault 2001). CS at reproductive stage of chickpea plant caused flower abortion and skimpy pod setting (Nayyar et al. 2005). Statistically, it has been predicted that CS in temperate regions is accountable for 30–40% drop in rice yield because of spikelet deterioration, meager spikelet fertility, and panicle deformation (Andaya and Mackill 2003). Similarly, Thakur et al. (2010) mentioned that CS occurred during reproductive phase of cereal grain crops lead to pollen tube deformation, pollen sterility, ovule abortion, flower abscission, meager fruit set, and drastic reduction in final grain yield. In case of legume crops, Junior et al. (2005) reported that chilled rhizospheric temperature drastically hinders root nodulation process and results in significant declination in nodule size, nodule number, and growth rate of nodule formation. Similarly, CS during wheat stem elongation stage resulted in spikelet death and reduction in biomass accretion and total grain yield (Whaley et al. 2004). Moreover, severe decline in the number of productive wheat tillers per plant has been noticed when CS occurred at jointing and booting stages of wheat (Li et al. 2015). CS can also attack photosynthetic machinery of plants and hence responsible for drastic decline of chlorophyll content, stomatal carbon-di-oxide (CO_2) concentration, net photosynthesis, and photosystem quantum yield (Karabudak et al. 2014; Mishra et al. 2011). This in turn can deteriorate plant robustness and reduce nutrient uptake efficiency from soil. Fernandez et al. (2012) noticed that exposure of grapevine plantlets to low temperature resulted in growth reduction and declination of photosynthetic rate of plantlets. Chinnusamy et al. (2007) mentioned that CS impairs membrane fluidity, disrupts genetic material (DNA and RNA) and protein structures, obstructs nutrient and water uptake, and causes notable modifications in the plant transcriptome. Additionally, it also severely affected cellular metabolism by declining the rates of biochemical reactions and reprogramming gene expression. At low temperature, cell membranes of cold susceptible plants become stiff and hard that further leading to significant level of disturbances in membrane-related processes, for instance, opening of ion channels and membrane-related electron transfer reactions (Uemura and Steponkus 1999). In turn, this can influence plant physiology negatively by reducing photosynthetic and growth rates (Ait Barka et al. 2006). Erdal (2012) observed that low temperature pessimistically influence the photosynthetic pigment production and thus cause etiolation in leaves. Cell signaling and gene expression alteration due to calcium (Ca^{2+}) ion influx from extracellular compartments triggered by cold stress in various plants has been well documented (Polisensky and Braam 1996; Monroy and Dhindsa 1995; Mahajan and Tuteja 2005). Exposure to low temperature alters cellular homeostasis status of the plant and as a consequence accumulation of reactive oxygen species (ROS) observed as a key product of CS triggered cellular modifications. ROS, such as hydrogen peroxide (H_2O_2), singlet oxygen (O_2^{-}), and hydrogen radical ($HO^{\cdot}$), disintegrate biological macromolecules (e.g., DNA, carbohydrates, lipids, and proteins) and ultimately results in programmed cell death (Xu et al. 2011; Ruelland et al. 2009).

14.3 Diversity of Plant Growth-Promoting Cold-Tolerant Microbes

Low temperature environment dominates major portion of Earth's biosphere. It acts as a reservoir of CTMs with the ability to thrive with low metabolic activity at subzero temperature (Kumar et al. 2019). Generally, psychrophilic bacteria include *Arthrobacter*, *Bacillus, Flavobacterium, Micrococcus, Moraxella, Moritella, Pseudoalteromonas*, *Pseudomonas*, *Polaromonas*, *Psychrobacter*, *Psychroflexus*, *Polaribacter*, and *Vibrio*. Besides this, several other types of cold-tolerant microbial species representing Archaea, fungi, and microalgae have been reported (Feller and Gerday 2003). Johnson et al. (1987) documented the presence of *Trichoderma* strains in cold climatic conditions of Alaska and Tennessee. Later, McBeath

(1995) identified several strains *Trichoderma* spp. showing biocontrol activity towards different kinds of pathogenic fungi at low temperatures ranged from 4 to 10 °C. Ghildiyal and Pandey (2008) also isolated cold-tolerant strains of *T. harzianum, T. koningii* and *T. viride* displaying biocontrol abilities from glacial sites of Indian Himalayan soil. Prevost et al. (1999) identified cold-tolerant strains of *Mesorhizobium* sp. and *Rhizobium leguminosarum* from Canadian soils. Later, a superior strain of *Sinorhizobium meliloti* adapted for nodulation of alfalfa at low temperatures have been described by Prevost et al. (2003). Pandey and colleagues (2002) identified *Pseudomonas corrugata* strains as cold-tolerant phosphate solubilizer. Similarly, siderophore producing cold-tolerant mutant of *P. fluorescens* has been generated by Katiyar and Goel (2004). Negi et al. (2005) explored Garhwal region of Indian Himalayas and documented several strains of *Pseudomona*s with strong cold adaptation. Additionally, these strains were identified as siderophore producer with excellent plant growth-promoting features at wide range of temperature (4–25 °C). Similarly, microbial exploration of subalpine regions of central Himalayas of India by Pandey and colleagues (2006) resulted in the identification of cold-adaptive *P. putida* strains with phosphate solubilizing and antagonistic capabilities. Cold tolerance and plant growth-promoting features of *Serratia marcescens* strain SRM obtained from *Cucurbita pepo* have been described by Selvakumar et al. (2008a, b). Later, *P. corrugata* NRRL B-30409 mutants with increased potential of organic acid production, phosphate solubilization, and plant growth promotion at chilling temperature have been reported by Trivedi and Sa (2008). Gulati et al. (2009) described *Acinetobacter rhizosphaerae* from the cold deserts of Himalaya and established its high competence for crop growth promotion (Gulati et al. 2009). *Exiguobacterium acetylicum* strain 1P showing siderophores production and biocontrol capabilities from North Western Himalayas of India were reported by Selvakumar et al. (2009). Malviya et al. (2009) explored glacial sites of the Indian Himalayas and reported psychrotolerant *Streptomyces* strains with strong antagonistic and chitinolytic activity. Besides these features, *Streptomyces* strains were also found to curb the growth of multiple phytopathogenic fungi. Later, Selvakumar and associates (Selvakumar et al. 2009) also reported cold-adaptive *Pseudomonas fragi* strain with excellent phosphorous solubilization capability. Vyas and colleagues (2010) reported a series of phosphorous solubilizing fluorescent *Pseudomonas* strains displaying tolerance towards salinity, alkalinity, temperature, calcium salts, and desiccation-induced stresses from trans-Himalayan regions of India. Singh et al. (2011) found two very efficient strains of *Aspergillus niger* which demonstrated excellent solubilizing activity at 20 °C in the presence of tri-calcium phosphate. Similarly, Rinu and Pandey (2011) reported *Paecilomyces hepiali* as a cold-adaptive phosphate solubilizing fungus from rock soil of Indian Himalayas. Sati et al. (2013) identified several cold-tolerant strains of genus *Bacillus*, *Penicillium,* and *Pseudomonas* along with yeasts and actinomycetes from soil under potato farming in cold regions of Indian Himalayas. Further, they observed that the isolated microbes were endowed with strong antagonistic and multifarious plant growth-promoting attributes. Several cold-adapted nitrogen-fixing bacterial species were isolated from Himalayan soil, and proteome of psychrophilic diazotroph *Pseudomonas migulae* S10724 (Suyal et al. 2014) and psychrotroph *Pseudomonas palleroniana* N26 (Soni et al. 2015) was studied to document the protein profile under low temperature diazotrophy. Yadav and coworkers (2015) have mentioned that cold-adapted *Arthrobacter nicotianae, Brevundimonas terrae,* and *P. cedrina* can display diverse plant growth-promoting features. Later, it has been observed that the bacteria isolated from root nodule of pea crop cultivated under low temperature environment exhibited excellent plant growth-promoting attributes in addition to strong biofertilizer capabilities under CS conditions (Meena et al. 2015). Verma and associates (2015) identified cold-adaptive bacterial strains of genus *Arthrobacter*, *Acinetobacter Bacillus*, *Bordetella*, *Providencia*, *Pseudomonas,* and *Stenotrophomonas* associated with wheat seedlings in northern hill zone of India. Fungal diversity in soil at higher altitudes of Sikkim and Uttarakhand Himalaya has shown that *Penicillium*, *Aspergillus*, *Epicoccum*, *Fusarium*, *Myrothecium*, *Cladosporium*, *Paecilomyces*, *Gangronella,* and *Trichoderma* were the most abundant and diverse genus (Rai and Kumar 2015). *Amanita*, *Russula*, *Boletus*, *Lactarius*, *Suillus,* and *Hygrophorus* are the common ectomycorrhizal fungal genera associated with oaks and conifers in temperate forest of Western Himalaya (Wang et al. 2015). Kumar et al. (2018) documented *Dyadobacter* sp. as a potential growth-promoting potential psychrotolerant from Bhowali, which is a temperate region of Western Indian Himalaya. Qin et al. (2017) identified cold-adapted bacterium *Pseudochrobactrum kiredjianiae* from cave soil of Russia. Tiryaki et al. (2019) reported cold-tolerant bacterial isolates belonging to *Brevibacterium frigoritolerans, P. chlororaphis*, *P. fluorescens*, *P. fragi,* and *P. proteolytica* from foliage apoplast of *Colchicum speciousum*, *Draba nemorosa*, *Erodium cicutarium*, *Galanthus gracilis,* and *Scilla siberica* plants (Tiryaki et al. 2019). Gautam et al. (2019) identified a psychrotrophic *Virdibacillus arenosi* PH15 strain from rhizosphere of *Podophyllum hexandrum* Royle, a medicinal plant widely grown in Sangla valley of Himachal Pradesh, India, and characterized for various plant growth-promoting attributes. Similarly, *Arthrobacter humicola*, *Brevibacillus invocatus*, *Pseudomonas mandelii,* and *Pseudomonas helmanticensis* have been documented as psychrophilic diazotrophs from high altitude Gangotri soil ecosystem (Kumar et al. 2019). More recently, Awasthi et al. (2019) documented and characterized cold-adaptive *Pseudomonas koreensis* P2 strain from cold desert of Arunachal Pradesh (India).

14.4 Mechanism of Microbial Mediated Cold Stress Tolerance in Crop Plants

The beneficial effects of CTMs in determining specific plant responses that are connected with cold injury tolerance have been reported in several crops. Sun et al. (1995) highlighted that a major mechanism of CTMs under CS could be efficient synthesis and release of antifreeze proteins and their strong affinity with plant root growth promotion. For instance, cold-adaptive *B. japonicum* strain could enhance nodule formation and nitrogen fixation efficiency in soybean crop under low non-freezing temperature (Mishra et al. 2009), while *Burkholderia phytofirmans* inoculation could improve chilling resistance by tumbling electrolyte leakage in grapewine seedlings (Ait Barka et al. 2006). Zhu and associates (2010) indicated that arbuscular mycorrhizae (AM) inoculated maize seedlings had higher superoxide dismutase (SOD) and catalase (CAT) activities than nonmycorrhizal (NM) seedlings under CS. Abdel Latef and Chaoxing (2011) revealed that the AM fungus alleviates CS injury in tomato plants by plummeting membrane lipid peroxidation and enhancing accumulation of osmotic adjustment compounds, antioxidant enzyme, and photosynthetic pigments. Similar enhancements in the activities of SOD and peroxidase (POD) enzymes have been noticed by Zhou et al. (2012) in AM colonized *Tectona grandis* seedlings under CS. Later, it has been explained by Liu et al. (2014a) that under CS, AM colonization stimulates plasma membrane ATPase activities and ATP accumulation in *Cucumis sativus* plants that in turn accountable for regulation of intracellular pH and electrochemical gradient generation for active ion transport (Kim et al. 2013). The plasma membrane H^+-ATPase is active in AM and provides sufficient energy for plant–microbe exchanges at the symbiotic interface around arbuscule (Gianinazzi-Pearson et al. 1995). Further, it has been observed that AM inoculation is responsible for upregulated expression of proton pump and calcium-transporting ATPase-related genes (*CsHA2*, *CsHA3*, *CsHA4*, *CsHA8*, *CsHA9*, *CsHA10*, *CA1*, and *CA9*) in root zone of cucumber seedlings under CS. Chen and coworkers (2013) noticed that AM inoculation in cucumber plants triggered rapid build up of phenolics, flavonoids, and lignin compounds. Further, they also observed significant and high level activities of phenylalanine ammonia-lyase, shikimate dehydrogenase, glucose-6-phosphate dehydrogenase, cinnamyl alcohol dehydrogenase, polyphenol oxidase, guaiacol peroxidase, caffeic acid peroxidase, and chlorogenic acid peroxidase in AM inoculated cucumber plants than non-AM plants under CS. Parallel reports regarding the enhanced activities of sucrose phosphate synthase (SPS) in AM inoculated maize and rice plants have been demonstrated several researchers (Liu et al. 2013; Zhu et al. 2015), which further indicates the sucrose metabolism role in improving CS tolerance capability of plants due to AM symbiosis. Liu et al. (2014b) demonstrated that increase in the expression of trehalose phosphate phosphatase (TPP) and trehalose phosphate synthase (TPS)-related genes (OsTPS1, OsTPS2, and OsTPP1) could enhance trehalose biosynthesis and higher trehalose accumulation in the AM colonized rice plants under CS. Endophytic *Burkholderia phytofirmans* PsJN primed grape seedlings enhanced cold tolerance and adaptation process of plant via antioxidant scavenging process (Theocharis et al. 2012). Further, modulation of carbohydrate metabolism is involved in minimizing chilling stress in inoculated grapevine plantlets with *Burkholderia phytofirmans* PsJN (Fernandez et al. 2012). Some other physiological changes such as activation of gene machinery linked with C-repeat binding factor (*CBF*), alterations of sugar metabolism pathway, maintenance of plant photosynthetic ability, and significant rise in the total phenolic contents have been observed in grapevine plantlets inoculated with psychrotolerant bacteria (Fernandez et al. 2012; Mishra et al. 2011; Ait Barka et al. 2006). Fernandez et al. (2012) experimentally confirmed that trehalose metabolism is involved in

Burkholderia phytofirmans mediated cold resistance in grapevine plantlets. Similarly, in case of arbuscular mycorrhiza (AM), Chen et al. (2013) observed that under cold stress significant rise in the production of total phenols and flavonoids occurred in AM inoculated cucumber seedlings than non-AM seedlings. Turan et al. (2013) mentioned that inoculation of *Azospirillum brasilense, B. megaterium*, *B. subtilis*, and *Raoultella terrigena* in wheat and barley helped in recovering plants from cold injury by maintaining antioxidant enzymes activity as well as minimum freezing injury. Further, Subramanian et al. (2015) also reported the enhanced level of cold acclimatization gene(s) expression and antioxidant activity in *P. frederiksbergensis* OS261 and *P. vancouverensis* OB155 inoculated tomato (*Solanum lycopersicum*) plants is involved in shielding tomato from low temperatures stress. Subramanian et al. (2016) reported that *P. frederiksbergensis* OS211*, Flavobacterium glaciei* OB146*, P. vancouverensis* OB155, and *P. frederiksbergensis* OS261 conferred chilling resistance in tomato seedlings via activation of antioxidant enzymes, rapid proline synthesis, and membrane damage minimization under low temperature (15 °C) exposure. Kang et al. (2015) documented that application of *Serratia nematodiphila* enhances pepper growth under low temperature by maintaining the high level gibberellic acid (GA4) and abscisic acid (ABA) production and low levels of salicylic acid (SA) and jasmonic acid (JA). Chu et al. (2016) reported that like bacteria, arbuscular mycorrhizal fungi (AMF) inoculation also improves *E. nutans* seedlings tolerance to cold stress by modulating redox balance by activating ROS scavenging system and other stress-related defense mechanisms. Later, these observations have been supported by the studies of Pedranzani et al. (2016) that improved photosynthetic efficiency, shoot dry mass, and enzymatic activities of CAT, APX, and SOD with a decrease in H_2O_2 and MDA contents were noticed after inoculation of *Digitaria eriantha* plants with AM under low temperature conditions. Tiryaki et al. (2019) revealed that inoculation of bean (*Phaseolus vulgaris* L.) seedlings with bacterial (*B. frigoritolerans, P. fragi*, *P. chlororaphis*, *P. fluorescens,* and *P. proteolytica*) assisted in regulating freezing injury, ice nucleating activity, and lipid peroxidation content along with ROS generation. In addition, the inoculations of these strains improved the functionalizing of apoplastic antioxidant enzyme machinery [e.g., glutathione reductase (GR), SOD, CAT, and peroxidase] and therefore improve the cold resistance of bean under low temperature. On the basis of the above studies, it can be concluded that microbes enhance plant growth and resistance to chilling stress by adopting more than one mechanism of action (Fig. 14.1).

14.5 Microbial Mediated Cold Stress Management in Agricultural Crops

CTMs have been reported to possess multifarious plant growth-promoting attributes in addition to their strong relationship with series of agricultural crops and found to persuade several manifold advantages to plants grown under CS environment (Table 14.1) has been summarized in the following sections.

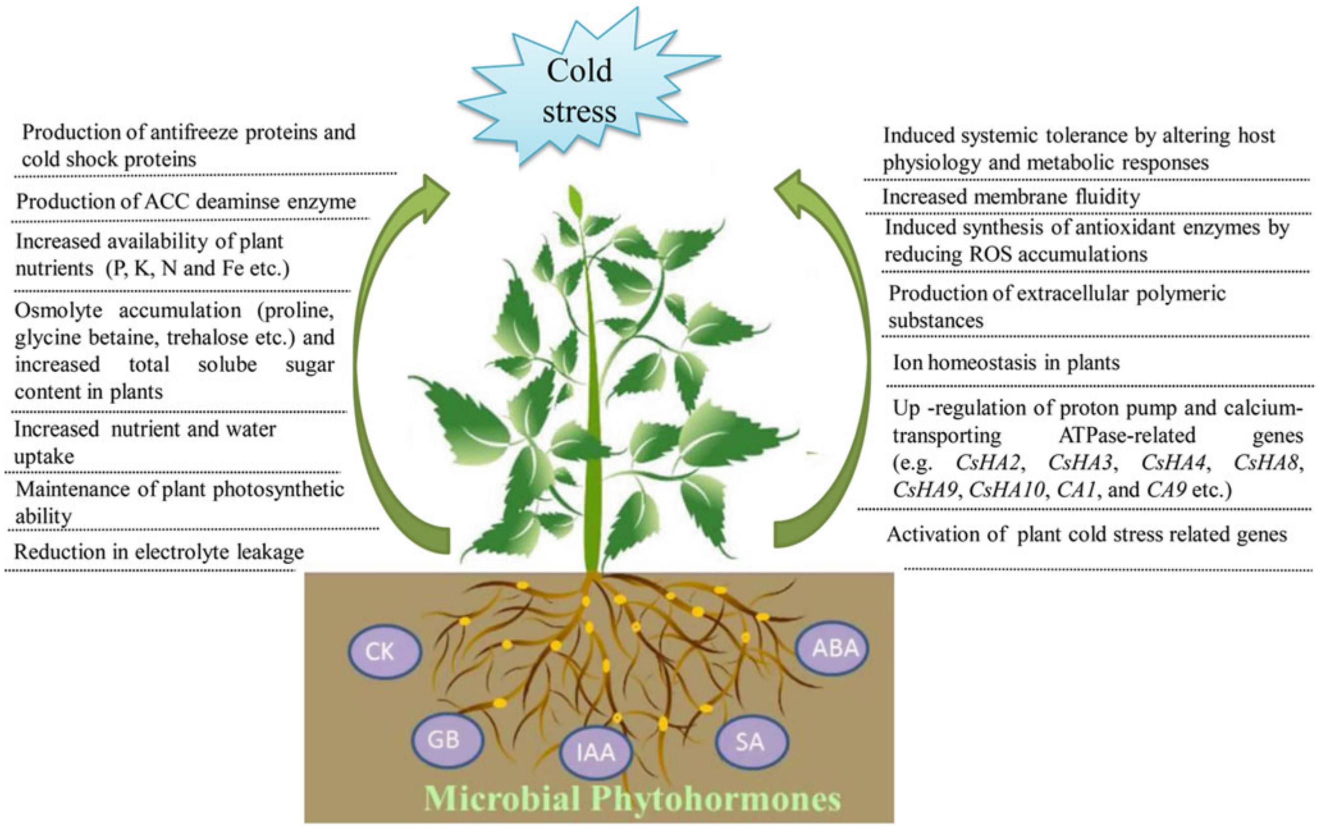

Fig. 14.1 Mechanism of microbial mediated cold stress tolerance in plants

Table 14.1 Principal examples of microbial mediated cold stress tolerance in plants

Microbe	Plant	Effect on plant growth	Mechanism of action	Growth conditions	Reference
Bacillus megaterium M3, *Bacillus subtilis* OSU142, *Azospirillum brasilense* Sp245 and *Raoultella terrigena*	Wheat (*Triticum aestivum* spp. *vulgare* cv 'Bezostiya') and barley (*Hordeum vulgare* cv 'Tokak')	Ameliorated the deleterious effects of stress condition on plant growth and increased biomass	Increased chlorophyll content, photosynthetic activity and relative water content, altering mineral uptake, and decreasing membrane damage	Pot trials	Turan et al. (2013)
Bradyrhizobium japonicum 532 C	Soybean	Improved nodulation and nitrogen fixation	–	Field trails	Zhang et al. (2003)
Burkholderia phytofirmans PsJN	*Vitis vinifera* L. cv. Chardonnay	Stimulates grapevine growth (root growth and plant biomass) and improves its ability to withstand cold stress	Significantly increased levels of starch, proline, and phenolics	Controlled plant growth chamber	Ait Barka et al. (2006)
Burkholderia phytofirmans strain PsJN	Arabidopsis thaliana	Reduces impact of freezing temperatures on photosynthesis	Differential accumulation of pigments, and reduced expression of RbcL and COR78 genes and prevent the plasmalemma disruption under freezing stress	Controlled plant growth chamber	Su et al. (2015)
Dyadobacter sp.	Chickpea (Cicer arietinum), black gram (Vigna mungo), green gram (*Vigna radiata*), pigeon pea (*Cajanus cajan*), and finger millet (*Eleusine coracana*).	Promote plant growth by fixing atmospheric N_2 and making it available to plant	Enhancements in agronomical parameters, leaf nitrate reductase activity and total chlorophyll content	Pot trial	Kumar et al. (2018)
Exiguobacterium acetylicum 1P	Wheat	Positively influenced the growth and nutrient uptake parameters	Phosphate solubilization, IAA, siderophore and HCN production	Pots in glass house	Selvakumar et al. (2010)

Flavobacterium sp. OR306 and *Pseudomonas frederiksbergensis* OS211	Tomato	Improve the cold resistance of seedlings under low temperature	Reduction of ethylene, increased expression of cold induced LeCBF1 and LeCBF3 genes in addition to reduced expression of ethylene-responsive transcription factor 13 (ETF-13) and ACO genes	Controlled plant growth chamber	Subramanian et al. (2015)
Glomus intraradices	*Phaseolus vulgaris*	Enhanced the cold tolerance of plants	Alterations in plasma membrane aquaporins (PIP)	Controlled plant growth chamber	Aroca et al. (2007)
Glomus mosseae	Tomato	Enhanced the cold tolerance of tomato plant, which increased host biomass and promoted plant growth.	Reducing membrane lipid peroxidation and increasing the photosynthetic pigments, accumulation of osmotic adjustment compounds, and antioxidant enzyme activity	Controlled plant growth chamber	Abdel Latef and Chaoxing (2011)
P. fragi, *P. chloropaphis*, *P. fluorescens*, *P. proteolytica* and *Brevibacterium frigoritolerans*	Bean (*Phaseolus vulgaris* L.)	Improve the cold resistance of seedlings under low temperature	Decreased freezing injury, ice nucleating activity and lipid peroxidation content in parallel with the decrease of reactive oxygen species level, stimulated the activity of apoplastic antioxidant enzymes	Controlled plant growth chamber	Tiryaki et al. (2019)

(continued)

Table 14.1 (continued)

Microbe	Plant	Effect on plant growth	Mechanism of action	Growth conditions	Reference
P. frederiksbergensis OS211, *Flavobacterium glaciei* OB146, *Pseudomonas vancouverensis* OB155, and *P. frederiksbergensis* OS261	Tomato	Improve germination, plant growth and induce antioxidant capacity in tomato plants	Reduction in membrane damage and activation of antioxidant enzymes along with proline synthesis	Controlled plant growth chamber	Subramanian et al. (2016)
Pantoea dispersa 1A	Wheat	Enhanced plant growth and nutrient uptake ability	Phosphate solubilization, IAA, siderophore and HCN production	Pot	Selvakumar et al. (2008a)
Pseudomonas corrugata NRRL B-30409	Wheat	Enhanced growth of wheat plants under low temperature	Increased phosphate solubilization, organic acid production	Greenhouse	Trivedi and Sa (2008)
Pseudomonas fragi CS11RH1	Wheat	Increased germination rate, plant biomass and nutrient uptake	Phosphate solubilization, indole acetic acid (IAA) and hydrogen cyanide (HCN) production	Pot	Selvakumar et al. (2009)
Pseudomonas jesenii MP1	*Cicer arietinum* (L.), *Vigna mungo* (L.) Hepper; *Vigna radiata* (L.) Wilczek., *Cajanus cajan* (L.) Millsp.	Stimulated growth of shoot length, root length, plant fresh weight and plant dry weight	Significant increase in chlorophyll content, nitrate reductase activity and phosphorous content	Pot trials	Kumar et al. (2014)
Pseudomonas lurida M2RH3	Wheat	Enhanced plant growth and nutrient uptake parameters	Phosphate solubilization, IAA and siderophore production	Pot	Selvakumar et al. (2011)
Pseudomonas putida GR12-2	Canola	Promote root elongation of both spring and winter canola at 5 °C temperature	Production of antifreeze protein	Petri dish	Sun et al. (1995)
Pseudomonas sp.	*Deschampsia antarctica*	Promoted root development	P-Solubilization	Petri dishes	Berríos et al. (2012)

Pseudomonas sp.	Lentil	Increased lentil shoot length, root length, root biomass, and shoot biomass	–	Pot trials in green house	Bisht et al. (2013)
Pseudomonas sp. NARs9	wheat	Enhancement in the germination, shoot and root lengths	IAA production and phosphate solubilization	Glass house	Mishra et al. (2009)
Pseudomonas sp. PGERs17	Wheat	Enhanced germination of wheat seedlings with higher root and shoot lengths	IAA production, tricalcium phosphate solubilization, HCN and siderophore production and antagonistic activity against plant pathogens	Pot	Mishra et al. (2008)
Pseudomonas spp.	Wheat	Significant increase in shoot length, root length, root biomass, and shoot biomass	IAA production, phosphate solubilization, HCN and siderophore production and increase in N, Fe and nutrient uptake	Pots in glass house	Mishra et al. (2011)
Serratia marcescens SRM	Wheat	Enhanced plant biomass and nutrient uptake	Phosphate solubilization, IAA, HCN and siderophore production	Pot	Selvakumar et al. (2008b)
Trichoderma gamsii NFCCI 2177	Maize, soybean, wheat and lentil	Positive influence plant growth as well as on rhizosphere based parameters	Phosphate solubilization, chitinase activity, and production of ammonia and salicylic acid	Green house	Rinu et al. (2014)

14.5.1 Cereal Crops

Kaushik and colleagues (2001) reported the role of *Azospirillum brasilense* inoculation in improving wheat crop growth at sub-optimal temperatures. Similarly, at 16 °C temperature, application of *Mycobacterium* sp., *Pantoea agglomerans,* and *P. fluorescens* isolated from German soil with typical semi-continental climate enhanced winter wheat growth and nutrient [Nitrogen (N), phosphorous (P), and potassium (K)] uptake efficiency but found less effective at 26 °C in loamy sand soil. Contrarily, Egamberdiyeva and Höflich (2003) reported highly efficient nutrient uptake capabilities of *Mycobacterium phlei* and *Mycoplana bullata* strains under both nutrient-rich and nutrient-poor soil at 16 °C and 38 °C, respectively. Saleem et al. (2007) highlighted that ACC deaminase enzyme produced by bacterial strains play significant role in reducing ethylene production under freezing temperatures and therefore assist in plant growth promotion. Selvakumar et al. (2008a, b) documented *Serratia marcescens* SRM as a promising cold-tolerant strain with potential capabilities to promote wheat growth under low temperature hilly terrains. Further, they also observed that *S. marcescens* has the ability to solubilize phosphorous and produce indole acetic acid, HCN, and siderophore at 15 °C and also reflected all the plant growth promotion attributes at 4 °C too. Moreover, seed treatment of wheat seedlings with *S. marcescens* strain showed improved wheat biomass and nutrient uptake under cold temperatures and therefore can be utilized as a prospective bioinoculant to protect wheat from cold injury. Later, *Pseudomonas* strains displaying excellent cold resistance as well as plant growth promotion attributes have been evaluated as seed bioinoculants under greenhouse conditions at 10 ± 2 °C temperature (Mishra et al. 2009). Experimental findings clearly concluded that seed bacterization significantly enhanced wheat biomass and found superior in comparison to non-bacterized seedlings. Further, a significant rise in total chlorophyll content, anthocyanin, free proline, total phenolics, and starch content along with rapid decline in Na^+/K^+ ratio, and electrolyte leakage have been recorded in *Pseudomonas* primed wheat seedlings. Selvakumar and workers (2011) also identified *P. lurida* M2RH3 as a potential psychrotolerant wheat growth-promoting bacterium owing to its inherent capacity to solubilize phosphate, produce siderophores, IAA, and hydrogen cyanide (HCN). These above-mentioned studies clearly indicate the potential of the bacteria to alleviate cold-induced stress in cereal crops. Turan et al. (2013) reported that *A. brasilense*, *B. megaterium*, *B. subtilis*, and *Raoultella terrigena* can enhance cold resistance in wheat and barley plants under chilling stress. Similarly, an endophytic psychrotolerant potassium solubilizing bacterium (*B. amyloliquefaciens* IARI-HHS2-30) have been isolated from North Western Indian Himalayas and identified as an excellent cold stress alleviator (Verma et al. 2015). Further, they noticed significant increment in plant biomass and chlorophyll "a" content under low temperature (4 °C) conditions, when wheat (cv. HS507) seed treated with (*B. amyloliquefaciens* IARI-HHS2-30). Recently, Qin et al. (2017) identified a cold-adapted bacterium with broad-spectrum biocontrol and wheat growth-promoting activity. They observed that under greenhouse conditions, *Pseudochrobactrum kiredjianiae* A4 strain improved physiological parameters as well as enhanced defense enzymes activities of wheat plants for effective mycelia growth suppression of phytopathogenic fungus *Rhizoctonia cerealis.* Overall above-mentioned studies clearly indicate that the cold-adapted microbes provide a promising solution to maintain crop growth and health under low temperature farming systems.

14.5.2 Leguminous Crops

Earlier studies of Prevost et al. (1987) indicated that rhizobia isolates of arctic region showed better nitrogenase activities at low temperatures than rhizobia isolates of temperate regions when tested their symbiotic association with *Onobrychis viciifolia*. Similarly, *R. trifolii* strains from subarctic regions of Scandinavia displayed better growth, fast nodulation, and enhanced nitrogenase activity with clover plant at 10 °C in comparison to *R. trifolii* strains isolated from southern regions (Ek-Jander and Fahraëus 1971). Further, they did not notice any significant differences in nitrogenase activity between strains of both regions at higher temperature (20 °C). Hume and Shelp (1990) found that inoculation of soybean with *B. japonicum* strain resulted in improved soybean yields in Ontario (Canada). Further, Zhang et al. (2003) also noticed that psychrotolerant strains of *Bradyrhizobium japonicum* also helpful in improving nodulation and nitrogen-fixing capability of soybean plants cultivated under low chilling temperature. Similarly, Mishra et al. (2011) found that cold-tolerant strains of *Pseudomonas* spp. and *R. leguminosarum*-PR1 protect lentil from CS as well as enhance iron acquisition, nutrient uptake, and plant growth. A study conducted by Katiyar and Goel (2004) revealed that *P. flouresens* ATCC13525 mutant strain is also able to produce significant amount of siderophores and able to promote *Vigna radiata* growth with significant increase in rhizosphere competitiveness. A psychrotrophic actinobacterium *Rhodococcus erythropolis* was also identified and described by Trivedi et al. (2007). During their investigation, they found that *R. erythropolis* was able to transform toxic and high concentration of chromium (Cr^{6+}) ions to less hazardous chromium (Cr^{3+}) ions and hence provide better growth of pea plants. A study made by Aroca et al. (2007) to decipher the role of AM symbiosis in improving *Phaseolus vulgaris* resistance to cold, salt, and drought stress revealed that in response to stress exposure, AM regulate root hydraulic properties, which were closely linked with the regulation of PIP2 protein levels and phosphorylation state. Gulati et al. (2009) identified *Acinetobacter rhizosphaerae* bacterium displaying IAA producing character from *Hippophae rhamnoides* plant, commonly found in the cold deserts of Himalayas. This strain was found promising in terms of chickpea growth promotion under controlled in vitro conditions and pea growth promotion under field conditions. Later, *Rahnella* sp. identified as a novel psychrotrophic enterobacteriaceae member by Vyas et al. (2010). This strain was found to augment plant growth of chickpea and pea under in vitro and field conditions by producing siderophores, phytohormones, organic acids, and enzymes like phytase and ACC deaminase (Vyas et al. 2010). Soybean plants inoculated with

Trichoderma gamsii NFCCI 2177 improved soybean growth under chilling temperature and used as a bioformulation (Rinu et al. 2014). Kumar and associates (2014) identified psychrotolerant *Pseudomonas jesenii* strain MP1 and tested for relative plant growth-promoting potential against *Cicer arietinum*, *V. mungo*, *V. radiata,* and *Cajanus cajan* pulse crops. They recorded significant stimulation in plant biomass of *Trichoderma gamsii* inoculated plants in comparison to their non-inoculated checks. Additionally, bacterium inoculated plants displayed significant rise in nitrate reductase activity, chlorophyll content, and phosphorous content too. Recently, Kumar et al. (2018) revealed the plant growth-promoting potential of psychrotolerant *Dyadobacter* sp. against four pulses (pigeon pea, green gram, black gram, and chickpea) and finger millet. They demonstrated that the bacterium was able to grow at nitrogen (N) deficient medium at both 10 and 28 °C and gave positive *nifH* amplification that confirms the diazotrophic nature of this psychrotolerant bacterium. Further, their pot trial-based study we concluded that psychrotolerant *Dyadobacter* sp. isolated from cold region of western Indian Himalaya has the potential to promote plant growth of pulses and finger millet by fixing atmospheric N_2 and making it available to plant. Overall, all the above-mentioned examples indicated that plant growth-promoting capabilities psychrotolerant bacterium and hence such microbes can be exploited to improve plant growth in cold climate agriculture.

14.5.3 Other Crops

Rapid augmentation of cold tolerance of *Burkholderia phytofirmans* strain PsJN inoculated grapevine plantlets have been documented by Ait Barka et al. (2006). During their study, they found significant and positive correlation of starch, proline, and phenolics in treated grapevine plantlets with plant ability to withstand CS. Halotolerant *P. putida* UW4 and GR12-2 were reported to enhance canola crop stand and growth in low chilling temperatures (Cheng et al. 2007; Sun et al. 1995). Kytöviita and Ruotsalainen (2007) observed that the biopriming of *Gnaphalium norvegicum* seeds with *Glomus claroideum* fungus significantly improved seed germination percentage, plant biomass, percent shoot nitrogen (N%), and root AM colonization at 8 °C than 15 °C. Similarly, Abdel Latef and Chaoxing (2011) indicated that *G. mosseae* fungus is proficient to enhance CS tolerance of tomato plant which increased host biomass and plant growth promotion by rapid production of osmotic adjustment compounds, increasing photosynthetic pigment productions, and regulating antioxidant enzyme activity and membrane lipid peroxidation. Theocharis et al. (2012) proved that *B. phytofirmans* PsJN primed grapevine plants exerted enhanced protection towards low non-freezing temperature (4 °C). They also observed a rapid and quick rise of both CS-related gene transcripts and metabolite levels in *B. phytofirmans* PsJN treated plantlets relative to non-bacterized counterparts. However, 1 week after CS exposure, more declination in the levels of stress-related metabolites in *B. phytofirmans* primed plants is observed. These results clearly indicated that the endophytic bacterium *B. phytofirmans* is involved in the cold-adaptive process via scavenging system. Later, Fernandez et al. (2012) experimentally revealed that trehalose metabolism is involved in *Burkholderia phytofirmans* induced chilling tolerance in grapevine. Subramanian et al. (2016) also established and confirmed the potential application of psychrotolerant bacteria (*P. frederiksbergensis* OS211*, F. glaciei* OB146*, P. vancouverensis* OB155, and *P. frederiksbergensis OS261*) in alleviating cold stress in tomato plants at low non-freezing temperature. Further, they found positive correlation of membrane damage reduction, rapid stimulation of antioxidant enzyme machinery, and proline synthesis with improved plant growth under CS conditions (15 °C). In another study, it was observed that 15.56% of survival rate of tomatoes achieved after *Bacillus cereus* AR156, B. *subtilis* SM21, and *Serratia* sp. XY21 application from 15.56 to 92.59% at 4 °C (Wang et al. 2016a, b). The experimental findings of Pedranzani et al. (2016) indicated that AM symbiosis can improve plant biomass, photosynthates, and enzymatic (CAT, APX, and SOD) activities of *D. eriantha* plants under CS condition and further play crucial role in supporting plants to with stand unfavorable CS environment. Similarly, studies of Matsubara et al. (2004) also demonstrated the advantageous role of inoculation of different species of AMF inoculation in growth promotion of strawberry plants. More elaborately, Chu et al. (2016) demonstrated that AMF inoculation improve CS tolerance level of *E. nutans* seedlings by scavenging ROS, modulating redox balance, and activating stress-related defense mechanisms.

14.6 Challenges and Opportunities

Cold-tolerant microbes (CTMs) play an important task as an ecological engineer to reduce low temperature stress problem of high altitude agriculture. On the basis of the information compiled in this chapter, microbial based approach is the most sustainable and prospective future plan for solving the biggest environmental challenges of CS to make global economy and food security intact. Therefore, considering current scenario of agriculture problems of high altitude agriculture, future research is required on the following directions to create more opportunities for sustainable growth of agriculture under cold stress environment:

- Development of highly efficient laboratory methodologies for preparation and formulation of cold-tolerant microbial inoculants on large scale. For instance, bioencapsulation and solid-state fermentation processes.
- Genetic and molecular interactions between soil, plants, and cold-tolerant microbes and their complexity should be explored deeply under field conditions in order to enhance the overall ecological relevance, economic value, and social importance of these microorganisms in a world that needs scientific solutions for higher crop production in low temperature environments.
- Genomic information of CTMs will facilitate to discover and experimentally validate novel secondary metabolism implicated in adaptation to cold ecological niches and promotion of useful attributes for low temperature resilient agriculture.

- Identification and evaluations of diverse types of microbial strains for cold stress tolerance should be carried out to formulate effective microbial consortia for overcoming the negative impact of changing environment problems.
- The psychrophilic microorganisms that can grow under cold environment as well as normal ambient temperature have huge impact on agriculture and allied sector under current scenario of climate change. In this context, attending the problem associated with successful field delivery of prospective CTM-based technologies and their appraisal is of utmost importance.
- Exploitation of effective microbial consortia comprised of multiple types of compatible CTMs displaying synergistic interactions with symbionts in addition to stable and multiple plant growth-promoting attributes for improving crop yields under low temperature is also a powerful strategic tool.
- Utilization of microbial elicitors to enhance plant cold stress tolerance capabilities.
- Incorporation of microbial genes into cold stressed plants or cultivars of high agronomical values.

14.7 Conclusions

Cold-tolerant microbes (CTMs) are widely present in the agro-ecosystem and participated in myriads of beneficial activities related to enhancement of CS tolerance level of various agricultural crops. So far, major emphasis of research work has restricted to the identification and functional characterization of limited groups of bacterial, fungal, and AM species. Therefore, focused and targeted research initiatives are required to decipher the mechanism of plant–CTM interaction, particularly taking care of extremities of high altitude agriculture. Another fascinating domain where microbiological research desires to be targeted is the identification and functional cataloguing of CTMs that can reduce environmental pollution of heavy metal toxicity and detrimental agro-waste because most decomposition processes appear to be faster under low temperature environment. If research efforts succeed in identifying a consortium of potential CTMs that retain their plant growth-promoting potential at lower temperatures, it would be a huge contribution for the resource poor farmers of high altitudes to enhance their livelihood income all over the globe.

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