Chapter 8
Alleviation of Cold Stress by Psychrotrophic Microbes

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Abstract Psychrotrophs have the ability to survive in extreme conditions of lower temperature ranges from 0 °C to 20 °C. Psychrotrophic microorganisms mainly include bacteria, archaea and yeast, but among them, bacteria predominate in polar environment and archaea are more widespread in cold and deep ocean waters. They have evolved a variety of adaptation mechanisms such as gene expression modification and production of cold stress protein to cope up with stress induced at such a lower temperature. Cold active enzymes produced by psychrotrophs have wide applications in the food and pharmaceutical industry. Moreover these have wide applications in agriculture as they have the ability to promote plant growth at low temperature.

Keywords Adaptation · Agriculture cold stress · Microbes · Psychrotrophs

8.1 Introduction

Psychrotrophs are those microbes which can survive and thrive at extremely cold conditions and grow at a wide range of temperature from 0 °C to 20 °C. Psychrotrophs have the ability to sustain in soil, surface, deep sea water, food and Antarctic ecosystem. These are distributed widely in soil and water in temperate regions. In the

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permafrost soil and ice, microbial activity is mainly restricted to unfrozen water. They have high salt concentrations along with particulate matter, so fluid flow is regulated by gradients of concentration and temperature (D'Amico et al. 2006). They have adapted themselves to survive at low temperature by involving modification in expression of genes (Seki et al. 2003) and producing cold acclimation proteins, anti-freezing proteins, unsaturated fatty acids, increase in proline content, cold-active enzymes, high sugar concentration and total phenolics, carotenoids and cryoprotectants (Ait Barka et al. 2006). Alteration in physiological and metabolic activities permit osmotic adjustment for continuation of water uptake include production of osmotic regulator, i.e. proline, sucrose, sugar and alcohols (Kasuga et al. 2004; Zhu 2002; Hasegawa et al. 2000; Yadav 2015). Psychrotrophs have attracted interest of scientific community to study these adaptations. This adaptation can be used to encourage agricultural plant growth. Psychrotroph's ability to generate cold-adaptive enzymes can be used in a wide variety of agricultural, industrial and medical fields/processes.

Low temperature is one of the main abiotic stresses that lead to adverse effect on plant development and production. Psychrotroph's ability to survive at low temperature could be utilized for considerate adjustment at low temperatures. Cold-sensitive enzymes could be utilized in leather processing industry as cleaning agents. The other applications include xenobiotic compounds biodegradation at low temperature, heterologous gene expression at molecular level and food processing (bakery, cheese manufacture and fermentation). Psychrotrophic microbes can ameliorate cold stress in plants which could be valuable to use in agriculture (Yadav et al. 2019a, b, 2020). Climate changes due to greenhouse gases lead to increase in tempeature that are favourable for survival of microorganisms in extreme conditions. Moreover cropping cycle that is subjected to low temperature periods has a negative impact on plant growth and psychrotrophs are the solution, with ability to fix nitrogen and solubilize phosphorus under such extreme climate. In cold climatic conditions, the use of psychrophiles as biofertilizers, biocontrol agent and bioremediators opens a new window in agriculture field under low temperature climatic conditions.

8.2 Alleviation to Cold Stress by Microbes

Psychrotrophs has adapted them to grow at low temperature. Microbes survive in unfavourable conditions by triggering physiological response in them. Several mechanisms that have been adapted by psychrotrophs to cope with cold stress are mentioned in Fig. 8.1.

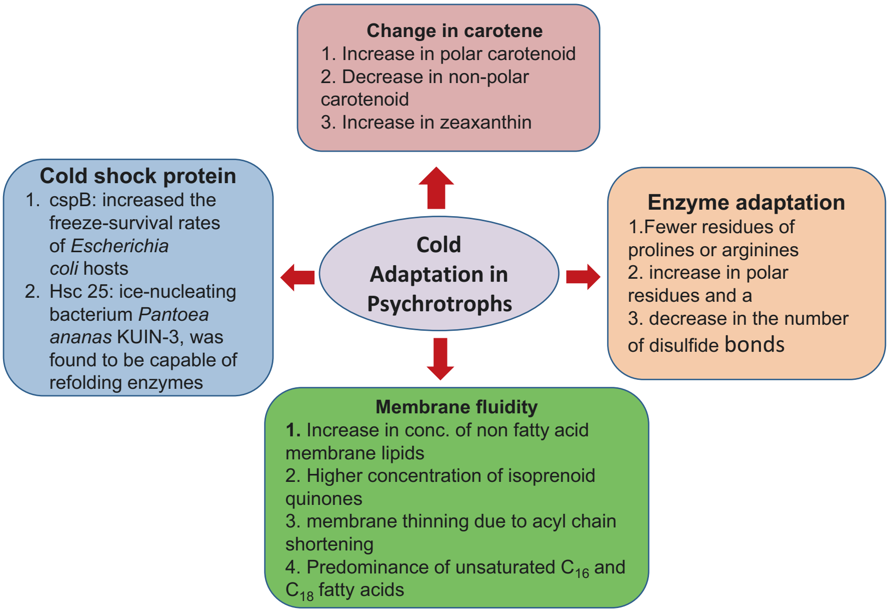

Fig. 8.1 Alleviation of cold stress by microbes

8.2.1 Membrane Fluidity

Maintenance of membrane fluidity plays an important role for adaptation to low temperature (Ray 2006). Lipid composition varies with change in habitat of organism. It was found that increases in nonfatty acid membrane lipid amount and higher concentration of isoprenoid quinones have been significantly improving adaptation to low temperature in *L. monocytogenes* strains as studied by Seel et al. (2018). In marine bacterium, *Synechococcus* responded to cold temperature, and membrane thinning due to acyl chain shortening with specific desaturation activities was observed. Along with it, membranes that were found almost devoid of C-18 rather contain C-14 and C-16 chains with no more than two unsaturated activities (Pittera et al. 2018). Singh et al. (2017) isolated *Leeuwenhoekiella aequorea, Pseudomonas pelagia, Halomonas boliviensis, Rhodococcus yunnanensis* and *Algoriphagus ratkwoskyi* from Kongsfjorden (an Arctic fjord) and found that the unsaturated fatty acids, primarily cis-10-penta-decenoic, palmitoleic and oleic acid, were mainly responsible constituents for adaptation capability to cold stress.

The Antarctic psychrotriphic bacterium *Pseudomonas syringae* was more sensitive to polymyxin B at 4 °C temperature than at 22 °C for growth. Due to this leads to increase the fluidity of lipopolysaccharides and improving outer membrane fluidity activities (Kumar et al. 2002). Mykytczuk et al. (2010) studied that psychrotrophic strains of *Acidithiobacillus ferrooxidans* had a comparatively higher rigid membrane with *P*- range (0.41–0.45), lower T_m (transition midpoint temperature), i.e. 2.0 °C, and broader transition range as compared to mesophilic strains (*P* range = 0.38–0.39; T_m = 2.0–18 °C) at low temperatures. Decrease in 12:0 fatty acids in psychrotrophic strains as compared to those of the mesophilic strains showing decreases in range of 16:0, 17:0 and cyclo-19:0 fatty acids clearly distinguished 5 °C fatty acid profiles of psychrotrophic strains. High amounts of unsaturated FAs that lead to the constitutive expression of FA desaturases in the bacterial cells is a major characteristic or feature of psychrotolerant bacteria.

8.2.2 Change in Carotene/Carotenoids

Carotenoids are polyisoprenoid hydrocarbon produced in response to extreme environmental stress. Pigments present in Antarctic bacteria have the ability to localize in the membrane and provide rigidity to the membrane. The amount of polar carotenoids increased with decreased temperature and the amount of nonpolar carotenoid also decreased (Chattopadhyay and Jagannadham 2001). The increase in decreased membrane fluidity due to polar carotenoid has been observed by Subczynski et al. (1992). Chattopadhyay and Jagannadham (2001) observed in the Antarctic bacteria that synthesized membrane-rigidifying polar carotenoids increase with synthesis of membrane-fluidizing fatty acids and compensate the effects of FA. Jousse et al. (2018) also reported key cold shock biomarkers that included cryoprotectants and their precursors, alkaloids and secondary metabolites involved in energy metabolism from *Pseudomonas syringae* isolated from cloud water. A psychrotrophic bacterium *Arthrobacter agilis* was isolated from the Antarctic sea ice. At low temperature the C-50 carotenoid production was observed that could contribute to cold stress membrane stabilization (Fong et al. 2001).

8.2.3 Enzyme Adaptation

In psychrotrophic organisms, different enzymes use multiple strategies to get adapted at lower temperature. These include reduction in number of ionic pairs and their hydrophobic interactions, decreased inter-subunit interactions, improved interaction with the solvent, core having reduced nonpolar fraction, active site with higher convenience, nonpolar residues improved in the solvent, decline in cofactor binding and glycine residues clustering with lower arginine and proline content (D'Amico et al. 2006). Cold-tailored microorganisms synthesize lipases which increase their tolerance to cope with the extremely frosty environment with elevated biocatalytic activity (Kour et al. 2019a). Cold tolerance of enzymes includes decrease in ratio of arginine to arginine + lysine, decrease in hydrophobic residues that attached with polar residue, smaller residues of prolines or arginines and also decrease in the number of disulfide bonds (D'Amico et al. 2006). In *Moritella marina*, malic dehydrogenase (MDH) was found to be stable between temperature 0° and 15 °C, and enzyme lost its properties with increase in temperature at 30 °C.

8.2.4 Cold Shock Protein

Proteins play a significant role in alleviating cold stress among organisms. Two types of proteins are formed in reaction to low temperature, viz. cold shock and cold acclimation proteins. The cold acclimation proteins are exclusively by psychrotrophs while cold shock proteins are produced in both mesophiles and psychrophiles. Cold shock proteins (Csps) inhibit mRNA secondary structure development by acting as nucleic acid chaperons at low temperature and thus make possible the commencement of translation. Cold shock proteins also contribute to osmotic, oxidative, starvation, pH and ethanol stress tolerance as well as to host cell invasion (Keto-Timonen et al. 2016). Gene coding for a Csp family protein, *cspB*, was cloned from an Arctic bacterium, *Polaribacter irgensii* KOPRI 22228, and overexpression of *cspB* increased the freeze-survival rates of *Escherichia coli* hosts (Jung et al. 2018). Thirteen proteins were induced in *Escherichia coli* when exposed to a temperature shock from 37 °C to 10 °C (Jones et al. 1987).

In the mesophilic bacteria, CSPs facilitated transcription and translation processes at low temperature, but their exact role is yet to be confirmed. Kawahara et al. (2000) found that *Pantoea ananas* KUIN-3 ice-nucleating bacterium produces cold acclimation protein (Hsc 25) which has an enzyme-refolding capability and further denature via high and low temperature and guanidine hydrochloride. Affinities of these proteins are higher for cold as compared to heat-denatured enzymes, as compared to Gro EL. Panicker et al. (2002) observed the superior expression of 8 kDa protein at 4 °C in *Pseudomonas* spp. 30–3 and suggested the role of Cap B protein in tolerance and survival at subzero temperatures. Drouin et al. (2000) studied that at 0 °C, the number of Csps synthesized was higher in the cold-adapted strains such as *R. leguminosarum* bv. *viciae* from the legumes *Lathyrus japonicus* and *Lathyrus pratensis* in northern Quebec than in the cold-sensitive strains. Mazzon et al. (2012) observed that cspA and csp B, cold shock genes from *Caulobacter crescentus*, have an important role in mRNA stabilization and cold adaptation. CspD, a cold shock domain protein, was produced in psychrotolerant Antarctic *Janthinobacterium* sp. Ant5–2 (ATCC BAA-2154) at low temperature (Mojib et al. 2011). H-NS and Huβ are plasmid-encoded cold shock proteins which participate in supercoiling of DNA when bacteria are exposed to cold stress. Metabolic state of the cell gets modified due to DNA structure reorganization and gene expression modification (Giangrossi et al. 2002).

8.3 Effect of Cold Stress on Agriculture

Cold stress held back the development and yield of plants (Janda et al. 2003). Response of plants towards lower temperature is given in Fig. 8.2. Cold stress leads to production of reactive oxygen species (ROS) in plants which are highly reactive and detrimental metabolic products. Plants had evolved a number of mechanisms to

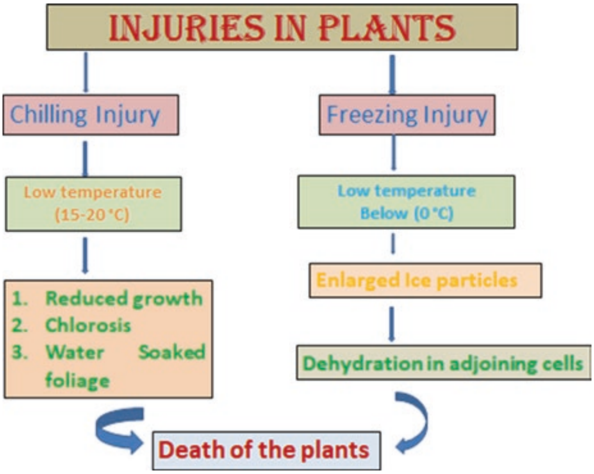

Fig. 8.2 Effect of cold stress on plants

reduce oxidative injuries in plants by evolving various enzymatic mechanisms that reduce reactive oxygen species. O_2 is converted to hydrogen peroxide (H_2O_2) by superoxide dismutase (SOD) which is then scavenged by catalase (CAT) by reducing the two electrons from oxygen. Peroxidase (POD) participates in lignin biosynthesis and indole acetic acid (IAA) degradation and converts H_2O_2 to H_2O (Agarwal et al. 2005). A MAPKK (maize mitogen-activated protein kinase kinase), gene *ZmMKK1*, was reported to induce chilling tolerance efficiency in tobacco by improving antioxidant enzyme activity and osmolyte accumulation and increased expression of reactive oxygen species (ROS)-related genes significantly (Cai et al. 2014). Accumulation of melatonin and sugars raffinose also confers chilling tolerance through the reactive oxygen species (ROS)-scavenging mechanism in plants (Zhang et al. 2015; ElSayed et al. 2014). Therefore, improvement of ROS-scavenging activity is the mechanism to perk up low temperature adaptation in the plants (Yadav et al. 2019a).

When warm-habitat plants such as maize (*Zea mays*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), tomato (*Lycopersicon esculentum*) and banana (*Musa* sp.) are exposed to low temperature, they exhibit symptoms of injuries (Lynch 1990; Guy 1990; Hopkins 1999). However, this symptom varies from plants to plants and depends upon the plant sensitivity to cold stress. Cold stress generally results in reduced germination, undersized reduced seedlings, yellowing of leaves, wilting, reduced tillering and necrosis in plants (Jiang et al. 2002). It also results in production of sterile pollen which leads to reduction in capitulate (Suzuki and Mittler 2008). The lower temperature leads to leaf tissue damage confirmed via observing electrolyte seepage and malondialdehyde concentration in tomato plant. Significantly improved root-and-shoot ratio and enhanced antioxidant enzyme were observed in tomato when its seeds were inoculated with plant growth-promoting psychrotolerant bacteria (Subramanian et al. 2016) (Fig. 8.3).

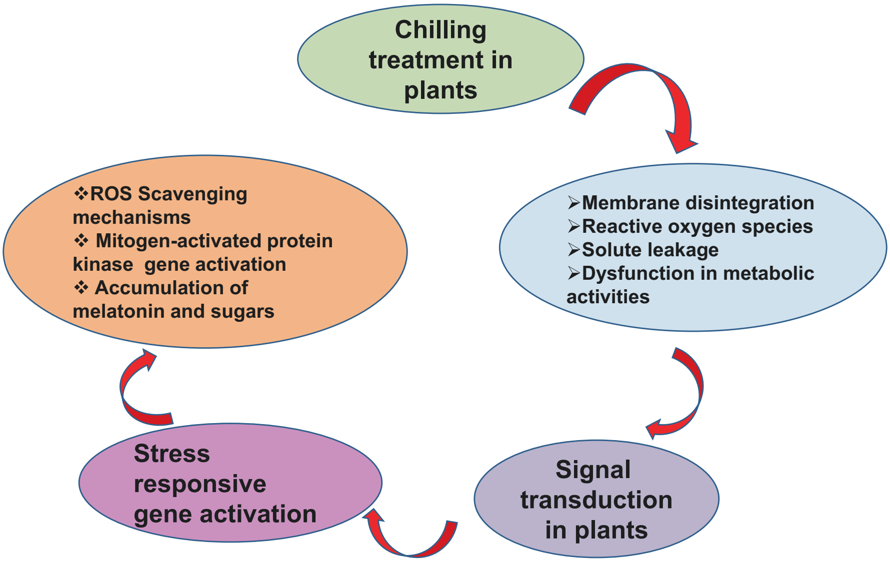

Fig. 8.3 Response of plants to cold temperature

8.4 Plant Growth-Promoting Rhizobacteria Ameliorates Cold Stress in Plants

Growth-promoting rhizobacteria are the bacteria living in the area around plant roots which are necessary for plant development. Novel group of microbes can be isolated from extreme environments representing unique ecosystems such as acidophiles, alkalophiles, halophiles, psychrophiles, thermophiles and xerophiles (Saxena et al. 2016; Yadav et al. 2017). Cold stress in the plants can be ameliorated with the help of cold-tolerant plant growth-promoting rhizobacterial strains (Ait Barka et al. 2006; Cheng et al. 2007). For sustainable agriculture, there is need to consider microbial diversity associated with crops. Under different abiotic stress conditions, PGPR associated with crops are able to promote the plant growth. Plant growth-promoting microorganisms have been reported and belong to the different genera including *Arthrobacter*, *Bacillus*, *Paenibacillus*, *Brevundimonas*, *Pseudomonas*, *Burkholderia*, *Flavobacterium*, *Citricoccus*, *Exiguobacterium*, *Janthinobacterium*, *Methylobacterium*, *Kocuria*, *Lysinibacillus*, *Microbacterium*, *Providencia* and *Serratia* (Saxena et al. 2015; Verma et al. 2015b; Singh et al. 2016; Yadav et al. 2016a, b, 2018).

At lower temperature *Bacillus*, *Exiguobacterium* and *Pseudomonas* have been found the good characteristics for plant growth promotion (Mishra et al. 2011; Selvakumar et al. 2011; Yadav et al. 2015c, 2016a, b). Under cold conditions and hilly areas, psychrophilic/psychrotrophic microbes could be used as a biofertilizers, biocontrols and bioremediators agent in agriculture. Cold-adapted enzymes produced by psychrophilic/psychrotolerant microbes have potential because they provide opportunities to study the adaptation of microbial life at lower temperature (Saxena et al. 2016; Yadav et al. 2019a, b). Subramanian et al. (2015) isolated psychrotolerant bacteria from soil of agricultural field in winter. Around 32 isolates were able to produce plant growth-promoting attributes such as ACC deaminase, salicylic acid, IAA, siderophores and tricalcium phosphate solubilization under lower temperature up to 5 °C. These psychrotrophs have ability to alleviate chilling stress in tomato plants (*Solanum lycopersicum* cv Mill).

Electrolyte seepage and lipid peroxidation in leaf tissues under cold stress was significantly reduced by strain *P. vancouverensis* OB155. Turan et al. (2013) studied that when Plant growth-promoting bacteria along with Boron were applied to wheat and barley, they induced the cold tolerance in plants by alteration in mineral uptake, enhancement of chlorophyll content, photosynthetic activity and relative water content and decreasing membrane damage.

Verma et al. (2015a) investigated that at lower temperature conditions, appreciable level of K solubilization was exhibited by *Bacillus amyloliquefaciens* IARI-HHS2-30. After 30 days of inoculation in wheat, *Bacillus amyloliquefaciens* IARI-HHS2-30 increases root/shoot length, fresh weight and chlorophyll content. PGP attributes having psychrophilic ability suggest that in low-temperature and high-altitude condition, these endophytic bacteria might be exploited as bio-inoculants for various crops. Yadav et al. (2016a, b) studied that PGP attributes in psychrotrophic bacterial species, viz. *Bacillus licheniformis*, *Bacillus muralis*, *Paenibacillus tylopili, Desemzia incerta* and *Sporosarcina globispora*. They observed that biofertilizers could be developed from these bacterial species for growing crops at low-temperature conditions.

8.4.1 ACC (1-Aminocyclopropane-1-Carboxylate) Deaminase Activity

At low temperature, there is an enormous increase in production of ethylene which triggers senescence and abscission in plants. ACC deaminase found in many bacteria can cleave ACC, intermediate of ethylene in plants. In this way, endophytic bacteria associated with plants help them to cope up with cold stress (Kour et al. 2019b; Verma et al. 2017). Tiryaki et al. (2019) isolated 6 psychrotolerants from the leaf apoplast of cold-adapted wild plants exhibiting ACC deaminase activity (57.60–166.11 nmol α-ketobutyrate/mg protein/h). These bacteria also secrete specific extracellular proteins at cold conditions. Bacterial inoculants decreased freezing injury and ROS levels while stimulating antioxidant system parameters in the bean seedlings. When canola plants were treated with ACC deaminase-producing bacterium *Pseudomonas putida* UW4, the plant growth was enhanced by lowering salt-induced ethylene synthesis (Cheng et al. 2007).

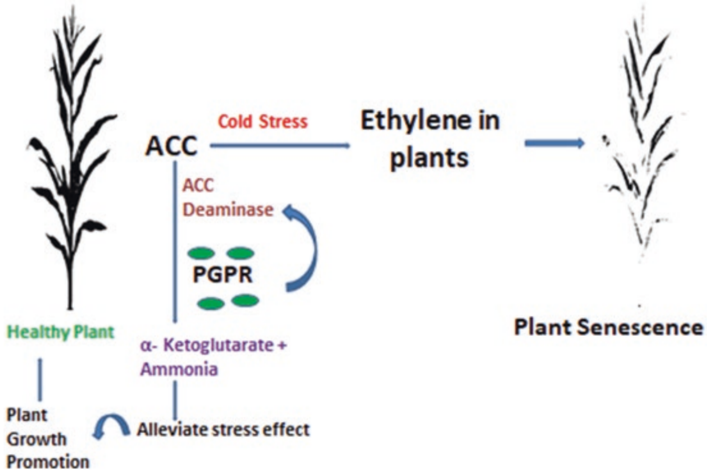

Fig. 8.4 ACC deaminase activity by PGPR in cold stress

Kadioglu et al. (2018) isolated 32 1-aminocyclopropane-1-carboxylic acid deaminase-producing cold-tolerant bacteria that were isolated from the 20 rhizospheric soils of wild plants collected from high altitudes (1760–2724 m) in different mountains in Erzurum, Eastern Anatolia, Turkey. The most effective four species in α-ketobutyrate producing potential from ACC were *Stenotrophomonas maltophilia* GBK 4 (1.207 mg^{-1} h^{-1}), *Leucobacter iarius* GBK 2 (0.993 mg^{-1} h^{-1}), *Pseudomonas fluorescens* GBK 3 (0.962 mg^{-1} h^{-1}) and *Pseudomonas migulae* GBK 1 (0.951 mg^{-1} h^{-1}), respectively. The plant growth-promoting bacteria has been reduced negative effect under cold stress condition in plants growth by antioxidant enzyme activities accumulation, decrease in reactive oxygen species (ROS) such as H_2O_2, O_2 and OH, hormonal, photosynthetic and other stress related pathways. ACC deaminase activity of psychrotrophs to degrade ACC is mentioned in Fig. 8.4.

8.4.2 Phytohormones

Psychrotolerant *Pseudomonas lurida* strain M2RH3 have produced various plant growth properties like indole-3-acetic acid production, siderophores, P-solubilization ability at low temperature and seed bacterization in *Triticum aestivum* with the positive results at cold growing temperature about the growth and nutrient uptake efficiency of wheat seedlings cv. VL 804 (Selvakumar et al. 2011). Cold-tolerant plant growth-promoting bacteria, e.g. *Pantoea dispersa* (strain 1A) and *Serratia marcescens* (strain SRM), have the ability for IAA production at 4 °C and 15 °C temperature, which have been isolated from the North-Western Indian Himalayas (Selvakumar et al. 2008a, b). At cold temperatures, seed bacterization of wheat seedlings inoculated with these bacterial strains had significantly enhanced plant growth, biomass and nutrient uptake efficiency in wheat plants.

IAA production at low temperature was reported by Mishra et al. (2008, 2009) in bacteria *Pseudomonas* sp. (strain PGERs17) and NARs9, respectively. At lower-temperature conditions, these bacterial strains have enhanced the seed germination as well as root and shoot lengths of wheat seedlings. Barka et al. (2006) reported that PGPR have the ability to produce or modify plant growth hormones, e.g. gibberellins, which play an important role in germination and thus help in cold stress alleviation. Kolesnichenko et al. (2003) and Chang et al. (2010) reported that in warm climate crops such as rice (*O. sativa* L.), cucumber, cassava and sunflower, PGPB ameliorated the harmful effects of stress condition on plant growth. Ortiz-Ojeda et al. (2017) observed that psychrotrophic bacteria associated with maca (*Lepidium meyenii* Walp.) show positive results for IAA production, 12 produced IAA at 22 °C, 8 at 12 °C and 16 at 6 °C. At 22 °C, LMTK39 produced maximum amount of the phytohormone (60.6 μg/ml) which decreased to 31.1 μg/ml at 12 °C. Strain LMTK11 showed the highest ability to produce IAA at 6 °C (14.1 μg/ml). Subramanian et al. (2016) reported that bacterial strains isolated from soils collected in regions with an average temperature of about 2 °C have the ability to produce IAA at 5 °C. IAA production by these strains was found to be in the range of 0.3 to 17 μg/ml.

Yadav et al. (2015a) isolated 12 bacteria from the cold desert of the Himalayan region that showed the ability to produce gibberellic acid. About two dozens of wheat combined with psychrotolerant bacterial strains also produced gibberellic acid which were isolated from the northern hills of India. Only 11 psychrotrophic bacterial strains that produced gibberellic acid were reported by Yadav et al. (2015b).

8.4.3 N_2 Fixation

Nitrogen is one of most important minerals which are essential for plant growth and development. Under extreme cold conditions, N_2 become deficient. Bacteria fix nitrogen by symbiotic and asymbiotic means. Competitiveness and functioning of nodule are affected by cold temperature. Various plant growth-promoting psychrotrophs can help plant to grow by providing nitrogen through symbiotic and asymbiotic means and help them to cope up with stress (Rana et al. 2019a, b). Zhang et al. (2003) studied that nitrogen fixation of soybean and its nodulation was positively influenced by *Rhizobia* originating from cooler climate of North America than that of warmer climate of South America. Psychrotolerant *Pseudomonas* sp. strain L10.10 (CP012676) bacteria isolated from Lagoon Island, Antarctica, having the ability of N_2 fixation along with other plant growth properties has been observed by See-Too et al. (2016).

Mishra et al. (2009) studied that co-inoculation of cold-tolerant *Pseudomonas* sp. Strain PGERs17 along with *Rhizobium leguminosarum*-PR1 significantly ($P > 0.05$) increased nodulation (156.2%) and 57.1% higher plant biomass. About

66.3% N uptake, 23.3% P uptake, 47.1% K uptake and 2.75-fold Zn uptake of shoots were enhanced on co-inoculation compared with uninoculated control. Zhang et al. (2006) studied that *Rhizobia* isolated from North America in colder region were able to influence the nodulation and nitrogen fixation of soybean positively. Prevost et al. (2003) studied that psychrotroph *Sinorhizobium meliloti* improves growth of alfalfa under cold and anaerobic (ice encasement) stresses after over-wintering, enhancing adaptation for abiotic stress. Kaushik et al. (2001) observed growth-promoting ability of two strains of *A. brasilense* in wheat crop. Devanand et al. (2002) observed that in pigeon pea yield, dry weight and plant height nodule number increased when *Azospirillum* spp. and *Pseudomonas striata* are coinoculated with *Rhizobium* spp. Ek-Jandér and Fåhraeus (1971) studied that clover rhizobia isolated from subarctic environment in Scandinavia showed earlier nodulation of their host plant and more vigorous acetylene reduction than that from southern Scandinavia.

8.4.4 Phosphorus Solubilization

In the rhizosphere ecosystem, plant growth-promoting rhizobacteria (PGPR) could be promoted growth by solubilization of insoluble phosphorous compounds (Gull et al. 2004). Katiyar and Goel (2003) observed that *P. fluorescens* having higher P-solubilization ability under cold stress increased plant growth at 10 °C in *Glycine max* and *Pisum sativum*. Organic acids produced by *Pseudomonas* which was isolated from glacial ice samples with various temperatures ranges from 4 °C to 30 °C and optimum conditions for P solubilization at 15 °C dissolve sparingly soluble P in the rhizosphere region and thus increased P availability to plant roots (Balcazar et al. 2015). Nineteen efficient fluorescent *Pseudomonas* having phosphate-solubilizing ability isolated from the cold deserts of the trans-Himalayas have been reported by Vyas et al. (2009).

Trivedi et al. (2007) suggested that at lower temperatures, bacteria isolated from the Himalayan soils have the ability to solubilize phosphate. The selected bacterial isolates showing low-temperature adaptation and possessing various plant growth promotion abilities are suitable for the development of carrier-based, easy-to-use inoculants for improved plant performance in colder regions. Auxin and phosphate-solubilizing *Pseudomonas* and Bacillus strains were isolated by Cakmakcl et al. (2007), and it was observed to be significantly increased in biomass, N, K and P uptake efficiency and enzyme activities as compared to control on wheat and spinach plants. Better results were found in growth parameters and nutrient uptake efficiency of wheat seedlings cv. VL 804 in pot-culture conditions under cold conditions when seed bacterization inoculated with *Pseudomonas lurida* M2RH3. Gulati et al. (2009) isolated *Acinetobacter rhizosphaerae*, a phosphate-solubilizing and rhizosphere-competent strain from cold desert of Indian Himalayas. Cold temperature causes significant reduction in plant growth. Psychrotrophs have abilities to tolerate chilling temperature. Moreover these have the ability to retain various plant growth-promoting characteristics, e.g. production of phytohormones, nitrogen fixation and phosphate solubilization under adverse conditions. These properties of psychrotrophs could be utilized to promote plant growth under different stress conditions. Thus, psychrotrophs could help to alleviate cold stress in plants.

8.4.5 Biocontrol Activity

The increased use of pesticides and insecticides has become the major cause for environmental pollution. Microorganisms having the ability to control pathogenic organisms can be used as biocontrol agents to reduce the use of chemical pesticides and insecticides. Yarzábal et al. (2018) isolated 25 *Pseudomonas* spp. bacterial strains from Antarctic soils at Greenwich Island of South Shetland Islands, Antarctic Peninsula. These isolates were found to possess antifungal activity against plant pathogenic fungi such as *Fusarium oxysporum*, *Pythium ultimum* and *Phytophthora infestans* which suggested that these could be used as biocontrol agent and biofertilizer. Balcazar et al. (2015) isolated nine psychrotrophic bacteria having phosphate solubilization ability from glacial ice collected from two small tropical glaciers which was located above 4.900 m in the Venezuelan Andes. Four *Pseudomonas* spp., PGV024, PGV284, PGV094 and PGV085, showed biocontrol activity against *P. infestans*, *P. ultimum* and *F. oxysporum.*

Raaijmakers et al. (2002) observed that several psychrophilic *Pseudomonas* spp. inhibited the growth of plant pathogenic fungi by cell wall degradation using hydrolytic enzymes, production of antibiotics such as 2,4-diacetylphloroglucinol (2,4-DAPG), pyoluteorin, pyrrolnitrin siderophore production and production of several cyclic lipodepsipeptides (LDP). Vero et al. (2013) studied that psychrotrophic yeasts isolated from Antarctic soils could be used as potential biocontrol agents for the management of postharvest and control the diseases of apple during cold storage. Isolate *Leucosporidium scottii* designated At17 showed biocontrol activity for blue and grey mould of two apple cultivars.

8.4.6 Siderophores Production

At low iron concentration, iron-chelating compounds called siderophores are produced by microorganisms. These are small in size molecules (500–1200 Da) that increasing the bioavailability of iron specifically by binding ferric iron with high affinity. Kube et al. (2013) studied iron acquisition by psychrophilic bacterium *Oleispira antarctica*. Bioprospecting studies suggested siderophore production by psychrotrophic bacterial species such as *Actinobacteria*, *Firmicutes*, b-Proteobacteria and c-Proteobacteria such as pyochelins, pyoverdines, aerobactins, bacillibactins and yersiniabactins (Yadav et al. 2015a).

Mishra et al. (2008) isolated *Pseudomonas* sp. PGERs17 (MTCC 9000) from the northern Indian Himalayas and produced pyoverdines and pyochelins siderophore at 4 °C. Three hundred and twenty-five bacterial isolates were isolated from cold desert soil by Yadav et al. (2015b). On CAS agar plates, 29 strains out of 325 isolates produced siderophore at low temperature. Siderophores were bacillibactin, sanguibactin, pyoverdine and pyochelin produced by *Bacillus*, *Sanguibacter*, *Arthrobacter* and other species. Psychrotrophilic *Bacillus* sp. PZ-1 was found to be siderophore producer (Ren et al. 2015). Seventeen-fold increases in root colonization with increased siderophore production in cold-tolerant mutant of *Pseudomonas fluorescens* was observed. Plant growth promotion in *Vigna radiata* was observed at 25 °C and 10 °C by this mutant strain. Selvakumar et al. (2009) isolated a novel siderophore producing bacterium *Exiguobacterium acetylicum* strain from north-western Indian Himalayas. This bacterium has the ability to be used as biocontrol agents that inhibit the fungal growth of *Fusarium oxysporum, Pythium, Rhizoctonia solani* and *Sclerotium rolfsii*.

8.4.7 Resistance Induction by Cold-Tolerant PGPR

Metabolic activities of the plants are affected by cold temperature which leads to yield reduction in plants. *Burkholderia phytofirmans* strain PsJN, a plant growth-promoting bacterium, increased physiological movement and grapevine growth at a temperature (low) in *Vitis vinifera* cv. Chardonnay explants. It was observed that the plantlet biomass increased sixfold at 26 °C and 2.2-fold at 4 °C, whereas root growth increased 11.8-fold at 26 °C and 10.7-fold at 4 °C, respectively (Barka et al. 2006). The psychrotolerant bacteria were isolated from the apoplast leaf of wild plants (cold-adapted) and inoculated on leaves of bean seedling that enhanced the cold resistance of bean seedlings. At cold conditions, these bacteria secreted specific extracellular proteins and showed ACC deaminase activity (Tiryaki et al. 2019).

Mishra et al. (2009) isolated a cold-tolerant bacterium *Pseudomonas* sp. NARs9 (MTCC9002) from the Indian Himalayas and also studied growth encouragement activities. Seed bacterization with isolate increased the germination, shooting and root lengths of 30-day wheat seedlings, respectively, by 19.2, 30.0 and 22.9 percent compared to uninoculated controls. Selvakumar et al. (2008a) studied *Pantoea dispersa* 1A (MTCC 8706), a cold-tolerant plant growth-promoting bacterium isolated from sub-alpine soil in the northwestern Indian Himalayas, to be used as an inoculant in cold wheat-growing environments to achieve the desired results of bacterization. Wu et al. (2019) studied that at 10 °C, *Bacillus pumilus*, *Bacillus safensis* and *Bacillus atrophaeus* promote the growth of winter wheat seedlings in pot house under cold condition. So these can act as promising candidates for sustainable agriculture under extreme climate of cold conditions. Various psychrotrophs having plant growth-promoting properties with isolation source are mentioned in Table 8.1.

Table 8.1 Plant growth-promoting psychrotolerant bacteria associated with crops

Microorganisms	Isolation source	PGP properties	References
P*seudomonas fragi, P. chlororaphis, P. fluorescens, P. proteolytica and Brevibacterium frigoritolerans*	Leaf apoplastic fluid of *Draba nemorosa*, Galanthus *gracilis*, Colchicum *speciosum*, Scilla *siberica*, *Erodium cicutarium*	ACC deaminase activity	Tiryaki et al. (2019)
Flavobacterium sp. OR306 and *Pseudomonas frederiksbergensis* OS211	Agricultural soil in winter	1-Aminocyclopropane-1-carboxylate deaminase (ACCD) gene	Subramanian et al. (2015)
Bacillus species	Qinghai-Tibetan plateau	Biocontrol activity	Wu et al. (2019)
Pseudomonas frederiksbergensis OS261	Chungbuk agricultural research and extension services, Ochang-eup, South Korea	ACC deaminase activity	Subramanian et al. (2016)
Pseudomonas sp. strain NARs1	Rhizospheric soil of *Amaranth* plant	Nutrient uptake, N_2 fixation	Mishra et al. (2011)
Pseudomonas lurida M2RH3 (MTCC 9245)	Uttarakhand Himalayas	Phosphorus solubilization	Selvakumar et al. (2011)
Pseudomonad strains	NW Himalayas	Biofertilizer	Mishra et al. (2011)
Serratia marcescens strain SRM *(MTCC 8708)*	Flowers of summer squash *(Cucurbita pepo)*	Phosphorus solubilization, IAA production, HCN, siderophore production	Selvakumar et al. (2011)
Pseudomonas spp.	Antarctic soils at Greenwich Island (South Shetland Islands, Antarctic peninsula)	Phosphorus solubilization, IAA production, HCN, biocontrol activity	Yarzábal et al. (2017)

8.5 Future Prospects and Challenges

Microorganisms have ubiquitous distribution all over the world. Microbes have the ability to grow under extreme conditions whether it is the colder regions of Himalayas and Alpine and polar region or thermal hot springs and deserts. The importance of microbes growing under such extreme conditions is increasing worldwide to study the adaptation they undergo for survival and growth under adverse conditions. Climate change has further enhanced the importance of their study among scientific communities. A temperate agro-ecosystem has a short growing season and low temperature which leads to cold temperature stress among plants and microbes. Cold stress has a negative impact on agriculture because it causes chilling and freezing injury among the plants. Moreover, in different parts of the world, cropping systems have to face transient colds which leads to negative impact on nitrogen fixation and plant growth promotion. Disease infestation also gets enhanced among plants at such a lower temperature. Psychrotrophs could be used as biofertilizer and biocontrol agents in such extreme conditions of lower temperature. There is a need to isolate microbes from extreme climates such as alpine and polar regions because these are adapted to grow under such adverse conditions, so it could be used to enhance plant growth, crop yield and agriculture productivity.

References

Agarwal S, Sairam RK, Srivastava GC, Tyagi A, Meena RC (2005) Role of ABA, salicylic acid, calcium, and hydrogen peroxide on antioxidant enzymes introduction in wheat seedlings. Plant Sci 169:559–570

Ait Barka E, Nowk J, Clement C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with plant growth promoting rhizobacteria *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72:7246–7252

Balcazar W, Rondón J, Rengifo M, Ball MM, Melfo A, Gómez W, Yarzábal LA (2015) Bioprospecting glacial ice for plant growth promoting bacteria. Microbiol Res 177:1–7

Barka EA, Nowak J, Clément C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl Environ Microbiol 72(11):7246–7252

Cai G, Wang G, Wang L, Pan J, Liu Y, Li D (2014) *ZmMKK1*, a novel group A mitogen-activated protein kinase gene in maize conferred chilling stress tolerance and was involved in pathogen defense in transgenic tobacco. Plant Sci 214:57–73

Cakmakcl R, Mustafa E, Ummugulsum E, Mesude FD (2007) The influence of plant growth promoting rhizobacteria on growth and enzyme activities in wheat and spinach plants. J Plant Nutr Soil Sci 170:288–295

Chang M, Chien W, Chao C, Lu M (2010) Effects of cold stress on alterations of physiochemical and chemical properties of rice polysaccharides. Carbohydr Polym 80:374–377

Chattopadhyay MA, Jagannadham MV (2001) Maintenance of membrane fluidity in Antarctic bacteria. Polar Biol 24:386–388

Cheng Z, Park E, Glick BR (2007) 1-Aminocyclopropane-1-carboxylate (ACC) deaminase from *Pseudomonas putida* UW4 facilitates the growth of canola in the presence of salt. Can J Microbiol 53:912–918

D'Amico S, Collins T, Marx JC, Feller G, Gerday C (2006) Psychrophilic microorganisms: challenges for life. EMBO Rep 7(4):385–389

Devanand BJ, Patil AB, Kulkaarni JH, Algawadi AR (2002) Effect of plant growth promoting rhizobacteria on growth and yield of pigeonpea (*Cajanus cajan* L.) by application of plant growth promoting rhizobacteria. Microbiol Res 159:371–394

Drouin P, Prevost D, Antoun H (2000) Physiological adaptation to low temperatures of strains of *Rhizobium leguminosarum* bv. *viciae* associated with *Lathyrus* spp. FEMS Microbiol Ecol 32:111–120

Ek-Jandér J, Fåhraeus G (1971) Adaptation of rhizobium to subarctic environment in Scandinavia. Plant Soil 35(1):129–137

ElSayed AI, Rafudeen MS, Golldack D (2014) Physiological aspects of raffinose family oligosaccharides in plants: protection against abiotic stress. Plant Biol 16(1):1–8

Fong N, Burgess M, Barrow K, Glenn D (2001) Carotenoid accumulation in the psychrotrophic bacterium *Arthrobacter agilis* in response to thermal and salt stress. Appl Microbiol Biotechnol 56(5–6):750–756

Giangrossi M, Giuliodori AM, Gualerzi CO, Pon CL (2002) Selective expression of the beta-subunit of nucleoid-associated protein HU during cold shock in *Escherichia coli*. Mol Microbiol 44:205–216

Gulati A, Vyas P, Rahi P, Kasana RC (2009) Plant growth-promoting and rhizosphere competent *Acinetobacter rhizosphaerae* strain BIHB 723 from the cold deserts of the Himalayas. Curr Microbiol 58:371–377

Gull M, Hafeez FY, Saleem M, Malik KA (2004) Phosphorus uptake and growth promotion of chickpea by co-inoculation of mineral phosphate solubilising bacteria and a mixed rhizobial culture. Aust J Exp Agric 44(6):623–628

Guy CL (1990) Cold acclimation and freezing stress tolerance: role of protein metabolism. Annu Rev Plant Phys 41:187–223

Hasegawa T, Mochida T, Kondo R, Kagoshima S, Iwasa Y, Akutagawa T, Nakamura T, Saito G (2000) Mixed-stack organic charge-transfer complexes with intercolumnar networks. Phys Rev 62:10059–10066

Hopkins WG (1999) The physiology of plants under stress. Volume 2: Introduction to plant physiology. Wiley, New York

Janda T, Szalai G, Rios-Ganzalez K, Veisz O, Paldi E (2003) Comparative study of frost tolerance and antioxidant activity in cereals. Plant Sci 164:301–306

Jiang QW, Kiyoharu O, Ryozo I (2002) Two novel mitogen-activated protein signaling components, OsMEK1 and OsMAP1, are involved in a moderate low-temperature signaling pathway in rice. Plant Physiol 129:1880–1891

Jones PG, VanBogelen RA, Neidhardt FC (1987) Induction of proteins in response to low temperature in *Escherichia coli*. J Bacteriol 169(5):2092–2095

Jousse C, Dalle C, Canet I, Lagrée M, Traïkia M, Lyan B, Delort AM (2018) Metabolomic study of the response to cold shock in a strain of *Pseudomonas syringae* isolated from cloud water. Metabolomics 14(1):11

Jung YH, Lee YK, Lee HK, Lee K, Im H (2018) CspB of an arctic bacterium, *Polaribacterirgensii* KOPRI 22228 confers extraordinary freeze-tolerance. Braz J Microbiol 49(1):97–103

Kadioglu GB, Koseoglu MS, Sezen A, Ozdal OG, Algur OF (2018) Isolation of cold tolerant and ACC deaminase producing plant growth promoting rhizobacteria from high altitudes. Romanian Biotechnol Letters 23:13479–13486

Kasuga M, Miural S, Shinozaki K, Yamaguchi-Shinozaki K (2004) A combination of the *Arabidopsis* DREB1A gene and stress inducible rd29A promoter improved drought- and low-temperature stress tolerance in tobacco by gene transfer. Plant Cell Physiol 45:346–350

Katiyar V, Goel R (2003) Solubilization of inorganic phosphate and plant growth promotion by cold tolerant mutants of *Pseudomonas fluorescens*. Microbiol Res 158(2):163–168

Kaushik R, Saxena AK, Tilak KVBR (2001) Selection and evaluation of *Azospirillum brasilense* strains capable of growing at sub-optimal temperature in rhizocoenosis with wheat. Folia Microbiol 46:327–332

Kawahara H, Koda N, Oshio M, Obata H (2000) A cold acclimation protein with refolding activity on frozen denatured enzyme. Biosci Biotechnol Biochem 64:2668–2774

Keto-Timonen R, Hietala N, Palonen E, Hakakorpi A, Lindström M, Korkeala H (2016) Cold shock proteins: a minireview with special emphasis on Csp-family of enteropathogenic *Yersinia*. Front Microbiol 7:1151

Kolesnichenko AV, Pobezhimova TP, Grabelnych OI, Tourchaninova VV, Korzun AM, Koroleva NA, Voinikov VK (2003) Difference between the temperature of non-hardened and hardened winter wheat seedling shoots during cold stress. J Therm Biol 28(3):235–244

Kour D, Rana KL, Kumar A, Rastegari AA, Yadav N, Yadav AN et al (2019a) Extremophiles for hydrolytic enzymes productions: biodiversity and potential biotechnological applications. In: Molina G, Gupta VK, Singh BN, Gathergood N (eds) Bioprocessing for biomolecules production. Wiley, Hoboken, pp 321–372

Kour D, Rana KL, Yadav N, Yadav AN, Kumar A, Meena VS et al (2019b) Rhizospheric microbiomes: biodiversity, mechanisms of plant growth promotion, and biotechnological applications for sustainable agriculture. In: Kumar A, Meena VS (eds) Plant growth promoting rhizobacteria for agricultural sustainability: from theory to practices. Springer, Singapore, pp 19–65. https://doi.org/10.1007/978-981-13-7553-8_2

Kube M et al (2013) Genome sequence and functional genomic analysis of the oil-degrading bacterium *Oleispira Antarctica*. Nat Commun 4:11

Kumar GS, Jagannadham MV, Ray MK (2002) Low-temperature-induced changes in composition and fluidity of lipopolysaccharides in the Antarctic psychrotrophic bacterium *Pseudomonas syringae*. J Bacteriol 184(23):6746–6749

Lynch DV (1990) Chilling injury in plants: the relevance of membrane lipids. In: Katterman F (ed) Environmental injury to plants. Wiley, New York, pp 451–475

Mazzon RR, Lang EA, Silva CA, Marques MV (2012) Cold shock genes cspA and cspB from *Caulobacter crescentus* are posttranscriptionally regulated and important for cold adaptation. J Bacteriol 194(23):6507–6517

Mishra PK, Mishra S, Selvakumar G, Bisht SC, Kundu S, Bisht JK, Gupta HS (2008) Characterization of a psychrotrophic plant growth promoting *Pseudomonas* PGERs17 (MTCC 9000) isolated from North Western Indian Himalayas. Ann Microbiol 58:1–8

Mishra PK, Mishra S, Bisht SC, Selvakumar G, Kundu S, Bisht JK, Gupta HS (2009) Isolation, molecular characterization and growth-promotion activities of a cold tolerant bacterium *Pseudomonas* sp. NARs9 (MTCC9002) from the Indian Himalayas. Biol Res 42:305–313

Mishra PK, Bisht SC, Ruwari P, Selvakumar G, Joshi GK, Bisht JK et al (2011a) Alleviation of cold stress in inoculated wheat (*Triticum aestivum* L.) seedlings with psychrotolerant *Pseudomonas* from NW Himalayas. Arch Microbiol 193:497–513

Mojib N, Nasti TH, Andersen DT, Attigada VR, Hoover RB, Yusuf N, Bej AK (2011) The antiproliferative function of violacein-like purple violet pigment (PVP) from an Antarctic *Janthinobacterium* sp. Ant5-2 in UV-induced 2237 fibrosarcoma. Int J Dermatol 50(10):1223–1233

Mykytczuk NC, Trevors JT, Twine SM, Ferroni GD, Leduc LG (2010) Membrane fluidity and fatty acid comparisons in psychrotrophic and mesophilic strains of *Acidithiobacillus ferrooxidans* under cold growth temperatures. Arch Microbiol 192(12):1005–1018

Ortiz-Ojeda P, Ogata-Gutiérrez K, Zúñiga-Dávila D (2017) Evaluation of plant growth promoting activity and heavy metal tolerance of psychrotrophic bacteria associated with maca (*Lepidium meyenii* Walp.) rhizosphere. AIMS Microbiol 3:279–292

Panicker G, Aislabie J, Saul D, Bej AK (2002) Cold tolerance of *Pseudomonas* sp. 30-3 isolated from oil-contaminated soil. Antarctica Polar Biol 25(1):5–11

Pittera J, Jouhet J, Breton S, Garczarek L, Partensky F, Maréchal E, Nguyen NA, Doré H, Ratin M, Pitt FD, Scanlan DJ (2018) Thermoacclimation and genome adaptation of the membrane lipidome in marine *Synechococcus*. Environ Microbiol 20(2):612–631

Prevost D, Drouin P, Laberge S, Bertrand A, Cloutier J, Levesque G (2003) Cold-adapted rhizobia for nitrogen fixation in temperate regions. Can J Bot 81:1153–1161

Raaijmakers JM, Vlami M, De Souza JT (2002) Antibiotic production by bacterial biocontrol agents. Antonie Van Leeuwenhoek 81(1–4):537

Rana KL, Kour D, Sheikh I, Dhiman A, Yadav N, Yadav AN et al (2019a) Endophytic fungi: biodiversity, ecological significance and potential industrial applications. In: Yadav AN, Mishra S, Singh S, Gupta A (eds) Recent advancement in white biotechnology through fungi. Volume 1: Diversity and enzymes perspectives. Springer, Cham, pp 1–62

Rana KL, Kour D, Sheikh I, Yadav N, Yadav AN, Kumar V et al (2019b) Biodiversity of endophytic fungi from diverse niches and their biotechnological applications. In: Singh BP (ed) Advances in endophytic fungal research: present status and future challenges. Springer, Cham, pp 105–144. https://doi.org/10.1007/978-3-030-03589-1_6

Ray MK (2006) Cold-stress response of low temperature adapted bacteria. In: Sreedhar AS, Srinivas UK (eds) Stress response: a molecular biology approach. Research Signpost India, Trivandrum, pp 1–23

Ren GM, Jin Y, Zhang CM, Gu HD, Qu JJ (2015) Characteristics of *Bacillus* sp PZ-1 and its biosorption to Pb(II). Ecotoxicol Environ Saf 117:141–148

Saxena AK, Yadav AN, Kaushik R, Tyagi SP, Shukla L (2015) Biotechnological applications of microbes isolated from cold environments in agriculture and allied sectors. In: Proceedings international conference on "Low temperature science and biotechnological advances". Society of Low Temperature Biology, New Delhi, p 104

Saxena AK, Yadav AN, Rajawat MVS, Kaushik R, Kumar R et al (2016) Microbial diversity of extreme regions: an unseen heritage and wealth. Indian J Plant Genet Resour 29(3):246–248

Seel W, Flegler A, Zunabovic-Pichler M, Lipski A (2018) Increased isoprenoid quinone concentration modulates membrane fluidity in *Listeria monocytogenes* at low growth temperatures. J Bacteriol 200(13):e00148–18

See-Too WS, Convey P, Pearce DA, Lim YL, Ee R, Yin WF, Chan KG (2016) Complete genome of *Planococcus rifietoensis* M8T, a halotolerant and potentially plant growth promoting bacterium. J Biotechnol 221:114–115

Seki M, Kamei A, Yamguchi-Shinozaki K, Schinozaki K (2003) Molecular responses to drought salinity and frost: common and different plants for plant protection. Curr Opin Biotechnol 14:194–199

Selvakumar G, Kundu S, Joshi P, Gupta AD, Nazim S, Mishra PK, Gupta HS (2008a) Characterization of a cold-tolerant plant growth-promoting bacterium *Pantoea dispersa* 1A isolated from a sub-alpine soil in the North Western Indian Himalayas. World J Microbiol Biotechnol 24:955–960

Selvakumar G, Mohan M, Kundu S, Gupta AD, Joshi P, Nazim S, Gupta HS (2008b) Cold tolerance and plant growth promotion potential of *Serratia marcescens* strain SRM(MTCC 8708) isolated from flowers of summer squash (*Cucurbita pepo*). Lett Appl Microbiol 46:171–175

Selvakumar G, Joshi P, Nazim S, Mishra PK, Kundu S, Gupta HS (2009) *Exiguobacterium acetylicum* strain 1P (MTCC 8707) a novel bacterial antagonist from the North Western Indian Himalayas. World J Microbiol Biotechnol 25:131–137

Selvakumar G, Joshi P, Suyal P, Mishra PK, Joshi GK, Bisht JK, Gupta HS (2011) *Pseudomonas lurida* M2RH3 (MTCC 9245) a psychrotolerant bacterium from the Uttarakhand Himalayas, solubilizes phosphate and promotes wheat seedling growth. World J Microbiol Biotechnol 27(5):1129–1135

Singh RN, Gaba S, Yadav AN, Gaur P, Gulati S, Kaushik R et al (2016) First, high quality draft genome sequence of a plant growth promoting and cold active enzymes producing psychrotrophic *Arthrobacter agilis* strain L77. Stand Genomic Sci 11:54. https://doi.org/10.1186/s40793-016-0176-4

Singh A, Krishnan KP, Prabaharan D, Sinha RK (2017) Lipid membrane modulation and pigmentation: a cryoprotection mechanism in Arctic pigmented bacteria. J Basic Microbiol 57(9):770–780

Subczynski WK, Markowska E, Gruszecki WI, Sielewiesiuk J (1992) Effect of polar carotenoids on dimyristoylphosphatidylcholine membranes: a spin-label study. Biochem Biophys Acta 1105:97–108

Subramanian P, Krishnamoorthy R, Chanratana M, Kim K, Sa T (2015) Expression of an exogenous 1-aminocyclopropane-1-carboxylate deaminase gene in psychrotolerant bacteria modulates ethylene metabolism and cold induced genes in tomato under chilling stress. Plant Physiol Biochem 89:18–23

Subramanian P, Kim K, Krishnamoorthy R, Mageswari A, Selvakumar G, Sa T (2016) Cold stress tolerance in psychrotolerant soil bacteria and their conferred chilling resistance in tomato (*Solanum lycopersicum* Mill.) under low temperatures. PLoS One 11(8):e0161592

Suzuki N, Mittler R (2008) Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. Physiol Plant 126:45–51

Tiryaki D, Aydın İ, Atıcı Ö (2019) Psychrotolerant bacteria isolated from the leaf apoplast of cold-adapted wild plants improve the cold resistance of bean (*Phaseolus vulgaris L.*) under low temperature. Cryobiology 86:111–119

Trivedi P, Pandey A, Sa T (2007) Chromate reducing and plant growth promoting activities of psychrotrophic *Rhodococcus erythropolis* MTCC 7905. J Basic Microbiol 47(6):513–517

Turan M, Gulluce M, Cakmak R, Sahin F (2013) Effect of plant growth-promoting rhizobacteria strain on freezing injury and antioxidant enzyme activity of wheat and barley. J Plant Nutr 36:731–748

Verma P, Yadav AN, Khannam KS, Kumar S, Saxena AK et al (2015a) Plant growth promotion and mitigation of cold stress in inoculated wheat (*Triticum aestivum* L.) by K-solubilizing psychrotolerant *Methylobacterium phyllosphaerae* strain IARI-HHS2-67. In: Proceeding of international conference on "Low temperature science and biotechnological advances". Society of Low Temperature Biology, New Delhi, p 175

Verma P, Yadav AN, Shukla L, Saxena AK, Suman A (2015b) Hydrolytic enzymes production by thermotolerant *Bacillus altitudinis* IARI-MB-9 and *Gulbenkiania mobilis* IARI-MB-18 isolated from Manikaran hot springs. Int J Adv Res 3:1241–1250

Verma P, Yadav AN, Shukla L, Saxena AK, Suman A (2015c) Alleviation of cold stress in wheat seedlings by *Bacillus amyloliquefaciens* IARI-HHS2-30, an endophytic pschrotolerant K-solubilizing bacterium from NW Indian Himalayas. Natl J Life Sci 12:105–110

Verma P, Yadav AN, Kumar V, Singh DP, Saxena AK (2017) Beneficial plant-microbes interactions: biodiversity of microbes from diverse extreme environments and its impact for crop improvement. In: Singh DP, Singh HB, Prabha R (eds) Plant-microbe interactions in agro-ecological perspectives. Volume 2: Microbial interactions and agro-ecological impacts. Springer, Singapore, pp 543–580. https://doi.org/10.1007/978-981-10-6593-4_22

Vero S, Garmendia G, González MB, Bentancur O, Wisniewski M (2013) Evaluation of yeasts obtained from Antarctic soil samples as biocontrol agents for the management of postharvest diseases of apple (malus× domestica). FEMS Yeast Res 13(2):189–199

Vyas P, Rahi P, Gulati A (2009) Stress tolerance and genetic variability of phosphate-solubilizing fluorescent *Pseudomonas* from the cold deserts of the Trans-Himalayas. Microb Ecol 58:425–434

Wu H, Gu Q, Xie Y, Lou Z, Xue P, Fang L, Schneider A (2019) Cold-adapted bacilli isolated from the Qinghai–Tibetan plateau are able to promote plant growth in extreme environments. Environ Microbiol 21(9):3505–3526

Yadav AN (2015) Bacterial diversity of cold deserts and mining of genes for low temperature tolerance. Ph.D. thesis, IARI, New Delhi/BIT, Ranchi, p 234. https://doi.org/10.13140/RG.2.1.2948.1283/2

Yadav AN, Sachan SG, Verma P, Saxena AK (2015a) Prospecting cold deserts of North Western Himalayas for microbial diversity and plant growth promoting attributes. J Biosci Bioeng 119(6):683–693

Yadav AN, Sachan SG, Verma P, Tyagi SP, Kaushik R, Saxena AK (2015b) Culturable diversity and functional annotation of psychrotrophic bacteria from cold desert of LehLadakh (India). World J Microbiol Biotechnol 31(1):95–98

Yadav AN, Verma P, Sachan S, Kaushik R, Saxena AK (2015c) Mitigation of cold stress for growth and yield of wheat (*Triticum aestivum* L.) by psychrotrophic *pseudomonads* from cold deserts of Indian Himalayas. In: Proceeding of 56th AMI and international symposium on emerging discoveries in microbiology. https://doi.org/10.13140/RG.2.1.4367.7523

Yadav AN, Sachan SG, Verma P, Kaushik R, Saxena AK (2016a) Cold active hydrolytic enzymes production by psychrotrophic Bacilli isolated from three sub-glacial lakes of NW Indian Himalayas. J Basic Microbiol 56:294–307

Yadav AN, Sachan SG, Verma P, Saxena AK (2016b) Bioprospecting of plant growth promoting psychrotrophic Bacilli from cold desert of north western Indian Himalayas. Indian J Exp Biol 54:142–150

Yadav AN, Verma P, Kumar V, Sachan SG, Saxena AK (2017) Extreme cold environments: a suitable niche for selection of novel psychrotrophic microbes for biotechnological applications. Adv Biotechnol Microbiol 2(2):1–4

Yadav AN, Verma P, Sachan SG, Kaushik R, Saxena AK (2018) Psychrotrophic microbiomes: molecular diversity and beneficial role in plant growth promotion and soil health. In: Panpatte DG, Jhala YK, Shelat HN, Vyas RV (eds) Microorganisms for Green Revolution. Volume

2: Microbes for sustainable agro-ecosystem. Springer, Singapore, pp 197–240. https://doi.org/10.1007/978-981-10-7146-1_11

Yadav AN, Kour D, Sharma S, Sachan SG, Singh B, Chauhan VS et al (2019a) Psychrotrophic microbes: biodiversity, mechanisms of adaptation, and biotechnological implications in alleviation of cold stress in plants. In: Sayyed RZ, Arora NK, Reddy MS (eds) Plant growth promoting rhizobacteria for sustainable stress management: Volume 1: Rhizobacteria in abiotic stress management. Springer, Singapore, pp 219–253. https://doi.org/10.1007/978-981-13-6536-2_12

Yadav AN, Yadav N, Sachan SG, Saxena AK (2019b) Biodiversity of psychrotrophic microbes and their biotechnological applications. J Appl Biol Biotechnol 7:99–108

Yadav AN, Singh J, Rastegari AA, Yadav N (2020) Plant microbiomes for sustainable agriculture. Springer, Cham

Yarzábal LA, Chica E (2017) Potential for developing low-input sustainable agriculture in the tropical Andes by making use of native microbial resources. In: Singh D, Singh H, Prabha R (eds) Plant-microbe interactions in agro-ecological perspectives, microbial interactions and agro-ecological impacts, vol 2. Springer, Singapore, pp 29–54

Yarzábal LA, Monserrate L, Buela L, Chica E (2018) Antarctic *Pseudomonas* spp. promote wheat germination and growth at low temperatures. Polar Biol 41(11):2343–2354

Zhang H, Prithiviraj B, Charles TC, Driscoll BT, Smith DL (2003) Low temperature tolerant *Bradyrhizobium japonicum* strains allowing improved nodulation and nitrogen fixation of soybean in a short season (cool spring) area. Eur J Agron 19:205–213

Zhang Y, Li D, Wang H, Xiao Q, Liu X (2006) Molecular diversity of nitrogen-fixing bacteria from the Tibetan Plateau, China. FEMS Microbiol Lett 260(2):134–142

Zhang N, Sun Q, Zhang H, Cao Y, Weeda S, Ren S (2015) Roles of melatonin in abiotic stress resistance in plants. J Exp Bot 66:647–656

Zhu JK (2002) Salt and drought stress signal transduction in plants. Annu Rev Plant Biol 53:247–273