Psychrotrophic Microbiomes: Molecular Diversity and Beneficial Role in Plant Growth Promotion and Soil Health

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Abstract

Prospecting the cold habitats has led to the isolation of a great diversity of psychrotrophic microbes belonging to different groups. The cold-adapted microbes have potential biotechnological applications in agriculture, medicine, and industry as they can produce cold-adapted enzymes (amylase, cellulase, chitinase, laccase, lipase, pectinase, protease, xylanase, β-galactosidase, and β-glucosidase), antifreezing compounds, and antibiotics and possess diverse multifunctional plant growth-promoting attributes (production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophores; solubilization of phosphorus, potassium, and zinc; 1-aminocyclopropane-1-carboxylate deaminase activity and biocontrol activity against plant pathogenic microbes). Cold-adapted microbes are ubiquitous in nature and have been reported from Antarctica, permanently ice-covered lakes, cloud droplets, ice cap cores from considerable depth, snow, glaciers, and those associated with plants growing in cold habitats. Cold-adapted microbial communities can be studied using culture-dependent and culture-independent

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techniques. Microbes recovered using both techniques revealed the occurrence of different and diverse major groups, *viz.*, Actinobacteria, Ascomycota, Bacteroidetes, Basidiomycota, Chlamydiae, Chloroflexi, Cyanobacteria, Euryarchaeota, Firmicutes, Gemmatimonadetes, Mucoromycota, Nitrospirae, Planctomycetes, Proteobacteria, Spirochaetes, Thaumarchaeota, and Verrucomicrobia. On the review of isolated cold-adapted microbes, it was found that Proteobacteria was the most dominant phylum followed by Firmicutes and Actinobacteria. This book chapter deals with the isolation, characterization, and biodiversity of cold-tolerant microbes from Antarctica; Himalayan cold desert; glaciers; ice-capped rivers; plant-associated, subalpine region of Uttarakhand; and different sub-glacial lakes. The biotechnological applications of cold-adapted microbes have been discussed. The benificial and potential cold-adapted microbes may have applications in diverse processes in agriculture, industry, and allied sectors.

Keywords
Antarctica · Biofertilizers · Biodiversity · Cold desert · Indian Himalayas · Psychrotrophic microbes · Sub-glacial lakes

11.1 Introduction

The microbiomes of cold environments are of particular importance in global ecology since the majority of terrestrial and aquatic ecosystems of our planet are permanently or seasonally submitted to cold temperatures. Earth is primarily a cold, marine planet with 90% of the ocean's waters being at 5 °C or lower. Permafrost soils, glaciers, polar sea ice, and snow cover make up 20% of the Earth's surface environments. Microbial communities under cold habitats have undergone the physiological adaptations to low temperature and chemical stress. Recently, these communities have attained the focus of applied research not only in terms of biotechnological prospects but also to understand the use of primitive analogues of biomolecules existed during early Earth environments (Yadav 2015; Saxena et al. 2016). The microbiomes of cold environments have been extensively investigated in the past few years with a focus on culture-dependent and culture-independent techniques. Cold-adapted microorganisms have been reported from Antarctic sub-glacial and permanently ice-covered lakes, cloud droplets, ice cap cores from considerable depth, snow, and glaciers (Srivastava et al. 2014; Yadav et al. 2015a, b, c). Many novel microbes have been sorted out from cold environments including *Halobacterium lacusprofundi* (Franzmann et al. 1988), *Sphingobacterium antarcticus* (Shivaji et al. 1992), *Octadecabacter arcticus* (Gosink et al. 1997), *Hymenobacter roseosalivarius* (Hirsch et al. 1998), *Cellulophaga algicola* (Bowman 2000), *Flavobacterium frigidarium* (Humphry et al. 2001), *Oleispira antarctica* (Yakimov et al. 2003), *Flavobacterium psychrolimnae* (Van Trappen et al. 2005), *Psychromonas ingrahamii* (Auman et al. 2006), *Exiguobacterium soli* (Chaturvedi et al. 2008), *Pseudomonas extremaustralis* (López et al. 2009), *Cryobacterium roopkundense* (Reddy et al. 2010), *Sphingomonas glacialis* (Zhang et al. 2011), *Pedobacter arcticus* (Zhou et al.

2012), *Sphingobacterium psychroaquaticum* (Albert et al. 2013), *Lacinutrix jangbogonensis* (Lee et al. 2014), *Massilia eurypsychrophila* (Shen et al. 2015), *Glaciimonas frigoris* (Margesin et al. 2016), and *Psychrobacter pocilloporae* (Zachariah et al. 2017). There are several reports on whole genome sequences of novel and potential psychrotrophic microbes (Kim et al. 2012; Singh et al. 2016).

The novel species of psychrotrophic microbes have been isolated worldwide and reported from different phylum of domain Archaea (Euryarchaeota and Thaumarchaeota), bacteria (Actinobacteria, Bacteroidetes, Chlamydiae, Chloroflexi, Cyanobacteria, Firmicutes, Gemmatimonadetes, Mucoromycota, Nitrospirae, Planctomycetes, Proteobacteria, Spirochaetes, and Verrucomicrobia), and fungi (Ascomycota, Basidiomycota, and Mucoromycota) (Franzmann et al. 1988; Shivaji et al. 1992; Gosink et al. 1997; Hirsch et al. 1998; Bowman 2000; Humphry et al. 2001; Yakimov et al. 2003; Van Trappen et al. 2005; Auman et al. 2006; Chaturvedi et al. 2008; López et al. 2009; Reddy et al. 2010; Zhang et al. 2011; Zhou et al. 2012; Albert et al. 2013; Lee et al. 2014; Shen et al. 2015; Margesin et al. 2016; Zachariah et al. 2017). Prospecting the cold habitats has led to the isolation of a great diversity of psychrotrophic microorganisms. The cold-adapted microbes have potential biotechnological applications in agriculture, medicine, and industry. The bacterial diversity from the cold environment could serve as a database for selection of bio-inoculants with PGP ability and could be used for improving the growth and yield of crops grown at high altitudes with prevailing low temperatures (Kumar et al. 2013; Yadav et al. 2014a, 2015d, 2017e; Kumar et al. 2016).

The psychrophilic/psychrotrophic/psychrotolerant microbes from Antarctica; Himalayan cold desert; glaciers; ice-capped rivers; plant-associated, subalpine region of Uttarakhand; and different sub-glacial lakes could be used in agriculture, medicine, and industry as they can produce cold-adapted enzymes (amylase, cellulase, chitinase, laccase, lipase, pectinase, protease, xylanase, β-galactosidase, and β-glucosidase), antifreezing compounds, and antibiotics and possess diverse multifunction plant growth-promoting attributes (production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophore; solubilization of phosphorus, potassium, and zinc; 1-aminocyclopropane-1-carboxylate deaminase activity and biocontrol activity against plant pathogenic microbes). Psychrotrophic plant growth-promoting (PGP) microbes have been shown to promote plant growth either directly by biological N_2-fixation; solubilization of minerals such as phosphorus, potassium, and zinc; and production of siderophores and plant growth hormones or indirectly via production of antagonistic substances by inducing resistance against plant pathogens under the native conditions from which they have been isolated (Verma et al. 2015a, 2016; Yadav et al. 2016c, 2017c). The psychrotrophic PGP microbes can have an impact on plant growth providing the plant with compound(s) of microbial origin for facilitating the uptake of nutrients from the environment. Psychrotrophic PGP microbes were found in several genera, including *Arthrobacter*, *Bacillus*, *Brevundimonas*, *Burkholderia*, *Pseudomonas*, *Citricoccus*, *Exiguobacterium*, *Flavobacterium*, *Janthinobacterium*, *Kocuria*, *Lysinibacillus*, *Methylobacterium*, *Microbacterium*, *Paenibacillus*, *Providencia*, and *Serratia* (Yadav 2009; Saxena et al. 2015b; Verma et al. 2015d, 2016; Yadav et al. 2016b). Among these taxa, *Pseudomonas* and *Exiguobacterium* have been the best characterized for PGP at low temperatures (Yadav et al. 2013, 2015f, 2017h, i). There are several studies have demonstrated the benefits of PGP microbes on the growth and yield of different crops at different climates, soils, and temperatures. The use of PGP microbes improves plant growth by supplying plant nutrients, which can help sustain environmental health and soil productivity.

Psychrophilic/psychrotolerant microbes are important for many reasons, particularly because they produce cold-active enzymes. Enzymes from psychrophiles have become interesting for industrial applications, partly because of ongoing efforts to decrease energy consumption. These enzymes provide opportunities to study the adaptation of life to low temperature and the potential for biotechnological exploitation (Yadav et al. 2016a; Saxena et al. 2016). Most of the work that has been conducted on psychrophilic bacteria is focused on cold-adapted enzymes such as amylase, protease, lipase, pectinase, xylanase, cellulase, β-galactosidase, β-glucosidase, and chitinase (Yadav et al. 2016a). Cold-active enzymes are produced by psychrophilic microbes, namely, *Acinetobacter*, *Aquaspirillum*, *Arthrobacter*, *Bacillus*, *Carnobacterium*, *Clostridium*, *Cytophaga*, *Flavobacterium*, *Marinomonas*, *Moraxella*, *Moritella*, *Paenibacillus*, *Planococcus*, *Pseudoalteromonas*, *Pseudomonas*, *Psychrobacter*, *Shewanella*, *Vibrio*, and *Xanthomonas* (Gerday et al. 2000; Groudieva et al. 2004; Yadav et al. 2014b, 2016a, 2017h; Singh et al. 2016). Psychrophilic microbes can be applied for biodegradation of agro-wastes at low temperatures. Shukla et al. (2016) have developed psychrotrophic microbial consortium of *Eupenicillium crustaceum*, *Paecilomyces* sp., *Bacillus atrophaeus*, and *Bacillus* sp., for its potential applications toward degradation of agri-residues and conversion to a value-added product like compost for enhancing soil fertility and decreasing environmental pollution caused by burning of agro-wastes. Psychrotrophic microbes produced antifreezing compounds at low temperatures (Yadav 2015; Singh et al. 2016; Yadav et al. 2017e). Antifreezing compounds are useful in cryosurgery and also in the cryopreservation of whole organisms, isolated organs, cell lines, and tissues. In food industry, antifreezing proteins (AFPs) can be used to improve the quality of frozen food. Improved cold tolerance in fishes has been achieved in some cases by direct injection of AFPs and in another case by transgenic expression of an AFP.

Biotechnology has opened up new possibilities for potential applications of beneficial microbiomes to the soil for the PGP and biocontrol of soilborne pathogens. An understanding of microbial diversity and its potential applications in agriculture is important and useful to arrive at measures that can act as indicators of plant growth, yield, and soil health. Cold-adapted microbes have attracted the attention of the scientific community due to their ability to promote plant growth and produce cold-active enzymes, with potential biotechnological applications in a broad range of industrial, agricultural, and medical processes. Psychrotrophic microbes could be valuable in agriculture as bio-inoculants and biocontrol agents for low-temperature habitats. The use of psychrophiles as biofertilizers, biocontrol agent, and bioremediators would be of great use in agriculture under cold climatic conditions. The present book chapter describes the method of isolation of psychrotrophic microbes from extreme cold environments, its characterization, identification, biodiversity, and distributions and biotechnological applications in agriculture, medicine, and industry.

11.2 Isolation and Characterization of Cold-Adapted Microbes

Cold-adapted microbial communities have received much attention, because Earth is primarily a cold, marine planet with 90% of the ocean's waters being at 5 °C or lower, and microbes from cold habitat could be applied in agriculture as PGP microbes, in medicine as antifreezing compounds (AFCs) for cryosurgery, and in industry for natural drugs, cold-active enzymes, and valuable bioactive metabolites. Cold-adapted microbes can be characterized using culture-dependent and culture-independent techniques, and microbes from cold habitat and those associated with plants growing at hilly and low-temperature condition should be isolated using culturable and unculturable techniques to know their diversity and distribution. Cold-adapted microbes could be isolated using enrichment and serial dilution methods followed by spread or pour plate technique. The populations of *Bacillus* and *Bacillus*-derived genera (BBDG) in the different samples were enumerated through enrichment and heat treatment using the standard serial dilution plating technique (Yadav et al. 2015d). The different specific growth mediums were used to isolate the maximum possible culturable morphotypes of different genera of cold-adapted microbes such as Archaea (chemically defined medium, standard growth media, and halophilic medium), *Arthrobacter* (trypticase soy agar), BBDG (T3 agar), fungus (potato dextrose agar), *Methylobacterium* (ammonium mineral salt), N_2-fixing bacteria (Jensen N_2-free agar), *Pseudomonas* spp. (Kings' B agar), *Rhizobium* (Congo red yeast mannitol), and soil-specific bacteria (soil extract agar) (Table 11.1). Along with microbes in natural cold environments, also other abiotic stress conditions can be used for isolation of halophilic psychrotrophic (with 5–20% NaCl concentration), acidophilic psychrotrophic (pH 3–5), and alkaliphilic psychrotrophic (pH 8–11) microbes (Fig. 11.1). The isolated microbes should be screened for tolerances to different temperatures for grouping of these microbes in three categories as psychrophilic, psychrotrophic, and psychrotolerant (Yadav et al. 2016b).

To know the PGP ability and other industrial applications of cold-adapted microbes, purified microbes should be screened qualitatively for direct PGP attributes which included biological N_2-fixation (Boddey et al. 1995); production of phytohormones indole-3-acetic acid (Bric et al. 1991), gibberellic acid (Brown and Burlingham 1968), and 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Jacobson et al. 1994); and solubilization of phosphorus (Pikovskaya 1948), potassium (Hu et al. 2006), and zinc (Fasim et al. 2002). The microbes should be also screened for qualitatively indirect PGP attributes which included production of ammonia (Cappucino and Sherman 1992), HCN (Bakker and Schippers 1987), siderophore (Schwyn and Neilands 1987), and lytic enzyme (Yadav et al. 2016a) and biocontrol against different fungal pathogens (Sijam and Dikin 2005) under different temperatures (5–40 °C). After qualitatively screening, the selected cold tolerant with PGP attributes should be quantitatively screened for N_2-fixing attributes by using the acetylene reduction assay (ARA) (Han and New 1998), P-solubilization (Mehta and Nautiyal 2001), K-solubilization (Verma et al. 2016), and IAA production (Patten and Glick 2002).

Table 11.1 The different media used for isolation of microbes from cold environments

Microbes	Media and composition per liter
Archaea	Chemically defined medium: 5 g casamino acids; 5 g yeast extract; 1 g sodium glutamate; 3 g trisodium citrate; 20 g $MgSO_4$; 2 g KCl; 100 g NaCl; 36 mg $FeCl_2$; 0.36 mg $MgCl_2$
	Standard growth media: 7.5 g casamino acids; 4 g $MgSO_4$; 2 g KCl; 150 g NaCl; 3 g trisodium citrate; 2.3 mg $FeCl_2$; 7 mg $CaCl_2$; 0.044 mg $MnSO_4$; 0.05 mg $CuSO_4$
	Halophilic medium: 100 g NaCl; 2 g KCl; 1 g $MgSO_4 \cdot 7H_2O$; 0.36 g $CaCl_2 \cdot 2H_2O$; 0.23 g NaBr; 0.06 g $NaHCO_3$; 5 g protease-peptone; 10 g yeast extract; 1 g glucose; trace FeCl3
Bacteria	Ammonium minerals salt: 0.70 g K_2HPO_4; 0.54 g KH_2PO_4; 1 g $MgSO_4$. $7H_2O$; 0.2 g $CaCl_2$. $2H_2O$; 4.0 mg $FeSO_4.7H_2O$; 0.5 g NH_4Cl; $ZnSO_4$. $7H_2O$; 30 μg $MnCl_2.4H_2O$; 300 μg H_3BO_3; 10 μg $CuCl_2$. $2H_2O$; 200 μg $CoCl_2$. $6H_2O$; 20 μg $NiCl_2.6H_2O$; 60 μg $Na_2MoO_4.2H_2O$
	Antarctic bacterial medium (ABM): 5 g peptone; 2 g yeast extract
	Jensen's agar: 20 g sucrose; 1 g K_2HPO_4; 0.5 g Mg_2SO_4; 0.5 g NaCl; 0.001 g Na_2MoO_4; 0.01 g $FeSO_4$; 2 g $CaCO_3$
	King's B agar: 20 g proteose peptone; 1.5 g K_2HPO_4; 1.5 $MgSO_4$.7H2O; 10 ml glycerol
	Nutrient agar: 5 g peptone; 5 g NaCl; 3 g beef extract
	R_2 agar: 0.5 g proteose peptone; 0.5 g casamino acids; 0.5 g yeast extract; 0.5 g dextrose; 0.5 g soluble starch; 0.3 g dipotassium phosphate; 0.05 g magnesium sulfate $7H_2O$; 0.3 g sodium pyruvate
	Sea water medium: 5 g tryptone; 10 g yeast extract; 5 g casamino acid; 3 g citrate solution; 2 g KCl; 20 g $MgSO_4 \cdot 7 H_2O$
	Soil extract agar: 2 g glucose; 1 g yeast extract; 0.5 g K_2HPO_4; 100 ml soil extract (soil extract: 250 g soil from sampling site +1 L H_20, autoclave and filter)
	Starch yeast peptone agar: 2 g starch; 0.8 g yeast extract; 0.1 g peptone
	T_3 agar: 3 g tryptone; 2 g tryptose; 1.5 g yeast extract; 0.005 g $MnCl_2$; 0.05 sodium phosphate
	Tryptic soy agar: 17 g tryptone; 3 g soya meal; 2.5 g dextrose; 5 g NaCl; 2.5 g K_2HPO_4
	Yeast extract mannitol agar: 1 g yeast extract; 10 g mannitol; 0.5 g $K_2HPO_4.H_2O$; 0.002 g $MgSO_4.7H_2O$; 0.1 g NaCl
Fungi	Czapek Dox Agar: sucrose 30 g; sodium nitrate 2 g; dipotassium phosphate 1 g; magnesium sulfate 0.5 g; potassium chloride 0.5 g; ferrous sulfate 0.01
	Potato dextrose agar: dextrose 20 g; potato extract 4 g (200 g of potato infusion)
	Rose Bengal agar: papaic digest of soya bean meal 5 g; dextrose 10 g; monopotassium phosphate 1 g; magnesium sulfate 0.5 g; Rose Bengal 0.05 g
	Sabouraud dextrose agar: mycological peptone 10 g; dextrose 40 g

For identification and phylogenetic profiling of microbes from cold habitat, the genomic DNA should be isolated from purified pelleted microbial cells of 1.5 mL broth and should be washed two to three times in 1.0 mL of TE buffer (10 mM Tris-HCl and 1 mM EDTA pH 8.0). Microbial lysis should be performed using 0.5 mL SET buffer (75 mM NaCl, 25 mM EDTA, and 20 mM Tris) with 10 μL of lysozyme (10 mg mL^{-1}) for 30 min at 37 °C and 10% SDS with 20 mg mL^{-1} proteinase K for 1 h at 55 °C. DNA should be extracted using phenol/chloroform/isoamyl alcohol,

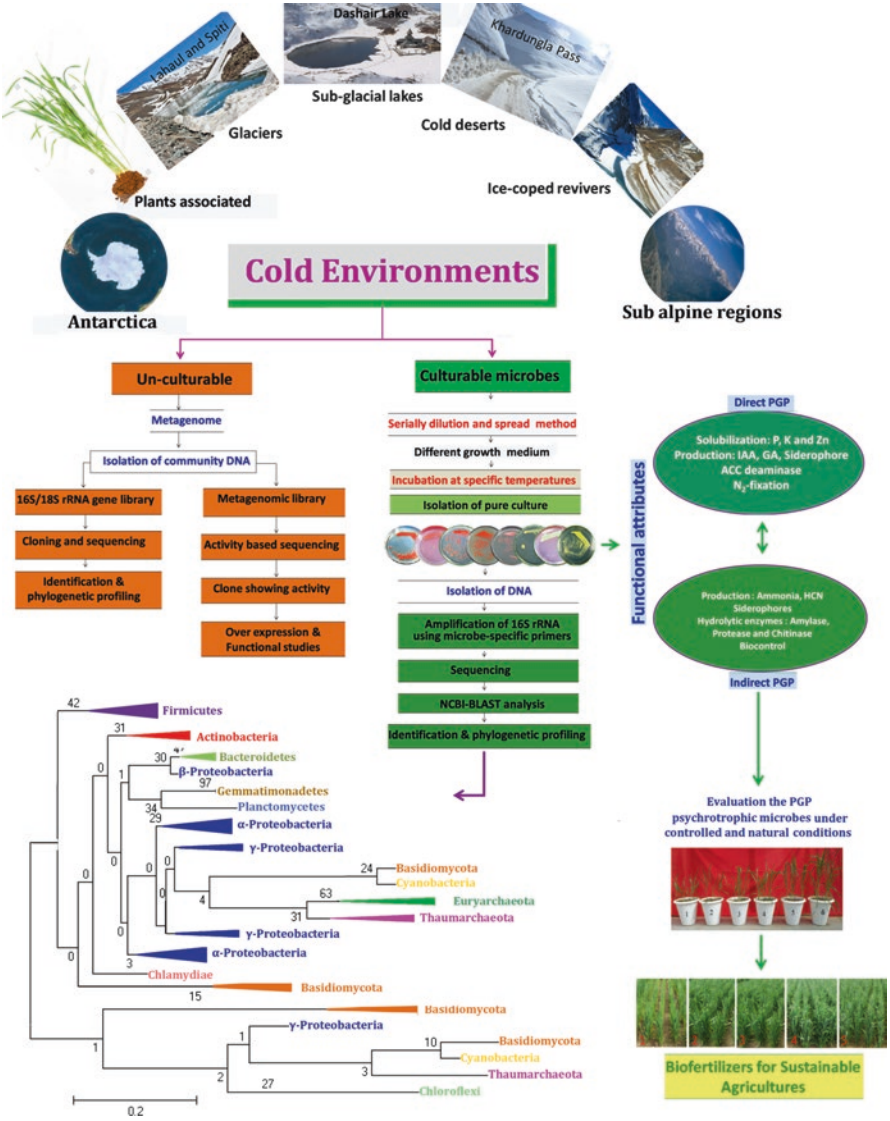


Fig. 11.1 A schematic representation of the isolation, identification, and potential applications of psychrotrophic microbes from different habitats of extreme cold environments

and aqueous phase can be transferred to a fresh tube. Finally, the washed DNA pellet should be incubated at 37 °C for 25–30 min to completely remove ethanol and then resuspended in 50 μL of TE buffer. The amount of DNA extracted should be electrophoresed on 0.8% agarose gel. The primers universal 16S rRNA/18S rRNA/ITS should be used for the amplification of conserved genes. The PCR-amplified 16S rRNA/18S rRNA/ITS should be purified with a Qiaquick purification kit (Qiagen).

The partial 16S rRNA/18S rRNA/ITS gene sequences should be compared with those available in the NCBI databases. Identification at the species level was determined using a 16S rRNA/18S rRNA/ITS gene sequence similarity of ≥97% with that of a prototype strain sequence in the GenBank. Sequence alignment and comparison can be performed, using the program CLUSTAL W. The phylogenetic tree can be constructed on the aligned datasets using the neighbor-joining method (Saitou and Nei 1987) implemented in the program MEGA 4.0.2 (Tamura et al. 2007).

11.3 Diversity and Distribution of Psychrotrophic Microbes

Earth is primarily a cold, marine planet with 90% of the ocean's waters being at 5 °C or lower. Permafrost soils, glaciers and ice sheets, polar sea ice, and snow cover make up 20% of the Earth's surface environments. Habitats for cold-adapted microorganisms represent a large proportion of the Earth's area. Much of the oceans, which cover some 70% of the Earth's surface, are at an average temperature of −1 to +5 °C. Alpine and Polar region constitute 25% of the world's land surface area. Man-made habitats (such as refrigeration and freezer systems) contribute only a small proportion of potential habitats for cold-adapted organisms. The diversity of microorganisms inhabiting cold environments has been extensively investigated in the past few years with a focus on culture-dependent techniques. The different groups of microbes have been reported such as archaea, eubacteria, and fungi, which included different phylum mainly Actinobacteria, Ascomycota, Bacteroidetes, Basidiomycota, Chlamydiae, Chloroflexi, Cyanobacteria, Euryarchaeota, Firmicutes, Gemmatimonadetes, Mucoromycota, Nitrospirae, Planctomycetes, Proteobacteria, Spirochaetes, Thaumarchaeota, and Verrucomicrobia (Fig. 11.2). Overall the distribution of psychrotrophic microbes varied in all bacterial phyla; Proteobacteria were the most dominant followed by Firmicutes and Actinobacteria. The least number of microbes was reported from phylum Mucoromycota followed by Gemmatimonadetes, Nitrospirae, and Thaumarchaeota (Fig. 11.3).

On the review of different extreme cold environments (Antarctica, permanently ice-covered lakes, ice-capped rivers, glaciers, and those associated with plants growing in cold habitat), it was found that 17 different phyla have been sorted out belonging to different domains of Archaea, Bacteria, and Eukarya. The overall percentages of different phyla included are Actinobacteria (12), Ascomycota (0.96), Bacteroidetes (5.18), Basidiomycota (4.22), Chlamydiae (1.15), Chloroflexi (0.96), Cyanobacteria (1.54), Euryarchaeota (1.34), Firmicutes (21.31), Gemmatimonadetes (0.38), Mucoromycota (0.19), Nitrospirae (0.38), Planctomycetes (0.77), Proteobacteria (48.08), Spirochaetes (0.58), Thaumarchaeota (0.38), and Verrucomicrobia (0.58) (Fig. 11.3). On the review of seven different extreme cold environments, Antarctica, plant associated [*Amaranthus*, *Brassica*, cabbage, garlic, maize, pea, and wheat], glacier [Gangotri Glacier, Kafni Glacier, Lahaul and Spiti, Pindari Glacier, Roopkund Glacier, Union Glacier, and Zangser Kangri Glacier], sub-glacial lakes [Chandratal Lake, Dal Lake, Dashair Lake, Gurudongmar Lake, and Pangong Lake], cold desert of Himalayas [Chumathang, Khardungla Pass, and

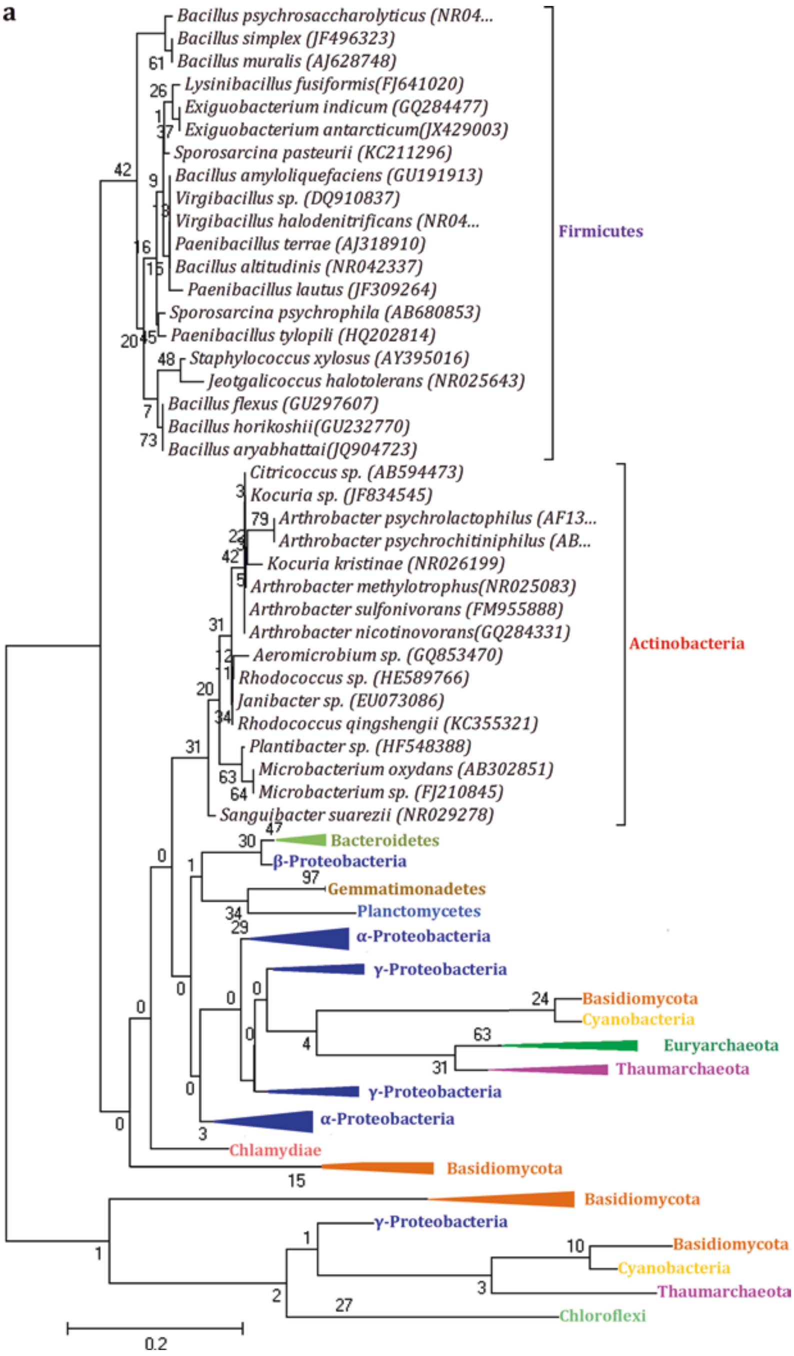
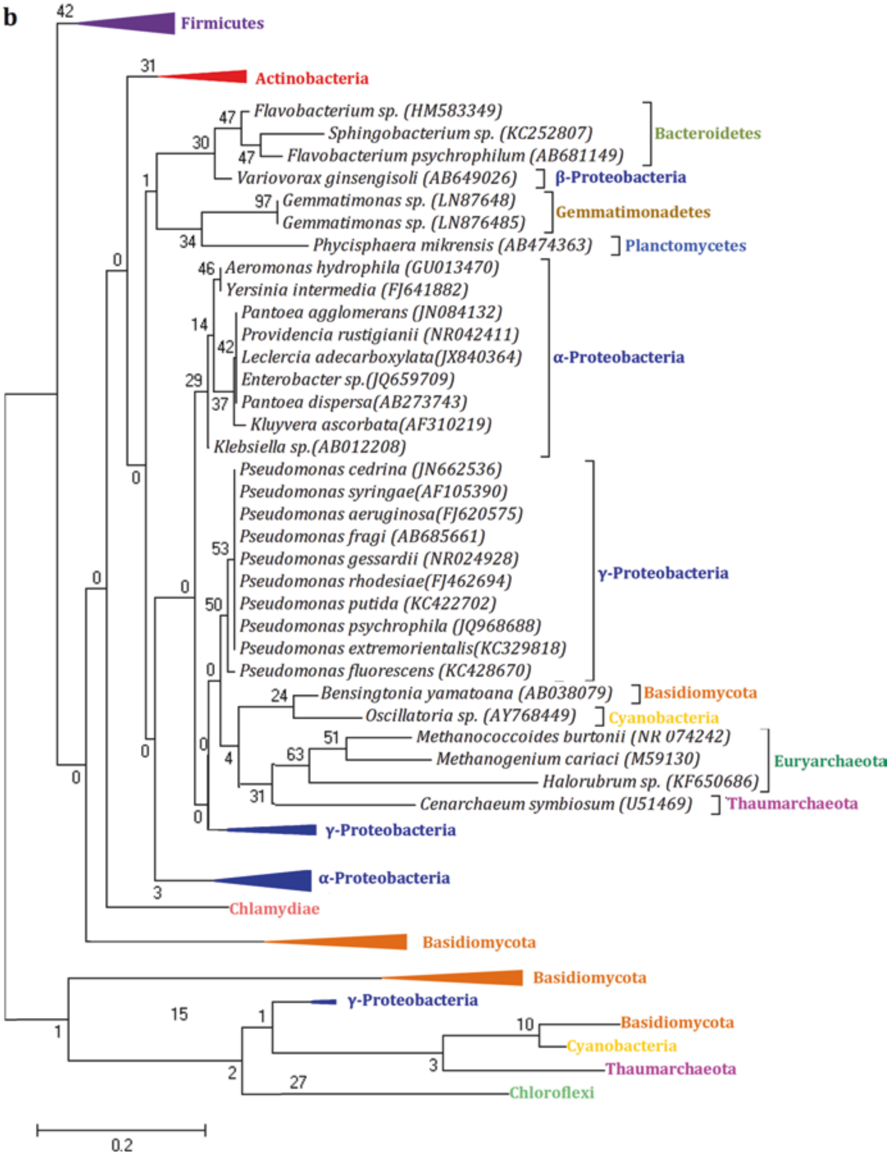


Fig. 11.2 (**a**, **b**, **c**) Phylogenetic tree showing the relationship among psychrotrophic microbes, isolated from diverse habitat of cold environments



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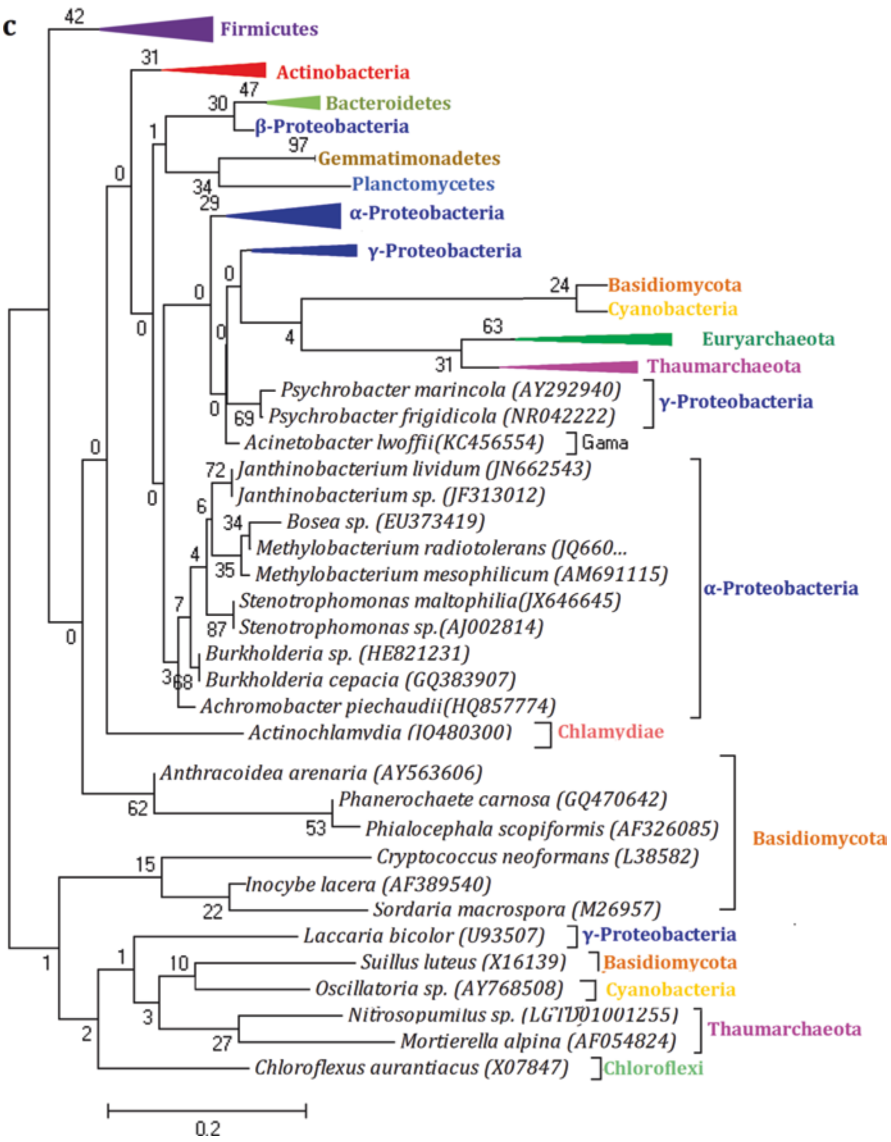

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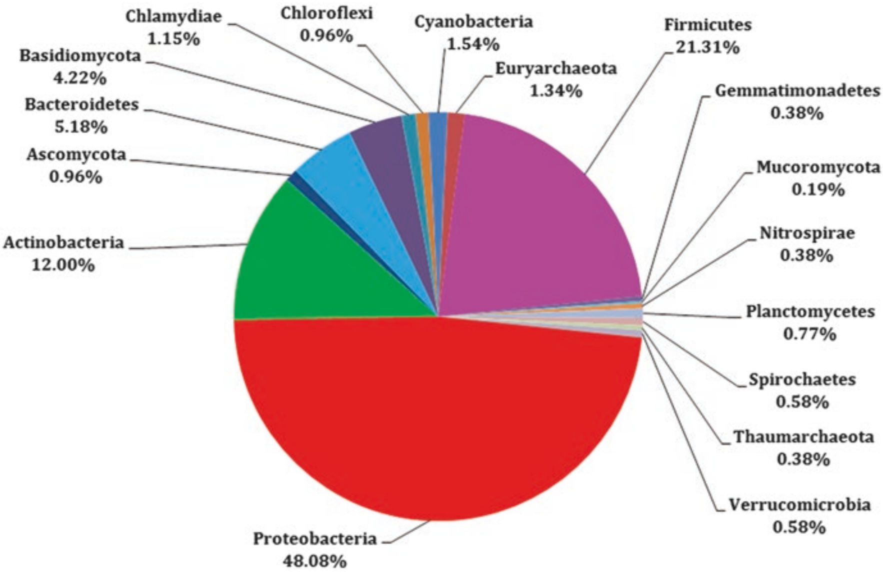

Fig. 11.3 Distribution of different phyla of psychrotrophic microbes, isolated from diverse habitat of cold environments

Rohtang Pass], ice-capped rivers [Indus River, Zanskar River, and Beas River], and subalpine Uttarakhand, it was found that, among 17 different phyla, four phyla, namely, Bacteroidetes, Cyanobacteria, Firmicutes, and Proteobacteria, are found at all site surveys (Fig. 11.4). Among all 17 phyla, the microbes of seven phyla, namely, Ascomycota, Euryarchaeota, Mucoromycota, Nitrospirae, Spirochaetes, Thaumarchaeota, and Verrucomicrobia, were reported of only one site to be niche-specific microbes (Fig. 11.4). On deciphering different habitats of extreme cold environments, it was found that more than 120 different genera of 17 different phyla have been sorted out and characterized. On the basis of different research, it may be concluded that among all reported cold-adapted genera, the five genera namely *Bacillus*, *Exiguobacterium*, *Pseudomonas*, *Psychrobacter*, and *Sphingobacterium* were ubiquitous in nature and have been reported from the all site survey (Fig. 11.5). The cold-adapted microbes have been characterized by both culture-dependent and culture-independent approach. It is possible to assess only a small fraction of the microbial diversity associated with plants using the isolation methods described above because few microbial species can be cultivated using traditional laboratory methods. The sizes of microbial communities as determined using culture-independent methods might be 100- to 1000-fold larger than communities uncovered via traditional isolation. Archaea were also reported to be associated with maize and rice using unculturable method only. There are very few reports for niche-/crop-specific microbes, but there were many reports on niche specificity of microbes from different extreme habitats (Kumar et al. 2014a, b; Pandey et al. 2013; Saxena et al. 2016; Suman et al. 2015; Yadav et al. 2015a, c, 2017h).

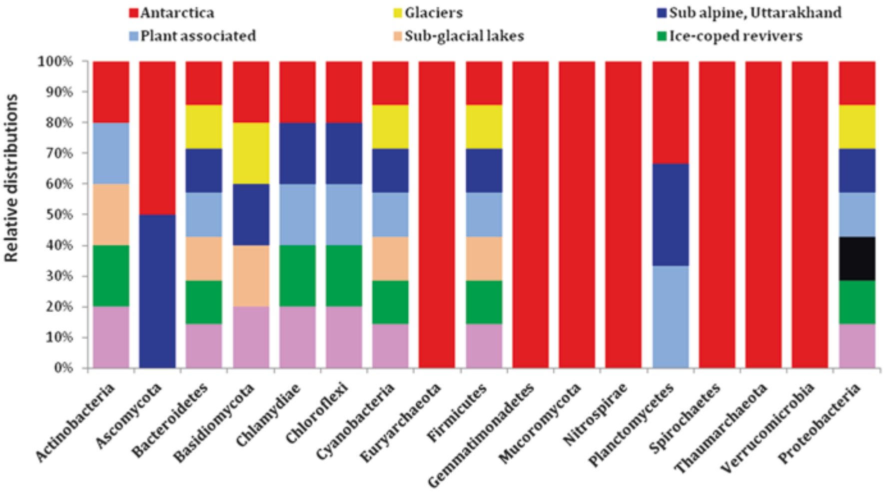

Fig. 11.4 Relative distribution of different phyla of psychrotrophic microbes, isolated from diverse habitat of cold environments

Many novel psychrotrophic microbes have been sorted out from cold environments including *Halobacterium lacusprofundi* (Franzmann et al. 1988), *Sphingobacterium antarcticus* (Shivaji et al. 1992), *Octadecabacter arcticus* (Gosink et al. 1997), *Hymenobacter roseosalivarius* (Hirsch et al. 1998), *Cellulophaga algicola* (Bowman 2000), *Flavobacterium frigidarium* (Humphry et al. 2001), *Oleispira antarctica* (Yakimov et al. 2003), *Flavobacterium psychrolimnae* (Van Trappen et al. 2005), *Psychromonas ingrahamii* (Auman et al. 2006), *Exiguobacterium soli* (Chaturvedi et al. 2008), *Pseudomonas extremaustralis* (López et al. 2009), *Cryobacterium roopkundense* (Reddy et al. 2010), *Sphingomonas glacialis* (Zhang et al. 2011), *Pedobacter arcticus* (Zhou et al. 2012), *Sphingobacterium psychroaquaticum* (Albert et al. 2013), *Lacinutrix jangbogonensis* (Lee et al. 2014), *Massilia eurypsychrophila* (Shen et al. 2015), *Glaciimonas frigoris* (Margesin et al. 2016), and *Psychrobacter pocilloporae* (Zachariah et al. 2017). There are several reports on whole genome sequences of novel and potential psychrotrophic microbes (Kim et al. 2012; Singh et al. 2016). The novel species of psychrotrophic microbes have been isolated worldwide and reported from different domain Archaea, Bacteria, and Eukarya which included members of phylum Actinobacteria, Proteobacteria, Bacteroidetes, Basidiomycota, Firmicutes, and Euryarchaeota. Along with novel species of psychrotrophic microbes, some microbial species including *Arthrobacter nicotianae*, *Brevundimonas terrae*, *Paenibacillus tylopili*, and *Pseudomonas cedrina* have been reported first time from cold deserts of NW Himalayas and exhibited multifunctional PGP attributes at low temperatures (Yadav et al. 2015a). In a study by Yadav et al. (2015b), the microbial species *Alishewanella* sp., *Aurantimonas altamirensis*, *Bacillus baekryungensis*, *Bacillus marisflavi*, *Desemzia incerta*, *Paenibacillus xylanexedens*, *Pontibacillus* sp., *Providencia* sp., *Pseudomonas frederiksbergensis*, *Sinobaca beijingensis*, and

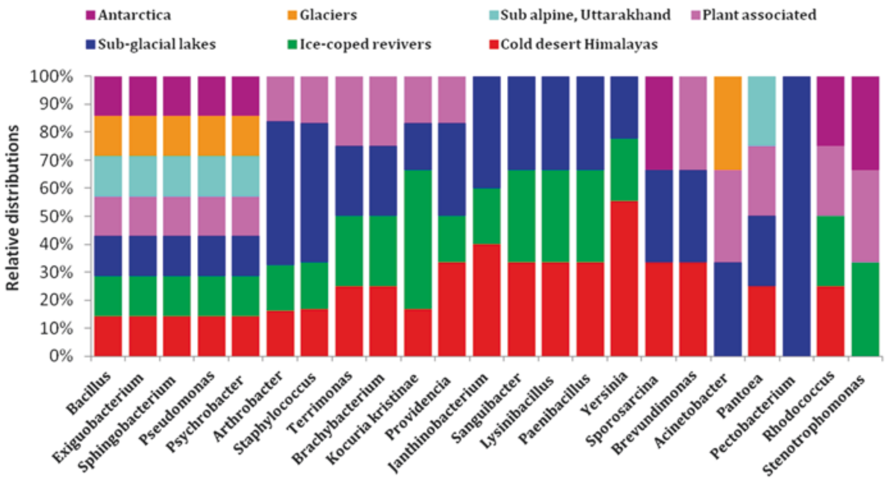

Fig. 11.5 Relative distribution of different genera of psychrotrophic microbes, isolated from diverse habitat of cold environments
Antarctica (Franzmann et al. 1992, 1997, 1988; Deming 2002; von Klein et al. 2002; Könneke et al. 2005; Marx et al. 2007; Chaturvedi et al. 2008; Kostadinova et al. 2009; Turchetti et al. 2011; Lee et al. 2016; Choi et al. 2016; He et al. 2017), *plant associated* [*Amaranthus*, *Brassica*, cabbage, garlic, maize, pea, and wheat] (Bisht et al. 2013; Verma et al. 2014b, 2015a, b, c, d, 2016, 2017a; Yadav et al. 2015a; Rana et al. 2016b, 2017; Kaur et al. 2017), *glacier* [Gangotri Glacier, Kafni Glacier, Lahaul and Spiti, Pindari Glacier, Roopkund Glacier, Union Glacier, and Zangser Kangri Glacier] (Baghel et al. 2005; Gulati et al. 2008; Malviya et al. 2009; Vyas et al. 2010; Pradhan et al. 2010; Shivaji et al. 2011; Srinivas et al. 2011; Barahona et al. 2016; Lee et al. 2017), *sub-glacial lakes* [Chandratal Lake, Dal Lake, Dashair Lake, Gurudongmar lake, and Pangong Lake] (Anupama et al. 2011; Yadav et al. 2012, 2013; Sahay et al. 2013; Pandey et al. 2013; Saxena et al. 2014; Srivastava et al. 2014; Yadav et al. 2014a, b, c, 2015a, b, d, e, f, 2016a, b, c, 2017h; Venkatachalam et al. 2015; Singh et al. 2016), *cold desert of Himalayas* [Chumathang, Khardungla Pass, and Rohtang Pass] (Pandey et al. 2013; Saxena et al. 2014, 2016; Srivastava et al. 2014; Yadav et al. 2015a, b, 2016a, b, c, 2017h; Shukla et al. 2016), *ice-capped rivers* [Indus River, Zanskar River, and Beas River] (Pandey et al. 2013; Saxena et al. 2014; Srivastava et al. 2014; Yadav et al. 2015a, b, 2016a, b, c, 2017h; Saxena et al. 2016), *subalpine, Uttarakhand* (Mishra et al. 2008; Selvakumar et al. 2008, 2009a, b, c, 2011; Mishra et al. 2009, 2011; Bisht et al. 2013; Nazir et al. 2017)

Vibrio metschnikovii have been reported first time from high-altitude and low-temperature environments of Indian Himalayas. Wheat-associated psychrotrophic bacteria *Arthrobacter methylotrophus* and *Pseudomonas rhodesiae* have been reported first time from wheat growing in north hills zone of India (Verma et al. 2015a). In a specific search of economically important *Bacillus* and *Bacillus*-derived genera (BBDG) at low temperature, various BBDG such as *Bacillus psychrosaccharolyticus*, *B. amyloliquefaciens*, *B. altitudinis*, *B. muralis*, *Paenibacillus tylopili*, *P. pabuli*, *P. terrae*, and *P. lautus* with efficient PGP attributes have been reported first time by Yadav et al. (2016b).

11.3.1 Archaea

Archaea are unique microorganisms that are present in ecological niches of high/low temperature and pH and high salinity. Archaea may be present freely or associated with plant rhizosphere. Archaea have been reported as ubiquitous and present in a wide range of environments, from cold environment (Dong and Chen 2012) and thermal springs (De León et al. 2013) and those associated with different plants (Saxena et al. 2015a; Yadav et al. 2015c, 2017b; Gaba et al. 2017). Archaea are a common component of different extreme environments. The largest proportion and greatest diversity of archaea exist in cold environments including Antarctic subglacial and permanently ice-covered lakes, cloud droplets, ice cap cores from considerable depth, snow deep sea, and glaciers. Most of the Earth's biosphere is cold, and archaea represent a significant fraction of the biomass. Although psychrophilic archaea have long been the neglected majority, the study of these microorganisms is beginning to come of age.

Psychrophilic archaea have diverse functional roles in a wide range of cold environments, and their environmental impact is well illustrated by their abundance in the ocean. There are no report of cold-adapted archaea in crop improvements, whereas as other groups of archaea including thermophilic, halophilic, and acidophilic have been reported for PGP under the respective abiotic stresses such as phosphorus solubilization by haloarchaea (Yadav et al. 2015c, 2017b), nitrogen fixation by methanogens (Leigh 2000), siderophore production (Dave et al. 2006), and IAA production (Saxena et al. 2015a; White 1987; Yadav et al. 2017b). It has become clear that cold-adapted archaea contribute to global energy cycles through the processing of organic and inorganic carbon and nitrogen compound.

A diverse group of methanogens and Crenarchaeota are among the most abundant members of the domain Archaea in the cold biosphere. The archaea that are most readily reported from naturally cold environments and that are most acquiescent to laboratory cultivation are methanogens, such as *Methanosarcina*, *Methanospirillum*, *Methanocorpusculum*, and *Methanomethylovorans* which can be isolated from Antarctic lake, freshwater lake, cold marine sediment, and the Baltic Sea (Franzmann et al. 1997; von Klein et al. 2002), and *Methanosarcina baltica*, isolated from the Gotland Deep of the Baltic Sea (von Klein et al. 2002). The eurypsychrophilic archaeon *Halorubrum lacusprofundi* was isolated from Deep Lake, Vestfold Hills, Antarctica (Franzmann et al. 1988).

Franzmann et al. (1992) reported a methylotrophic, methanogenic bacterium that was isolated from the anoxic hypolimnion of Ace Lake, Antarctica, which has been identified as *Methanococcoides methylutens*. The optimum and maximum temperatures for growth were 23.4 and 29.5 °C, respectively. The strain grew in artificial media at in situ lake temperature (1.7 °C), provided growth was first initiated in the media at higher temperatures. The strain had a theoretical minimum temperature for growth of −2.5 °C. The mol% G + C content of DNA from the strain was 39.6% (T_m).

Franzmann et al. (1997) reported *Methanogenium frigidum* from the perennially cold, anoxic hypolimnion of Ace Lake in the Vestfold Hills of Antarctica. The cells were psychrophilic, exhibiting the most rapid growth at 15 °C and no growth at temperatures above 18–20 °C. The cells were slightly halophilic; good growth occurred in medium supplemented with 350–600 mM Na^+, but no growth occurred with 100 or 850 mM Na^+. The pH range for growth was 6.5–7.9; no growth occurred at pH 6.0 or 8.5. Growth was slow (maximum specific growth rate, 0.24 day^{-1}; doubling time, 2.9 days). This is the first report of a psychrophilic methanogen growing by CO_2 reduction.

Wagner et al. (2013) reported that a methanogenic archaeon, strain SMA-21^T, was isolated from a permafrost-affected soil by serial dilution in a liquid medium. The cells were non-motile, were stained gram-negative, and grew as irregular cocci with a diameter of 1.3–2.5 μm. Optimal growth was observed at 28 °C, pH 7.8, and 0.02 M NaCl. The strain grew on H_2/CO_2, methanol, and acetate, but not on formate, ethanol, 2-butanol, 2-propanol, monomethylamine, dimethylamine, trimethylamine, or dimethyl sulfide. The 16S rRNA gene sequence was closely related to those of *Methanosarcina mazei* DSM 2053^T (similarity 99.9%) and *Methanosarcina horonobensis* HB-1^T (similarity 98.7%). On the basis of the level of DNA-DNA hybridization (22.1%) between strain SMA-21^T and *Methanosarcina mazei* DSM 2053^T as well as of phenotypic and genotypic differences, strain SMA-21^T was assigned to a novel species of the genus *Methanosarcina*, for which the name *Methanosarcinasoligelidi* sp. nov. is proposed. The type strain is SMA-21^T (=DSM 20065^T = JCM 18468).

11.3.2 Bacteria

Among different groups of microbes isolated and reported from extreme cold environments, the most dominant groups/domain was Bacteria which include different phylum mainly: Actinobacteria, Bacteroidetes, Chlamydiae, Chloroflexi, Cyanobacteria, Firmicutes, Gemmatimonadetes, Nitrospirae, Planctomycetes, Proteobacteria, Spirochaetes, and Verrucomicrobia (Figs. 11.3 and 11.4). The Actinobacteria is a phylum of gram-positive bacteria. The members of bacteria belonging to phylum Actinobacteria are classified into six classes, namely, Acidimicrobiia, Actinobacteria, Coriobacteriia, Nitriliruptoria, Rubrobacteria, and Thermoleophilia (Yadav et al. 2017f). Among six different classes, members of class Actinobacteria are the most dominant and contain one of the largest of bacterial genera, *Streptomyces*. The bacterial species of phylum Actinobacteria are ubiquitous in nature and have been isolated from different extreme environments (extreme temperatures, pH, salinities, pressure, and drought) and those associated with plants growing in different habitats (Yadav et al. 2017e, h, i). Based on a comprehensive literature analysis, psychrotrophic members of phylum Actinobacteria have been reported from different genera such as *Acidimicrobium*, *Actinomyces*, *Arthrobacter*, *Bifidobacterium*, *Cellulomonas*, *Clavibacter*, *Corynebacterium*, *Frankia*, *Microbacterium*, *Micrococcus*, *Mycobacterium*, *Nocardia*, *Propionibacterium*, *Pseudonocardia*, *Rhodococcus*, *Sanguibacter*, and *Streptomyces*. Among the members of class Actinobacteria, the species of *Arthrobacter* were the most dominant in cold environments which included *Arthrobacter antarcticus*, *A. aurescens*, *A. chlorophenolicus*, *A. defluvii*, *A. equi*, *A.*

globiformis, *A. ilicis*, *A. koreensis*, *A. methylotrophus*, *A. nicotianae*, *A. nicotinovorans*, *A. nitroguajacolicus*, *A. oryzae*, *A. oxydans*, *A. pascens*, *A. polychromogenes*, *A. psychrochitiniphilus*, *A. psychrolactophilus*, *A. ramosus*, *A. sulfonivorans*, *A. sulfurous*, and *A. ureafaciens* (Verma et al. 2015a; Yadav et al. 2015a, b, 2017c, g; Rana et al. 2016a, 2017; Singh et al. 2016; Suman et al. 2016b).

The bacterial species of *Bacillus* and *Bacillus*-derived genera (BBDG), which are associated with different plants, show different plant growth-promoting attributes. The PCR-denaturing gradient gel electrophoresis (DGGE) technique was developed to study the diversity of *Bacillus* (including the groups separated as *Paenibacillus*, *Alicyclobacillus*, *Aneurinibacillus*, *Virgibacillus*, *Salibacillus*, and *Gracilibacillus*). The genus *Bacillus* consists of a heterogenic group of gram-positive rods, able to form endospores that allow them to survive for extended periods under adverse environmental conditions, better than nonsporulating bacterial enteropathogens. Endospore formation is the dominant feature in the characterization of *Bacillus*. There is a boundary that separates this genus from other genera in which endospores are produced. The genus *Clostridium* is distinguished from *Bacillus* by its inability to grow on the surface of agar media in air, or, if growth does occur under these conditions, it is slight and does not lead to sporulation. There is also little or no catalase activity. *Sporosarcina* is sharply separated from *Bacillus* by the coccal form of its vegetative cells.

Many BBDG have been reported from cold environments such as *Bacillus aerius*, *B. aerophilus*, *B. stratosphericus*, *B. altitudinis* (Shivaji et al. 2006), *B. thuringiensis* (Das and Dangar 2008), *B. megaterium* (Trivedi and Pandey 2008), *Paenibacillus glacialis* (Kishore et al. 2010), and *Bacillus cereus*, *B. amyloliquefaciens*, *B. cibi*, *B. pumilus*, and *Lysinibacillus fusiformis* (Sahay et al. 2013, 2017). Among BBDG, several species of *Bacillus* have been sorted out from cold habitat, e.g., *Bacillus acidicola*, *B. altitudinis*, *B. amyloliquefaciens*, *B. anthracis*, *B. aryabhattai*, *B. asahii*, *B. baekryungensis*, *B. cereus*, *B. cibi*, *B. circulans*, *B. firmus*, *B. flexus*, *B. horikoshii*, *B. kochii*, *B. licheniformis*, *B. marisflavi*, *B. megaterium*, *B. mojavensis*, *B. muralis*, *B. pseudomycoides*, *B. psychrosaccharolyticus*, *B. pumilus*, *B. safensis*, *B. simplex*, *B. sonorensis*, *B. subtilis*, *B. thuringiensis*, and *B. weihenstephanensis*. Among the members of Firmicutes, *Bacillus* were reported as the most dominant genera from cold environments followed by *Exiguobacterium mexicanum*, *E. acetylicum*, *E. antarcticum*, *E. artemiae*, *E. aurantiacum*, *E. homiense*, *E. indicum*, *E. marinum*, *E. sibiricum*, and *E. soli*; *Paenibacillus amylolyticus*, *P. lautus*, *P. pabuli*, *P. terrae*, *P. tylopili*, and *P. xylanexedens*; and *Planococcus antarcticus*, *P. donghaensis*, and *P. kocurii* (Pandey et al. 2013; Verma et al. 2015a; Yadav et al. 2015a, b, c, d, e, f, 2016a, b, c, 2017e; Rana et al. 2016a, 2017; Saxena et al. 2015b; Singh et al. 2016; Kumar et al. 2017).

Verma et al. (2015d) investigated 41 endophytic bacteria that were isolated from surface-sterilized roots and culms of wheat *var.* HS507, growing in NW Indian Himalayas. These bacteria were screened *in vitro* for multifarious plant growth-promoting attributes such as solubilization of phosphorus, potassium, and zinc; production of indole-acetic acids, hydrogen cyanide, gibberellic acid, and siderophore; nitrogen fixation; ACC deaminase activity; and biocontrol against *Rhizoctonia* *solani* and *Macrophomina phaseolina* at low temperature (4 °C). One isolate, IARI-HHS2-30, showed that appreciable level of potassium solubilization was further characterized *in vivo* at control condition of low temperature. Based on 16S rRNA gene sequence analysis, this isolate was identified as *Bacillus amyloliquefaciens* assigned with accession number KF054757. Analysis of the phylogenetic characterization showed close homology with typical psychrotolerant bacteria *Bacillus amyloliquefaciens*, *Bacillus methylotrophicus*, *Bacillus polyfermenticus*, *Bacillus siamensis*, *Bacillus subtilis*, and *Bacillus vallismortis*. Endophytic nature and plant growth-promoting ability of IARI-HHS2-30 was tested qualitatively and followed by inoculation onto wheat seedlings in low-temperature conditions. At 30 days after inoculation, *Bacillus amyloliquefaciens* IARI-HHS2-30 to wheat plants resulted in significant increase in root/shoot length, fresh weight, and chlorophyll content. Plant growth-promoting features coupled with psychrophilic ability suggest that this endophytic bacterium may be exploited as bio-inoculants for various crops in low-temperature and high-altitude condition.

Yadav et al. (2016b) reported and characterized psychrotrophic bacilli from different sites in northwestern Indian Himalayas. A total of 247 morphotypes were obtained from different soil and water samples and were grouped into 43 clusters based on 16S rDNA-RFLP analysis. Sequencing of representative isolates from each cluster led to their identification, and 43 bacilli belonged to different species of 11 genera, *viz.*, *Desemzia*, *Exiguobacterium*, *Jeotgalicoccus*, *Lysinibacillus*, *Paenibacillus*, *Planococcus*, *Pontibacillus*, *Sinobaca*, *Sporosarcina*, *Staphylococcus*, and *Virgibacillus*. With an aim to develop microbial inoculants that can perform efficiently at low temperatures, all representative isolates were screened for different plant growth-promoting traits at low temperatures (5–15 °C). Among the strains, variations were observed for production of ammonia (22%), indole-3-acetic acid (20%), siderophores (8%), gibberellic acid (4%), and hydrogen cyanide (3%); solubilization of phosphate (12%), zinc (16%), and potassium (8%); 1-aminocyclopropane-1-carboxylate deaminase activity (5%); and biocontrol activity (19%) against *Rhizoctonia solani* and *Macrophomina phaseolina*. Among all the strains, *Bacillus licheniformis*, *Bacillus muralis*, *Desemzia incerta*, *Paenibacillus tylopili*, and *Sporosarcina globispora* were found to be potent candidates to be developed as inoculants as they exhibited multiple PGP traits at low temperature.

The phylum Proteobacteria is a major group of gram-negative bacteria which included α/β/γ/δ-Proteobacteria. The α-Proteobacteria grows at very low levels of nutrients and includes agriculturally important bacteria capable of inducing *Azospirillum* and fixing nitrogen in symbiosis with plants. The β-Proteobacteria is highly metabolically diverse and contains chemolithoautotrophs, photoautotrophs, and generalist heterotrophs, while the γ-Proteobacteria is the largest class in terms of species, *Pseudomonas* and *Azotobacter*. Among the Proteobacteria, γ-Proteobacteria were the most dominant, in which the members of the genus *Pseudomonas* were predominant in extreme cold environments such as *Pseudomonas aeruginosa*, *P. antarctica*, *P. azotoformans*, *P. baetica*, *P. cedrina*, *P. corrugate*, *P. costantinii*, *P. deceptionensis*, *P. extremaustralis*, *P. extremorientalis*, *P. fluorescens*, *P. fragi*, *P. frederiksbergensis*, *P. geniculata*, *P. gessardii*, *P. graminis*, *P. jessani*, *P.*

kilonensis, *P. koreensis*, *P. lurida*, *P. mediterranea*, *P. moraviensis*, *P. orientalis*, *P. pavonaceae*, *P. peli*, *P. plecoglossicida*, *P. poae*, *P. psychrophila*, *P. putida*, *P. reactans*, *P. rhodesiae*, *P. simiae*, *P. stutzeri*, *P. syringae*, *P. teessidea*, *P. tolaasii*, *P. trivialis*, *P. vancouverensis*, and *P. xanthomarina* (Srivastava et al. 2014; Verma et al. 2015a; Saxena et al. 2015b; Singh et al. 2016; Rana et al. 2017; Yadav et al. 2017i; Kumar et al. 2017).

Verma et al. (2013) reported 135 wheat-associated plant growth-promoting bacteria from acidic soil; among all isolates, *Pseudomonas chlororaphis* IARI-THD-13, *Pseudomonas fluorescens* IARI-THD-21, *Pseudomonas rhodesiae* IARI-THD-11, and *Pseudomonas rhodesiae* IARI-THD-28 exhibited direct and indirect plant growth-promoting attributes. The plant growth-promoting (PGP) traits were done *in vitro* at different pH which included solubilization of phosphorus, potassium, and zinc; production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophore; nitrogen fixation; 1-aminocyclopropane-1-carboxylate deaminase activity; and biocontrol against *Fusarium graminearum*, *Rhizoctonia solani*, and *Macrophomina phaseoli.* Acidotolerant isolates may have application as inoculant plant growth-promoting and biocontrol agents in crops growing under acidic condition.

Verma et al. (2014a, b) investigated thermotolerant wheat-associated plant growth-promoting bacteria which have been identified using 16S rRNA gene sequencing. A total of 348 isolates belonged to three phyla, namely, Actinobacteria, Firmicutes, and Proteobacteria, with 38 distinct species of 17 genera. *Bacillus* and *Pseudomonas* were dominant in rhizosphere while *Methylobacterium* were in phyllosphere. Different species of *Pseudomonas fuscovaginae* IARI-IIWP-29, *Pseudomonas lini* IARI-IIWP-33, *Pseudomonas monteilii* IARI-IIWP-27, *Pseudomonas stutzeri* IARI-IHD-4, and *Pseudomonas thivervalensis* IARI-IHD-3 have been sorted out from wheat as endophytic, rhizospheric, as well as epiphytic. *In vitro* plant growth-promoting activities of bacteria exposed more than three beneficial traits which may act independently or concurrently. P-solubilization and siderophores production are the predominant traits exhibited by these microbes. The many species of genera *Bacillus*, *Exiguobacterium*, *Micrococcus*, *Pseudomonas*, and *Psychrobacter* showed antagonistic properties against fungal pathogens *Fusarium graminearum*, *Rhizoctonia solani*, and *Macrophomina phaseoli.* These promising isolates showing a range of useful plant growth-promoting attributes insist to be explored for agricultural applications.

Verma et al. (2015a) reported psychrotolerant wheat-associated bacteria from northern hills zone of India. A total of 247 bacteria were isolated from 5 different sites. 16S rRNA gene-based phylogenetic analysis revealed that 65, 26, 8, and 1% bacteria belonged to four phyla, namely, Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes, respectively. Overall 28% of the total morphotypes belonged to *Pseudomonas* followed by *Bacillus* (20%); *Stenotrophomonas* (9%); *Methylobacterium* (8%); *Arthrobacter* (7%) and *Pantoea* (4%); *Achromobacter*, *Acinetobacter*, *Exiguobacterium*, and *Staphylococcus* (3%); *Enterobacter*, *Providencia*, *Klebsiella*, and *Leclercia* (2%); and *Brevundimonas*, *Flavobacterium*, *Kocuria*, *Kluyvera*, and *Planococcus* (1%). Representative strains from each cluster were screened in vitro for plant growth-promoting traits, which included solubilization of phosphorus, potassium, and zinc; production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophore; nitrogen fixation; 1-aminocyclopropane-1-carboxylate deaminase activity; and biocontrol against *Fusarium graminearum*, *Rhizoctonia solani*, and *Macrophomina phaseolina.* Cold-adapted isolates may be applied as inoculants for plant growth promotion and as biocontrol agents for crops growing under cold climatic condition.

11.3.3 Fungi

The psychrophilic fungi have an optimum growth temperature near 10 °C or below and that 10 °C was the minimum growth temperature required for most of the fungi. Many researchers agree with Morita's definition of psychrophiles that psychrophilic fungi grow well at 15 °C or lower, whereas psychrotrophic fungi require temperatures above 20 °C for their maximum growth. Microorganisms that can be recovered from the interior of deep-core samples of Arctic and Antarctic ice are expected to be millions of years old. Various ancient fungi, ranging from 10,000 to 140,000 years in age, have been isolated and documented from Arctic and Antarctic ice (Fisher et al. 1995; Babjeva and Reshetova 1998; Tosi et al. 2002; Malviya et al. 2009; Srivastava et al. 2014; He et al. 2017). Psychrophilic fungi exist in some of the coldest environments throughout the world because of their great efficiency of adaptation to cold environment of deep sea, glacier, the Arctic, and Alps regions. There is a wide range of natural habitats where low temperatures occur continuously or intermittently due to seasonal effects. These regions include oceans, the tundra, and subarctic regions. These fungi may be present either because they are true psychrophiles or because they are psychrotolerant with the ability to survive but not actively grow at temperatures <5 °C. *Penicillium* is a genus of ascomycetous fungi and it has an important role in various natural processes. A wide and ubiquitous presence of *Penicillium* species has been witnessed in several studies. Based on a comprehensive literature analysis Penicillium has been reported as one of the most common fungi occurring in various environments such as soils, air, extreme environments (temperature, salinity, water deficiency and pH) and also associated with plants and specific food products. It's huge diversity and existence in extreme environments provide great opportunity in exploring this fungus for various environmental, biotechnological and industrial applications (Yadav et al. 2017g). *Penicillium* and different groups of microbes have attracted significant attention because of the interest in cold-active enzymes and plant growth-promoting attributes at low temperatures (Yadav 2015; Yadav et al. 2015e, 2017g; Singh et al. 2016).

Cold-tolerant species of *Penicillium* have been primarily reported in connection with subarctic vegetation (Fisher et al. 1995; Babjeva and Reshetova 1998; Tosi et al. 2002), in snow and below snow-covered tundra (Vishniac 1993; Babjeva and Reshetova 1998; Pennisi 2003; Schadt et al. 2003), and in permafrost (Dmitriev et al. 1997; Babjeva and Reshetova 1998; Golubev 1998; Soina et al. 2000; Tosi et al. 2002) and offshore polar waters (Broady and Weinstein 1998). Very few studies describe their presence in Arctic glaciers. Viable fungi have, however, been isolated from Arctic and Antarctic ice, ranging in age from 10,000 and up to 140,000 years (Abyzov 1993; Ma et al. 1999, 2000; Christner et al. 2000, 2003). In these cases, the few isolated filamentous fungi were considered as randomly entrapped fungal Aeolian propagules originating from close and distant locations. Fungi have been only rarely isolated from glacial ice in extremely cold polar regions and were in these cases considered as random, long-term preserved Aeolian deposits. Fungal presence has so far not been investigated in polar sub-glacial ice, a recently discovered extreme habitat reported to be inhabited exclusively by heterotrophic bacteria.

Sonjak et al. (2006) reported on the very high occurrence (up to 9 × 10^3 CFU/L) and diversity of filamentous *Penicillium* spp. in the sediment-rich sub-glacial ice of three different polythermal Arctic glaciers. The dominant species was *P. crustosum*, representing the average half of all isolated strains from all three glaciers. The other most frequently isolated species were *P. bialowiezense*, *P. chrysogenum*, *P. thomii*, *P. solitum*, *P. palitans*, *P. echinulatum*, *P. polonicum*, *P. commune*, *P. discolor*, *P. expansum*, and new *Penicillium* species. This was the first report on the presence of large populations of *Penicillium* spp. in sub-glacial sediment-rich ice. *Penicillium crustosum* is an important and panglobal contaminant of lipid- and protein-rich foods and feeds. Although it is infrequent in extremely cold environments, we isolated a high number of *P. crustosum* strains from Arctic coastal, but particularly, sub-glacial environments in Svalbard, Norway, *P. crustosum* is extremely consistent in its phenotypic properties, including morphology, physiology, and secondary metabolite production. However, some Arctic isolates differed from other Arctic and non-Arctic strains in their weak growth on creatine and in the production of the secondary metabolite and rastin A. Penicillia strains that populate glacial ice must be physiologically adaptable and able to retain their viability throughout the dynamic processes of ice melting and freezing and extremes in pressure. Such enrichment would select for *Penicillium* populations best adapted to dark, cold, oligotrophic environments with shifting osmotic pressures (Yadav et al. 2017g).

Lyhne et al. (2006) reported that *Penicillium jamesonlandense* is a novel species from Greenland that grows exceptionally slow at 25 °C and has an optimum temperature for growth of 17–18 °C. The novel species is more psychrotolerant than any other *Penicillium* species described to date. Isolates of this novel species produce a range of secondary metabolites with a high chemical diversity, represented by kojic acid, penicillic acid, griseofulvin, pseurotin, chrysogine, tryptoquivalins, and cycloaspeptide. *Penicillium ribium*, another novel psychrotolerant species from the Rocky Mountains, Wyoming, USA, produces asperfuran, kojic acid, and cycloaspeptide.

Sonjak et al. (2007) reported that *Penicillium crustosum* is a panglobally distributed foodborne fungus, extremely consistent in its morphological and physiological properties. It is also known for its consistent production of several mycotoxins and other secondary metabolites such as penitrems, roquefortines, viridicatins, and terrestric acids. It is important in temperate regions as a contaminant of oil seeds, nuts, cheese, and meat and as producer of rot in apples. In spite of its ubiquitous nature and copious amounts of conidia produced, it has only rarely been reported from extremely cold environments. According to Sonjak et al. (2007), study of mycobiota in coastal Arctic environment resulted in isolation of a high number of *P. crustosum* strains from different niches, such as seawater and sea ice, but primarily from the sediment-rich subglacial ice of three different polythermal Arctic glaciers. Although phenotypic properties were very homogenous in all *P. crustosum* isolates, some Arctic isolates differed from all other Arctic and non-Arctic strains in their weak growth on creatine, used otherwise as a very reliable taxonomic marker, and furthermore in the production of andrastin A (Gunde-Cimerman et al. 2003; Sonjak et al. 2005; Yadav et al. 2017g).

Dhakar et al. (2014) isolated and identified 25 *Penicillium* species from the Indian Himalayan regions. Based on the phenotypic characters (colony morphology and microscopy), all the isolates were designated to the genus *Penicillium*. Exposure to low temperature resulted in enhanced sporulation in 23 isolates, while it ceased in the case of 2. The fungal isolates produced watery exudates in varying amounts that in many cases increased at low temperature. All the isolates could grow between 4 and 37 °C (optimum 24 °C), hence considered psychrotolerant. While all the isolates could tolerate pH from 2–14 (optimum 5–9), 7 isolates tolerated pH 1.5 as well. While all the fungal isolates tolerated salt concentration above 10%, ten isolates showed tolerance above 20%. Based on ITS region (ITS1-5.8S-ITS2) analysis, the fungal isolates belonged to 25 different species of *Penicillium*. Characters like tolerance for low temperature, wide range of pH, and high salt concentration and enhancement in sporulation and production of secondary metabolites such as watery exudates at low temperature can be attributed to the ecological resilience possessed by these fungi for survival under low-temperature environment of mountain ecosystem.

Barsainya et al. (2016) isolated the salt-tolerant and chromium-resistant fungal strains from Pangong Lake of Ladakh. They carried out on interaction of *Penicillium* sp. with chromium and NaCl and report the ability of *Penicillium* sp. to bind with chromium and NaCl in aqueous solution. It is demonstrated in the study that NaCl reduced the extent of Cr biosorption and promote the fungal strains of *Penicillium* for better growth. The present finding suggests that NaCl might reduce the toxicity of hexavalent chromium in *Penicillium* sp. and may be used as a potential organism for remediation of chromium in high-salinity environments.

11.4 Beneficial Role in Plant Growth Promotion, and Soil Health

The extreme environment of high salt, drought, and low temperature affects the productivity of several commercial crop plants. The low temperature plays a significant role in reducing agricultural production worldwide as 20% of the Earth's surface were covered with frozen soils (permafrost), glaciers and ice sheets, and snow. Cold-tolerant microorganisms are widely distributed in the agroecosystem and play a variety of roles extending from nitrogen fixation, plant growth promotion, and alleviation of cold stress in plants. Though most research work conducted so far has largely focused on psychrophilic/psychrotolerant bacteria, it is a welcome sign that many agriculturally important resourceful microbes are being described from various parts of the Earth.

Phosphate (P) is the major essential macronutrient for biological growth and development. In spite of that, these sources constitute the biggest reservoirs of P in soil because, under appropriate conditions, they can be solubilized and become available for plants. Microorganisms play a central role in the natural P cycle. There are considerable populations of P-solubilizing bacteria (PSB) in soil and in plant rhizospheres. PSB have the ability to solubilize inorganic phosphate compounds, such as tricalcium phosphate, hydroxyapatite, and rock phosphate. It has been reported that indolic compounds (indole-3-acetic acid, indolepyruvic acid, and indoleacetamide) have a positive effect on root growth and cause rapid establishment of roots beneficial for young seedlings as they increase their capacity to anchor themselves to the soil and to obtain water and nutrients from their environment. We have also tested the ability of isolates to produce IAA.

The capacity to synthesize IAA is widespread among soil- and plant-associated bacteria. It has been estimated that 80% of bacteria isolated from the rhizosphere can produce the plant growth regulator IAA. Iron, the fourth most abundant element in the Earth's crust, is largely required by all living organisms for direct microbial assimilation. In aqueous solution, iron can exist in either the ferrous (Fe^{2+}) or (Fe^{3+}) forms, the latter being the less soluble. However, in highly oxidized and aerated soils, the predominant form of iron is the ferric form, which is soluble in water (pH 7.4) at about 10^{-18} M. This is too low to support the growth of microorganisms, which generally need concentrations approaching 10^{-6} M for normal growth. Consequently, to survive in such environments, organisms secrete iron-binding ligands (siderophores) that can bind ferric iron and make it available to the host microorganisms. In the present study, 20 isolates were identified that could produce siderophore at low temperatures. Sustainable agriculture requires the use of strategies to increase or maintain the current rate of food production while reducing damage to the environment and human health. The use of microbial plant growth promoters is an alternative to conventional agricultural technologies. Plant growth-promoting microbe can affect plant growth directly or indirectly. The direct promotion of plant growth by PGP microbes, for the most part, entails providing the plant with a compound that is synthesized by the bacterium or facilitating the uptake of certain nutrients from the environment. The indirect promotion of plant growth occurs when PGP microbes decrease or prevent the deleterious effects of one or more phytopathogenic organisms (Verma et al. 2017b; Yadav et al. 2017a-i).

There are several ways in which different PGP microbes have been reported to directly facilitate the proliferation of their plant hosts. PGP microbes can fix atmospheric nitrogen and supply it to plants; they synthesize siderophores that can solubilize and sequester iron from the soil and provide it to the plant; they synthesize several different phytohormones that can act to enhance various stages of plant growth; they may have mechanisms for the solubilization of minerals such as phosphorus, potassium, and zinc that will become more available for plant growth; and they may synthesize some less well-characterized, low-molecular-mass compounds or enzymes that can modulate plant growth and development (Kloepper et al. 1989; Glick 1995; Quadt-Hallmann et al. 1997; Glick et al. 1999a, b; Yadav et al. 2017d). A particular PGP microbe may affect plant growth and development by using any one or more of these mechanisms (Yadav et al. 2017a) (Table 11.2).

Table 11.2 Psychrotrophic microbes with multifarious plant growth-promoting attributes

	Plant growth promoting attributes						
Microbes	P	K	NF	IAA	Sidero.	ACC	References
Actinobacteria							
Arthrobacter methylotrophus IARI-HHS1-25	55.9±1.4	–	+	21.4±1.3	4.9±0.1	+	Verma et al. (2015a)
Arthrobacter sulfonivorans IARI-L-16	25.6±1.2			27.6±0.7	4.7±0.9	–	Yadav et al. (2015b)
Cellulosimicrobium cellulans IARI-ABL-30	15.5±1.1			18.4±0.8	–	+	Yadav et al. (2015b)
Kocuria kristinae IARI-HHS2-64	64.0±1.0	–	–	20.4±1.1	2.1±0.1	–	Verma et al. (2015a)
Sanguibacter antarcticus IARI-L-33	20.1±0.1			9.3±0.9	10±0.8	+	Yadav et al. (2015b)
Sanguibacter suarezii IARI-R-7	18.1±0.5			76.8±0.3	5±0.15	+	Yadav et al. (2015a)
Firmicutes							
Bacillus altitudinis IARI-HHS2-2	43.9±0.7	–	+	6.6±1.0	–	–	Verma et al. (2015a)
Bacillus amyloliquefaciens IARI-HHS2-30	54.2±1.5	+	+	28.8±1.5	3.5±0.2	+	Verma et al. (2015d)
Bacillus amyloliquefaciens IARI-R-25	39.4±2.4			14.2±1.0	4.8±1.2	–	Yadav et al. (2015a)
Bacillus aryabhattai IARI-HHS1-30	45.6±1.0	–	+	15.6±0.7	–	–	Verma et al. (2015a)
Bacillus firmus IARI-L-21	35.2±3.3			35.2±1.0	6.0±0.8	+	Yadav et al. (2015b)
Bacillus licheniformis IARI-AL38	19.2±1.0	–		13.2±1.0	4.5±0.5		Yadav et al. (2016)
Bacillus muralis IARI-AR28	–	+		22.5±0.5	5.7±1.2	–	Yadav et al. (2016)
Bacillus pumilus IARI-L-54	36.1±0.8			32.3±1.2	4.3±0.9	–	Yadav et al. (2015b)
Bacillus subtilis IARI-L-69	19.8±0.5			27.7±0.9	5.3±0.5	+	Yadav et al. (2015b)
Desemzia incerta IARI-L-46	47.5±1.2			28.6±1.0	4.7±0.5	–	Yadav et al. (2015b)
Exiguobacterium antarcticum IARI-HHS2-49	–	+	–	22.8±0.8	3.1±0.1	–	Verma et al. (2015a)
Lysinibacillus sphaericus IARI-AR11		+		14.4±1.2	–	+	Yadav et al. (2016)
Paenibacillus tylopili IARI-AR36	48.4±2.4	+		39.4±2.4	3.8±1.2	–	Yadav et al. (2016)
Sporosarcina globispora IARI- AR111	–	+		37.6±0.3	–	+	Yadav et al. (2016)
Proteobacteria							
Acinetobacter rhizosphaerae BIHB 723	785 ± 1.2	–	–	15.6 ± 1.2	+	+	Gulati et al. (2009)
Aeromonas hydrophila IARI-R-6	31.5±1.8			21.4±1.0	2.4±1.5	–	Yadav et al. (2015a)

(continued)

Table 11.2 (continued)

Microbes	Plant growth promoting attributes						References
	P	K	NF	IAA	Sidero.	ACC	
Bordetella bronchiseptica IARI-HHS2-29	48.6±0.9	–	+	15.2±1.1	1.6±0.2	–	Verma et al. (2015a)
Pantoea agglomerans IARI-R-87	22.0±1.4			43.9±1.1	6.8±0.5	–	Yadav et al. (2015a)
Pantoea dispersa 1A	44.5±0.2	–	–	4.4±0.5	+	–	Selvakumar et al. (2008)
Providencia rustigianii IARI-R-91	131.7±1			51.0±2.0	5.2±0.7	+	Yadav et al. (2015a)
Pseudomonas cedrina IARI-R-53	182.6±1			9.99±1.0	5.2±1.2	+	Yadav et al. (2015a)
Pseudomonas fluorescens PPRs4	90.2 ± 1.7	–	–	9.4 ± 0.2	+	–	Mishra et al. (2011)
Pseudomonas fragi IARI-R-57	45.5±1			11.3±0.5	4.6±0.7	+	Yadav et al. (2015a)
Pseudomonas geniculata IARI-HHS1-19	45.0±1.2	–	+	66.7±0.5	2.5±0.2	–	Verma et al. (2015a)
Pseudomonas jessani PGRs1	7.9 ± 0.1	–	–	16.2 ± 0.3	+	–	Mishra et al. (2011)
Pseudomonas koreensis PBRs7	97.3 ± 1.9	–	–	15.8 ± 0.3	+	–	Mishra et al. (2011)
Pseudomonas lurida M2RH3	305.0±2.4	–	–	16.8 ± 0.2	+	–	Selvakumar et al. (2011)
Pseudomonas lurida NPRs3	69.7 ± 1.5	–	–	9.9 ± 0.2	+	–	Mishra et al. (2011)
Pseudomonas moraviensis IARI-R-132	44.2±2.1			154.6±1.	2.2±0.5	+	Yadav et al. (2015a)
Pseudomonas putida IARI-R-131	–			137.9±1	2.4±0.7	–	Yadav et al. (2015a)
Pseudomonas putida PGRs4	169.9 ± 3.9	–	–	10.1 ± 0.2	+	–	Mishra et al. (2011)
Pseudomonas reactans IARI-ABR-38	23.23±1			61.4±0.5	4.2±0.5	–	Yadav et al. (2015a)
Pseudomonas sp. NARs9	15.7±1.82	–	–	21.8±0.2	+	–	Mishra et al. (2009)
Pseudomonas sp. PGERs17	74.1±0.3	–	–	13.2±0.8	+	–	Mishra et al. (2008)
*Psychrobacter frigidicola*IARI-R-127	20.83±1			65.9±1.0	2.8±1.5	+	Yadav et al. (2015a)
Rahnella sp. BIHB 783	805.0±1.	–	–	24.5±1.5	88.0±3	+	Vyas et al. (2010)
Stenotrophomonas maltophilia IARI-HHS1-20	55.7±0.5	+	–	66.1±0.7	2.4±0.1	+	Verma et al. (2015a)
Bacteroidetes							
Flavobacterium psychrophilum IARI-HHS2-37	66.0±0.7	–	–	11.4±1.5	2.6±0.1	+	Verma et al. (2015a)

P Phosphorus, *K* Potassium, *NF* Nitrogen Fixation, *IAA* Indoleacetic acids, *Sidero.* Siderophore

11.4.1 Biological N_2-Fixation

Nitrogen is the major limiting factor for plant growth; the application of N_2-fixing bacteria as biofertilizers has emerged as one of the most efficient and environmentally sustainable methods for increasing the growth and yield of crop plants. Biological nitrogen fixation (BNF) is one of the possible biological alternatives to N fertilizers and could lead to more productive and sustainable agriculture without harming the environment. A variety of nitrogen-fixing bacteria like *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Gluconacetobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, and *Serratia* have been reported to fix nitrogen under low-temperature condition (Verma et al. 2015a, b, c, d, 2016; Yadav 2015; Rana et al. 2016a, b, 2017).

Verma et al. (2015a) reported psychrotolerant wheat-associated bacteria from northern hills zone of India. A total of 247 bacteria were isolated from 5 different sites. Representative strains from each cluster were screened in vitro for plant growth-promoting traits, which included solubilization of phosphorus, potassium, and zinc; production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophore; nitrogen fixation; 1-aminocyclopropane-1-carboxylate deaminase activity; and biocontrol against *Fusarium graminearum*, *Rhizoctonia solani*, and *Macrophomina phaseolina*. Among all, *Arthrobacter nicotinovorans* IARI-HHS1-1, *Arthrobacter methylotrophus* IARI-HHS1-25, *Bacillus flexus* IARI-HHS1-24, *Bacillus aryabhattai* IARI-HHS1-30, *Bacillus altitudinis* IARI-HHS2-2, *Bacillus amyloliquefaciens* IARI-HHS2-30, *Bordetella bronchiseptica* IARI-HHS2-29, *Providencia* sp. IARI-HHS1-3, *Pseudomonas fluorescens* IARI-HHS1-4, *Pseudomonas mediterranea* IARI-HHS1-5, *Pseudomonas peli* IARI-HHS1-8, *Pseudomonas geniculata* IARI-HHS1-19, *Pseudomonas azotoformans* IARI-HHS1-23, *Pseudomonas syringae* IARI-HHS1-29, and *Acinetobacter lwoffii* IARI-HHS2-26 show nitrogen fixation under low-temperature conditions. Cold-adapted isolates may be applied as inoculants for plant growth promotion and as biocontrol agents for crops growing under cold climatic condition.

Verma et al. (2016) reported the nitrogen-fixing bacilli from wheat growing in northern hills of India. A total of 395 bacilli were isolated by heat enrichment and employed in different growth media. Phylogenetic analysis based on 16S rRNA gene sequencing led to the identification of 55 distinct bacilli that could be grouped in 5 families, *Bacillaceae* (68%), *Paenibacillaceae* (15%), *Planococcaceae* (8%), *Staphylococcaceae* (7%), and *Bacillales incertae sedis* (2%), which included 8 genera, namely, *Bacillus*, *Exiguobacterium*, *Lysinibacillus*, *Paenibacillus*, *Planococcus*, *Planomicrobium*, *Sporosarcina*, and *Staphylococcus*. That study was the first to report for the presence of *Bacillus endophyticus*, *Paenibacillus xylanexedens*, *Planococcus citreus*, *Planomicrobium okeanokoites*, *Sporosarcina* sp., and *Staphylococcus succinus* in wheat rhizosphere which exhibit multifunctional PGP attributes. Among all screened bacteria, *Bacillus barbaricus* BSH5 (18.2 ± 1.6 nmol ethylene h^{-1} mg^{-1} protein), *Bacillus circulans* BSH11 (45.3 ± 1.5 nmol ethylene h^{-1} mg^{-1} protein), *Lysinibacillus fusiformis* BSH2 (43.5 ± 1.6 nmol ethylene h^{-1} mg^{-1} protein), and *Lysinibacillus sphaericus* BSH6 (19.5 ± 1.0 nmol ethylene

h^{-1} mg^{-1} protein) fixed the atmospheric nitrogen under the hilly area and low-temperature condition.

11.4.2 Solubilization of Phosphorus, Potassium, and Zinc

Phosphate (P) and potassium (K) are the major essential macronutrients for biological growth and development. However, the concentrations of soluble P and K in soil are usually very low, as the biggest proportions of P and K in soil are in soluble rocks, minerals, and other deposits (Goldstein 1994). Phosphorus is one of the major growth-limiting nutrients in plants and is often the limiting mineral nutrient for biomass production in natural ecosystems. It is important for the plant growth and promotes root development, tillering, and early flowering and performs other functions like metabolic activities, particularly in synthesis of protein. Thus, P is a key element in several metabolic pathways and biochemical reactions including glycolysis and numerous steps in the C3 and C4 pathways of the Calvin cycle. Phosphorus is an essential element for the establishment and development of plants because it improves the entire root system, consequently improving the shoot. In later stages of growth, the lack of phosphorus can lead to atrophy and death of the stems and leaves and can also delay fruit maturation. It is only taken up in monobasic or dibasic soluble forms. Phosphates applied to agricultural soils are rapidly immobilized and rendered inaccessible for plants. Due to this rapid immobilization, many agricultural soils have large reservoirs of phosphates in inaccessible forms. In this scenario, phosphorus-solubilizing activity is determined by the ability of microorganisms to release metabolites such as organic acids, which through their hydroxyl and carboxyl groups chelate the cation bound to phosphate, the latter being converted to soluble forms.

Gulati et al. (2008) reported fluorescent pseudomonads with phosphate-solubilizing ability from the cold desert region of Lahaul and trans-Himalayas, India. Among 216 phosphate-solubilizing isolates, 12 exhibiting high solubilization of tricalcium phosphate (TCP) in NBRIP liquid culture were identified as *Pseudomonas trivialis*, *P. poae*, *P. fluorescens*, and *Pseudomonas* spp. on the basis of phenotypic features, whole-cell fatty acid methyl ester (FAME) profiles, and 16S rDNA sequencing. These isolates also showed relatively high solubilization of North Carolina rock phosphate (NCRP) in comparison to the solubilization of Mussoorie rock phosphate (MRP) and Udaipur rock phosphate (URP). The solubilization of phosphate substrates by *P. trivialis* and *P. poae* is reported for the first time.

Vyas et al. (2010) deciphered phosphate-solubilizing bacteria isolated from *Hippophae rhamnoides* rhizosphere which was identified as *Rahnella* sp. based on its phenotypic features and 16S rRNA gene sequence. The bacterial strain showed the growth characteristics of a cold-adapted psychrotroph, with the multiple plant growth-promoting traits of inorganic and organic phosphate solubilization, 1-amino cyclopropane-1-carboxylate-deaminase activity, ammonia generation, and siderophore production. The strain also produced indole-3-acetic acid, indole-3-acetaldehyde, indole-3-acetamide, indole-3-acetonitrile, indole-3-lactic acid, and indole-3- pyruvic acid in tryptophan-supplemented nutrient broth. Gluconic, citric, and isocitric acids were the major organic acids detected during tricalcium phosphate solubilization. A rifampicin-resistant mutant of the strain exhibited high rhizosphere competence without disturbance to the resident microbial populations in pea rhizosphere. Seed bacterization with a charcoal-based inoculum significantly increased growth in barley, chickpea, pea, and maize under the controlled environment. The attributes of cold tolerance, high rhizosphere competence, and broad-spectrum plant growth-promoting activity exhibited the potential of *Rahnella* sp. BIHB 783 for increasing agriculture productivity.

Yadav et al. (2016b) investigated plant growth-promoting psychrotrophic bacilli from different sites in northwestern Indian Himalayas. A total of 247 morphotypes were obtained from different soil and water samples and were grouped into 43 clusters based on 16S rDNA-RFLP analysis with 3 restriction endonucleases. Sequencing of representative isolates from each cluster led to their identification, and 43 bacilli belonged to different species of 11 genera, viz., *Desemzia*, *Exiguobacterium*, *Jeotgalicoccus*, *Lysinibacillus*, *Paenibacillus*, *Planococcus*, *Pontibacillus*, *Sinobaca*, *Sporosarcina*, *Staphylococcus*, and *Virgibacillus*. With an aim to develop microbial inoculants that can perform efficiently at low temperatures, all representative isolates were screened for different plant growth-promoting traits at low temperatures (5–15 °C). Among the strains, variations were observed for production of ammonia (22%), indole-3-acetic acid (20%), siderophores (8%), gibberellic acid (4%), and hydrogen cyanide (3%); solubilization of phosphate (12%), zinc (16%), and potassium (8%); 1-aminocyclopropane-1-carboxylate deaminase activity (5%); and biocontrol activity (19%) against *Rhizoctonia solani* and *Macrophomina phaseolina*. Among all the strains, *Bacillus licheniformis*, *B. muralis*, *Desemzia incerta*, *Paenibacillus tylopili*, and *Sporosarcina globispora* were found to be potent candidates to be developed as inoculants as they exhibited multiple PGP traits at low temperature.

Verma et al. (2016) have reported 395 bacilli from wheat, and these bacteria have been screened for direct and indirect PGP traits, and result has been represented by 55 representative bacilli. Of 55 representatives, 39, 18, and 40 strains exhibited solubilization of phosphorus, potassium, and zinc, respectively. Among P, K, and Zn solubilizers, *Paenibacillus polymyxa* BNW6 solubilized the highest amount of phosphorus 95.6 ± 1.0 mg L^{-1} followed by *Sporosarcina* sp. BNW4 (75.6 ± 1.0 mg L^{-1}). *Planococcus salinarum* BSH13 (46.9 ± 1.2 mg L^{-1}) and *Bacillus pumilus* BCZ15 (7.5 ± 0.5 mg L^{-1}) solubilized the highest amount of potassium and zinc, respectively. Among plant growth-promoting activities, ammonia-producing bacilli were highest (79.0%), when compared to P solubilizer (73.9%), Zn solubilizers (67.1%), protease producers (56.7%), IAA producers (55.2%), siderophore producers (49.1%), biocontrol activity (47.8%), K solubilizers (39.2%), N2-fixers (31.4%), HCN producers (27.3%), and gibberellic acid producers (24.8%).

11.4.3 Phytohormones Production

Plant-associated microbes typically produce plant growth hormones such as cytokinins, auxins, and gibberellins. The gibberellin production is most typical for the root-associated microbes, cytokinins have been identified in some leaf isolates, and auxin production is common to all plant-associated microbes. Auxins are a group of indole derivatives that have various growth-promoting functions in plants, such as promotion of root formation, regulation of fruit ripening, and stimulation of cell division, extension, and differentiation. Indoleacetic acid (IAA) is the most well-known auxin. Auxins can promote the growth of roots and stems quickly (by increasing cell elongation) or slowly (through cell division and differentiation). The production of such growth regulators by endophytes provides numerous benefits to the host plant including the facilitation of root system expansion, which enhances the absorption of water and nutrients and improves plant survival. There are several types of bacterial auxins, and the well-studied of these is indoleacetic acid (IAA). IAA does not function as a hormone in microbial cells; therefore, the ability of bacteria to produce IAA may have evolved as the plant-microorganism relationship developed. The ability to synthesize these phytohormones is widely distributed among plant-associated microbes, and IAA may potentially be used to promote plant growth or suppress weed growth. Many studies have described the ability of endophytic bacteria to produce phytohormones and auxins, such as IAA (Hallmann et al. 1997), and the ability to produce IAA is considered to be responsible for plant growth promotion by beneficial bacteria, such as *Azospirillum*, *Alcaligenes faecalis*, *Klebsiella*, *Enterobacter*, *Acetobacter diazotrophicus*, and *Herbaspirillum seropedicae*. Cytokinins are a group of compounds with the backbone of adenine having a substitution at the N-6 atom of the purine ring. These compounds are important in many steps of plant development, as they stimulate plant cell division, induce germination of seeds, activate dormant buds, and play a role in apical dominance. Cytokinins also induce the biosynthesis of chlorophyll, nucleic acids, and chloroplast proteins at the early stages of leaf development. Both pathogenic and beneficial plant-associated bacterial species are capable of synthesizing cytokinins. Among plant-associated methylotrophs, species such as *Methylovorusmays* and *Methylobacterium mesophilicum* JCM2829 synthesize and excrete cytokinins (Ivanova et al. 2001, 2008).

Verma et al. (2015a) deciphered the biodiversity of wheat-associated bacteria from the northern hills zone of India. A total of 247 bacteria were isolated from 5 different sites. Analysis of these bacteria by amplified ribosomal DNA restriction analysis (ARDRA) using 3 restriction enzymes, *Alu*I, *Msp*I, and *Hae*III, led to the grouping of these isolates into 19–33 clusters for the different sites at 75% similarity index. Among all isolated bacteria, 14% showed IAA production in which strain IARI-HHS1-3 showed the highest IAA production (70.8 ± 1.5 μg mg^{-1} protein day^{-1}) followed by IARI-HHS1-8 (69.1 ± 0.5 μg mg^{-1} protein day^{-1}). On the basis of 16S rRNA gene sequencing, the strains IARI-HHS1-3 and IARI-HHS1-8 were identified as *Providencia* sp. and *Pseudomonas peli* respectively. The potential utility of such cold-active bacterial strains in the context of hill and mountain agro-ecosystems is immense, considering the unique crops growing in the climatic conditions of high altitude agricultural systems. Such systems require situation-specific microbial inoculants that withstand extremities of cold and retain their functional traits for PGP. The PGP potential of the bacterial strains dealt with in this study requires further evaluation and validation before their use as bio-inoculants.

The selection of native functional PGP microorganisms is a mandatory step for reducing the use of energy-intensive chemical fertilizers.

11.4.4 ACC Deaminase Activity

Ethylene is a stress-induced plant hormone that can inhibit plant growth. Some bacteria can lower the level of ethylene in the plant by cleaving the plant-produced ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC). Inoculation of such bacteria can mitigate the effect of various stressors by sustaining plant growth in the face of ethylene. ACC deaminase-producing bacteria may play a role in regulating ethylene levels after such bursts, ensuring that ethylene levels stay below the point where growth is impaired (Glick 1995). Ethylene is a key regulator of the colonization of plant tissue by bacteria which in turn suggests that the ethylene-inhibiting effects of ACC deaminase may be a bacterial colonization strategy. Regardless of why plant-associated bacteria produce ACC deaminase, their application can clearly be a very useful strategy to mitigate the effects of various stressors on cultivated plants. Generally, ethylene is an essential metabolite for the normal growth and development of plants (Khalid et al. 2004, 2006). This plant growth hormone is produced endogenously by approximately all plants and is also produced by different biotic and abiotic processes in soils and is important in inducing multifarious physiological changes in plants. Apart from being a plant growth regulator, ethylene has also been established as a stress hormone. Under stress conditions like those generated by salinity, drought, water logging, heavy metals, and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. Plant growth-promoting bacteria which possess the enzyme ACC deaminase facilitate plant growth and development by decreasing ethylene levels, inducing salt tolerance and reducing drought stress in plants. Microbial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia*, *Rhizobium*, etc. (Khalid et al. 2006; Verma et al. 2014a, b, 2015a; Xu et al. 2014; Yadav and Saxena 2017).

In the study by Verma et al. (2015a) the wheat associated psychrotrophic bacteria from Indian Himalayas has been deciphered. The bacterial isolated exhibited multifunctional PGP attributes. Among 247 bacterial isolates, 15 strains showed ACC deaminase activity under the low temperature conditions. On the basis of 16S rRNA sequencing these bacteria were identified as *Arthrobacter methylotrophus* IARI-HHS1-25, *Flavobacterium psychrophilum* IARI-HHS2-37, *Bacillus horikoshii* IARI-HHS2-13, *Methylobacterium mesophilicum* IARI-HHS1-36, *Methylobacterium radiotolerans* IARI-HHS1-45, *Methylobacterium phyllosphaerae* IARI-HHS2-67, *Methylobacterium* sp. IARI-HHS2-69, *Providencia* sp. IARI-HHS1-3, *Pseudomonas fragi* IARI-HHS1-10, *Pseudomonas fluorescens* IARI-HHS1-4, *Stenotrophomonas maltophilia* IARI-HHS1-20, *Pseudomonas syringae* IARI-HHS1-29, *Pseudomonas aeruginosa* IARI-HHS2-12, *Leclercia adecarboxylata* IARI-HHS2-42 and *Enterobacter* sp. IARI-HHS2-44.

11.4.5 Antifungal Activity and Production of Siderophores, Antibiotics, and Lytic Enzymes

The indirect mechanism of plant growth occurs when microbes lessen or prevent the detrimental effects of pathogens on plants by production of inhibitory substances or by increasing the natural resistance of the host. The pathogenic microorganisms can be controlled by releasing siderophores; β-1,3-glucanase; chitinases; antibiotics; and fluorescent pigment or by hydogen cyanide production. World agriculture faces a great loss every year incurred from infection by pathogenic organisms. Application of microorganism for the control of diseases seems to be one of the most promising ways. Biocontrol systems are eco-friendly and cost-efficient and involved in improving the soil consistency and maintenance of natural soil flora. To act efficiently, the biocontrol agent should remain active under large range of conditions, *viz*., varying pH, temperature, and concentrations of different ions. Biocontrol agents limit growth of pathogen as well as few nematodes and insects. Biocontrol bacteria can limit pathogens directly by producing antagonistic substances, competition for iron, detoxification, or degradation of virulence factors or indirectly by inducing systemic resistance (ISR) in plants against certain diseases, signal interference, competition for nutrients and niches, and interference with activity, survival, germination, and sporulation of the pathogen (Verma et al. 2017b). Recent studies have indicated that biological control of bacterial wilt disease could be achieved using antagonistic bacteria. Different bacterial species, namely, *Alcaligenes* sp., *Bacillus pumilus*, *B. subtilis*, *B. megaterium*, *Clavibacter michiganensis*, *Curtobacterium* sp., *Flavobacterium* sp., *Kluyvera* sp., *Microbacterium* sp., *Pseudomonas alcaligenes*, *P. putida*, and *P. fluorescens*, have been reported as endophytes and were inhibitory to plant pathogens (Inderiati and Franco 2008; Ramesh et al. 2009; Nagendran et al. 2013; Gholami et al. 2014; Purnawati 2014; Verma et al. 2015a, b, c, d, 2016; Suman et al. 2016b) (Table 11.2).

Selvakumar et al. (2009c) reported *Exiguobacterium acetylicum* strain 1P (MTCC 8707) from rhizospheric soil sample. The species level identification was achieved on the basis of 16S rRNA gene sequencing. The sequence showed 98% similarity with sequences of *E. acetylicum* available in the public domain. The strain was positive for siderophores and HCN production. In separate *in vitro* assays, it was found to inhibit the growth and development of *Rhizoctonia solani*, *Sclerotium rolfsii*, *Pythium*, and *Fusarium oxysporum*. The volatile compound produced by the bacterium was found to be the most potent in inhibiting the hyphal development of *R. solani*, *S. rolfsii*, *Pythium*, *and F. oxysporum* by 45.55, 41.38, 28.92, and 39.74%, respectively. Commonly observed deformities caused by the diffusible and volatile compounds produced by the bacterium included hyphal inhibition, constriction, and deformation. Under pot culture conditions, the bacterium improved the germination and early growth parameters of pea (*Pisum sativum*) in the presence of *R. solani* and *S. rolfsii*.

Growth enhancement through enzymatic activity is another mechanism used by plant growth-promoting bacteria. Plant growth-promoting bacterial strains can produce certain enzymes such as chitinases, dehydrogenase, β-glucanase, lipases, phosphatases, proteases, etc., and exhibit hyperparasitic activity, attacking pathogens by excreting cell wall hydrolases. Through the activity of these enzymes, plant growth-promoting bacteria play a very significant role in plant growth promotion particularly to protect them from biotic and abiotic stresses by suppression of pathogenic fungi including *Botrytis cinerea*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Phytophthora* sp., *Rhizoctonia solani*, and *Pythium ultimum* (Arora 2013; Yadav 2017).

The production of antibiotics that is considered to be one of the most powerful and studied biocontrol mechanisms of plant growth-promoting bacteria against phytopathogens has become increasingly better understood over the past two decades (Shilev 2013; Gupta et al. 2015). A variety of antibiotics have been identified, including compounds such as amphisin, 2,4-diacetylphloroglucinol (DAPG), oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by pseudomonads and oligomycin A, kanosamine, zwittermicin A, and xanthobaccin produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas* sp. to prevent the proliferation of plant pathogens (generally fungi). *Bacillus amyloliquefaciens* is known for lipopeptide and polyketide production for biological control activity and plant growth promotion activity against soilborne pathogens (Ongena and Jacques 2008). Apart from the production of antibiotic, some bacteria are also capable of producing volatile compound known as hydrogen cyanide (HCN) for biocontrol of black root rot of tobacco, caused by *Thielaviopsis basicola* (Sacherer et al. 1994). Lanteigne et al. (2012) also reported the production of DAPG and HCN by *Pseudomonas* contributing to the biological control of bacterial canker of tomato.

Iron is a necessary cofactor for many enzymatic reactions and is an essential nutrient for virtually all organisms. In aerobic conditions, iron exists predominantly in its ferric state (Fe^{3+}) and reacts to form highly insoluble hydroxides and oxyhydroxides that are largely unavailable to plants and microorganisms. To acquire sufficient iron, siderophores produced by bacteria can bind to Fe^{3+} with a high affinity to solubilize this metal for its efficient uptake. Bacterial siderophores are low-molecular-weight compounds with high Fe^{3+} chelating affinities responsible for the solubilization and transport of this element into bacterial cells. Some bacteria produce hydroxamate-type siderophores, and others produce catecholate types. In a state of iron limitation, the siderophore-producing microorganisms are also able to bind and transport the iron-siderophore complex by the expression of specific proteins. The production of siderophores by microorganisms is beneficial to plants because it can inhibit the growth of plant pathogens. Siderophores have been implicated for both direct and indirect enhancement of plant growth by plant growth-promoting bacteria. The direct benefits of bacterial siderophores on the growth of plants that have been demonstrated by using radiolabeled ferric siderophores as a sole source of iron showed that plants are able to take up the labeled iron by a large number of plant growth-promoting bacteria including *Aeromonas*, *Azadirachta*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* sp. (Gulati et al. 2009; Mishra et al. 2011; Vyas et al. 2010; Yadav et al. 2015a, b; Verma et al. 2013, 2015a) (Table 11.2).

11.5 Biofertilizers: Microbes with Multifarious Plant Growth-Promoting Attributes

Biofertilizers are basically the microbes which bring about the enrichment of the nutrients of the soil by enhancement of the availability of the nutrients to the crops. Plant nutrients are one of the most essential components of the sustainable agriculture. The production of the healthy crops so as to meet the demands of the world's expanding population mainly relies on the type of the fertilizers which are basically used to supplement all the nutrients to the plants, but more reliability the chemical fertilizers are damaging the environmental ecology as well as affecting the human health with great severity. Thus, the use of the microbes as biofertilizers is considered as an alternative to chemical fertilizers so as to improve the fertility of the soil as well as increase the productivity of the crops in sustainable farming. These microbes are considered to be the biopotential and a novel tool for providing substantial benefits to the agriculture. These microbes basically colonize the roots and stimulate the growth, and these are referred to as the PGP microbes. PGP microbes stimulate the growth by various direct and indirect mechanisms such as the production of various plant growth regulators, biological nitrogen fixation, phosphorus solubilization, and production of the siderophores, HCN, and various lytic enzymes. Extensive work on the biofertilizers is available which reveals that these microbes have the capability of providing the required nutrients to the crops in amounts which are sufficient for the enhancement of yield of the crops (Suman et al. 2016a; Verma et al 2017c; Yadav et al. 2017a).

Selvakumar et al. (2008) reported and characterized a *Pantoea dispersa* strain 1A with multifarious PGP attributes. It is endowed with multiple plant growth-promoting attributes such as phosphate solubilization, IAA production, siderophore production, and HCN production, which are expressed differentially at suboptimal temperatures (15 and 4 °C). It was able to solubilize phosphate (17.6 μg of P_2O_5 ml^{-1} day^{-1}), and produce IAA (3.7 μg ml^{-1} day^{-1}), at 15 °C.

Mishra et al. (2008) deciphered a psychrotolerant, *Pseudomonas vancouverensis*, which possesses various PGP attributes. The isolate produced 8.33 and 1.38 μg/ml of IAA at 15 °C and 4 °C, respectively, on the third day after incubation. It solubilized 42.3, 66.3, and 74.1 μg/ml of tricalcium phosphate at 4, 15, and 28 °C, respectively, after 7 days of incubation. The strain also possessed HCN and siderophore production abilities at 4 °C. It exhibited inhibitory activity against several phytopathogenic fungi in three different bioassays. The maximum relative growth inhibition was recorded against *Sclerotium rolfsii* and *Rhizoctonia solani* (100%), followed by *Pythium* sp. (73.1%) and *Fusarium oxysporum* (19.7%), in volatile compound assays.

Gulati et al. (2009) isolated and characterized *Acinetobacter rhizosphaerae* strain BIHB 723 with multifunctional PGP activities of phosphate solubilization, auxin production, 1-aminocyclopropane-1-carboxylate deaminase activity, ammonia generation, and siderophore production. A significant increase in the growth of pea, chickpea, maize, and barley was recorded for inoculations under controlled conditions. Field testing with the pea also showed a significant increment in plant growth and yield.

Verma et al. (2015a) reported psychrotolerant wheat-associated bacteria from northern hills zone of India. A total of 247 bacteria were isolated from 5 different sites. Representative strains from each cluster were screened in vitro for plant growth-promoting traits, which included solubilization of phosphorus, potassium, and zinc; production of ammonia, hydrogen cyanide, indole-3-acetic acid, and siderophore; nitrogen fixation; 1-aminocyclopropane-1-carboxylate deaminase activity; and biocontrol against *Fusarium graminearum*, *Rhizoctonia solani*, and *Macrophomina phaseolina.* Cold-adapted isolates may be applied as inoculants for plant growth promotion and as biocontrol agents for crops growing under cold climatic condition.

11.6 Conclusion and Future Prospect

In conclusion, utility of such cold-active microbial strains in the context of hill and mountain agro-ecosystems is immense considering the unique crop-growing situations and the climatic conditions of the high-altitude agricultural systems. Such systems require situation-specific microbial inoculants that withstand extremities of cold and retain their functional traits for plant growth promotion. Microbial strains with multifarious plant growth promotion potential could be used as bio-inoculants (biofertilizers and biocontrol agents) in the hill and mountain agro-ecosystems, where temperature is a major determinant of plant and microbial activity. The selection of native functional plant growth-promoting microorganisms is a mandatory step for reducing the use of energy-intensive chemical fertilizers. The benificial and potential cold-adapted microbes may have applications in diverse processes in agriculture, industry, and allied sectors.

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