Understanding Cold-Adapted Plant Growth-Promoting Microorganisms from High-Altitude Ecosystems

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Himani Singh, Nupur Sinha, and Prachi Bhargava

Abstract

Psychrophiles are found almost in all the ecosystems at low temperatures. They are of great importance as they act as models to study the mechanics for survival at low temperature and can be used to extract several enzymes and secondary metabolites which are useful in various industries say healthcare, food, detergent, tannery, etc. This chapter focuses on the basic modifications of psychrophiles at cellular, molecular and functional levels, their applications in different spheres of life and how these strategies can be mimicked in human lives.

Keywords

Psychrophiles · PGPR · High altitude · Cold-adapted enzymes

13.1 Ecological Diversity of Cold-Adapted Microorganisms

Low temperature suits best to psychrophiles for their growth and reproduction. The cold-adapted microorganisms are present at higher altitudes and in deep blue seas where the temperature is below 15 °C. Though these ecosystems are too harsh for survival, still diverse microbial communities survive facing all the challenges with the help of adaptations at various levels. The challenges include availability of

H. Singh
Institute of Biosciences and Technology, Shri Ramswaroop Memorial University, Barabanki, Uttar Pradesh, India

N. Sinha
Amity Institute of Biotechnology, AUUP, Noida, Uttar Pradesh, India

P. Bhargava (✉)
Institute of Agricultural Sciences and Technology, Shri Ramswaroop Memorial University, Barabanki, Uttar Pradesh, India
e-mail: prachi.bio@srmu.ac.in

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nutrients, IR radiations, excessive UV radiations, change in pH and very high osmotic pressure (De Maayer et al. 2014). Psychrophiles may be autotrophic, chemotrophic or heterotrophic based on their mode of nutrition. They play an important role in nutrient turn over and production of biomass in low-temperature environments and have significant role in various industries. Psychrophilic microbes find their importance in food preservation and degradation of organic matter in low temperatures where artificial cold environmental conditions are generated in vitro. Ironically most of the food spoiling bacteria are adapted to man-made cryo-environments. Pse*udomonas*, *Psychrobacter*, *Staphylococcus* and *Photobacterium* have often been isolated from psychrotolerant bacteria in artificial cold environments. Some of the factors that govern the existence of the genera in artificial cold environments have been summarized below:

- Possibility of shift of ambient environment to cold environment
- Possibility of invasion by their own basic cellular and molecular components
- Ability to propagate rapidly
- Presence or absence of oxygen at low temperatures

These genera are considered to be genetically diverse and have mechanisms for adapting to cold environments.

In addition to the above attributes, marine psychrophiles have cell membranes made up of lipids that do not harden in cold environment. Moreover, the presence of catalase atoms in psychrophiles help them to adapt to the natural conditions (higher concentration of hydrogen peroxide at low temperatures) under which these microbes endure. Three types of psychrotolerant H_2O_2-safe microscopic organisms have been disengaged from channel reservoirs of a fish egg preparing plant that utilizes H_2O_2 as a fading operator. Certain varieties of obscure bacterial species exist with specific varieties of natural adjustment systems (e.g., enzymatic efficiency of catalase and its cellular localization) contingent upon the natural H_2O_2 focus and delicacy of cells. Therefore, it is really hard to surmise general rules that may clarify the limit with respect to numerous psychrophiles to adjust their genomic and metabolic highlights to their local cold natural surroundings. The physiological studies of individual strain of proteins and genes show high level of psychrophilic adaptation (Rodrigues and Tiedje 2008; Casanueva et al. 2010). Various omics technologies have been utilized to ponder different capacities in microorganisms developed under various cold temperatures (Allen et al. 2009; Fondi et al. 2016). These adaptations work in a synergistic way at both genomic and metabolic levels to help the microorganism lead a smooth life in cold environment (Math et al. 2012). One of the example is the adenylate cyclase present in the cell membrane which gets activated at low temperature, aiding in smooth functioning of metabolic pathways. Various such cold adaptations will be discussed in detail in this chapter.

13.2 Effects of Low Temperature on Microbes

Low temperature can affect the microorganism in various ways. Reduction in growth rate and number of cell, variation in cell composition and nutritional requirements are some direct effects while other indirect effects include solute solubility, cell density, nutrient distribution and osmotic adjustment of the membrane. Microbes sense the decrease in environmental temperature with the help of their cellular responses like stiffness in their membrane, which is a very important membrane-associated sensor. Cold signal transduction pathway in microorganism is a two-component system. The signal with the help of sensors reaches the response regulator which in turn upregulate the genes involved in membrane fluidity in cold-adapted microorganism. The lipid bilayer maintains the cell permeability and transportation of essential solutes in liquid–crystalline phase. When temperature decreases, the functional phase of lipid transits into gel form due to which membrane fluidity is lost. Gene for fatty acid desaturases includes membrane lipid and protein phosphorylation and dephosphorylation, which induce phosphorylation of cytosolic protein (Jagtap and Ray 1999). Composition of fatty acid varies according to external temperature. At low temperature, there is more unsaturation owing to saturases, more methyl branching, alteration in fatty chain length, increase in the ratio of ante-iso to iso branching and change in the ratio of sterol and phospholipid contents. In 2008, Coa-Hoang et al. stated that cold shock induced membrane injury which triggered high rate of cell inactivation in microbes like *Escherichia coli* and *Bacillus subtilis.* Other adapting features like secretion of cold-shock proteins (Czapski and Trun 2014), molecular RNA chaperones, osmotic solutes (cryoprotectants) (Kawahara et al. 2008), enzymatic denaturation, incorrect protein tertiary and quaternary structures and intracellular ice formation play a pivotal role in the existence of microbes in cold environments.

13.2.1 Cell Membrane-Associated Changes

Microorganisms exhibit significant tolerance to chilling by reducing the damage in their membranes. Downshift in temperature reduces membrane fluidity and induce permeability in response to increased phase transition of membrane phospholipids (Cao-Hoang et al. 2010). Cells growing at 37 °C have more saturated fatty acid content (laurate) while at low temperature the content of laurate decreases and is substituted by unsaturated fatty acid (palmitoleate), which increases membrane fluidity and decreases membrane phase separation. Enzyme fatty acid desaturase causes unsaturation of fatty acids in *Bacillus subtilis* in preexisting membrane phospholipids (Aguilar et al. 2001). The gene of enzyme desaturase is regulated by a sensor called DesK kinase which activates the transcriptional activators DesR at cold temperature (Albanesi et al. 2004). Figure 13.1 illustrates the mechanism of unsaturation of already present fatty acids and maintenance of membrane fluidity by desaturase enzyme.

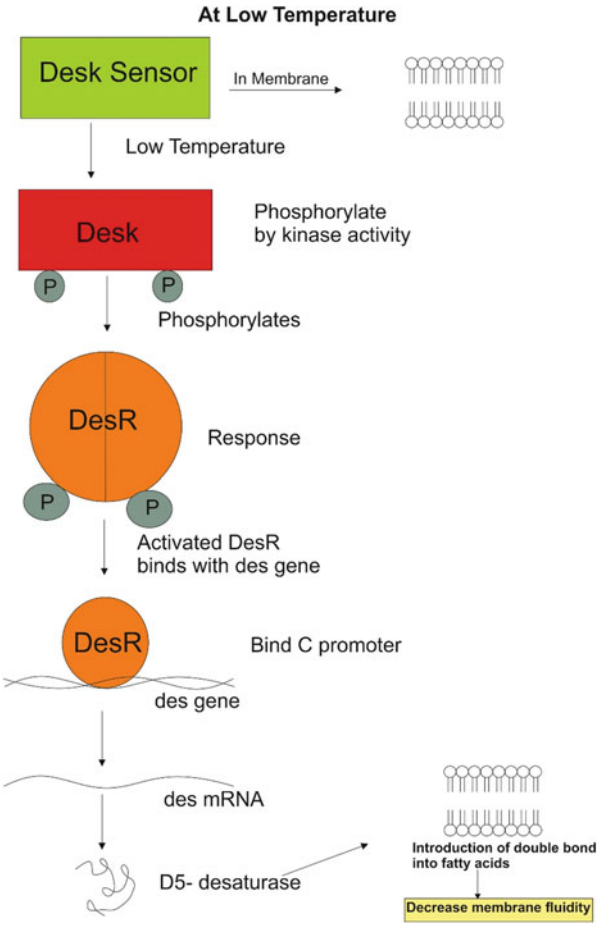

Fig. 13.1 Mechanism of unsaturation of already present fatty acids by desaturase enzyme at low temperature

13.2.2 Role of Cryoprotectants

Cryoprotectants (CRPs) are small molecules or chemical chaperones that provide defence mechanism against cold stress (Kawahara et al. 2008). These compounds include sugars like monosaccharides (glucose, fructose), disaccharides (sucrose, trehalose, etc.), polyamines, polyols (alcohol sugars such as glycerol and sorbitol) and amino acids (glycine, alanine, and proline). CRPs may be secreted outside the cell or may be located at intracellular level. Secreted CRPs can lower the freezing of water (Bouvet and Ben 2003) while their intracellular counterparts increase the total internal solute concentrations so as to regulate the osmotic pressure and maintain the osmolarity prior to freezing. CRPs have been reported in various bacteria like *Lactobacillus*, *Pseudomonas* and *Pantoea*. During cold shock, glycine betaine controls the aggregation of cellular proteins and regulates the fluidity of the membrane (Chattopadhyay 2002). Almost similar conditions have been reported in food-borne pathogen *L. monocytogenes*, where glycine betaine maintains high osmolarity

at chilling stress (Angelidis and Smith 2003). Another cryoprotectant trehalose accumulates on both sides of the cell membrane and conserves intracellular water to stabilize cell membrane against freezing (Sano et al. 1999). Exopolysaccharides (EPS) synthesized by psychrophiles in cold environment have polyhydroxyls which prevent ice nucleation of water, enzyme denaturation and lysis of cell (Feng et al. 2014). ESPs store water and minerals and assist in cell aggregation, cell coating and formation of biofilm (microbial cells adhere to each other within an indigenous matrix of extracellular polymer) and maintain the viability of cells (Qin et al. 2007). Fungi *Mortierella elongata*, has some characteristics which favour their growth at low temperatures. These features include increased the amounts of intracellular trehalose, stearidonic acid and absence of ergosterol lipid when subjected to cold stress (Weinstein et al. 2000). Ergosterol is the main sterol in fungi which makes lipid membranes more rigid and decrease their membrane permeability; hence, deficiency of ergosterol causes the membrane more liable to cold-induced damage. Therefore, *M. elongata* increases the production of trehalose as an adaptation method in low temperature. Trehalose is the most effective cryoprotectants in thermotolerance in the fungi *Neurospora crassa* and *Cunninghamella japonica* (Neves et al. 1991; Tereshina et al. 1991). Dong and Chen found that at 4 °C cultured cell extracts of *Methanolobus psychrophilus* R15, there is upregulation of a new type of adenosine derivative which acts as osmotic solute in cold condition. Another cryoprotectant Cor26 is accumulated in *Pseudomonas fluorescens* KUIN-1 bacteria and aspartate in *Methanococcoides burtoni* in response to cold temperature. Aspartate is known to increase the affinity of GTP binding to elongation factor 2 while the action of Cor26 is unknown.

13.3 Cold Acclimation Proteins and Cold-Shock Proteins

Psychrophiles release a group of ~20 proteins during steady-state growth at cold temperature referred as cold-acclimation proteins (CAPs). The level of these proteins increases constitutively at low temperatures which help microorganism to adapt in cold climate (Phadtare 2004). They regulate protein synthesis and are essential for viability in cold condition. RNA chaperone CspA are usually cold-shock proteins reported in mesophiles and function as Caps in cold-adapted bacteria. The function of CAPs is not yet explored much; however, it has been revealed that these proteins regulate cell cycle and cell growth at lower temperature. *Pantoea ananas* KUIN-3 release a cold acclimation protein, Hsc 25, which has the potential of refolding the cold-denatured enzymes (Kawahara et al. 2008).

When environmental temperature comes down suddenly, psychrophilic bacteria show cold-shock response and release cold-shock proteins (Csps). These are (65–75 aa in length) nucleic acid-binding proteins (Czapski and Trun 2014). Cold-shock proteins neutralize various detrimental effects of fall in temperature and hence facilitate the cells to adjust with a transient overexpression that affect a number of molecular and cellular processes (Phadtare 2004). At cryo-temperature, RNA structures stabilize and become non-dynamic that induce premature transcription and translation termination. However, protein folding is disorganized, and ribosome

function is hindered. Csps function as RNA chaperones helping in the sliding of ribosomes on target mRNA. This activity can be inhibited due to secondary structures of RNA at cold stress. Due to chaperone activity of Csps, single-stranded state of RNA is maintained (Barria et al. 2013). All Csps are ancient proteins which have some key conserved structure which includes five antiparallel strands that makes a ß-barrel. Csps that comprise a single nucleic acid-binding domain are known as cold-shock domain (CSD). CSD consists of two RNA binding motifs referred as ribonucleoprotein 1 and 2 (Lee et al. 2013). These binding motifs open tightly packed nucleic acid molecules which are inaccessible for translation (Chaikam and Karlson 2010).

Proteins that are constitutively synthesized in cell are called housekeeping proteins. Cold shock does not lower the production of these proteins, whereas the expression of Csps is enhanced with aggravated cold shock (Ermolenko and Makhatadze 2002). These CSPs reduce the expression of housekeeping gene and maintain the folding of important proteins. Hence cells adapt for temperature downshift at slower rate. Chaikam and Karlson (2010) reported that Csps are actively associated with the maintenance of chromosome folding. CspA was the first reported cold-shock protein in *Escherichia coli* (Goldstein et al. 1990). Previously it was reported that *E. coli* CspAs consist of nine homologous proteins (CspA to CspI). CspA consists of 13% of total cell proteins at cold condition while at 37–40 °C it is declined to lower levels (Lee et al. 2013). During cold or before freezing, Csp proteins are overexpressed in *Lactobacillus* strains which increase the survival rate of the cells. Human pathogen *Listeria monocytogenes* becomes less virulent under refrigerated condition due to the removal of *cspA*, *cspB*, and *cspD* genes which regulate the synthesis of the virulence factor listeriolysin O (Schärer et al. 2013). CspA from psychrophilic *Psychromonas arctica* was overexpressed in *E. coli* which increases the rate of cell survival and cold resistance in hosts by tenfold after repetitive freezing and thawing in polar environments (Jung et al. 2010). In Antarctic bacterium *Psychrobacter* sp. G, three CSP genes *Csp1137*, *Csp2039* and *Csp2531* have been identified with their regulatory sequence (Song et al. 2012). Csp genes of *Yersinia enterocolitica* 8081 and *Yersinia pseudotuberculosis* IP32953 share the maximum homology with csp genes of *E. coli* K-12 W3110 (Kanehisa et al. 2016). Enteropathogenic *Yersinia* psychrotrophs (spread by eatables and cause enteric illness yersiniosis) bear a locus having CspA duplication gene (cspA1 and A2) (Neuhaus et al. 1999).

13.4 Ice Nucleators and Antifreeze Proteins

Ice nucleators are the proteins that act as an ice crystal surface at low temperature (0 °C). They induce freezing and control the energy required for ice formation by ice crystal surface arrangement on water. Some bacteria have the potential of ice formation at low temperature. These bacteria are reported as “ice plus” bacteria. They have ice nucleation-active protein (Ina protein) located on the outer bacterial wall, which act as potent nucleating centre for ice crystals. *Erwinia herbicola* produces highly potent ice nucleators which show optimum activity at subfreezing

temperature (Kozloff et al. 1983). Hirano et al. (1985) found that ice-nucleating bacteria live on the surface of leaves and induce frost damage when the temperature goes down. *Pantoea* (Lindow 1983), *Xanthomonas* (Kim et al. 1987) and *Pseudomonas* (Obata et al. 1987) are some examples of cryotolerant ice-nucleating bacteria.

Antifreeze proteins (AFPs) are ice-binding proteins that inhibit ice crystal formation and growth in any bacterium (Gilbert et al. 2005). They control the ice from melting by binding irreversibly to its surface. AFPs induce high thermal hysteresis activity and inhibit ice recrystallization even at milli-molar concentrations. Fungal AFP from a mold *Typhula ishikariensis* also possesses ice-binding properties (Cheng et al. 2016). Re-crystallization of ice is robustly reduced due to binding of antifreeze proteins with multiple ice planes. Ice-nucleating and antifreeze activities of AFP have also been identified in Arctic rhizobacterium *Pseudomonas putida* GR12-2, which is an extracellular glycolipo protein (Muryoi et al. 2004). There are three domains in ice-nucleating proteins, namely N, R and C. N domain facilitate the binding of ice-nucleating proteins (INP) to lipids and carbohydrates, and ice formation and ice nucleation activity are related to R-domain and C-terminal domain (Kawahara et al. 2008). Yamashita et al. (2002) reported that *Moraxella* was the first reported bacteria in Antarctic region that synthesizes an AFP for its survival in extreme cryo-environment. Ca^{2+}-dependent AFPs have been reported from *Marinomonas primoryensis* bacteria which is dominantly found in Antarctic lake (Gilbert et al. 2005). Psychrophilic phytopathogenic fungi have extracellular AFPs which check the freezing of hyphae (Robinson 2001) and make sure the accessibility of substrate by checking the rate of freezing of nutrients. Hoshino et al. (2009) reported that various genera belonging to Basidiomycetes, Oomycetes and Ascomycetes release AFPs which control freezing of extracellular environment and check the growth of mycelia at very low temperature.

13.5 Cold-Adapted Enzyme

In low temperature, the rate of chemical reactions is very slow because there is inadequate kinetic energy to conquer enzyme activation barriers (in ground state (substrate) and activated state). Psychrophiles release enzymes that show high specific activities at lower temperatures called as cold-adapted enzymes. These include cellulases, lipases, proteases, amylases, xylanases, pectinases, keratinases, esterases, catalases, peroxidases and phytases are perform important role under very harsh climatic as they represent low activation energy and high catalytic activity (Kuddus et al. 2011). Reaction rate (*kcat*) of cold-adapted enzymes is highly independent of temperature.

Cold-adapted enzymes increase structural flexibility to cope with freezing at low temperature (Collins et al. 2008). These adaptations involve molecular dynamic simulations of distinct stabilizing interactions either in the enzyme or at the active site of enzyme (implicated in catalysis). Some relevant factors include electrostatic interactions like reduced no of ion pairs, hydrogen bonds and hydrophobic interaction, reduced proline and arginine residues in loops, location of glycine residues,

decreased cofactor binding, increased interaction with the solvent and reduced inter-subunit interactions (Siddiqui and Cavicchioli 2006). Amylases are very common enzyme found in microorganisms, plants and animals. The α-amylase reported in *Pseudoalteromonas haloplanktis* (AHA), also the most studied cold-adapted enzyme is monomeric, has multiple domains and shows Ca^{2+}- and Cl^{-}-dependent properties (Siddiqui and Cavicchioli 2006). D'Amico et al. (2003) reported that activation energy is reduced in psychrophilic α-amylase (35 kJ mol^{-1}) as compared to thermophilic α-amylase (70 kJ mol^{-1}), so k_{cat} of psychrophilic α-amylase is increased 21-folds at low temperature. Binding of substrates require low energy, so binding affinity of cold-adapted enzymes is lesser, and substrate binding is highly accessible. Several cold-adapted enzymes comprise a more labile and localized flexibility (flexible catalytic site) than other protein structure (Siddiqui et al. 2005). In cold-adapted enzymes, buried amino acids are smaller and show lesser hydrophobicity than their mesophilic and thermophilic counterparts. Hydrolysis and transesterification of fatty acid esters are catalysed by another class comprising of hydrolytic enzymes called esterases and lipases. Esterases differ from lipases on mode of their kinetics and specificity of substrate (Chahiniana and Sarda 2009). EstSL3 esterase, a novel cold-adapted enzyme from *Alkalibacterium* sp. SL3, shows close similarity to lipases extracted from *Alkalibacterium* and *Enterococcus* (Wang et al. 2016). Many cold-adapted enzymes have broad cavities to contain H_2O molecules and/or ligands (Giordano et al. 2015). Cold active pectinases abundantly used in the food-processing industry isolated from *Cryptococcus* have pectinolytic activity (35–36 U/mL at 9 °C) and synthesizes pectinase by glucose as carbon substrate (Birgisson et al. 2003). Some psychrophilic yeasts reported in Japan have pectinolytic activity only at 5 °C and are not capable to survive at high temperature (Tomoyuki et al. 2002). *Aureobasidium pullulans* strain produces pectinase enzyme at cryo-temperature which shows higher pectinase activity of 0.7–0.8 U/mL at 12 °C (Merín et al. 2011). Fungal strains *Aspergillus awamori* isolated from Himalayan region not only has maximum pectinase activity but also produce high amount of psychrophilic xylanases and cellulases (Anuradha et al. 2010)

13.6 RNA Degradosomes in Psychrophiles

Psychrophilic microbes have a multiprotein complex called degradosome which is engaged with the debasement of delivery moiety RNA and the handling of ribosomal RNA which is directed by non-coding RNA. The degradosome consists of enzymes like RNA helicase B, polynucleotide phosphorylase and RNase E (Carpousis 2002; Feng et al. 2001; Cho 2017). The amount of RNA in any cell varies with time for instance, in *Escherichia coli*, the time period of messenger RNA is approximately in the range of 2–25 min, whereas it may live more in other microscopic organisms. RNA is degraded even in resting cells, and the resulting nucleotides are reused for crisp rounds of nucleic acid synthesis. The amount of RNA formed by degradosomes is significant as related to quality guideline and quality control.

All life forms have numerous enzymatic tools for debasing RNA, for example, ribonucleases, helicases, 3′-end nucleotidyltransferases, 5′-end topping and decapping catalysts and RNA-restricting proteins which utilize RNA as substrate. RNA degradosome of *Escherichia coli* comprises four essential parts: (1) hydrolytic endo-ribonuclease RNase E, (2) phosphorolytic exoribonuclease PNPase, (3) adenosine triphosphate (ATP)-subordinate RNA helicase (Rh1B), and (4) glycolytic compound enolase. The degradosome of Antarctic bacterium *Pseudomonas syringae* contains ribonuclease E and RNA helicase. Polynucleotide phosphorylase is present in *Escherichia coli*, and this enzyme controls the quality of ribosomal ribonucleic acid. But the composition of degradosome of the Antarctic counterpart possess another exoribonuclease, ribonuclease R. In *Escherichia coli*, it is well known that ribonuclease R can degrade RNA molecules, and in this process, it does not require (ATP) but helicase requires ATP due to which energy is conserved by cells at low temperatures as well (Purusharth et al. 2005; Hardwick et al. 2010; Carpousis et al. 2009). The metabolic enzyme aconitase is found in *C. crescentus* and phosphofructokinase is found in *B. subtilis* degradosomes though enolase enzyme is present in both the psychrophiles. The bacteria regularly adjusts the gene expression to survive in the harsh environments. Ribonucleases (RNases) control the expression of regulatory proteins and protein-coding RNA by degradation and maturation. Exoribonucleolytic capacities are available in polynucleotide phosphorylase (PNPase) and RNase R in the human pathogen *Streptococcus pyogenes*. An exoribonuclease, PNPase is the focal 3′-to-5′ exoRNase partaking in RNA damage (Lécrivain et al. 2018; Chandran and Luisi 2006; Chandran et al. 2007). A considerable number of the Csp family proteins are in charge of RNA adjustment and debasement. Moreover, mRNA is stable in cold conditions due to the presence of chaperon functions of Csps. CspA also destabilizes the secondary structure and maintains its structure in a single-stranded state, which is necessary for its degradation. CspE acts in the opposite manner, and it stops RNA degradation. CspE binds to poly-A tails, which interfere with their degradation by PNPase, and it stops RNA cleavage by RNase E (Feng et al. 2001; Khemici et al. 2008; Prud'homme-Généreux et al. 2004). A DEAD-box helicase called DeaD in *E. coli* is added into the degradosome which can degrade RNA, under cold conditions.

13.7 Plant Growth Promotion by Agricultural Microbes in Cold Climate

The psychrophilic microorganisms help in the growth of plants under adverse conditions, their promotion and adaptations under harsh environments such as extremes of temperatures, high salt conditions, extremes of pH and drought stresses and are termed as plant-associated extremophilic microorganisms. They possess diverse plant development advancing characteristics, and hence, these productive and potential organisms might be used as biofertilizers to enhance the productivity and maintain the well-being of soil giving a push to the highly talked sustainable agriculture (Verma et al. 2016).

Certain strains of rhizospheric microorganisms, known as plant growth-promoting bacteria (PGPB), invigorate plant development and wellness. Various microorganisms promoting the yields are significant for keeping up the supportability of harvest generation in horticulture. Microorganisms related with harvests can be rhizospheric, phyllospheric, and endophytic based on their location. The rhizosphere contains roots and is affected by the addition of substrates that influence microbial action. A number of microorganisms are found to be associated with the plant rhizosphere which helps in the growth and development of the plant belonging to genera *Azospirillum, Bacillus*, *Pseudomonas*, *Rhizobium,* etc. (Verma et al. 2014). The epiphytic microorganisms are most versatile in nature as they endure high temperature (40–55 °C) and UV radiation. The phyllospheric microorganisms include *Agrobacterium, Pseudomonas,* etc. which can survive in harsh conditions such as extremes of temperature (Nutaratat et al. 2014).

The endophytic living beings are those microorganisms that colonizes in various aerial and subaerial parts of the plant, viz. root, stem or seeds without expediting any ruinous effect on the host plant. These microorganisms have been extracted from plants including wheat (Verma et al. 2013), soybean, pea, common bean, chickpea, pearl millet and rice (Suman et al. 2016). Various examples of endophytic microbial species are *Achromobacter, Azoarcus*, etc. (Verma et al. 2014). Microscopic organisms isolated from harsh temperature conditions are adjusted to live under stressful temperature conditions. Many optimizations have been used to isolate psychrotolerant and psychrophilic microbes from soil. The growth of cold-tolerant Antarctic bacterium can be increased by supplementing the minimal media supplements like amino acids which improved the growth rate of psychrophilic bacteria when the temperature was lowered from 11 °C to almost freezing point of water, i.e. 5 °C.

Indole-3-acetic acid (IAA) is a vital phytohormone secreted by PGPR which enhances overall plant development (Selvakumar et al. 2008). This IAA-secreting capacity of psychrophilic microorganisms acts as a marker tool for their identification while looking at the physiological or environmental conditions. Auxin production in microscopic organisms is controlled by the proline amino acid-dependent pentose phosphate pathway (Sahay et al. 2017). *Pantoea dispersa* and *Serratia marcescens* show their maximum IAA-creating capacity at 4 and 15 °C, respectively. Seed treatment with these bacterial strains significantly improved plant biomass and supplement take-up of wheat seedling developed at cold temperatures. Introduction of seeds with these mentioned strains upgraded the seed germination, root growth and shoot lengths of wheat plantlets developed at low temperatures (Sahu and Ray 2008).

Another bacterial framework that influences plant advancement is the nearness of compound 1-aminocyclopropane-1-carboxylate (ACC) deaminase. This catalyst enhances the overall development and improvement of plants. Bacterial strains that have ACC deaminase can diminish the ethylene combination even in virus infections, thus curbing the negative impact on plants. Plants having ACC deaminase may adjust to this troublesome situation by cutting down ethylene level similar to normal stresses. Few psychro-tolerant bacteria producing ACC deaminase

promote plant development even at low temperature that too under high osmotic pressure.

13.7.1 Nitrogen Fixation

Nitrogen fixation is a very essential process in the soil which is performed by many bacterial species that have the capacity to absorb atmospheric nitrogen and convert it into nitrogenous substances that furnish important nutrients for plants. These microbes synthesize the nitrogenase enzymes that form ammonia from nitrogen N_2. These processes require biological energy in the form of adenosine triphosphate (ATP). The nitrogen-fixing microbes may be free-living or symbiotic. The basic source of energy for some of the nitrogen-fixing microbes living freely is sunlight while others depend on organic matter present in soil. Soil microorganism *Azotobacter* is an aerobic heterotroph, and *Clostridium species* are active in conditions that do not have oxygen. Both the groups of microorganisms (free-living and symbiotic) can fix only minimal amounts of nitrogen, but still they are important for the survival of various plants in the environment.

Symbiotic microbes thrive on plant roots, forming root nodules. *Rhizobium* is an important member of this group which lives symbiotically with various members of leguminaseae family (peas, clover, beans, peanuts, soybeans). *Frankia* is an actinomycete associate with several plant families including species of temperate region trees, for example, *Alnus* and *Myrica*, the arid-region *Acacia*, and the tropical-region *Casuarina* and *Ceanothus*. Crop rotation helps to introduce good amounts of N_2 into the soil for efficient crop production.

Cyanobacteria have a pioneering role in fixing atmospheric nitrogen. They are very active in media which is very shallow such as flooded rice fields and marshy areas. An aquatic microbe, *Anabaena,* lives in a shallow medium in association with *Azola* which is a water fern, and its symbiosis can produce a high quantity of nitrogen per hectare annually, which is sufficient for rice production.

Nitrogen cycle involves various processes such as fixation, ammonification, nitrification and denitrification. Each step involves specialized microbes, and the consequences depend on the physiological state of the soil. The nitrogen cycle in the soil is also affected by the atmospheric processes. Partial removal of nitrogen in the soil releases N_2O, which is a very harmful and strong greenhouse gas responsible for global warming. Carbon dioxide and methane are other greenhouse gases that come out from the soil in special circumstances. N_2 fixation in the deep Arctic or Atlantic Ocean is the most important source of nitrogen where nitrogen is limited in system. N_2 fixation that occurs in ice-free summer waters contributes up to 30% of the N_2 fixation in the Arctic Ocean. Nitrogen fixation in freshwater is relatively common at high altitudes, but still nitrogen fixation in oceans is considered to be common. In Arctic region, when ice melts due to increase in temperature, the net production of nitrogen is increased in Arctic Ocean due to marine nitrogen fixers (Arrigo et al. 2012). A sufficient amount of nitrogen fixers is required to increase the productivity of nitrogen via Arctic nitrogen cycle which affects the primary producers that form

the foundation of the food chain (Popova et al. 2012). This data helps us to conclude that N_2 fixation can also occur at minimum temperatures (Moisander et al. 2010) and at very high altitudes (Sohm et al. 2011; Díez et al. 2012) where it was believed that nitrogen fixation would not be possible.

13.7.2 Phosphate Solubilization

The availability of phosphorus is very important for the cultivation of healthy crops to cope up with the universal requirement of food. Various metabolic and physiological processes like energy transfer, photosynthesis, respiration, signal transduction and nitrogen fixation in plants of the family leguminaceae require P as essential macronutrient. Although P is the most abundant macronutrient found in almost all types of soils, it acts as the major limiting factor for the plant growth because of its unavailability to plants. Inorganic P occurs mostly in insoluble mineral complexes in soil, some are present in chemical fertilizers, and the plants are unable to absorb the insoluble and precipitated forms. Soil microorganisms help in the transformation of phosphorus and make it easily available to plant roots as they possess the ability to solubilize and mineralize phosphorus from inorganic phosphorus (Rodriduez et al. 1999). P-solubilizing bacteria and fungi have been isolated from both rhizospheric and non-rhizospheric soils and phyllosphere (Zaidi et al. 2009). In addition to bacteria and fungi, various microbial species that exhibit P solubilization capacity are actinomycetes and algae. Examples of P solubilization microorganisms are *Pseudomonas species, Bacillus species, Rhodococcus species*, *Arthrobacter species, Serratia species, Chryseobacterium species,* etc. (Wani et al. 2005; Chen et al. 2006), *Azotobacter species* (Sharma et al. 2013), *Xanthomonas species* (Srinivasan et al. 2012), *Enterobacter species,* etc., (Zhu et al. 2012), and *Vibrio species and Xanthobacter species* (Babalola and Glick 2012). The *Rhizobium* species that fixes atmospheric nitrogen to the host plants also show P solubilization property. *Rhizobium species* and *Crotalaria* species (Jorquera et al. 2011) increase the P content in plants by making P easily available to plants. *Kushneria* species is a halophilic bacteria that was extracted from the soils of Daqiao saltern on the eastern coast of China, which have proved to be very beneficial for saline soils. Phosphate-solubilizing fungi include strains of *Fusarium, Alternaria, Sacchromyces,* etc. For better usage of amassed phosphorus in soils their use is very promising in the form of biofertilizers enhancing sustainable agriculture one step further (Richardson and Simpson 2011).

One of the enzymes that cause P solubilization is glucose dehydrogenase which is a membrane-bound enzyme and causes oxidation of glucose to gluconic acid. The gluconic acid is then converted to 2-ketogluconic acid and 2,5-diketogluconic acid by the action of enzymes. P is solubilized effectively by 2-ketogluconic acid as compared to gluconic acid. Although most of the studies on P solubilizing microorganisms were performed at mesophilic temperatures but some reports are also available of studies at low temperatures such as 10 °C (Vassilev et al. 2006).

P mineralization means debasement of the remaining portion of the molecule after solubilization of organic phosphorus which results in dissolution of Ca-P compounds. Phytase is another enzyme responsible for organic P mineralization. This enzyme causes the formation of phosphorus from organic materials which are stored in the form of phytate in soil (Yi et al. 2008). Other enzymes involved in P mineralization are NSAPs (non-specific acid phosphatases) which remove the phosphate group from phosphoester bonds of organic compounds. Various non-specific acid phosphatase (NSAPs) enzymes released by P-solubilizing microorganisms belonging to the family of phosphormonoesterases. The acid phosphatase enzymes play an important role in solubilization, though alkaline phosphatases are also present. Various solubilization and mineralization processes that involve different enzymes play an important role in recycling of phosphorus.

13.7.3 Stress Management

Cold-tolerant microbes permanently sustain low temperature in cryo-environments such as deep sea, mountains, and polar regions. These organisms are also known as psychrotolerant, psychrotroph, or psychrophiles as they grow better at very low temperatures (Morita 1975). Psychrophiles can overcome two main challenges because of their unique properties: First challenge is the survival of psychrophiles at very low temperatures because if there is decrease in temperature, the biochemical reactions are affected exponentially. Second, the viscous aqueous environments are considerably increased as temperature is decreased. Their growth rate is maximum between temperatures of 2 and 12 °C (Xu et al. 2003).

The membrane functions are also affected, which leads to decreased membrane fluidity and the loss of membrane functions. The physical properties of membranes are affected by fatty acid composition, and it changes with the environment of the microbes. In general, reduced temperature produces a higher content of branched fatty acids both saturated and unsaturated (Pandey et al. 2004). Another adaptation of psychrophiles is an increased content of big and more compact head groups of lipids, proteins, and carotenes (Deming 2002). In some psychrophiles, there is less non-polar carotenoid pigment synthesis (Chintalapati et al. 2004).

Microbial activity at temperatures around −20 °C occurs in normal water inside the ice. These contain increased concentrations of sodium chloride (NaCl) or other particulate matters which maintain the fluid flow. Different factors such as hydrostatic and osmotic pressure, solar radiations, availability of nutrients and stress also strongly affect the growth of psychrophilic microbes. Various specialized proteins are expressed in microbes when they are subjected to sudden change in temperatures. These proteins are involved in cellular processes like protein folding and the control of membrane fluidity (Russell 2000). In psychrophiles, Caps are expressed at low temperatures though they are similar to the Caps present in mesophiles. This shows that a sensory system that senses temperature is present in psychrophiles, and these thermosensors sense membrane fluidity as well (Arthur and Watson 1976).

Anti-freeze proteins (AFPs) or ice-restricting proteins have been recognized in microorganisms living in Antarctic lake (Gilbert et al. 2005) that can tie to ice precious stones in an expansive surface and brings down the temperature at which a life form can openly develop (Jia and Davies 2002). AFP from certain organisms is Ca^{2+}-reliant and hyperactive ice surfaces and control ice precious. AFPs bind to stone development and recrystallization by bringing down the point of solidification (warm hysteresis) (Krembs et al. 2002).

Other molecules that have an important role in protecting psychrophiles against cold conditions are disaccharide trehalose and exopolysaccharides. Trehalose binds the molecules together and helps in the prevention of protein denaturation and protein aggregation (Nichols et al. 2005). The trehalose disaccharide also rummage-free radicals and stabilize cellular membranes under cold climatic conditions. Increased concentrations of exopolysaccharides have been found in bacteria of sea of Antarctica water (Muryoi et al. 2004) and in sea ice of Arctic water (Nichols et al. 2005). These change the physiological environment of bacterial cells, participate in adhering of cells to surfaces and retain water, increase the nutrient concentration, retain and save extracellular enzymes against cold denaturation, and most importantly, it acts as cyoprotectant (Tosco et al. 2003). EPS have elevated amounts of polyhydroxyl which brings down the point of solidification of water. EPS can likewise trap water, supplements and metal particles and encourage surface grip, cell collection and biofilm arrangement and may likewise assume a job in securing extracellular catalysts against cold denaturation and autolysis. EPS have high levels of polyhydroxyl which lowers the freezing point of water (Campanaro et al. 2011). EPS influenced the species colonization and survival of the present organisms in the natural surroundings near the oceans ice by lowering the rate of development of ice because of higher saltiness (Mykytczuk et al. 2011).

The combination of cytoplasmic ice crystals is incited by cell solidifying. The accumulation of substances like sucrose, glycine, betaine and mannitol results in the bringing down of the point of solidification of cytoplasm consequently giving assurance against solidifying.

Ongoing transcriptome investigations have demonstrated that introduction to cold temperatures initiates a fast up-guideline of qualities engaged with layer biogenesis, for example, unsaturated fat and LPS biosynthesis, peptidoglycan biosynthesis, glycosyltransferases and outer membrane proteins (Deming 2002). Similar genomic studies have additionally uncovered that genes engaged with the synthesis of cell membrane are overexpressed in the genomes of psychrophilic microorganisms. General membrane transport proteins are elevated as seen by transcriptomic contemplates, against the lower dispersion rates over the cell layers experienced at colder temperature (Qiu et al. 2006). Specifically, the dimensions of peptide transporters are expanded which encourages cold and hyperosmotic stress which improves the take-up of supplements (Reva et al. 2006).

Another class of layer smoothness modulators are carotenoid pigments. Both polar and non-polar carotenoid pigments are delivered by different Antarctic microorganisms and have been proposed to keep up layer smoothness and aid in keeping up equalization amid changes in temperatures (Fig. 13.1). Wax esters

additionally assume a significant job in cool balanced film ease. In *Psychrobacter urativorans*, they may represent up to 14% of the cell lipid content, and in *P. arcticus*, the wax ester synthase is constitutively communicated, paying little heed to the development temperature (Sung et al. 2011).

13.8 Industrially Important Cold Enzymes

Psychrophilic microorganisms produce enzymes that can sustain low temperature and other stresses of cold climatic conditions. These enzymes are used in paper, pulp, pharmaceutical and food industries (Whitman 1998). Psychrozymes or cold-adapted enzymes can sustain temperatures between 10 and 5 °C. There is an increasing demand of psychrozymes in industries because of their withstanding nature in adverse conditions. Nowadays more attention is paid on the use of proteins isolated from cold-loving microorganisms as they act at their optimum temperature enhancing the recovery of the products of enzymatic reaction (D'Amico et al. 2006).

The psychrozymes have the ability to degrade a wide range of polymeric substances and the substance that can produce enzymes like amylases, cellulases, pectinases, β-galactosidase, oxidases, protease and lipase. A huge amount of money is invested in psychrozymes worldwide due to their extreme potential. The industrially important psychrozymes are used in the fields of food industry (such as pectinase, β-galactosidase), bio-polishing of textile products and detergent formulation industries. Moreover, these psychrozymes are also used in bioremediation (such as oxidases), for biotransformations (methylases and aminotransferases) (Okuyama et al. 1999) and in biomedical applications. Psychrozymes are used in:

1. Industrial processes including food technology
2. Bioremediation and other pollution control technologies
3. Medical and other pharmaceutical uses

Psychrozymes have many benefits such as high specific activities at low temperature, they can offer many other advantages like saving energy, saving volatile compounds, contamination prevention and easy inactivation of enzymes. Most of the food industries treat the products with psychrozymes for maintaining the quality of food during their transportation and storage. Psychrozymes are also frequently utilized in detergent and textile industries. Similarly pectinases and cellulases are used in the clarification of fruit juices; proteases helps in the removal of fish skin.

Apart from food industry, psychrozymes are used for the low-temperature biodegradation, and they are best alternatives to physicochemical methods for the bioremediation of solids and waste waters polluted by hydrocarbons, oils and lipids (Violot et al. 2005). Biodegradation with psychrozymes have several advantages over other existing traditional methods. It has been observed that the treatment of contaminated soil with psychrozymes is much more cost-effective than traditional methods such as incineration, storage or concentration. In 1997, Brun et al. studied the recombinant Antarctic *Pseudoalteromonas haloplanktis* which secretes toluene-0-xylene monooxygenase (T0MO). This enzyme efficiently converts several

aromatic compounds into their corresponding catechols in a broad range of temperature. It has been suggested that the genetically engineered Antarctic bacterium is used in the bioremediation of contaminated marine environments. The interest on psychrozymes have increased greatly because of their high activity at low temperatures which offers potential economic benefits (Margesin and Schinner 1994). For example, the "peeling" of leather by cold adapt protease can be done with normal water instead of at 37 °C. An important achievement in the field of cold-adapted enzymes has been the construction of a host-vector system that allows the overexpression of genes in psychrophilic bacteria even at low temperatures which prevents the formation of inclusion bodies and protects heat-sensitive gene products. A single PUFA is produced using psychrozymes, rather than the complex mixture which is yielded from fish or algal oils.

13.9 Conclusion

Microbes play a vital role in sustainable environment and affect both flora and fauna of any ecosystem. Cold environment has its own challenges which can be countered by using the strategies used by nature. Exploring the adaptations used by psychrophiles help us to mimic them in our day to day life. Many low-temperature microbes have a great role to play in all low temperature-based industries.

References

Aguilar PS, Hernandez-Arriaga AM, Cybulski LE, Erazo AC, de Mendoza D (2001) Molecular basis of thermosensing: a two component signal transduction thermometer in Bacillus subtilis. EMBO J 20(7):1681–1691

Albanesi D, Mansilla MC, de Mendoza D (2004) The membrane fluidity sensor DesK of Bacillus subtilis controls the signal decay of its cognate response regulator. J Bacteriol 186 (9):2655–2663

Allen MA, Lauro FM, Williams TJ, Burg D, Siddiqui KS, De Francisci D, Chong KW, Pilak O, Chew HH, De Maere MZ, Ting L (2009) The genome sequence of the psychrophilic archaeon, Methanococcoides burtonii: the role of genome evolution in cold adaptation. ISME J 3(9):1012

Angelidis AS, Smith GM (2003) Role of the glycine betaine and carnitine transporters in adaptation of Listeria monocytogenes to chill stress in defined medium. Appl Environ Microbiol 69 (12):7492–7498

Anuradha K, Padma PN, Venkateshwar S, Reddy G (2010) Fungal isolates from natural pectic substrates for polygalacturonase and multienzyme production. Indian J Microbiol 50 (3):339–344

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, Van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bahr F, Bates NR (2012) Massive phytoplankton blooms under Arctic sea ice. Science 336(6087):1408

Arthur HE, Watson KE (1976) Thermal adaptation in yeast: growth temperatures, membrane lipid, and cytochrome composition of psychrophilic, mesophilic, and thermophilic yeasts. J Bacteriol 128(1):56–68

Babalola OO, Glick BR (2012) Indigenous African agriculture and plant associated microbes: current practice and future transgenic prospects. Sci Res Essays 7(28):2431–2439

Barria C, Malecki M, Arraiano CM (2013) Bacterial adaptation to cold. Microbiology 159 (12):2437–2443

Birgisson H, Delgado O, Arroyo LG, Hatti-Kaul R, Mattiasson B (2003) Cold-adapted yeasts as producers of cold-active polygalacturonases. Extremophiles 7(3):185–193

Bouvet V, Ben RN (2003) Antifreeze glycoproteins. Cell Biochem Biophys 39(2):133–144

Brun E, Moriaud F, Gans P, Blackledge MJ, Barras F, Marion D (1997) Solution structure of the cellulose-binding domain of the endoglucanase Z secreted by Erwinia chrysanthemi. Biochemistry 36(51):16074–16086

Campanaro S, Williams TJ, Burg DW, De Francisci D, Treu L, Lauro FM, Cavicchioli R (2011) Temperature-dependent global gene expression in the Antarctic archaeon Methanococcoides burtonii. Environ Microbiol 13(8):2018–2038

Cao-Hoang L, Dumont F, Marechal PA, Le-Thanh M, Gervais P (2008) Rates of chilling to 0 C: implications for the survival of microorganisms and relationship with membrane fluidity modifications. Appl Microbiol Biotechnol 77(6):1379–1387

Cao-Hoang L, Dumont F, Marechal PA, Gervais P (2010) Inactivation of Escherichia coli and Lactobacillus plantarum in relation to membrane permeabilization due to rapid chilling followed by cold storage. Arch Microbiol 192(4):299–305

Carpousis AJ (2002) The Escherichia coli RNA degradosome: structure, function and relationship to other ribonucleolytic multienyzme complexes. Biochem Soc Trans 30(2):150–155

Carpousis AJ, Luisi BF, McDowall KJ (2009) Endonucleolytic initiation of mRNA decay in Escherichia coli. Prog Mol Biol Transl Sci 85:91–135

Casanueva A, Tuffin M, Cary C, Cowan DA (2010) Molecular adaptations to psychrophily: the impact of 'omic' technologies. Trends Microbiol 18(8):374–381

Chahiniana H, Sarda L (2009) Distinction between esterases and lipases: comparative biochemical properties of sequence-related carboxylesterases. Protein Pept Lett 16(10):1149–1161

Chaikam V, Karlson DT (2010) Comparison of structure, function and regulation of plant cold shock domain proteins to bacterial and animal cold shock domain proteins. BMB Rep 43(1):1–8

Chandran V, Luisi BF (2006) Recognition of enolase in the Escherichia coli RNA degradosome. J Mol Biol 358(1):8–15

Chandran V, Poljak L, Vanzo NF, Leroy A, Miguel RN, Fernandez-Recio J, Parkinson J, Burns C, Carpousis AJ, Luisi BF (2007) Recognition and cooperation between the ATP-dependent RNA helicase RhlB and ribonuclease RNase E. J Mol Biol 367(1):113–132

Chattopadhyay MK (2002) The cryoprotective effects of glycine betaine on bacteria. Trends Microbiol 10(7):311

Chen YP, Rekha PD, Arun AB, Shen FT, Lai WA, Young CC (2006) Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. Appl Soil Ecol 34(1):33–41

Cheng J, Hanada Y, Miura A, Tsuda S, Kondo H (2016) Hydrophobic ice-binding sites confer hyperactivity of an antifreeze protein from a snow mold fungus. Biochem J 473(21):4011–4026

Chintalapati S, Kiran MD, Shivaji S (2004) Role of membrane lipid fatty acids in cold adaptation. Cell Mol Biol (Noisy-le-Grand) 50(5):631–642

Cho KH (2017) The structure and function of the gram-positive bacterial RNA degradosome. Front Microbiol 8:154

Collins T, Roulling F, Piette F, Marx JC, Feller G, Gerday C, D'Amico S (2008) Fundamentals of cold-adapted enzymes. In: Margesin R, Schinner F, Gerday C, Marx JC (eds) Psychrophiles: from biodiversity to biotechnology. Springer, Berlin, pp 211–227

Czapski TR, Trun N (2014) Expression of csp genes in E. coli K-12 in defined rich and defined minimal media during normal growth, and after cold-shock. Gene 547(1):91–97

D'Amico S, Marx JC, Gerday C, Feller G (2003) Activity-stability relationships in extremophilic enzymes. J Biol Chem 278(10):7891–7896

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

De Maayer P, Anderson D, Cary C, Cowan DA (2014) Some like it cold: understanding the survival strategies of psychrophiles. EMBO Rep 15(5):508–517

Deming JW (2002) Psychrophiles and polar regions. Curr Opin Microbiol 5(3):301–309

Díez B, Bergman B, Pedrós-Alió C, Antó M, Snoeijs P (2012) High cyanobacterial nifH gene diversity in Arctic seawater and sea ice brine. Environ Microbiol Rep 4(3):360–366

Ermolenko DN, Makhatadze GI (2002) Bacterial cold-shock proteins. Cell Mol Life Sci 59 (11):1902–1913

Feng Y, Huang H, Liao J, Cohen SN (2001) Escherichia coli poly (A)-binding proteins that interact with components of degradosomes or impede RNA decay mediated by polynucleotide phosphorylase and RNase E. J Biol Chem 276(34):31651–31656

Feng S, Powell SM, Wilson R, Bowman JP (2014) Extensive gene acquisition in the extremely psychrophilic bacterial species Psychroflexus torquis and the link to sea-ice ecosystem specialism. Genome Biol Evol 6(1):133–148

Fondi M, Bosi E, Giudice AL, Fani R (2016) A systems biology view on bacterial response to temperature shift. In: Biotechnology of extremophiles. Springer, Cham, pp 597–618

Gilbert JA, Davies PL, Laybourn-Parry J (2005) A hyperactive, Ca2+−dependent antifreeze protein in an Antarctic bacterium. FEMS Microbiol Lett 245(1):67–72

Giordano D, Pesce A, Boechi L, Bustamante JP, Caldelli E, Howes BD, Riccio A, Prisco G, Nardini M, Estrin D, Smulevich G (2015) Structural flexibility of the heme cavity in the cold-adapted truncated hemoglobin from the Antarctic marine bacterium Pseudoalteromonas haloplanktis TAC125. FEBS J 282(15):2948–2965

Goldstein J, Pollitt NS, Inouye M (1990) Major cold shock protein of Escherichia coli. Proc Natl Acad Sci 87(1):283–287

Hardwick SW, Chan VS, Broadhurst RW, Luisi BF (2010) An RNA degradosome assembly in Caulobacter crescentus. Nucleic Acids Res 39(4):1449–1459

Hirano SS, Baker LS, Upper CD (1985) Ice nucleation temperature of individual leaves in relation to population sizes of ice nucleation active bacteria and frost injury. Plant Physiol 77 (2):259–265

Hoshino T, Xiao N, Tkachenko OB (2009) Cold adaptation in the phytopathogenic fungi causing snow molds. Mycoscience 50(1):26–38

Jagtap P, Ray MK (1999) Studies on the cytoplasmic protein tyrosine kinase activity of the Antarctic psychrotrophic bacterium Pseudomonas syringae. FEMS Microbiol Lett 173 (2):379–388

Jia Z, Davies PL (2002) Antifreeze proteins: an unusual receptor–ligand interaction. Trends Biochem Sci 27(2):101–106

Jorquera MA, Crowley DE, Marschner P, Greiner R, Fernández MT, Romero D, Menezes-Blackburn D, De La Luz Mora M (2011) Identification of β-propeller phytase-encoding genes in culturable Paenibacillus and Bacillus spp. from the rhizosphere of pasture plants on volcanic soils. FEMS Microbiol Ecol 75(1):163–172

Jung YH, Yi JY, Jung HJ, Lee YK, Lee HK, Naicker MC, Uh JH, Jo IS, Jung EJ, Im H (2010) Overexpression of cold shock protein A of Psychromonasarctica KOPRI 22215 confers cold-resistance. Protein J 29(2):136–142

Kanehisa M, Furumichi M, Tanabe M, Sato Y, Morishima K (2016) KEGG: new perspectives on genomes, pathways, diseases and drugs. Nucleic Acids Res 45(D1):D353–D361

Kawahara H, Omori N, Obata H (2008) Cryoprotective activity of mannoprotein from the cell membrane of Pichiaanomala. CryoLetters 29(5):437–445

Khemici V, Poljak L, Luisi BF, Carpousis AJ (2008) The RNase E of Escherichia coli is a membrane-binding protein. Mol Microbiol 70(4):799–813

Kim HK, Orser C, Lindow SE, Sands DC (1987) Xanthomonas campestris pv. translucens strains active in ice nucleation. Plant Dis 71(11):994–997

Kozloff LM, Schofield MA, Lute M (1983) Ice nucleating activity of Pseudomonas syringae and Erwinia herbicola. J Bacteriol 153(1):222–231

Krembs C, Eicken H, Junge K, Deming JW (2002) High concentrations of exopolymeric substances in Arctic winter sea ice: implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep-Sea Res I Oceanogr Res Pap 49(12):2163–2181

Kuddus M, Roohi AJ, Ramteke PW (2011) An overview of cold-active microbial α-amylase: adaptation strategies and biotechnological potentials. Biotechnology 10(3):246–258

Lécrivain AL, Le Rhun A, Renault TT, Ahmed-Begrich R, Hahnke K, Charpentier E (2018) In vivo 3′-to-5′ exoribonuclease targetomes of Streptococcus pyogenes. Proc Natl Acad Sci 115 (46):11814–11819

Lee J, Jeong KW, Jin B, Ryu KS, Kim EH, Ahn JH, Kim Y (2013) Structural and dynamic features of cold-shock proteins of Listeria monocytogenes, a psychrophilic bacterium. Biochemistry 52 (14):2492–2504

Lindow SE (1983) The role of bacterial ice nucleation in frost injury to plants. Annu Rev Phytopathol 21(1):363–384

Margesin R, Schinner F (1994) Properties of cold-adapted microorganisms and their potential role in biotechnology. J Biotechnol 33(1):1–4

Math RK, Jin HM, Kim JM, Hahn Y, Park W, Madsen EL, Jeon CO (2012) Comparative genomics reveals adaptation by Alteromonas sp. SN2 to marine tidal-flat conditions: cold tolerance and aromatic hydrocarbon metabolism. PLoS One 7(4):e35784

Merín MG, Mendoza LM, Farías ME, De Ambrosini VI (2011) Isolation and selection of yeasts from wine grape ecosystem secreting cold-active pectinolytic activity. Int J Food Microbiol 147 (2):144–148

Moisander PH, Beinart RA, Hewson I, White AE, Johnson KS, Carlson CA, Montoya JP, Zehr JP (2010) Unicellular cyanobacterial distributions broaden the oceanic N2 fixation domain. Science 327(5972):1512–1514

Morita RY (1975) Psychrophilic bacteria. Bacteriol Rev 39(2):144

Muryoi N, Sato M, Kaneko S, Kawahara H, Obata H, Yaish MW, Griffith M, Glick BR (2004) Cloning and expression of afpA, a gene encoding an antifreeze protein from the arctic plant growth-promoting rhizobacterium Pseudomonas putida GR12-2. J Bacteriol 186 (17):5661–5671

Mykytczuk NC, Trevors JT, Foote SJ, Leduc LG, Ferroni GD, Twine SM (2011) Proteomic insights into cold adaptation of psychrotrophic and mesophilic Acidithiobacillus ferrooxidans strains. Antonie Van Leeuwenhoek 100(2):259–277

Neuhaus K, Francis KP, Rapposch S, Görg A, Scherer S (1999) Pathogenic Yersinia species carry a novel, cold-inducible major cold shock protein tandem gene duplication producing both bicistronic and monocistronic mRNA. J Bacteriol 181(20):6449–6455

Neves MJ, Jorge JA, François JM, Terenzi HF (1991) Effects of heat shock on the level of trehalose and glycogen, and on the induction of thermotolerance in Neurosporacrassa. FEBS Lett 283 (1):19–22

Nichols CM, Lardière SG, Bowman JP, Nichols PD, Gibson JA, Guézennec J (2005) Chemical characterization of exopolysaccharides from Antarctic marine bacteria. Microb Ecol 49 (4):578–589

Nutaratat P, Srisuk N, Arunrattiyakorn P, Limtong S (2014) Plant growth-promoting traits of epiphytic and endophytic yeasts isolated from rice and sugar cane leaves in Thailand. Fungal Biol 118(8):683–694

Obata H, Saeki Y, Tanishita J, Tokuyama T, Hori H, Higashi Y (1987) Identification of an ice-nucleating bacterium KUIN-1 as Pseudomonas fluorescens and its ice nucleation properties. Agric Biol Chem 51(7):1761–1766

Okuyama H, Morita N, Yumoto I (1999) Cold-adapted microorganisms for use in food biotechnology. In: Biotechnological applications of cold-adapted organisms. Springer, Berlin, pp 101–115

Pandey KD, Shukla SP, Shukla PN, Giri DD, Singh JS, Singh P, Kashyap AK (2004) Cyanobacteria in Antarctica: ecology, physiology and cold adaptation. Cell Mol Biol 50 (5):575–584

Phadtare S (2004) Recent developments in bacterial cold-shock response. Curr Issues Mol Biol 6 (2):125–136

Popova EE, Yool A, Coward AC, Dupont F, Deal C, Elliott S, Hunke E, Jin M, Steele M, Zhang J (2012) What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry. J Geophys Res Oceans 117(C8): C00D12

Prud'homme-Généreux A, Beran RK, Iost I, Ramey CS, Mackie GA, Simons RW (2004) Physical and functional interactions among RNase E, polynucleotide phosphorylase and the cold-shock protein, CsdA: evidence for a 'cold shock degradosome'. Mol Microbiol 54(5):1409–1421

Purusharth RI, Klein F, Sulthana S, Jäger S, Jagannadham MV, Evguenieva-Hackenberg E, Ray MK, Klug G (2005) Exoribonuclease R interacts with endoribonuclease E and an RNA helicase in the psychrotrophic bacterium Pseudomonas syringae Lz4W. J Biol Chem 280 (15):14572–14578

Qin G, Zhu L, Chen X, Wang PG, Zhang Y (2007) Structural characterization and ecological roles of a novel exopolysaccharide from the deep-sea psychrotolerant bacterium Pseudoalteromonas sp. SM9913. Microbiology 153(5):1566–1572

Qiu Y, Kathariou S, Lubman DM (2006) Proteomic analysis of cold adaptation in a Siberian permafrost bacterium–Exiguobacterium sibiricum 255–15 by two-dimensional liquid separation coupled with mass spectrometry. Proteomics 6(19):5221–5233

Reva ON, Weinel C, Weinel M, Böhm K, Stjepandic D, Hoheisel JD, Tümmler B (2006) Functional genomics of stress response in Pseudomonas putida KT2440. J Bacteriol 188(11):4079–4092

Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability update on microbial phosphorus. Plant Physiol 156(3):989–996

Robinson CH (2001) Cold adaptation in Arctic and Antarctic fungi. New Phytol 151(2):341–353

Rodriduez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol Adv 17:319–339

Rodrigues DF, Tiedje JM (2008) Coping with our cold planet. Appl Environ Microbiol 74 (6):1677–1686

Russell NJ (2000) Toward a molecular understanding of cold activity of enzymes from psychrophiles. Extremophiles 4(2):83–90

Sahay H, Yadav AN, Singh AK, Singh S, Kaushik R, Saxena AK (2017) Hot springs of Indian Himalayas: potential sources of microbial diversity and thermostable hydrolytic enzymes. 3 Biotech 7(2):118

Sahu B, Ray MK (2008) Auxotrophy in natural isolate: minimal requirements for growth of the Antarctic psychrotrophic bacterium Pseudomonas syringae Lz4W. J Basic Microbiol 48 (1):38–47

Sano F, Asakawa N, Inoue Y, Sakurai M (1999) A dual role for intracellular trehalose in the resistance of yeast cells to water stress. Cryobiology 39(1):80–87

Schärer K, Stephan R, Tasara T (2013) Cold shock proteins contribute to the regulation of listeriolysin O production in Listeria monocytogenes. Foodborne Pathog Dis 10(12):1023–1029

Selvakumar G, Kundu S, Joshi P, Nazim S, Gupta AD, Mishra PK, Gupta HS (2008) Characterization of a cold-tolerant plant growth-promoting bacterium Pantoeadispersa 1A isolated from a sub-alpine soil in the North Western Indian Himalayas. World J Microbiol Biotechnol 24 (7):955–960

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA (2013) Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. Springerplus 2(1):587

Siddiqui KS, Cavicchioli R (2006) Cold-adapted enzymes. Annu Rev Biochem 75:403–433

Siddiqui KS, Feller G, D'Amico S, Gerday C, Giaquinto L, Cavicchioli R (2005) The active site is the least stable structure in the unfolding pathway of a multidomain cold-adapted α-amylase. J Bacteriol 187(17):6197–6205

Sohm JA, Webb EA, Capone DG (2011) Emerging patterns of marine nitrogen fixation. Nat Rev Microbiol 9(7):499

Song W, Lin X, Huang X (2012) Characterization and expression analysis of three cold shock protein (CSP) genes under different stress conditions in the Antarctic bacterium Psychrobacter sp. G. Polar Biol 35(10):1515–1524

Srinivasan R, Yandigeri MS, Kashyap S, Alagawadi AR (2012) Effect of salt on survival and P-solubilization potential of phosphate solubilizing microorganisms from salt affected soils. Saudi J Biol Sci 19(4):427–434

Suman A, Yadav AN, Verma P (2016) Endophytic microbes in crops: diversity and beneficial impact for sustainable agriculture. In: Microbial inoculants in sustainable agricultural productivity. Springer, New Delhi, pp 117–143

Sung MS, Im HN, Lee KH (2011) Molecular cloning and chaperone activity of DnaK from cold-adapted bacteria, KOPRI22215. Bull Kor Chem Soc 32(6):1925–1930

Tereshina VM, Mikhailova MV, Feofilova EP (1991) Physio-logical role of trehalose and an antioxidant in Cun-ninghamelia japonica during high temperature stress. Microbiology 60:533–540

Tomoyuki N, Kaichiro Y, Tatsuro M, Noboru T (2002) Cold-active pectinolytic activity of psychrophilic-basidiomycetous yeast Cystofilobasidium capitatum strain PPY-1. J Biosci Bioeng 94(2):175–177

Tosco A, Birolo L, Madonna S, Lolli G, Sannia G, Marino G (2003) GroEL from the psychrophilic bacterium Pseudoalteromonas haloplanktis TAC 125: molecular characterization and gene cloning. Extremophiles 7(1):17–28

Vassilev N, Vassileva M, Nikolaeva I (2006) Simultaneous P-solubilizing and biocontrol activity of microorganisms: potentials and future trends. Appl Microbiol Biotechnol 71(2):137–144

Verma P, Yadav AN, Kazy SK et al (2013) Elucidating the diversity and plant growth promoting attributes of wheat (Triticumaestivum) associated acidotolerant bacteria from southern hills zone of India. Natl J Life Sci 10(2):219–227

Verma P, Yadav AN, Kazy SK et al (2014) Evaluating the diversity and phylogeny of plant growth promoting bacteria associated with wheat (Triticumaestivum) growing in central zone of India. Int J Curr Microbiol Appl Sci 3(5):432–447

Verma P, Yadav AN, Khannam KS, Kumar S, Saxena AK, Suman A (2016) Molecular diversity and multifarious plant growth promoting attributes of bacilli associated with wheat (Triticumaestivum L.) rhizosphere from six diverse agro-ecological zones of India. J Basic Microbiol 56(1):44–58

Violot S, Aghajari N, Czjzek M, Feller G, Sonan GK, Gouet P, Gerday C, Haser R, Receveur-Brechot V (2005) Structure of a full length psychrophilic cellulase from Pseudoalteromonas haloplanktis revealed by X-ray diffraction and small angle X-ray scattering. J Mol Biol 348 (5):1211–1224

Wang G, Wang Q, Lin X, Ng TB, Yan R, Lin J, Ye X (2016) A novel cold-adapted and highly salt-tolerant esterase from Alkalibacterium sp. SL3 from the sediment of a soda lake. Sci Rep 6:19494

Wani PA, Zaidi A, Khan AA, Khan MS (2005) Effect of phorate on phosphate solubilization and indole acetic acid releasing potentials of rhizospheric microorganisms. Ann Plant Protect Sci 13 (1):139–144

Weinstein RN, Montiel PO, Johnstone K (2000) Influence of growth temperature on lipid and soluble carbohydrate synthesis by fungi isolated from fellfield soil in the maritime Antarctic. Mycologia 92:222–229

Whitman WB (1998) The unseen majority. Proc Natl Acad Sci U S A 74:5088–5090

Xu Y, Nogi Y, Kato C, Liang Z, Rüger HJ, De Kegel D, Glansdorff N (2003) Moritella profunda sp. nov. and Moritella abyssi sp. nov., two psychropiezophilic organisms isolated from deep Atlantic sediments. Int J Syst Evol Microbiol 53(2):533–538

Yamashita Y, Nakamura N, Omiya K, Nishikawa J, Kawahara H, Obata H (2002) Identification of an antifreeze lipoprotein from Moraxella sp. of Antarctic origin. Biosci Biotechnol Biochem 66 (2):239–247

Yi Y, Huang W, Ge Y (2008) Exopolysaccharide: a novel important factor in the microbial dissolution of tricalcium phosphate. World J Microbiol Biotechnol 24(7):1059–1065

Zaidi A, Khan MS, Ahemad M, Oves M, Wani PA (2009) Recent advances in plant growth promotion by phosphate-solubilizing microbes. In: Microbial strategies for crop improvement. Springer, Berlin, pp. 23–50

Zhu HJ, Sun LF, Zhang YF, Zhang XL, Qiao JJ (2012) Conversion of spent mushroom substrate to biofertilizer using a stress-tolerant phosphate-solubilizing Pichia farinose FL7. Bioresour Technol 111:410–416