An Overview of Survival Strategies of Psychrophiles and Their Applications

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Abstract

Psychrophiles are capable of surviving under extreme cold conditions, subzero temperatures. They have adapted various mechanisms like altered membrane fluidity, antifreeze proteins, cold shock proteins, chaperones, trehalose, exopolysaccharides, synthesis of carotenoid pigments, production of ice nucleating proteins, decreased flagellar motility, etc. Psychrophiles mainly find their application in environmental bioremediation, in preventing food spoilage, as cell factories for production of various enzymes, and also in degradation of oil spills in oceans. They have proved to be a boon for the agriculture due to their plant growth-promoting properties at low temperatures. Development of microbial consortium and genetic engineering may be fruitful in the coming future in plant biotechnology. This chapter describes the cold tolerance mechanisms in psychrophilic microorganisms and the application of such microbes in different industrial sectors and agriculture. We also included the gaps and overcome strategies in the agriculture application of cold-tolerant microorganisms.

Keywords

Extremophiles · Psychrophiles · Antifreeze proteins · Psychrophilic enzymes · Agriculture

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6.1 Introduction

In the last few decades, the pioneer conditions in which existence will thrive are regularly fluctuating with higher ranges of temperature, pH, pressure, radiation, salinity, energy, and restriction on supplements. Under such a wide range of parameters, not only can microorganisms thrive on earth, but they can also survive extreme space conditions (Horneck et al. 2010; Yamagishi et al. 2018). When taking extremophilic (instead of extremotolerant) organisms into account, it is imperative to remember that these living beings are exceptionally adjusted for extreme conditions establishing the standard under which the life form can metabolically and biochemically operate. In the course of the recent years, researchers have been captivated by the interesting life forms that occupy extraordinary conditions. All such organisms, regarded as extremophiles, live in such intolerably hazardous or even lethal environment in which other life forms cannot survive such as high acidic or alkaline pH, high and low pressure, high salt condition, and cold and hot springs (Rampelotto 2013).

The majority of extremophiles are microorganisms in which *Archaea* accounts a major portion. In *Archaea*, most of the organisms are hyperthermophilic, acidophilic, alkaliphilic, and halophilic microorganisms. The archaeal strain *Methanopyrus kandleri* 116 has been reported to show growth at 122 °C temperature, while the genus *Picrophilus* has potential to grow at 0.0 pH to 0.06. In *Eubacteria*, cyanobacteria are the prominent species adapted to different extreme environments. Cyanobacteria can survive to hypersaline, high-metal, and xerophilic conditions. On the other hand, fungi are also reported to survive in mining areas, high pH conditions, hot and cold deserts and metal-contaminated water. In eukaryotic invertebrates, *Tardigrade* is known as polyextremophiles for surviving under extreme temperatures ranging from −272 °C to 151 °C, 6000 atm pressure, and radiation environment (Rampelotto 2013).

6.2 Types of Extremophiles

6.2.1 Thermophiles

Some microbial life can survive at moderately high temperatures, between 45 °C and 80 °C, and are known as thermophiles. In fact, hyperthermophiles are especially outrageous thermophiles with ideal temperatures of over 80 °C (Madern et al. 2006). In numerous geothermally warmed districts on Earth, such microorganisms include volcanic deposits infiltrated by hot gases and deep-sea hydrothermal vents (Nakagawa and Takai 2006). Usually, such extreme regions are abundant in decreased synthetics from the inside of the Earth, and subsequently, numerous thermophilic microorganisms are chemoautotrophs (Amend et al. 2003). During chemoautotrophic nature, acidic condition is created in the surrounding environment due to production of acid and product. These reactions produce sulfuric acid as a result of removing energy by oxidizing sulfur compounds, thereby also rendering geothermal waters extremely acidic. Thus, many heat-loving microorganisms are additionally adjusted to highly acidic environments (Satyanarayana et al. 2005). For instance, *Picrophilus* spp. are reported to survive at pH 0.7 and at temperature of 60 °C (Schleper et al. 1995). In Japan, they were secluded from volcanically induced dry land. Hydrothermal deep ocean vent populations are located near subsurface volcanoes and at the border between seawater and magma, typically kilometers underneath the sea surface (Desbruyères et al. 2000). As no light is visible and the oxygen content is extremely limited, chemoautotrophic anaerobes are the large proportion of thermophilic isolates found in these areas.

For high temperatures, the subatomic explanation for changes to outrageous conditions has been more intensively researched than for any other parameter. Biomolecules, for example, catalysts, denature, lose their potential at high temperatures, and then subsequently halt metabolism at high temperatures. In addition, membrane's fluidity rises exponentially, disrupting the cell. A number of mobile diversifications are presented by thermophiles to protect them. The membrane lipids comprise greater straight and saturated fatty acids than mesophiles (Ulrih et al. 2009). By supplying the exact degree of fluidity needed for membrane operation, this allocates thermophiles to expand at elevated temperatures. Thermophilic proteins seem to be smaller and mainly greater in a few instances, which can also contribute to prolonged stability (Kumar and Nussinov 2001). An additional mechanism for protection of proteins is the action of chaperones, which facilitate the refolding of denatured proteins (Jaenicke 1996). In addition, monovalent and divalent salts upgrade the stability of nucleic acids (Hickey and Singer 2004). Another approach to stabilize out DNA is more compaction of genome into chromatin (Marguet and Forterre 1998).

6.2.2 Psychrophiles

Psychrophiles have an ideal growth temperature of 15 °C and an upper limit of 20 °C that expand at or below 0 °C (Rothschild 2007). Such microbes establish in an assortment of cold conditions, from the stratosphere to the deep ocean. A significant part of the deep sea is at a stable temperature of 2 °C, while liquid sea water can also be cooled to below 0 °C across the polar ice caps, when the usual salt content of ocean water (3.4%) takes the freezing edge down to −1.8 °C (Atkins and Locke 2004). At the point when the seawater freezes up, salt turns out to be progressively gathered in little compartments. Under these conditions, the edge of water freezing may be discouraged to −20 °C (Margesin et al. 2008). Table 6.1 represents the diversity of psychrophiles in different areas.

Psychrophiles such as *Psychrobacter cryopegellai* have shown regular digestion and metabolic activity at frozen temperature such as −10 °C (Rodrigues et al. 2009). For this cause, numerous psychrophiles are halophiles as well (microorganisms that develop in elevated salt concentrations). To endure and thrive at low temperatures, psychrophiles need to beat a few issues identified with perpetual cold conditions. Enzymes also become unbending at minimal temperatures, and solute

Table 6.1 List of psychrophiles present in different habitats

Soil	River	Lake water	Stream water
Acidobacteria sp., *Ascomycota* sp., *Zygomycota* sp., *Methylobacter* sp., *Methylosinus* sp., *Eurotium* sp., *Aspergillus* sp., *Deinococcus* sp., *Chytridiomycetes* sp., *Streptococcus* sp., *Crenarchaeota* sp., *Cryptococcus* sp., *Mrakia* sp., *Arthrobacter* sp., *Actinobacteria* sp.	*Actinobacteria* sp. *Firmicutes* sp. *Proteobacteria* sp. *Pseudomonas fluorescens Trematomus* sp.	*Actinobacteria* sp., *Hydrogenophilus thermoluteolus*, *Methanococcoides frigidum*, *Methanococcoides burtonii*	*Cyanobacteria* sp.

concentrations are at elevated, possibly destructive levels (Cavicchioli 2006). In addition, ice crystals can pierce the cell membranes until the water is frozen, compromising cellular integrity (D'Amico et al. 2006). Membranes of psychrophiles comprise of expanded degrees of unsaturated fatty acids that further growth with the reduction in temperature so that it will modulate membrane fluidity (Nichols et al. 2004). At low temperatures, psychrophiles generate cold-adapted catalysts that have highly explicit activities (Feller and Gerday 2003). These enzymes are able to maintain transcription and translation at low temperatures. The existence of some genes active at low temperatures has also been seen in studies (Goodchild et al. 2004). In addition, antifreeze proteins are also involved to resist such bacteria under cold environment by reducing formation of ice (Gilbert et al. 2004).

6.2.3 Acidophiles

Acidophiles are microorganisms that can grow at pH 2.0 optimally (Morozkina et al. 2010). Sulfur and its minerals are oxidized by acidophiles to gain energy that creates intense acidic conditions (Rohwerder and Sand 2007). In reality, the greater part of the firm acidophilic microorganisms characterized has been detached from volcanic regions or corrosive mine seepage. Some *Archaea* sp. like *Picrophilus oshimae* and *P. torridus* were isolated from volcanically heated soils of 60 °C (Schleper et al. 1995). The intracellular pH value of these microorganisms is held at 4.6, while the other acidophiles retain their pH at 6.0. In Iron Mountain, California, *Ferroplasma acidarmanus* was secluded from acid mine discharge and is capable of increasing at a pH of 0 (Dopson et al. 2004). The Tinto River is regarded as a fascinating model for acidic conditions due to its scale and convenient accessibility. Low-pH conditions can cause protein denaturation in a cell. Many organisms survive in such conditions by inducing more neutral amino acid production (Baker-Austin and Dopson 2007).

6.2.4 Alkaliphiles

Alkaliphiles are a group of microorganisms that can grow at pH above 9.0 (Horikoshi 1999) as shown by the hyperalkaline spring waters in lake and deserts and semi-arid environments, including the broad desert in the western United States and other regions of the world with elevated Ca^{2+} concentrations induced by silicate serpentinization (Grant 2003).

There can be a range of microorganisms living at a pH of 10.5 (Martins et al. 2001). In the soda lakes of Maqarin, Jordan, microbial populations exist at 12.9 pH (Pedersen et al. 2004). Alkaliphiles are often excluded from natural habitats, which often appear to contain elevated levels of NaCl, and are therefore referred to as haloalkalophiles (Gareeb and Setati 2009). In alkaline conditions, the convergences of hydrogen particles are extremely short, and cells experience difficulty utilizing ATP synthase to deliver energy and other fundamental particles (Krulwich et al. 1998). By continuously pumping in certain ions and exporting others to preserve their interior at near neutrality, base-loving microbes overcome these concerns. In addition, the alkalophile cell wall functions as a defense system from harsh environmental conditions (Horikoshi 2006).

6.2.5 Halophiles

Halophiles are microorganisms that thrive from around 10% sodium chloride to saturation at elevated salt concentrations, and a few of them can also flourish in salt crystals (Das Sarma 2002). Aquatic ecosystems with variable salinity, salt marshes, surface salt lakes, subterranean salt lakes, and several other areas are the habitats where halophilic microorganisms are located (Litchfield and Gillevet 2002). The Great Salt Lake in Utah and the Dead Sea in the Middle East are two of the largest and most examined recent hypersaline conditions. The hypersaline conditions are created in Antarctica regions, where high salt content can preserve water in liquid state under −20 °C temperature (Madern et al. 2006; Das Sarma 2006).

All these adapted microorganisms produce more number of solutes inside the cell to maintain osmotic balance. In their cells, halophilic *Archaea* retain extraordinarily high amounts of potassium chloride (Oren 2004). Under saturated salt conditions, all the halophiles follow the same machinery as thermophiles for survival (Michael et al. 1999). Therefore, in conjunction with thermophilic and mesophilic proteins, researchers explored the sequences of amino acids, arrangements, and functional properties of halophilic proteins to acquire intuition into the evolutionary techniques (Michael et al. 1999).

6.2.6 Piezophiles

The microorganisms which, under high hydrostatic pressure conditions, can protect themselves under elevated atmospheric pressure are referred to as piezophiles (Abe and Horikoshi 2001). Piezophiles are more prevalent in the depths of the ocean and Earth's crust. These microorganisms have been isolated at a depth of 10.5 km from the lowest portion of the ocean and have the potential to survive at pressures of up to 110 Mpa at 2 °C and 40 Mpa at temperatures above 100 °C (Yayanos 1995).

These microbes are accustomed to high temperatures and limited resources in subsurface environments embedded within the Earth's crust. Iron-reducing bacterial species were recovered from the Siijan (Sweden) granite at a depth of 6.7 km (Kotelnikova 2002). Complex microbial habitats have been confirmed in extreme conditions like in South African gold mines, inside freshly mined rocks about 3 km down the earth (Takai et al. 2001). Similarly, in the Columbia River basin, methanogenic microbes were obtained from several hundred meters (Washington State, USA) (Thomas-Keprta et al. 1997).

Some researchers have calculated that "deep biota" approaches the aggregate total of all surface living systems (Dartnell 2007). These subterranean fissures are suitable ecosystems in several aspects, since they have a stable atmosphere with steady chemical energy flow. These ecosystems often shield microbes from harmful radiations. The challenge in collecting samples from deep-sea environments and various complexities involved in performing biochemical experiments in the laboratory under high pressure conditions are the major reasons responsible for making it one of the least studied areas in the field of science. There are recent reports, though, in progress. Interactions between protein and protein are very susceptible to changes in strain, which may be the cause for the dissociation of enzymes and inhibition of gene expression (Sharma et al. 2002; Nakasone et al. 1998). Under extreme conditions, lipid membrane molecules stack closer, resulting in diminished fluidity of the membrane (Bartlett 2002). Increment in the level of unsaturated fatty acids in their membranes can also circumvent this issue (Aertsen et al. 2009). Table 6.2 represents categorized microbes for different extreme conditions with their ecological importance.

6.3 Survival Strategies Adapted by Psychrophiles

Around 10% of the area is surrounded by ice and glaciers that are not ideal for the reproduction of normal living beings in this vast planet consisting of living creatures. Prokaryotic life has occupied much of our planet's evolutionary history, expanding to fill nearly all available environmental niches, and it is a current reality that cold conditions are prevalent on earth. Psychrophilic microorganisms have effectively colonized all types of extreme situations. A portion of these life forms, contingent upon their ideal development temperature, are likewise known by the terms psychrotolerant or psychrotroph (Morita 1975). The potential of psychrophiles to flourish and propagate at low temperatures suggests that core challenges intrinsic to

Table 6.2 Types of microbes with their ecological importance

Types of microorganisms	Examples	Ecological importance
Thermophiles and hyperthermophiles	*Methanopyrus kandleri*, *Geobacillus stearothermophilus*, *Caldicellulosiruptor*, *Thermococcus*, *Sulfolobus*, *Thermotoga*, *P. furiosus*, *T. kodakarensis*	Thermophilic microorganisms have demonstrated many metabolic capacities and may have biotechnological use in anaerobic processes either as a source of thermostable enzymes or as an inoculum. In addition, by forming a syntrophy with hydrogenotrophic *Archaea*, they can accelerate protein degradation
Psychrophiles	Bacteria: *Arthrobacter* sp., *Psychrobacter* sp., *Chryseobacterium greenlandense*, *Halomonas*, *Pseudomonas* *Lichens*: *Umbilicaria antarctica*, *Xanthoria elegans*	In cold climates, psychrophiles play an essential part in bioremediating fat-contaminated waste water and eliminating harmful substances such as hydrocarbons, heavy metals, and fuel oils
Acidophiles	Archaea: *Sulfolobus solfataricus*, *Halobacteriaceae* *Bacteria*: *Acidobacteria*, *Alicyclobacilli*, *Acetobacter* *Eukarya*: *Urotricha*, *Dunaliella acidophila*, *Mucor racemosus*	Acid-stable enzymes have great applications in food and beverages industries
Alkaliphiles	*Natronomonas*, *Halorhodospira halochloris*, *Thiohalospira alkaliphila*	In industrial applications, alkaliphiles have had a great influence. Biological detergents produce alkaline enzymes that have been formed from alkaliphiles, such as alkaline cellulases and/or alkaline proteases. The commercial development of cyclodextrin by alkaline cyclomaltodextrin glucanotransferase is another significant use. This enzyme lowered the cost of processing and opened the way for vast amounts of cyclodextrin in foodstuffs, pesticides, and pharmaceuticals. Alkali-treated wood pulp has also been documented to be biologically bleached by xylanase produced by alkaliphiles
Halophiles	*Wallemia chthyophaga*, *Chromohalobacter beijerinckii*, *Tetragenococcus halophilus*	Halophiles have great potential in saline soil remediation
Piezophiles	*Shewanella*, *Colwellia*, *Photobacterium*, *Moritella*, *and Psychromonas*, *Pyrococcus yayanosii*, *Pyrococcus abyssi*	In the food industry; have great potential in industrial and biotechnological perspective. The high efficiency of the detergent has been demonstrated by piezophilic proteins

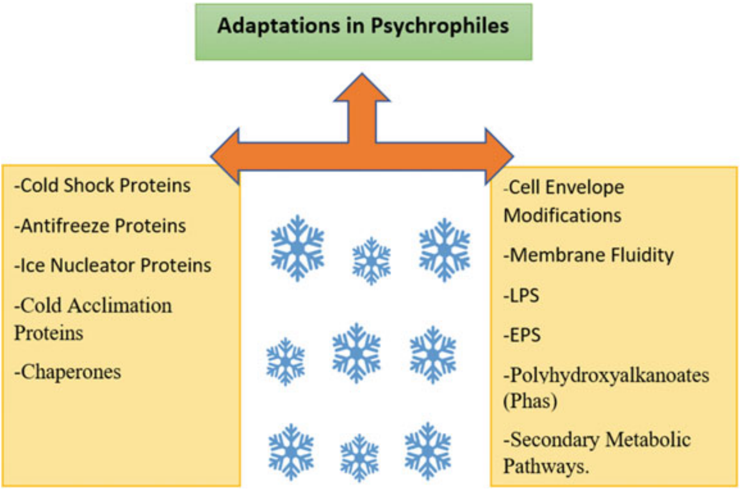

Fig. 6.1 Representation of different cellular and molecular adaptation strategies of psychrophiles under cold conditions

chronically cold conditions have been solved. These challenges include membrane fluidity, enzyme inactivation, ceasing of transcription and translation machinery, etc. Cold-adapted species such as *Moritella profunda* and many more have developed several changes at physical and genetic level within them to protect against low temperatures (Xu et al. 2003). In addition, most experiments have discussed the heat susceptibility of cold-adapted microorganisms, which is no longer the source of cold tolerance, although it is of concern. A lot of testing has been conducted in recent decades to assess the ability of psychrophiles. Psychrophiles can retain temperatures ranging from 10 °C to –20 °C, and the optimum temperature for most of them is 5 °C. However, in a permafrost bacterium, the low-temperature cutoff of psychrophiles was not addressed, and proliferation was accounted for at −12 °C and metabolic potential at −20 °C.

The strategies adapted by different organisms to survive under cold conditions result in different prospects regarding fundamental attributes of various biological processes like genetic sequence responsible for construction of macromolecules which are stable even in extreme conditions and biochemical limitations which may alter stability of macromolecules (Fig. 6.1). Such microorganisms adapted to extreme environments possess a broad range of metabolic diversity along with uncommon physiological potential to support their survival. Though the molecular, biochemical, or physiological strategies adapted by such microorganisms are not fully clarified, still, a detailed study of the involved pathways is of great importance for biotechnological sectors. Their adaptability and tolerance to such extreme conditions make them a better alternative for mesophilic enzymes which may have potential to remain active in extreme environmental conditions. Industrial biotechnology harbors wide application of such extraordinary microbes, as few enzymes may express polyextremophilicity (i.e., tolerance to more than one extreme condition) which are beneficial.

Psychrophiles inhabit many unique attributes like presence of unsaturated fatty acids in cell membranes, as unsaturated fatty acid has the capability to remain in liquid state under low temperatures and enable transport of solutes, antifreeze proteins, cold shock proteins, and cryoprotectants. Survival in low temperature is a combined result of various changes in fluidity of membrane, decreased levels RNA and protein synthesis, and alteration in structures of ribosomes, which ultimately modify the functioning of cellular machinery. Accumulation of glycine, betaine, sucrose, and mannitol for synthesis of antifreeze proteins which prevent ice crystals is also the type of technique used by psychrophiles to confirm their survival. Production of exopolysaccharides among psychrophiles is regarded as a mechanism against cryoprotection (Salwan and Sharma 2020).

Few compounds which possess properties of an osmoprotectant and cryoprotectant and also can act as source of carbon, nitrogen, and energy include sucrose, glycerol, glycine, sorbitol, and mannitol, as they reduce the freezing point of cytoplasm and prevent accumulation of macromolecules and increase stability of cell membrane. Collins and Deming (2013) conducted a study on *P. haloplanktis* and found that the uptake of compounds which confirm tolerance to low temperatures such as spermine, glutathione, and ornithine was enhanced due to thiolation of protein-S, which is regulated by glutathionyl spermidine, and glutathione seemed to show a possible cold adaptation mechanism (Mocali et al. 2017). Genes coding for proteins which are responsible for synthesis and breakdown of nitrogen reserves polymers and polyamides were found during genome analysis of *Colwellia psychrerythraea* (Nunn et al. 2015). In a study, *Mesorhizobium* sp. strain N33 was found to grow at 4 °C and accumulate a number of different cryoprotective compounds like sarcosine and threonine (Ghobakhlou et al. 2015).

Synthesis of polyhydroxyalkanoates (PHAs) is common in psychrophiles as it has an important physiological role. PHAs enable the survival and resistance of bacteria to various environmental stresses along with ability to produce and degrade fatty acids. Phasins are among the important PHAs that could help in stress protection and fitness enhancement (Mezzina and Pettinari 2016).

6.3.1 Cell Membrane Fluidity

Membrane fluidity is an important aspect of cellular functioning. Temperature at the either ends of biotic thermal range alters membrane fluidity. Cell membrane structure, composition, and response to varied temperature ranges differ among *Eubacteria* and *Archaea* (Deming 2002). In psychrophiles, membrane lipid composition is different from other organisms with increased ratio of polyunsaturated and saturated fatty acids that confers their survival in extreme climates (Guan et al. 2013).

Metabolic imbalance and growth cessation can be observed as a result of low temperature. Cell membranes and envelopes are considered as a vital link between the cell and its surrounding environment; thus, modification in its structure is an important aspect of cold adaptation. Commonly involved mechanisms at low temperatures to manage fluidity of membrane and avoid rigidness include alteration in lipid composition of cell membrane, preferring smaller chains, and lowering saturation of lipids (De Maayer et al. 2014). According to a study, widening of cell wall provides protection from cell damage caused due to formation of ice and osmotic pressure as observed in *E. sibiricum* at −2.5 °C. Growth of *Planococcus halocryophilus* Or1 in cold conditions was supported by synthesis of cell membrane, cell wall, and components of envelop along with uncommon cell envelop attributed by encrustations around the cell during subzero growth at −15 °C (Mykytczuk et al. 2013).

Many studies prove that few genes are responsible for maintenance of lipid membrane and cell wall synthesis at low temperatures as observed in *P. arcticus* (Bergholz et al. 2009). Cell wall, membrane related proteins and envelope synthesis was 289 enhanced gradually. In the Antarctic strains of *Pseudomonas syringae* and *P. extremaustralis rise*, high amount of hydroxy fatty acids was observed along with modification in fluidity and constitution of LPS (Benforte et al. 2018). Increasing hydrophobicity and amount of calcium carbonate, peptidoglycan, and choline along the cell membrane is closely related to cold adaptation. Copies of genes responsible for biosynthesis of carbonic anhydrase and peptidoglycan increased in low-temperature conditions indicating precipitation of calcium carbonate by microbes (Mykytczuk et al. 2016). *P. halocryophilus* at low temperature is known to possess increased fatty acid saturation as at low temperatures, fatty acid desaturases are in inactive state (Ronholm et al. 2015). Alteration in lipid composition was noted when the microbial cells were incubated at low temperatures. The level of unsaturated fatty acids increased in bacteria and yeasts with decrease in growth temperature which is beneficial for proper membrane functioning (Russell et al. 1995; Berry and Foegeding 1997). Decreases in temperature result in transformation of cellular fluid components to gel which inhibits the proper functioning of proteins causing leakage in microbial cell membrane. Exopolysaccharides, which constitute the polymers around the microbial cells, are a major aspect supporting tolerance to cold conditions (Tribelli and López 2018). However, change in constituents of membrane enables the membrane to maintain its fluidity, thus preventing gel formation and promoting survival of microbes at low temperatures. Carotenoid pigments have been recognized as fluidity modulators in various Antarctic bacteria.

6.3.2 Antifreeze Proteins (AFPs)

The antifreeze proteins have the ability to reduce the size and shape of ice crystals, which was first time observed in *Micrococcus cryophilus* and *Rhodococcus erythropolis* soil bacterium (Duman and Olsen 1993). The AFPs are present between the solid ice and liquid water and thus prevent the growth of ice crystals. At low concentrations of antifreeze proteins, ice recrystallization inhibition occurs.

Complementary structures present on ice crystals act as binding sites for antifreeze proteins and result in formation of thermal hysteresis thereby increasing the capacity of organism to survive in low temperature (Jia and Davies 2002).

Freeze avoidance and freeze tolerance are the major categories of antifreeze proteins. Freeze avoidance refers to avoiding low-temperature conditions generally by mobile organisms and mainly depends on high thermal hysteresis activity (D'Amico et al. 2006). Freeze tolerance involves minimization of damage caused to immobile organisms especially by ice recrystallization inhibition (Middleton et al. 2012). The antifreeze proteins studied in Antarctica Lake bacteria *Marinomonas primoryensis* were found to be Ca^{2+} dependent and hyperactive, while AFP showing antifreeze and ice nucleating activities was identified in Arctic plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2 (Muryoi et al. 2004; Gilbert et al. 2004). Ice structuring and shaping is also a type of adaptation in psychrophiles. According to Wilson et al. (2006), AFPs from *Pseudomonas putida* GR12-2 alter the morphology of ice in its supercooled state into either a hexagonal or hexagonal bipyramid.

6.3.3 Cold Shock Proteins

Cold shock proteins (CSPs) are involved in nucleic acid protection through binding with binding motifs RNP1 and RNP2. In bacteria, CSPs are activated during downshift of temperature to tolerate cold stress and are also present under general circumstances to manage other biological functions like enhancement of normal growth and stress adaptation responses. CSPs counteract the effects of cold shock by mimicking nucleic acid chaperons. Enzymes involved in transcription and translation like elongation factor, RNA polymerase, and peptidyl prolyl *cis-trans* isomerase are adapted to be optimally active at low temperatures. While cold shock proteins (CSPs) and RNA helicases are overexpressed at low temperatures (Lim et al. 2000). Thus, CSPs efficiently cope with deleterious effect of downshift in temperature by reestablishment of membrane fluidity by incorporation of unsaturated fatty acids into their membranes along with restoration of ribosome function and inducing proper protein folding. CSPs also help the cell handle various other conditions like osmosis, starvation, pH, and ethanol stress tolerance. Goldstein et al. (1990) first described CspA in *E. coli* and suggested that its homologous proteins are cold inducible and involved in chaperone role for RNA protection. In a study, CspA expression was found to be induced in *E. coli under repeated* freezing and thawing (Jung et al. 2010). The production of trehalose and other exopolysaccharides also has an important role in the survival of psychrophiles (Phadtare 2004). It was observed that, under extreme cold environments like the Antarctica, microbes produced more numbers of exopolysaccharide to protect cells and adhere on the surface and for water retention (Krembs et al. 2002; Nichols et al. 2005a, b).

6.4 Applications of Cold Adapted Microbes

6.4.1 Psychrophilic Enzymes in Different Industries

Psychrophiles are the cellular factories for production of various enzymes that remain active in the presence of detergents, oxidants, and alkaline environments, thus, expressing their potential in several industries. Various psychrophiles have proved themselves as better sources of cellulase which can be used in food industry, wastewater, and soil bioremediation and molecular biology. Psychrophilic cellulases having potential at lower washing temperatures and reduced water consumption are preferred. Cellulases, lipases, and proteases from psychrophiles also find application in environmental bioremediation, food industry, and molecular biology, and a lot is still unexploited (Souza et al. 2015). The cryophilic enzymes limit the undesirable reactions which may occur at higher temperatures and thus can be used for enzymatic reactions which require low temperatures like in the food industry to prevent spoilage and alter nutritional value and taste of heat-labile substrates. The cryophilic enzymes are economically beneficial due to low-energy requirements and higher catalytic efficiency at low temperatures. As they are functional at low temperatures, they can be used to precede a reaction along with preventing spoilage at temperatures where microbial contamination is less prevalent. Heat inactivation as an alternative to chemical inactivation is facilitated by psychrophilic enzymes, evidencing their role in vaccine and other large-scale industries.

Psychrophilic enzymes which are heat labile find their application in molecular biosciences where sequential reactions take place and each enzyme needs to be inactivated after each step. Thus, heat inactivation of enzymes may be attained by just a mild increase in temperature upholding the double-stranded DNA in stable state (Cavicchioli et al. 2011).

In the food industries, psychrophilic microorganisms and their metabolites have a wide variety of utilization. Coagulating enzymes have a great benefit in regulating case coagulation in order to preserve the consistency of whey from the cheese industry. For example, Marzyme®, Rennilase 50TL, and Moelilase are used in the market of developed countries (Divya and Naga 2015). Applications of β-galactosidase obtained from psychrophilic bacteria will produce 70–80% of product yields, which is far greater than the processes derived from mesophilic microorganisms utilizing enzymes. The commercial cold activated neutral protease is derived predominantly from *Bacillus subtilis* and is brought to market under the trade name Eutrase.

6.4.2 Use of Psychrophilic Microorganisms in Bioremediation

Psychrophilic microorganisms in the ecosystem have the potential to biodegrade different substances. They can be effective at low temperatures in bioremediation or multiple contaminants. Dodecane, hexadecane, naphthalene, and toluene were identified to be mineralized at cold temperatures by strains of bacteria (Watson et al. 1978). It has been manifested in laboratory and field studies, by means of particular bacterial cultures. A few of the decaying genes like naphthalene (ndoB) and toluene (xyIE, todC I) were also recorded in psychrotrophic bacteria. Likewise, *Rhodococcus* sp. strain Q15 has been found to degrade n-alkanes and diesel fuel at low temperature (Mahdieh et al. 2014).

6.4.3 Role of Psychrophiles in Medicine and Pharmaceuticals

In order to develop antifungal, anticancer, and antitumor agents, multiple strains of bacteria, *Streptomyces*, and fungi have been identified. A species of *Alteromona*s that synthesizes 2,3-indolinedione (isatin) has been identified. This formulation preserves the shrimp *Palaemon macrodactylus* from *Lagenidium callinectes*, which is a pathogenic fungus from *Moraxella* sp. and *Flavobacterium* sp. Antiviral and antitumor medicines can be manufactured. Polysaccharide, an antitumor, has been known as Narinactin. The *Bacillus subtilis* protease and amylase combination is effective in removing dental plaque(s) (Ramana et al. 2000). Poly-unsaturated fatty acids (PUFA) isolated from psychrophilic archaea have also conferred its use in development of neutraceuticals and other dietary supplements.

6.4.4 Role of Psychrophiles in Domestic Purposes

In domestic operations, the enzymes of psychrophilic species can be utilized. Low-temperature cleaning of clothes can preserve fabric colors and reduce power consumption. Few enzymes that are applied to detergents for the hydrolysis of macromolecular stains, such as subtilisin, lipase, and glycosidases, are poorly effective at tap water levels; psychrophilic enzymes may replace them (Feller and Gerday 2003).

6.4.5 Application of Psychrophiles in Textile-Based Industries

The extremozymes of few psychrophilic microbes are an extremely good source of enzymes for the textile industries. Since the twentieth century, amylases are often used for desizing. The most recent commercial developments are the use of cellulases for denim finishing and lacquers for clothing effluent decolorization and textile bleaching. It also encourages the production of environmentally sustainable fiber manufacturing systems and techniques to increase the efficiency of the finished product (Araújo et al. 2009).

6.5 Psychrophiles Used in Fine Chemical Synthesis

Colwellia psychrerythraea are reported to produce polyhydroxyalkanoate (PHA), a polyester that has thermoplastic and elastomeric properties, and are of great economic interest. During chemical process, cold adapted esterase(s) and lipases are mainly used for industrial purposes (Methé et al. 2005).

6.6 Role of Psychrophiles in Agriculture

The microbiomes found in low-temperature conditions are of great importance to the agriculture sector as they are permanently adapted to such extreme conditions. Diverse genera of bacteria like *Sphingobacterium* sp., *Octadecabacter* sp., *Hymenobacter roseosalivarius*, *Flavobacterium* sp., *Oleispira* sp., *Glaciimonas frigoris*, and *Psychrobacter pocilloporae* have been found in cold environments. Various species of psychrotrophs have been determined among different domains, i.e., bacteria, archaea, and fungi. Few microbes isolated from the cold deserts of Northwestern Himalayas reported plant growth-promoting (PGP) properties which included *Arthrobacter nicotianae*, *Brevundimonas* sp., *Paenibacillus tylopili*, and *Pseudomonas* sp. (Yadav et al. 2015a, b). In the northern regions of India, some psychrophiles like *Arthrobacter methylotrophus* and *Pseudomonas rhodesiae* have been recovered from wheat plant (Verma et al. 2016). Several economically beneficial *Bacillus* sp. possessing efficient plant growth-promoting potential have been determined by Yadav et al. (2015a, b). *Pseudomonas* and *Exiguobacterium* are considered best PGP at low temperatures.

Among the wide diverse psychrotrophic microbiome, various bio-inoculants enriched with PGP potential can be used to enhance crop production by assisting nitrogen fixation, stimulating phytohormones and release of siderophores, and facilitating solubilization and uptake of minerals like phosphorus, potassium, and zinc, by expressing antagonistic activity against plant pathogens as a biocontrol agent, or by inducing resistance against the pathogen. Psychrophiles can also be used for biodegradation of agricultural residues and wastes. Other studies developed microbial consortium comprised of three bacterial species, namely, *Eupenicillium crustaceum*, *Paceliomyces* sp., and *Bacillus atrophaeus*, for degradation of agricultural residues and the use of generated compost for enhancing soil fertility (Ajar et al. 2017; Shukla et al. 2016). Antifreeze proteins are also used for cryopreservation and improving quality of frozen food. Moreover, a soil actinomycete has been identified as *Streptomyces* sp. which produced antibiotics showing toxicity against many gram-positive bacteria at low temperatures (Ogata et al. 1971).

6.7 Conclusion and Future Prospectives

Psychrophiles are of great importance in agriculture and industrial biotechnology. Although several researches have been successful in exploring cold-tolerant microbes and their derivatives, still, much is to be explored with diversity in cold-tolerant microbes. In many hill agriculture regions, cold temperatures and less fertile soils are two major challenges. Under cold temperature, soils are acidic and phosphorus-deficient, limiting crop productivity. In such areas, green biotechnology has a great impact on agricultural productivity of small farm holders and their economies. Several efforts have been made by the scientific community to increase crop productivity through application of bio-inoculants. However, current biofertilizers used in cold climates have been found ineffective. The results obtained so far indicate that cold-tolerant or cold-loving microbes are more effective as compared to general biofertilizers. But still, much work is needed to explore more diversity of psychrophiles and finally achieve the desired bio-inoculant formulations which could perform efficiently under cold climate conditions.

Likewise, microbial symbionts associated with plants growing at low temperature are also required to explore the management of cold stresses under natural environment. In addition, we suggest further research to explain symbiotic mechanism for applying microbial species in general condition. A promising approach in this research area is the use of metagenomics sequencing to identify potential symbionts and their metabolic characteristics. We recommend exploring yeast endophytes or unicellular algae in cold environment, as they are majorly reported in symbiotic mechanism. We also recommend the study on secondary metabolites of symbiotic microbes associated with cold-tolerant plants for producing antimicrobial compounds and ameliorating chilling and freezing events in plants.

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