Chapter 9
Adaptation Mechanisms and Applications of Psychrophilic Fungi

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9.1 Introduction

Frozen environments (cryosphere) represent world's largest share of psychrophilic habitats including snow, ice sheets, ice lake, ice caps, permafrost, glaciers, frozen parts of the ocean, frozen rivers and lakes (Musilova et al. 2015; Kudryashova et al. 2013), in both polar regions (NOAA 2018), glaciers and lakes of nonpolar mountain ranges (Walsh et al. 2016; Salazar and Sunagawa 2017), and man-made freezers (Ahmad et al. 2010) and refrigerators (Flores et al. 2012). Psychrophilic environment is harsh due to low temperature along with at least one of these, i.e., UV rays, low nutrients and water availability, freeze-thaw cycles, and osmotic pressures, and yet these are of ecological and environmental importance. Cold conditions, and other limiting factors, strongly influence survival of organisms in a cold habitat (Margesin and Miteva 2011). Freezing temperature damages cells by disrupting them via ice crystals, stops the activity of enzymes and other proteins, and decreases fluidity of cytoplasm and membranes, thus hindering their normal function in low-temperature environment without proper adaptation tools (Raymond et al. 2007). Cold temperature freezes cell wall and cell membrane that leads to inability to carry out transportation in or out of the cells. Similarly, a frozen cytoplasm is unable to offer favorable environment for enzymes to perform the biochemical processes of a cell. Low temperature affects structure of enzymes which could not achieve their activation energy required to metabolize a reaction (Chandler 2018).

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For survival in extreme environments soil fungi compete with microbes of the soil, acquire the intermittent nutrients, and also utilize secondary metabolites for survival (Yogabaanu et al. 2017). Ice veins inside the glaciers and ice sheets represent microenvironment that serves as habitat for existence of microbes (Thomas and Dieckmann 2002). Microorganisms in the ice veins face many physicochemical stresses, i.e., low water activity and pH, lowered solute diffusion rates, and damage to the membranes owing to ice crystal formation. Psychrophiles demonstrate various structural and functional approaches for their survival under reduced liquid water, extremely cold temperature, high solar radiation, and nutrient scarcity (Garcia-Lopez and Cid 2017).

Psychrophiles and psychrotrophs include all three domains of life such as archaea, prokaryotes (e.g., bacteria), and eukaryotes (e.g., fungi) (Margesin and Miteva 2011; Boetius et al. 2015; Hassan et al. 2016); inhabit stressful low-temperature environments; and are dependent on each other for active ecological processes. Fungi are widely distributed in the cryosphere (Hoshino and Matsumoto 2012), and play an important role in nutrient recycling; thus they are termed as "the survivor community." They also decompose organic compounds under subzero temperatures (Tsuji 2016).

Cold environment constitutes extremely diverse cold-adapted fungi including representatives of all phyla (Wang et al. 2017). Cold-tolerant fungi, belonging to phyla Ascomycota, Deuteromycota, Zygomycota and Basidiomycota, including *Mucor*, *Cladosporium*, *Alternaria*, *Aspergillus*, *Penicillium*, *Lecanicillium*, *Botrytis*, *Geomyces*, *Monodictys*, and *Rhizopus*, have been reported from Antarctica (Kostadinova et al. 2009). Cold-adapted fungi are varied; dwell as saprobes, symbionts, parasites, and pathogens of plant and animal; and also carry out critical functions in diverse ecosystems. Few fungal species cause diseases in plants and animals in cold regions (Wang et al. 2017) and can have both ecologic as well as economic impact on vegetation or animal life.

Adaptation to low temperature makes fungi an appealing resource for obtaining new enzymes and secondary metabolites for use in biotechnology and pharmaceuticals (Wang et al. 2017). Fungi secrete cellulose, hemicellulose and lignin-degrading enzymes, secondary metabolites, and bioactive compounds, and have great potential in biotechnological applications. In nature, soil fungi decompose dead plants, carry out mineral cycling to maintain soil fertility, and thus have an important role in biogeochemistry (Watkinson 2016), the same role of fungi in low-temperature habitats. Scientists have reviewed cold-adapted fungi, properties of enzymes, biotechnological applications and use of metagenomics to screen for enzymes, cold gene expression systems and enzymes used for washing purpose (Cavicchioli et al. 2011), synthesis of biotechnologically important cold-active enzymes, genome sequences, proteomics and transcriptomics of adaptation mechanisms under cold conditions (Feller 2013; Alcaíno et al. 2015), and influence of climate change on microbes of permafrost and their function (Jansson and Taş 2014). Boetius et al. (2015) explained microbial ecology, composition of frozen waters and biogeochemical activities of the microbial communities, and living strategies and ecological functions of cold-adapted fungi reviewed by Wang et al. (2017). This chapter elaborates strategies used by cold-adapted fungi to survive in cold and avenues to exploit their strategies as potential applications in various industries and biotechnology.

9.2 Adaptation Mechanisms

In cold temperature, fatty acid tails of phospholipids become rigid due to less movement, and fluidity of membrane is decreased, thus decreasing permeability to molecules (oxygen and glucose) into the cell. Long exposure to temperatures below-freezing points freezes the liquid inside the cell and forms crystals that damages the membrane, resulting in death of cell (Chandler 2018).

Low temperature affects the cells by impeding chemical reaction rate, denaturing proteins, enhancing water viscosity, limiting activities of microbial enzymes and fluidity of cell membrane (Hassan et al. 2016), and restraining water availability as a solvent for biochemical reactions (Wynn-Williams and Edwards 2000) and frequent freeze-thaw cycles (Montiel 2000).

Eukaryotic microorganisms survive in hypersaline environments by accumulation of "compatible solutes" in their cytoplasm (Oren 1999) and maintain intracellular concentrations of sodium ions below the toxic level (Plemenitaš et al. 2008).

In fungi, melanin provides protection against the undesirable effects of UV radiation (Gessler et al. 2014), drying, high amount of salts, heavy metals, and radionuclides. Melanin helps fungi to live under high electromagnetic radiation in higher altitudes and deserts and on plant surfaces (Zhdanova et al. 2005; Dighton et al. 2008; Grishkan 2011).

Radiations from sunlight comprise UV-A and -B radiations with shorter wavelengths that cause damage to biological systems in glaciers (Cockell and Knowland 1999). To counteract this, organisms have developed repair processes like photoreactivation, base excision repair, nucleotide excision repair, and mismatch repair (Rastogi et al. 2010a, b). UV-absorbing pigments are produced by some organisms (Rastogi et al. 2010a, b). Solar UV-A interacts with cellular photosensitizers that generate reactive oxygen species and induce oxidative stress with proteins as the main target for damage. UV-B negatively affects ecology and evolution of biological systems (Cockell and Blaustein 2001).

Various strategies of cold tolerance in fungi include production of antifreeze proteins (AFPs), plasma membrane fluidity, trehalose, compatible solutes, and many other cold-shock proteins and mechanisms (Robinson 2001). Scientists are looking for molecular or genetic basis of adaptations. High expression of unknown or novel genes in *Glaciozyma antarctica* PI12 could have an important role in cold adaptation (Firdaus-Raih et al. 2018).

9.2.1 Plasma Membrane Fluidity Maintenance

Microorganisms living in cold habitats deal with low temperature by changing composition of lipid membrane (Russell 1990) and increasing level of unsaturated fatty acids. Increased unsaturation of lipids is observed at low temperature in *Geomyces pannorum*, with decrease in production of ergosterol in *Mortierella elongate* (Weinstein et al. 2000). *M. elongate* showed increase in production of stearidonic acid, a fatty acid previously reported in psychrotrophic zygomycetes. *Rhodosporidium diobovatum* (psychrotolerant Arctic yeast) demonstrates increased membrane fluidity through unsaturation of fatty acids (Turk et al. 2011).

9.2.2 Compatible Solutes

Compatible solutes are low-molecular-weight osmoregulators that stabilize the cells and provide favorable environment for function of enzymes and other molecules inside cell in cold, heat, drought, and other stress conditions. These solutes have cryoprotective ability and maintain membrane and cytoplasm's structure and function. Different classes of compatible solutes produced by psychrophilic fungi to cope with low temperature include polyols, melanin, mycosporines, trehalose, and betaine (Ruisi et al. 2007). Cold-adapted fungi also adapt to repeated freeze-thaw cycles, low water availability, osmotic stress, desiccation, low nutrient availability, and high UV radiation (Ruisi et al. 2007).

9.2.2.1 Polyols

Polyols are organic compounds which contain more than two hydroxyl functional groups, for example sugar alcohol, including mannitol and glycerol. Synthesis of compatible solutes by enzymatic activities is elicited by induced dehydration and osmotic stress in fungi at low temperature, and glycerol is one of them (Pascual et al. 2003). Fungi use mannitol to store carbon, balance redox, and serve as an antioxidant and stress tolerant (Son et al. 2012). Turgor pressure can be controlled against decline in external water potential by raising mannitol and glycerol concentrations (Grant 2004). It is known that mannitol has protective role in water stress condition and can be used as a protective agent in cryoenvironment (Weinstein et al. 1997). Han and Prade (2002) reported glycerol and erythritol synthesis in *Aspergillus nidulans*, triggered by exposure to high salinity.

9.2.2.2 Trehalose

Increase in trehalose concentration is observed on exposure of fungi (e.g., *Hebeloma* sp., *Humicola marvinii,* and *Mortierella elongate*) to cold environment (Tibbett et al. 1998a; Weinstein et al. 2000).

Lack in ergosterol and increase in trehalose concentration in *Mortierella elongate* at low temperature have been documented by Weinstein et al. (2000). Trehalose accumulates in fungal hyphae and reproductive bodies to protect from adverse effects of low temperature (Robinson 2001).

9.2.2.3 Betaine

Betaine is glycerolipid with a non-phosphorous, polar moiety attached to diacylglycerol through ether linkage. It is found in many lower eukaryotes like bryophytes, algae, protozoa and fungi, and some prokaryotic bacteria. There are three types of betaine: diacylglyceryl-trimethyl-homoserine, diacylglyceryl-hydroxymethyl-trimethyl-β-alanine, and diacylglyceryl-carboxyhydroxymethylcholine (Murakami et al. 2018). Betaine is soluble in water and protects the cells by two mechanisms:

i) by osmoregulation to adjust osmotic pressure in and outside the cell, and ii) also acting as scavenger of reactive oxygen species. Studies indicated the presence of gene responsible for production of betaine on genome of *Aspergillus fumigatus.* Betaine is produced in a two-step process of oxidation followed by dehydration. Substrate choline is converted to betaine aldehyde (BA) by monooxygenase and BA is transformed to betaine by BA dehydrogenase (Chen and Murata 2011). Hoffmann and Bremer (2011) and Bashir et al. (2014) reported that bacteria can use betaine both as antistress molecule in extreme environment and a source of energy, whereas Lambou et al. (2013) reported fungi to use betaine as a source of carbon and energy.

9.2.2.4 Mycosporines

Mycosporine having oxo-carbonyl chromophores has been found in terrestrial fungi (Shick and Dunlap 2002). Basidiomycetous yeasts, *Rhodotorula minutia* and *R. slooffiae*, produced mycosporine-glutaminol-glucoside (Sommaruga et al. 2004). An Antarctic fungus *Arthrobotrys ferox* produced carotenoid pigments and mycosporines, having a strong role in UV protection (Arcangeli and Cannistraro 2000). Cold-adapted *Dioszegia patagonica* sp. nov, a yeast from Patagonia, accumulated carotenoid and mycosporines (Trochine et al. 2017). Mycosporines are not extensively studied in fungi inhabiting polar and nonpolar regions, but their occurrence in other fungi enables them to shield from UV.

9.2.2.5 Melanin

In mesophilic fungi, melanin plays a role as virulence factor in pathogenesis of fungi, stress protection (e.g., oxidative, UV), attachment, and penetration of appressorium (Yu et al. 2013). All biological kingdoms synthesize melanin (Eisenman and Casadevall 2012) which protects them from UV and ionizing radiation and desiccation.

9.2.3 Cold-Active Enzymes

These are known for sustaining microbial proliferation including fungi, at a very low temperature (Kuddus et al. 2011; Hassan et al. 2017). In cold environment, psychrophiles face low enzyme activity, modified transport systems, reduced membrane fluidity, and protein cold-denaturation among others (D'Amico et al. 2006). Elevated amounts of unsaturated and methyl-branched fatty acids and shorter acyl-chain fatty acids are produced by psychrophiles that increase fluidity of membrane (Chintalapati et al. 2004). Cold-shock proteins are also produced to assist in membrane fluidity or protein folding (Phadtare 2004), and antifreeze proteins hinder growth of ice crystal (Sarmiento et al. 2015). As temperature drops, proteins are denatured due to decrease in water molecule availability (Karan et al. 2012). A number of structural adaptations are known in cold-adapted enzymes that makes these enzymes flexible as compared to mesophilic or thermophilic enzymes. It makes them catalytically active at low temperatures (Siddiqui and Cavicchioli 2006), as well as thermolabile. Psychrophilic enzymes have more flexibility and activity at reduced temperatures: high surface hydrophobicity, reduced core hydrophobicity, decreased ratio of arginine/lysine, increased glycine residues, less proline in loops, with more α-helices, more nonpolar residues on surface of protein, weaker protein interactions, hydrogen bonds and other electrostatic interactions, and less/weaker metal-binding sites, less disulfide bridges, reduced secondary structures, with increased number and size of loops, and increased conformational entropy of the unfolded protein state (Feller 2010; Cavicchioli et al. 2011). Therefore, rate of reaction in psychrophilic enzymes decreases when temperature decreases (Feller 2013). Interestingly, cold-adapted xylanases are reported more active at low temperatures, and more thermolabile at higher temperatures (Collins et al. 2002). Psychrophilic *Humicola fuscoatra* and *H. marvinii* recovered from Antarctica and solubilized produced phosphatase and extracellular protease at 15 °C (Weinstein et al. 1997). Hassan et al. (2017) reported production of lipases, amylases, phosphatases, proteases, and DNAase from different fungal species isolated from Siachen glacier, Pakistan. He et al. (2017) gave new insights into *Aspergillus oryzae* cold-adapted amylase and application of gene AmyA1 in the food and starch industries. Cold-adapted *Cladosporium herbarum* ER-25 produced extracellular invertase and assisted in removal of toxical dark-brown pigments (melanoidins) along with laccase and manganese peroxidase (Taskin et al. 2016).

9.2.4 Antifreeze Proteins (AFP)

Antifreeze protein is an effective strategy used by psychrophilic organisms, for survival at subzero temperature (Duman 2001). AFP DUF3494-type proteins are present in all domains of life specifically restricted to cold-adapted taxa (Bowman 2017). Ice growth and nucleation are hindered by AFPs and organism stays supercooled until atmospheric temperature is lowered below freezing point.

New fungal AFP has been identified and purified from psychrophilic *Antarctomyces psychrotrophicus* (Ascomycetes) (Xiao et al. 2010). AFP-producing fungi are pathogenic for different plant species (Snider et al. 2000; Hoshino et al. 2003; Hoshino 2005).

9.2.5 Exopolysaccharides (EPS)

Exopolysaccharide production is an adaptive strategy used by fungi to survive in extreme condition by preventing damages in subzero temperature. *Phoma herbarum* CCFEE 5080 from Antarctica was observed for EPS production (Selbmann et al. 2002).

9.3 Applications

Psychrophilic fungi (metabolite or whole cell) can be used as biotechnological product (Fig. 9.1) for production of compounds, and bioremediation in cold regions and their proteins can be used in medical research, molecular biology, biotechnology, detergents or cosmetics, and food or feed technologies (Margesin and Feller 2010; Tiquia-Arashiro and Rodrigues 2016).

9.3.1 Novel Source of Cold-Active Enzymes

Low-temperature-active enzymes represent a striking reserve for biotechnological applications (Santiago et al. 2016; Hamid et al. 2014; Cavicchioli et al. 2011; Tiquia and Mormile 2010), with uses in food processing, textile, detergents, feed stocks, bioremediation, cosmetics, paper, and pharmaceutical industries (Javed and Qazi 2016). Psychrophilic yeasts produce cold-active enzymes, used in fine chemical synthesis, and various domestic and environmental applications (Hamid et al. 2014). They do not require processes requiring heating that hampers the quality, sustainability, and cost-effectiveness of production at industrial level (Santiago et al. 2016), and elimination of heating results in saving substantial energy, efficient function at low temperatures, increased yield, and high stereo-specificity, and avoids the unwanted chemical reactions that occur at high temperatures. Psychrophilic fungi produce various intra- and extracellular enzymes, which enable them to confront

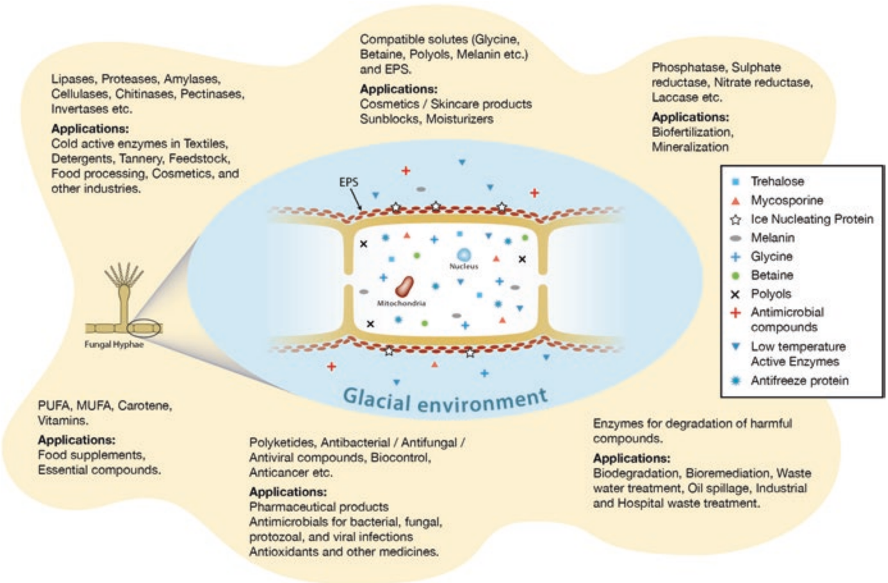

Fig. 9.1 Schematic representation of adaptation mechanisms of psychrophilic fungi that can be used for potential biotechnological purposes

and aid in harsh conditions and in degradation of large molecules and uptake of nutrients (Gerday et al. 2000; Feller and Gerday 2003; Gomes and Steiner 2004; Margesin et al. 2005).

Yeast and fungi from cold habitats deliver usefulness of fermentation procedures feasible at room temperature, that reduce production cost and influence on environment (Perfumo et al. 2018), and are economically important based on their activity at moderate and low temperatures (Allen et al. 2002; Margesin et al. 2002).

Poveda et al. (2018) isolated pectinase producing *Geomyces* sp. strain F09-T3-2 from marine sponges in Antarctica, with probable uses in food and beverage industry. Psychrophilic fungi from Baramulla (Jammu and Kashmir) produced cold-active pectinases (pectin esterase, exo-galacturanase, and endo-galacaturanase) for potential in the wine making and juice industries (Singh et al. 2012). Polygalacturonase from psychrophilic *Sclerotinia borealis* (Takasawa et al. 1997) has applicability in fruit ripening, pollen, and abscission.

Yusof et al. (2017) characterized the sequence of a chitinase produced by psychrophilic yeast, *Glaciozyma antarctica* PI12. Fungi belonging to Ascomycota and Basidiomycota from Antarctic soil and sea samples produced cold-adapted hydrolytic enzymes (e.g., phytase, glucosidase, chitinase, invertase, tannase, pectinase, lipase, protease, α-amylase, cellulase, subtilase, and xylanase) and oxidoreductases (laccase and superoxide dismutase) (Duarte et al. 2018). Cold and pH-tolerant *Penicillium* spp. produced cold-active lipases (Pandey et al. 2016).

Ascomycetes, Deuteromycetes, Basidiomycetes, and white-rot fungi produce laccases that degrade lignin and have been used in petrochemical, pulp, paper, and textile industries; food processing; medical and health care; and designing of biosensors and nanotechnology (Upadhyay et al. 2016).

Cold-active cellulases by psychrophilic microorganisms can hydrolyze biomass at low temperature and convert cellulosic biomass into monomeric sugars for bioethanol production (Tiwari et al. 2015). *Aspergillus niger* SH3 from Himalayan region (India) produced endoglucanase, *β*-glucosidase, FPase, and xylanase and can be a potential candidate for biofuel production (Tiwari et al. 2015). Cellulose decomposing *Cladosporium* (WR-C1) was isolated from a hypothermal litter layer (Da-qing et al. 2016). Cellulases and lipases produced by *M. arctica* reported to be highly active at 3 °C and have significant role in biogeochemical cycle of glacial ecosystems (Tsuji et al. 2018). *Verticillium* sp. *AnsX*1 having enhanced cellulytic activity in cold was recovered from Antarctic and has potential for bioconversion of lignocellulosic biomass into biofuels (Wang et al. 2013).

Efficient activity of endo-1, 4-β-glucanase (endoglucanase) is reported at low temperature from *Cladosporium, Penicillium, Cadophora,* and *Geomyces* by Duncan et al. (2006), and Gawas-Sakhalkar et al. (2012) reported phosphatase activity of *Penicillium citrinum, Aspergillus niger*, whereas *Aspergillus aculeatus* exhibited amylase and pectinase activity.

Psychrophilic enzymes have a great prospective as detergents for cleaning/washing at low temperature (Cavicchioli et al. 2011). Novozymes have developed Celluzyme® and Celluclean® using cellulases from cold-adapted *Humicola insolens* (Adapa et al. 2014). Mukherjee and Singh (2011) reported α-amylase with possible use in the food and textile industries and as additive in detergent for cold washing. They have a great potential of applications in "peeling" of leather at industrial scale, baking and wine industry, food and feed industry, molecular biology, cheese ripening, resizing denim jeans, and paper industry (Petrescu et al. 2000; Mayordomo et al. 2000).

Phytase was produced by *Morchella importuna*, a psychrophilic mushroom which can be used as fish feed additive enzyme (Taskin et al. 2016).

9.3.2 Pharmaceutical Products

Fungi are reported to produce pharmaceutical products (Schulz et al. 2002) but the recovery of such bioactive metabolites from fungi of cold regions is quite rare. *Penicillium lanosum* and *Penicillium soppii* synthesized bioactive secondary metabolites such as cycloaspeptide A and griseofulvin (Frisvad et al. 2006). Psychrophilic *Penicillium jamesonlandense* produced cyclic peptides cycloaspeptide A and D (Frisvad et al. 2006). *Penicillium ribium* was found to synthesize compound, cyclic nitropeptide psychrophilin A (Dalsgaard et al. 2004a; Frisvad et al. 2006), whereas *Penicillium rivulorum* produced communesin G and H and psychrophilin B and C (Dalsgaard et al. 2004b, 2005). *Penicillium algidum* synthesized cycloaspeptide A and D and psychrophilin D (Dalsgaard et al. 2005). These cyclic peptides reported only in fungal isolates from cold habitats showed antimalarial and insecticidal properties (Dalsgaard et al. 2005; Lewer et al. 2006), along with other biological activities.

Polyketides (PKs) have antimicrobial activity and other clinically important applications. PKs promote struggle for nutrients, to demote the potentials of its competitors and to establish chemical interaction with organisms in its vicinity (Mukherjee et al. 2012). Penilactones A and B, the oxygenated polyketides, were produced from *Penicillium crustosum* PRB-2 from deep sea of Antarctic (Wu et al. 2012), and 5 fungal hybrid polyketides, including cladosins, were obtained from deep-sea *Cladosporium sphaerospermum* 2005-01-E3. Cladosin C demonstrated slight activity against influenza A H1N1 virus (Wu et al. 2014). Chloro-trinoreremophilane sesquiterpene, eremophilane sesquiterpenes, and eremofortine recovered from an Antarctic *Penicillium* sp. PR19N-1 showed cytotoxic activity against cancer cell lines (Wu et al. 2013). *Dichotomomyces cejpii* F31-1, a marine fungus, produced polyketide Scequinadoline A showing inhibitory activity against dengue virus serotype 2 production (Wu et al. 2018). Polyketide, anthraquinone-xanthone**,** from *Engyodontium album* LF069 exhibited inhibition against methicillin-resistant *Staphylococcus aureus* (Wu et al. 2016).

Psychrophilic halophilic *Penicillium chrysogenum* from Vestfold Hills' saline lake produced bis-anthraquinone (rugulosin and skyrin) with possible application as insecticide and medicine (Parker et al. 2000; Sumarah et al. 2005). Some important and potential bioactive secondary metabolites by fungi of Antarctic were documented by Marinelli et al. (2004) and Rojas et al. (2009). Fungi from King George Island, Antarctic, and Svalbard, showed antimicrobial potential against *Bacillus subtilis*, *Bacillus cereus*, *Pseudomonas aeruginosa*, *Enterococcus faecalis,* and *Escherichia coli* (Yogabaanu et al. 2017).

Moghaddam and Soltani (2014) isolated psychrophilic endophytic fungi *Phoma* sp., *P. herbarum,* and *Dothideomycetes* spp., with an ability to synthesize metabolites active against phytopathogenic fungi and antibacterial activity against ice-nucleating *Pseudomonas syringae*. Depsipeptide, chaetomiamide, and diketopiperazines showing anticancer and cytotoxic activity were recovered from endophytic *Chaetomium* sp. (Wang et al. 2017).

9.3.3 Bioremediation Potentials

Psychrophilic microbes are useful for bioremediation of waste water and soil in temperate regions in winter. Bioremediation potential of psychrophilic fungi is not studied well yet; however, it would be quite effective in cold regions.

Mortierella sp. from Antarctica used dodecane as carbon and energy source and can be a good candidate for bioremediation of hydrocarbon spill (Hughes et al. 2007). Antarctic *Aspergillus fumigatus* degraded phenol via production of phenol hydroxylase, hydroquinone hydroxylase, and catechol 1,2-dioxygenase (Gerginova et al. 2013).

D'Annibale et al. (2006) reported *Allescheriella* sp. DABAC 1, *Stachybotrys* sp. DABAC 3, and *Phlebia* sp. DABAC 9 to produce laccase and peroxidases, and removed naphthalene, dichloroaniline isomers, o-hydroxybiphenyl, and 1,1-binaphthalene. *Stachybotrys* sp. DABAC 3 remediated 9,10-anthracenedione and 7H-benz[DE]anthracen-7-one. Dechlorination of polychlorinated biphenyls (PCBs) has been demonstrated by *Phanerochaete chrysosporium* (Bedard et al. 2006). *Candida antarctica* could degrade petroleum compounds (Hua et al. 2004).

9.3.4 Pigment/Lipid Production

Pigments and lipids synthesized by psychrophilic fungi confront low temperatures. Increased amount of lipids like fatty acids and polyunsaturated triglycerides has been found in psychrotolerant and psychrophilic fungi (Weinstein et al. 2000).

Singh et al. (2014) reported pigments (carotenoid) and fatty acids (linoleic, stearic, linolenic, myristic, heptadecanoic, and palmitic acid) from cold-tolerant fungus, *Thelebolus microspores*. Linolenic acid is used as a food supplement for patients of diabetic neuropathy, eczema, and cardiovascular disease. Carotenoid biosynthesis was also reported in *Neurospora crassa* at low temperature (Castrillo et al. 2018).

9.3.5 Exopolysaccharide (EPS) Production

The production of EPS is the response to stress or harsh conditions. Mycelium of fungi surrounded by EPS has high growth rate as compared to unembedded mycelium in response to repeated exposure to freeze-thaw cycles (Selbmann et al. 2002). *Phoma herbarum* CCFEE 5080, an Antarctic fungal isolate, showed production of exopolysaccharide identified as β 1-3, 1-6 glucan of 7.4 × 10 6 Dalton (Selbmann et al. 2002). Meristematic black fungi isolated from Antarctica were reported by Onofri (1999) and Selbmann et al. (2005) for production of extracellular polymeric substances around their hyphae that surround their multicellular conidia and same is the case found in *Friedmanniomyces endolithicus.*

Endolithic fungus *Cryomyces antarcticus* CCFEE 515 isolated from the most comparable referent for Mars environment present on Earth, McMurdo Dry Valleys of Antarctica. It is used as eukaryotic model for astrobiological studies and in space experiments under UV and ionizing radiation (Selbmann et al. 2018).

Melanized microorganisms are dominant in harsh environments, like soils contaminated with radionuclides (Dadachova et al. 2007). Upregulation of many genes is caused by exposure to radiation, and an inducible microhomology-mediated recombination pathway is expected as a possible mechanism for eukaryotic evolution.

Exopolysaccharide is often used in cryopreservation, e.g., alginate beads containing EPS preserve the sample from freezing damage (Martinez et al. 1999). Psychrophilic Antarctic *Thelebolus* sp. IITKGP-BT12 produced EPS characterized as glucan and showed antiproliferative activity in cancer cells (Mukhopadhyay et al. 2014).

9.3.6 Biofertilization Capabilities

In nature, phosphorus is found in both inorganic and organic states, and it is one of the principal nutrients required for the crop development and increased yield. Soil comprises inorganic phosphates in insoluble form and plants cannot uptake insoluble form, it is useless for plants until solubilized. Solubilization changes the inorganic phosphates into organic soluble state, which the plants can take up.

Microorganisms play a key role in solubilization of phosphates to its organic soluble counterpart via chelation, exchange reaction, and acidification (Narsian and Patel 2000; Reyes et al. 2002). Bacteria, actinomycetes, and fungi involved in phosphate solubilization have been reported (Trivedi and Pandey 2007; Stibal et al. 2009; Nenwani et al. 2010; Singh et al. 2011). Ectomycorrhizal macromycetes (Sharma and Baghel 2010) and ectomycorrhizal *Hebeloma* (Tibbett et al. 1998b) produce phosphatase, whereas *Penicillium* and *Aspergillus niger* from nonpolar cold habitats produced inorganic phosphatase (Goenadi and Sugiarto 2000; Pandey et al. 2008). *Aspergillus niger*-1 and 2, from tundra in Arctic Archipelago of Svalbard, showed an ability for phosphate solubilization. Cold-tolerant *Penicillium citrinum* PG162 produced intracellular acid phosphatase (Gawas-Sakhalkar et al. 2012). Cold-tolerant fungi with an ability to produce phosphatase (Singh et al. 2011; Tibbett et al. 1998a, b; Gawas-Sakhalkar et al. 2012) suggest a good potential of biofertilizers in place of chemical fertilizers with efficient activity and ecofriendly characters.

9.4 Conclusions

Present review gives a detailed account of adaptability processes of cold-adapted fungi and how their strategies could be exploited for applications in biotechnology and industry. Psychrophilic fungi are a splendid resource of new and unique products and can have numerous opportunities in food industry, pharmaceuticals, enzymes, and so on. Unfortunately, these are not studied extensively yet, and therefore hold a promising future. The fungi in low-temperature environments including icy habitats and deep-sea environments are of diverse nature and are in abundance. Their strategies to thrive under extreme conditions make them versatile and their metabolites can be of potential use in many dimensions.

9.5 Future Perspectives

This review provides a baseline or food for thought regarding the exploitation of cold-adapted fungi and their metabolites for biotechnology and industrial uses. Adaptive mechanisms of low-temperature fungi need to be investigated further on molecular and genetic basis. Two of the most important avenues are pharmaceuticals and replacing synthetic compounds with biobased or biologically synthesized metabolites of use in industry and biotechnology. Psychrophilic fungi need to be investigated in practical application for the bioremediation of domestic, industrial, and hospital wastes because they are active at low temperature and can effectively work in winter season all over the globe. Therefore, we strongly recommend bioprospecting for fungal diversity in cold habitats and investigate their processes in detail.

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