Rev Environ Sci Biotechnol (2016) 15:147–172
DOI 10.1007/s11157-016-9395-9

REVIEW PAPER

Psychrophilic and psychrotrophic fungi: a comprehensive review

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Abstract This article reviews the comparative diversity of psychrophilic and psychrotrophic fungi, their adaptability mechanisms for survival and potential applications in biotechnology and pharmaceuticals. Fungi are able to grow and survive at low temperature and exist widely in polar and non-polar habitats. These cold regions are known for very low temperature, high ultra violet-B radiation, frequent freeze and thaw cycles and low water and nutrient availability. Most of the fungi adapt to such harsh conditions by evolving various strategies in their metabolism and physiology. Psychrophilic and psychrotrophic fungi are of importance in biotechnological and pharmaceutical fields due to their diverse characteristics developed or evolved due to their adaptation and survival in extreme environments, like; production of cold-active enzymes, pharmaceutical or bioactive metabolites and exo-polysaccharides, have potential for bioremediation and can also be used as biofertilizer.

Keywords Psychrophilic fungi · Psychrotrophic fungi · Cold habitats · Diversity · Adaptation · Applications

1 Background

Approximately, 85 % of Earth is cold with temperatures ranging below 5 °C, permanently or seasonally (Hoshino and Matsumoto 2012; Margesin and Miteva 2011). Cold habitats range from deep sea to high mountains and from Antarctica to Arctic region. A large proportion of cold environment consists of deep sea. Around 71 % of the biosphere is occupied by oceans and provides temperature from −1 to 4 °C, the snow covers ~35 % of total terrestrial environment, frozen ground ~24 % of terrestrial environment, sea ice ~13 % of the Earth surface and glaciers ~10 % of terrestrial environment, providing a temperature of about −5 °C, along with some other low temperature environments comprising cold soils, lakes, caves and cold deserts (Singh et al. 2006; Margesin and Miteva 2011).

The living entities that have adapted to and live in cold environments are termed as psychrophiles and psychrotrophs. Psychrophiles and psychrotrophs are defined as the organisms that can grow at or near 0 °C (Ingram 1965; Morita 1975). More specifically, the optimum and maximum temperature for the growth of psychrophiles is ≤15 and ≤20 °C, respectively. Psychrotrophs grow well above 15 °C (Morita 1975; Gounot 1991; Cavicchioli et al. 2002). “Obligate psychrophiles” require 15 °C for their optimal growth, <20 °C for their maximal growth and 0 °C or lower for their minimum growth (Turchetti et al. 2008) and facultative psychrophiles grow well below 0 °C (Raspor and Zupan 2006).

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According to Deverall (1968), the psychrophilic fungi have an optimum growth temperature near 10 °C or below and that 10 °C was the minimum growth temperature required for most of the fungi. Many researchers agree with Morita's definition of psychrophiles that psychrophilic fungi grow well at 15 °C or lower, whereas, psychrotrophic fungi require temperatures above 20 °C for their maximum growth (Maheswari 2005; Cavicchioli et al. 2002; Robinson 2001). Bacteria and fungi are reported to remain viable for at least thousands of years (Shi et al. 1997; Catranis and Starmer 1991). Microorganisms that can be recovered from the interior of deep-core samples of Arctic and Antarctic ice are expected to be millions of years old (Taylor et al. 1997). Various ancient fungi, ranging from 10,000 to 140,000 years in age, have been isolated and documented from Arctic and Antarctic ice (Abyzov 1993; Christner et al. 2003).

2 Low temperature adapted life forms

The extremely cold environments such as Arctic and Antarctic areas are dominated by microorganisms e.g. bacteria, protists and fungi as well as microscopic animals e.g. nematodes, rotifers, tardigrades, springtails, mites (Hogg et al. 2006; Arenz and Blanchette 2011). The Arctic and Antarctica have been investigated for psychrophiles, belonging to bacteria and archaea, to some extent, for algae, but less for fungi (Ma et al. 1999; Gunde-Cimerman et al. 2003; Abyzov 1993). Fungi not only survive but can also grow and propagate in unusual environments. Diverse fungi have been documented from different extreme environments such as saline liquids (Gunde-Cimerman et al. 2000), surface of dried rocks (Steflinger 1998), ocean pits (Lopez-Garcia et al. 2001), dry and hot deserts (Abdel-Hafez et al. 1989), very low pH (Lopez-Archilla et al. 2001), as well as in the coldest polar environments (Tojo and Newsham 2012). Cold adapted fungal species are considered the most effective eukaryotic extremophiles and have adapted such strategies from prokaryotic extremophiles (Petrovic et al. 2002).

Many studies have found that primary biomass production in cold ecosystems is facilitated by fungi because of their endophytic and lichenic relationship with several primary producers (Rosa et al. 2009; Gianoli et al. 2004). Their ability to decompose wood (carboxymethyl cellulose) suggests their role in recycling of the nutrients in cold environments (Duncan et al. 2006). Several fungi have been isolated from various historic huts (built with woody materials) in Antarctica, showing their biodegradation potential (Blanchette et al. 2010; Arenz and Blanchette 2009). Moreover, well-known fungal pathogens such as *Pythium* species have also been found in cold habitats (Uspon et al. 2009; Bridge et al. 2008).

Psychrophilic fungi in cold environments are facing numerous extreme situations, including coldest temperatures (frequent freeze–thaw cycles), high salt concentrations, low moisture content, extreme UV and solar radiation and low nutrient availability. Such extreme factors may vary from one site to another, but all fungi must overcome such potential challenges (McKenzie et al. 2003; Selbmann et al. 2002; Robinson 2001). To combat such harsh conditions, fungi have adapted special features that are still not fully understood. Although, several cold adaptive mechanisms of psychrophilic fungi have been described, it is assumed that a combination of strategies including production of antifreeze proteins, compatible solutes (glycerol), trehalose, polyols (acyclic sugar alcohols) and cold-active enzymes, are employed by psychrophiles for their survival (Brown 1978; Lewis and Smith 1967; Weinstein et al. 2000; Robinson 2001).

3 Fungal diversity in cold habitats

Psychrophilic fungi exist in some of the coldest environments throughout the world because of their great efficiency of adaptation to cold environment (distribution of cold adapted fungi throughout the world is summarized in Fig. 1; Table 1). The presence of psychrophilic and psychrotrophic fungi in cold environments, including; permafrost (Golubev 1998), cold water (Tosi et al. 2000), glacial ice (Ma et al. 1999), off-shore polar waters (Broady and Weinstein 1998), glaciers, ice sheets and shelves, freshwater ice, sea ice, icebergs (Tojo and Newsham 2012), have been widely studied.

Cryoconite holes on glacier surfaces are the cold niches of microbial diversity and activity. Multivariate analysis of terminal-restriction fragment length polymorphism (T-RFLP) profiles of rRNA ITS amplicons detected fungal communities in cryoconite holes at

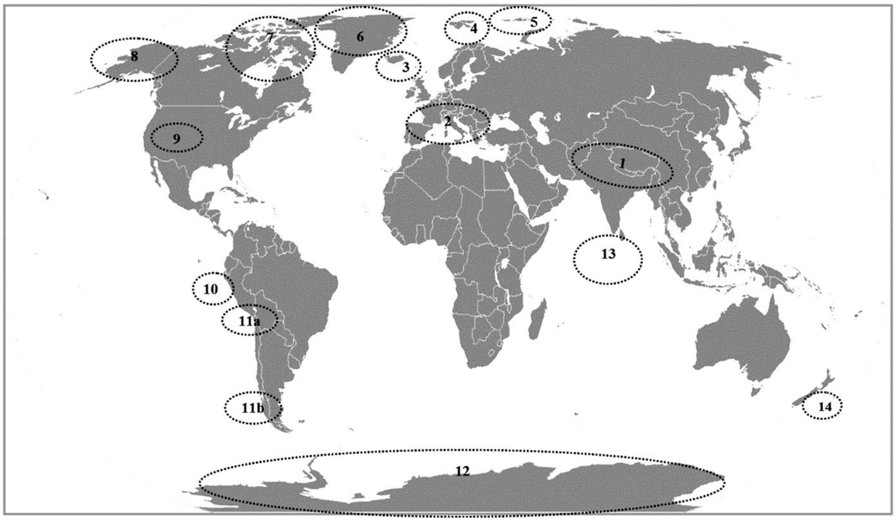

Fig. 1 Distribution of cold adapted fungi in different niches. Distribution of cold adapted fungi in different regions of the world. *1* Hindu Kush, Karakoram, Himalaya (HKKH), *2* European Alps, *3* Iceland, *4* Svalbard, *5* Arctic Ocean, *6* Greenland, *7* Canadian Arctic Islands, *8* North USA (Alaska), *9* Western USA (Utah), *10* North Pacific Ocean, *11* South America (*a* Bolivia, *b* Patagonia), *12* Antarctica, *13* Indian Ocean, *14* South Pacific Ocean (for detail refer to Table 1)

Kongsfjorden, Svalbard, and were compared to those from the soils of adjacent moraine and tundra sites. It was observed that the communities on glaciers with contrasting ice-surface hydrology differed remarkably. Most of the fungi cultured from cryoconite sediment were basidiomycetous yeasts or filamentous Ascomycota (Helotiales/Pleosporales), including aeroaquatic fungi, such as *Articulospora* and *Varicosporium*, indicating their role in cycling of carbon in cryoconite holes (Edwards et al. 2013).

It was reported by Zumsteg et al. (2012) that fungi shifted from an Ascomycota-dominated community in young soils to a more Basidiomycota-dominated community in old soils. Redundancy analysis indicated that base saturation, pH, soil C and N contents and presence of plant material related to soil age, associated with the microbial succession along the Damma glacier forefield in central Switzerland.

Arbuscular mycorrhizal (AM) and dark septate endophytic (DSE) fungi colonization in two dominant plant species (*Melandrium apetalum* and *Poa litwinowiana*) was observed on the forefront of Zhadang Glacier in Qinghai–Tibet Plateau, China. It was observed that AM dominated in *M. apetalum* and DSE dominated in *P. litwinowiana.* A total of five AM fungal spore morphotypes (*Acaulospora capsicula*, *Diversispora* sp., *Glomus constrictum*, *Glomus eburneum* and *Glomus* sp.) were found in the rhizosphere soils. Two AM fungal phylotypes: one *Claroideoglomus* phylotype from roots and one seaweed, also thought to be endemic phylotype from spores were identified (Pan et al. 2013).

3.1 Antarctica

Approximately, 99 % of the Antarctica continent is covered by ice throughout the year (Fox et al. 1994). The climate of Antarctica is one of the coolest and driest on the Earth, however, it contains variable climatic regions throughout the continent. The Antarctica is grouped into three different regions including the continental Antarctic, the Sub-Antarctic and the Maritime Antarctic (Peck et al. 2006). The biodiversity of fungi has been studied in different areas of the Antarctic continent (Onofri et al. 2005a; Bridge and Worland 2004). Biodiversity studies range from the floristic (Onofri and Tosi 1992; Mercantini et al. 1993), ecophysiologic (Tosi et al. 2002; Onofri et al. 2000), at molecular level (Vishniac and Onofri 2002) and phylogenetic (Selbmann et al. 2005).

Many mycological studies carried out in Antarctica, comprised different fungi that exist in lakes (Brunati et al. 2009; Goncalves et al. 2012), soil, historic woodlands (Fell et al. 2006; Arenz et al. 2006) as well as live on macroalgae (Loque et al. 2010) and on plants (Uspon et al. 2009; Rosa et al. 2009). About 0.6 % of fungi (water molds, Kingdom Chromista) and 99.4 % true fungi including yeasts (unicellular), and filamentous fungi (phylum Ascomycota, Basidiomycota, Chytridiomycota and Zygomycota) have been reported from Antarctica (Onofri et al. 2005b).

Table 1 Geographical distribution of cold adapted fungi in the world

No.	Region	Sampling site	References
1	HKKH (non polar)	1. Kumaun, Himalaya	Sati et al. (2014)
		2. Pangong Lake, Himalaya	Anupama et al. (2011)
		3. Nainital Kumaun, Himalaya	Sati et al. (2009)
2	European Alps	1. Damma glacier, Swiss Alps	Brunner et al. (2011)
		2. Forni and Sforzellina glacier, Ita. Alps	Turchetti et al. (2008)
		3. Stubaier glacier, Austria	Margesin et al. (2007)
3	Iceland	Iceland	Richardson (2004)
4	Svalbard	Kongsfjorden glaciers	Sonjak et al. (2006)
			Fujiyoshi et al. (2011)
5	Arctic Ocean	1. Franz Josef Land	Bergero et al. (1999)
		2. Kongsfjorden glaciers	Sonjak et al. (2006)
6	Greenland	1. GISP2 and Dye-3 sites	Ma et al. (2000)
7	Canadian Arctic Islands	Keewatin, Baffin Island, Ward Hunt Iceland, Saskatoon Island	Allen et al. (2006)
		Ellesmere Island	Olsson et al. (2004)
8	North USA	Alaska	Deslippe et al. (2011)
9	Western USA	Utah state	Kuddus et al. (2008)
10	South Pacific ocean	Peru Margin and Trench	Edgcomb et al. (2010)
11	South America	Bolivia	Flakus and Kukwa (2012)
		Patagonia	Garcia et al. (2013)
12	Antarctica	1. Peninsula	Laura et al. (2014)
		2. Intertidal transects, rocky coastline, Antarctica	Laura et al. (2013)
		3. King George Island	Vivian et al. (2013)
		4. Admiralty Bay, King George	Rosa et al. (2010)
		5. Livingston Island, West Antarctica	Kostadinova et al. (2009)
		6. Schirmacher Oasis	Singh et al. (2006)
		7. King George Island	Stchigel et al. (2003)
13	Indian Ocean	Central Indian Basin	Singh et al. (2010, 2012), Raghukumar et al. (2004), Damare et al. (2006a, b)
14	South Pacific Ocean region	Canterbury (New Zealand)	Ciobanu et al. (2014)

Paleobiological and paleoecological studies have shown that the Antarctic fossil fungal biota was present in degraded organic material, which proposes that perhaps they were initially saprophytic and acted as main decomposers (White and Taylor 1988; Stubblefield and Taylor 1983).

Blanchette et al. (2010) isolated 69 filamentous fungi from Nimrod Hut, Cape Royds, Antarctica that included the genera *Cadophora*, followed by *Thielavia* and *Geomyces*. *Thielavia* was studied in the Ross Sea Region (Blanchette et al. 2010), also reported from lichen on King George Island (Stchigel et al. 2001). Arenz et al. (2006) studied various filamentous Ascomycetes (New Harbor), Basidiomycetes (Allan Hills), Ascomycete yeasts, *Geomyces* sp. (Mt Fleming) and Zygomycetes (Lake Fryxell Basin). Duncan et al. (2006) isolated filamentous fungi from Terra Nova Hut which were mainly cold active and grow at 4 and 25 °C. *Geomyces pannorum* is reported from many locations of Antarctica (Loque et al. 2010; Rosa et al. 2010; Arenz and Blanchette 2011) which were thought to be indigenous (Vishniac 1996) and keratinophilic (Marshall 1998). The *Geomyces* and *Cadophora* sp. are widely present in Antarctica (Blanchette et al. 2010), playing significant role in the decaying and nutrient recycling (Arenz and Blanchette 2009; Arenz et al.

2006). In Antarctica, *Penicillium* species have been isolated from lakes (Ellis-Evans 1996), soils (Azmi and Seppelt 1998), historical woodlands (Arenz et al. 2006) and macroalgal thalli (Loque et al. 2010).

The extreme environment of Antarctica is accompanied by stressful conditions (Pugh 1980). Fungal genera including *Aspergillus*, *Candida*, *Cryptococcus*, *Cylindrocarpon*, *Glomerella*, *Golovinomyces*, *Penicillium* and *Phoma* have been reported from marine sediments (Singh et al. 2011; Lai et al. 2007; Calvez et al. 2009). *G. pannorum*, *Thelebolus* sp., mainly *Thelebolus microsporus* and *Mortierella* sp. are reported from Antarctic Peninsula (Goncalves et al. 2012; Arenz and Blanchette 2011). *Thelebolus* sp. is widely present in many other sites such as in benthic mats of Antarctic lakes (Brunati et al. 2009). The genus *Antarctomyces* is represented by the type species *A. psychrotrophicus*, isolated from Antarctic soil and seaweed, also thought to be endemic to Antarctic environment (Arenz et al. 2006; Arenz and Blanchette 2011; Stchigel et al. 2001; Loque et al. 2010).

King George Island, South Shetland archipelago, Antarctica, have an average temperature of 2 °C (min −20 °C, max 10 °C). Stchigel et al. (2003) reported two species of Ascomycetes, *Thielavia antarctica* and *Apiosordaria antarctica*, from King George Island (Antarctica). Moreover, Azmi and Seppelt (1997) reported many fungi from soils e.g. *Cadophora malorum* and from moss (Tosi et al. 2002) in the Windmill Islands, Antarctica. Mycological investigations in Victoria Land have been carried out by many authors, who provided lists of fungi present in the surrounding territories of that area (Broady et al. 1987). Park et al. (2015) studied lichen associated fungal species from King George Island, Antarctica, by pyrosequencing of eukaryotic large subunit (LSU) and revealed that fungal communities belonged to the Arthoniomycetes, Eurotiomycetes, Lecanoromycetes, Leotiomycetes, Sordariomycetes (Ascomycota) and Tremellomycetes and Cystobasidiomycetes (Basidiomycota). Litova et al. (2014) isolated *Aspergillus*, *Penicillium* and *Alternaria* as common genera from Antarctic soil probes.

McMurdo Dry Valley, one of the most unreceptive environments on Earth is favorable for the growth of microorganisms which love to grow in ice- free area including black meristematic fungi, persistent members of endolithic microbial communities such as lichen-dominated cryptoendolithic communities (Nienow and Friedmann 1993; Selbmann et al. 2008). Black meristematic fungi are known to be tolerant to extreme environmental conditions. The black fungi constitute melanized cell walls and meristematic development, which support survival and persistence in hostile environmental conditions (Selbmann et al. 2010). They are commonly isolated from environments that are almost devoid of other eukaryotic lifeforms, including saltpans (Plemenitas and Gunde-Cimerman 2005), acidic and polluted sites (Baker et al. 2004; Isola et al. 2013) and exposed rocks in dry and extremely hot or cold habitats (Staley et al. 1982). In Antarctica, the black meristematic fungi have been isolated from Northern and Southern Victoria Land (Selbmann et al. 2005; 2013).

Pythium belong to oomycete genera and are well-known fungal pathogens, usually infect small plants and arthropods in Antarctica (Humber 1989; Bridge et al. 2008). *Pythium* species, such as *Pythium tenue*, *Neozygites* sp. etc., have been reported from plants in vegetated sub-Antarctic islands such as Kerguelen, Macquarie and South Georgia (Knox and Paterson 1973; Hughes et al. 2003; Bridge and Denton 2007). Bridge et al. (2008) isolated pathogenic *Pythium* species from Antarctic hair grass *Deschampsia antarctica* in Signy Island, South Orkney Islands. Pathogenic *Pythium* species have also been reported from different Antarctic plants (Uspon et al. 2009; Bridge et al. 2008). The endophytic fungi have also been investigated in various plants such as *D. antarctica* and *Colobanthus quitensis* (Rosa et al. 2009; Gianoli et al. 2004). Taxonomically, most endophytic fungi were Ascomycetes but also belonged to Basidiomycota and Zygomycota (Huang et al. 2001). The endophytic fungal groups can help the plants to face abiotic (temperature, pH, osmotic pressure) and biotic stresses (bacteria, fungi, nematodes, and insects) (Rodriguez et al. 2001).

3.2 Arctic

The cold Arctic region comprises northern fringes of Ellesmere Island as well as Svalbard, Franz Joseph Land, Novaya Zemlya and the New Siberian Islands, all in the region of 80–85°N. The Arctic is divided into five bioclimatic sub zones (A–E), with A being the coldest and E the warmest (Ludley and Robinson 2008).

Fungi are found in all aerobic ecosystems, colonizing a diversity of substrates and performing a wide diversity of functions, some of which are not well understood (Table 2). Yeasts, black yeast-like fungi, melanized filamentous species as well as representatives of *Aspergillus* and *Penicillium* seem to be dominant among the mycobiota adapted to cold and saline niches (Cantrell et al. 2001).

Franz Joseph Land is a high-arctic desert or semi desert archipelago. The average air temperature during summer, ranges from 0.2 to 1.3 °C, with an average for the year as 14.1 °C (Bergero et al. 1999). Bergero et al. (1999) have isolated fungal species of *Geomyces*, *Phialophora*, *Phoma*, *Acremonium*, *Thelebolus* and *Mortierella* from Franz Joseph Land. The filamentous *Penicillium* species have been investigated in three different polythermal glaciers of Arctic region (Svalbard, Norway) (Sonjak et al. 2006). The most predominant species was *Penicillium crustosum*. Thirty-two genera of decomposer basidiomycetes, having around 100 species, have been collected and surveyed in Arctic tundra in North America (Lydolph et al. 2005). The Mycorrhizal fungal communities are common in arctic environment. They are important for growth and survival of their host plants as they provide water and limiting nutrients in exchange for photosynthetic carbon (Smith and Read 2002). Some of the ectomycorrhizal fungal communities have been investigated in the Arctic–Alpine ecosystems that were associated with *Dryas octopetala* or chronosequences (Cripps and Eddington 2005; Harrington and Mitchell 2002; Jumpponen et al. 2002). The Arbuscular mycorrhizal (AM) fungal communities have also been found in Arctic ecosytems (Allen et al. 2006; Olsson et al. 2004). Ectomycorrhizal fungi are widely distributed in arctic and alpine habitats on all continents. Some widely distributed EMF (Ectomycorrhizal fungi) genera include *Inocybe*, *Cortinarius*, *Hebeloma*, *Russula*, *Thelephora*, *Tomentella*, *Cenococcum* and *Laccaria* (Deslippe et al. 2011; Fujiyoshi et al. 2011).

There are about 2600 morphologically described macrofungi and at least 150 ectomycorrhizal species reported from Svalbard, the Russian Arctic and Iceland (Borgen et al. 2006). EMF have been collected from two arctic ectomycorrhizal host plants, *Salix*

Table 2 Fungal species/genera and their distribution in different Artic and Alps regions

No.	Distribution sites	Fungal genera/species	References
1	Franz Joseph Land	*Geomyces*, *Phialophora*, *Phoma*, *Acremonium*, *Thelebolus* and *Mortierella*	Bergero et al. (1999)
2	Colorado Front Range	*Saccharomyces cerevisiae*, *Taphrina communis*, *Neolecta vitellina*, *Phialophora gregata*, *Festcuca psuedostems*, *Hymenoscyphus ericae* and *Phialophora finlandia*	Schadt et al. (2001)
3	Lyman Glacier	*Cortinarius decipiens*, *C. tenebricus*, *Inocybe lacera*, *Laccaria* cf. *Montana*, *Suillus cavipes*	Jumpponen et al. (2002)
4	Northern Fennoscandia, Arctic	*Anthracoidea echinospora* and *Anthracoidea heterospora*	Scholler et al. (2003)
5	Western Beringia, Arctic	*Acanthophysium*, *Mortierella*, *Bensingtonia*, *Cryptococcus*, *Sordaria*, *Phanerochaete* and *Phialocephala*	Lydolph et al. (2005)
6	Svalbard, Norway	*Penicillium crustosum* and other *penicilium* species	Sonjak et al. (2006)
7	Tyrolean Alps	*Cenococcum geophilum*, *Sebacina* sp., *Tomentella* sp. and *Cortinarius* sp.	Muhlmann and Peintner (2008)
8	Cliff ledges, Arctic–Alpine	*Cenococcum geophilum*, Thelephoraceae sp., *Cortinarius* sp., and Sebacinales sp.	Ryberg et al. (2009)
9	Arctic tundra	*Cortinarius* sp. and *Russula*	Deslippe et al. (2011)
10	Austre Broggerbreen, Svalbard	*Geopora* sp. and *Cenococcum* sp.	Fujiyoshi et al. (2011)
11	High Arctic	*Cryptococcus*, *Rhizosphaera*, *Mycopappus*, *Melampsora*, *Mrakia*, *Tetracladium*, *Phaeosphaeria*, *Venturia*, and *Leptosphaeria*	Zhang and Yao (2015)

arctica and *Dryas integrifolia* that belong to the major genera *Thelephora*, *Tomentella*, *Sebacina*, *Inocybe*, *Cortinarius*, *Russula*, *Hebeloma*, *Laccaria* and *Clavulina* are characteristic of arctic and alpine environments (Muhlmann and Peintner 2008; Ryberg et al. 2009; Deslippe et al. 2011). Dark septate endophytes are present in the Arctic and Alpine plant roots but there is less knowledge about their phylogenetic antiquities or their effects on host plants (Jumpponen and Trappe 1998; Schadt et al. 2001). As in Antarctica, some of the fungal pathogens are also present in Arctic habitat, for example obligate basidiomycetes plant pathogens in Arctic ecosystems are *Exobasidium* (Nannfeldt 1981; Ing 1998) and rusts (belonging to Basidiomycetes that consist of a large group of obligate plant parasites) and smuts (obligate parasitic fungi of the genus *Anthracoidea*) (Scholler et al. 2003; Singh and Palni 2011). Zhang and Yao (2015) assessed the diversity and dissemination of endophytic fungal communities in High Arctic using 454 pyrosequencing by targeting the ITS region and found that the *Cryptococcus*, *Rhizosphaera*, *Mycopappus*, *Melampsora*, *Tetracladium*, *Phaeosphaeria*, *Mrakia*, *Venturia*, and *Leptosphaeria* were predominant fungal genera.

Cryoconite holes have biogeochemical, ecological and biotechnological importance. Culturable psychrophilic yeast and filamentous fungi from cryoconite holes at Midre Lovénbreen glacier have been studied. The microbes were identified through conventional and DNA sequencing techniques as *Cryptococcus gilvescens*, *Mrakia* sp., *Rhodotorula* sp., *Phialophora alba* and *Articulospora tetracladia*. *Rhodotorula* sp. expressed high amylase, while *Cryptococcus gilvescens* showed high lipase activity. *Mrakia* sp. showed phosphate solubilization between 4 and 15 °C. Filamentous fungi and yeast in the cryoconite holes drive the process of organic macromolecule degradation through secretion of cold-adapted enzymes, thereby having important role in nutrient cycling in these sub-glacial environments (Singh and Singh 2012).

Ribosomal DNA sequences were amplified from sub-fossils of the ascolichen *Umbilicaria cylindrica* (L.) Delise ex Duby collected at the ablating edges of Greenland glaciers. Phylogenetic analysis indicated that they were not closely related to those of the lichen-forming fungus but rather represented 2 groups of psychrophilic basidiomycetes (orders Cystofilobasidiales and Sporidiales) and one group of ascomycetes (order Leotiales). Sporidiales and the Leotiales, include fungi previously detected from grass clothing of the Tyrolean Iceman desiccated and frozen for over 3000 years and also in 2000 and 4000 year-old ice core samples from northern Greenland. Cystofilobasidiales were identical to those of the basidio yeast saprobe *Mrakia frigida* (DePriest et al. 2000).

3.3 Deep sea

Deep sea is an environment of extreme conditions, such as high hydrostatic pressure and low nutrient availability, with an average temperature between −1 and 4 °C in most areas of deep sea or high temperature (>400 °C in hydrothermal vents) and absence of sunlight. Living organisms in deep sea are considered to be adapted to cold environments. Yeast diversity commonly found in deep sea is represented by *Rhodosporidium* spp., *Rhodotorula* spp., *Candida* spp., *Cryptococcus* spp., *Pichia* spp., *Sporobolomyces* spp. and *Trichosporon* spp. As compared to prokaryotic microorganisms, yeasts in deep-sea environment remain relatively underexplored, with few studies carried out on their physiology (Nagano et al. 2013). The deep-sea is usually defined as the area of ocean beyond the photic zone (e.g. >200 m depth). Due to coldness, darkness and stability of the deep-sea bottom, it was presumed that most of life forms may be present in a suspended state.

Singh et al. (2010) have isolated filamentous fungi and yeasts that belong to phylum Ascomycota and Basidiomycota from sediments of Central Indian Basin. Similarly, *Aspergillus* sp., *Fusarium* sp., *Curvularia* sp., *Penicillium* sp. and *Cladosporium* sp. have been isolated at 5 °C from deep-sea sediment core of the Indian Ocean (Raghukumar et al. 2004; Damare et al. 2006a, b). Singh et al. (2012) also investigated fungal diversity in two sediment cores ~40 cmbsf (cm below seafloor) at a depth of ~5000 m in the Central Indian Basin, by culture-dependent as well as culture-independent approaches and recovered a total of 19 culturable fungi, of which two showed similarity to *Hortaea werneckii* and *Aspergillus versicolor*. Some of the fungi, such as *Cerrena*, *Hortaea* and *Aspergillus* sp., were recovered by culture-dependent as well as culture-independent approaches.

Most of the fungi of deep-sea environments are of psychrotrophic nature, but in some cases, deep-sea fungal isolates can also grow well at 30 °C than 5 °C (Damare and Chandralata 2008; Singh et al. 2010). Moreover, fungal communities belonging to Ascomycota and Basidiomycota phylum have been reported from the deep marine subsurface by DNA and RNA-based clone library analyses (Edgcomb et al. 2011; Orsi et al. 2013; Burgaud et al. 2013). Zhang et al. (2015) studied the presence of fungal communities in eight marine sediments of Kongsfjorden (Svalbard, High Arctic) using 454 pyrosequencing and revealed the *Pichia*, *Fusarium*, *Alternaria* and *Malassezia* as common fungal genera. Zhang et al. (2013) explored the diversity of fungal communities in different deep-sea sediment samples of the South China Sea by culture-dependent methods and isolated *Aspergillus*, *Cladosporium* and *Penicillium* as dominant genera. In an another study in the East India Ocean, fungal diversity of sediments from a depth of 4000 m have been studied using a mixture of metagenomics and conventional methods (Zhang et al. 2014). This tactic stemmed in the salvage of a total of 45 fungal operational taxonomic units (OTUs) and 20 culturable fungal phylotypes including fungal genera *Aspergillus*, *Alternaria*, *Cladophialophora*, *Cladosporium*, *Eurotium*, *Fusarium*, *Geomyces*, *Hypocrea*, *Leptosphaeria*, *Mortierella*, *Phoma*, *Rhizoscyphus* and *Trichoderma*.

3.4 The European Alpines

About 200 km long and 800 km wide, European Alpines extends across eight European Alpine countries. The highest peaks of Alpine mountain are approximately 4400–4800 m. The mean temperature in the valley floors range from −5 to 4 °C to as high as 8 °C during January, and in July it range between 15 and 24 °C. The variability of climate in European Alps is influenced by the North with huge Eurasian terrestrial physique, the Atlantic weather systems and Mediterranean Sea (Auer et al. 2005; Beniston and Jungo 2002; Begert et al. 2005).

The microbiological analysis of 78 samples taken from a boreal bog in Western Siberia and from a tundra wetland soil in Alaska showed the presence of 23 yeast species belonging to the genera *Bullera*, *Candida*, *Cryptococcus*, *Debaryomyces*, *Hanseniaspora*, *Metschnikowia*, *Mrakia*, *Pichia*, *Rhodotorula*, *Saccharomyces*, *Sporobolomyces*, *Torulaspora*, and *Trichosporon*. Peat samples from the boreal bog were dominated by eurytopic anamorphic basidiomycetous species, such as *Rhodotorula mucilaginosa* and *Sporobolomyces roseus*, and by the ascomycetous yeasts *Candida* spp. and *Debaryomyces hansenii*. These samples also contained *Candida paludigena* and *Schizoblastosporion starkeyi-henricii.* The wetland Alaskan soil was dominated by one yeast species (*Cryptococcus gilvescens*), which is a typical inhabitant of tundra soils (Poliakova et al. 2001).

In European Alps, psychrophilic yeasts have been documented in ice, subglacial sediments and melted water from two different Italian alpine glaciers including *C. gilvescens*, *Aureobasidium pullulans* (about half of the total), *Cryptococcus terricolus*, *Mrakia gelida*, *Naganishia globosa*, *Rhodotorula glacialis*, *Rhodotorula psychrophenolica*, *Rhodotorula bacarum*, *Rhodotorula creatinivora* and *Rhodotorula larynges* (Turchetti et al. 2008). Margesin et al. (2007) described three new psychrophilic species of the genus *Rhodotorula* comprises *Rhodotorula psychrophila*, *R. psychrophenolica* and *R. glacialis* collected from soil of an alpine railway area, from mud in the thawing zone of a glacier foot and from glacier cryoconite, respectively. Buzzini et al. (2005) reported the presence of viable yeast cells in melted waters running off from glaciers in Italian Alps. Similarly, a novel species of the genus *Acaulospora* has also been reported from numerous mountains in Southern Chile and Switzerland at 550–1600 and 1850–2050 m, respectively (Fritz et al. 2011). *Acaulospora alpine* a novel arbuscular mycorrhizal fungal species have been reported from Swiss Alp (Oehl et al. 2006). Brunner et al. (2011) isolated 45 fungi from sediments of fine granite of Damma glacier in the central Swiss Alps. A set of fungal species isolated from fine granitic sediment of the non-vegetated forefield of the Damma Glacier showed a high potential to weather powdered granite material in batch experiments. In particular, the zygomycete fungi *Mucor hiemalis*, *Mortierella alpina*, *Umbelopsis isabellina* and the ascomycete fungus *Penicillium chrysogenum* dissolved the granite powder most efficiently. It was shown that high concentrations of Ca, Fe, Mg and Mn in the solutions were the result of release of high amounts of organic acids, mainly citrate, malate and oxalate (Brunner and Schlumpf 2014). Muggia et al. (2015) isolated 248 lichen-associated fungi that belong to the Chaetothyriomycetes and Dothideomycetes, while a slight section represents Sordariomycetes and Leotiomycetes, from the Koralpe mountain range in the south eastern rim of the Austrian Alps. A total of 347 endophytic fungi were isolated from alpine plants, *Rhodiola crenulata*, *Rhodiola angusta* and *Rhodiola sachalinensis*, representing at least 57 genera in 20 orders of four phyla, namely, Ascomycota (88.89 %), Basidiomycota (2.78 %), Zygomycota (1.11 %), and Glomeromycota (0.56 %), which displayed high copiousness and diversity (Cui et al. 2015). Coleine et al. (2015) studied the presence of fungi in Alpine Tarfala Valley and the data showed that the mainstream of fungi isolated belonged to the Ascomycota and *Cryptococcus gilvescens* and *Pezoloma ericae* were the most frequently isolated species.

3.5 Glaciers of Hindu Kush–Karakoram–Himalayas (HKKH)

Hindu Kush–Karakoram–Himalayas hosts more than 20,000 glaciers, of which 5000 are in the Karakoram range (Inman 2010) and more than 12,000 are in the Himalayas that cover about 60,000 km area (Kaab et al. 2012). The HKKH glaciers have not been properly investigated earlier for presence of psychrophilic and psychrotrophic fungi and very few studies have been carried out. Five species of aquatic hyphomycetes belonging to the genus *Lemonniera* and aquatic hyphomycete, *Tetracladium nainitalense* a root endophyte has been isolated from Kumaun Himalaya, India (Sati et al. 2009, 2014; Sati and Belwal 2005). Anupama et al. (2011) reported the psychrophilic and halotolerant *Thelebolus microsporus* from the Pangong Lake, Himalayan region. Singh and Palni (2011) have collected 35 species belonging to 7 families of rust fungi from herbaceous and shrubby hosts in central Himalayan region. Moreover, 25 psychrophilic yeasts have been identified from Roopkund Lake soil of Himalayas, India (Shivaji et al. 2008). Wang et al. (2015) studied glaciers on the Qinghai–Tibet Plateau for the presence of cold-adapted fungi and isolated 1428 fungi, of which 150 were identified and *Phoma sclerotioides* and *Pseudogymnoascus pannorum* were the most dominant species and Helotiales (Leotiomycetes, Ascomycota) was the most commonly encountered group and also described six new species; *P. antarctica*, *P. lutea*, *P. olivacea*, *T. ellipsoideum*, *T. globosum* and *T. psychrophilum*.

Recently, few studies about the diversity of fungi in Hindu Kush and Karakoram mountain ranges of Pakistan have been conducted. A total of 77 fungal isolates were isolated from Batura, Passu and Siachen glaciers, representing 24 fungal genera, one class and one order (Hassan 2015). Most of the fungi from these glaciers belong to genus *Penicillium*, *Cladosporium*, *Mrakia*, *Geomyces*, *Leotiomycetes*, *Thelebolus*, *Trichoderma*, *Pueraria*, *Pseudogymnoascus*, *Beauveria*, *Pseudeurotium*, *Fontanospora*, *Cordyceps*, *Cadophora*, *Periconia*, *Cryptococcus*, *Trametes*, *Mortierella*, *Scopulariopsis*, *Candida*, *Antrodia*, *Sporobolomyces*, *Phoma*, *Eupenicillium*, while one fungal species to order *Pleosporales* and class *Dothideomycetes* each. *Antrodia juniperina* is isolated for the first time from any polar or non-polar habitats. In another study, Nadeem (2014) isolated 57 fungal strains from Tirich Mir glacier, Pakistan, with *Alternaria*, as predominant genus.

4 Adaptability in cold environment

Psychrophilic fungi in cold habitats of polar and non-polar regions are subject to extreme low temperature and various other stress conditions including high repeated freeze and thaw cycles (Ruisi et al. 2006), UV radiation (mainly UV-B), reduced moisture, increased salinity, low nutrient availability and desiccation. These potential challenges and stress conditions vary considerably from one environment to the other, and fungi must counter it for their survival. Coldness is a relative name (Smith 1993), which is defined as freezing temperature with a limit of −70 °C, beyond which life process stops (Robinson 2001). Such low temperature and regular freeze thaw cycles are also provided by Polar terrestrial regions (Montiel 2000). Low temperature influence fungal cells by increasing water viscosity, denaturing of proteins, slowing of chemical reactions and decreasing of membrane stability (Crowe et al. 1992; Russell 1990). Water unavailability and salinity are common in Antarctic island due to extreme dryness. Antarctica has almost 70 % of the world's fresh water which is entirely covered in ice. High winds enhance evaporation that leads to drought and the key source of humidity is fleeting water melted due to solar heating during the austral summer. Due to increased evaporation, salt concentrations in the soil, shallow ponds and rocks are

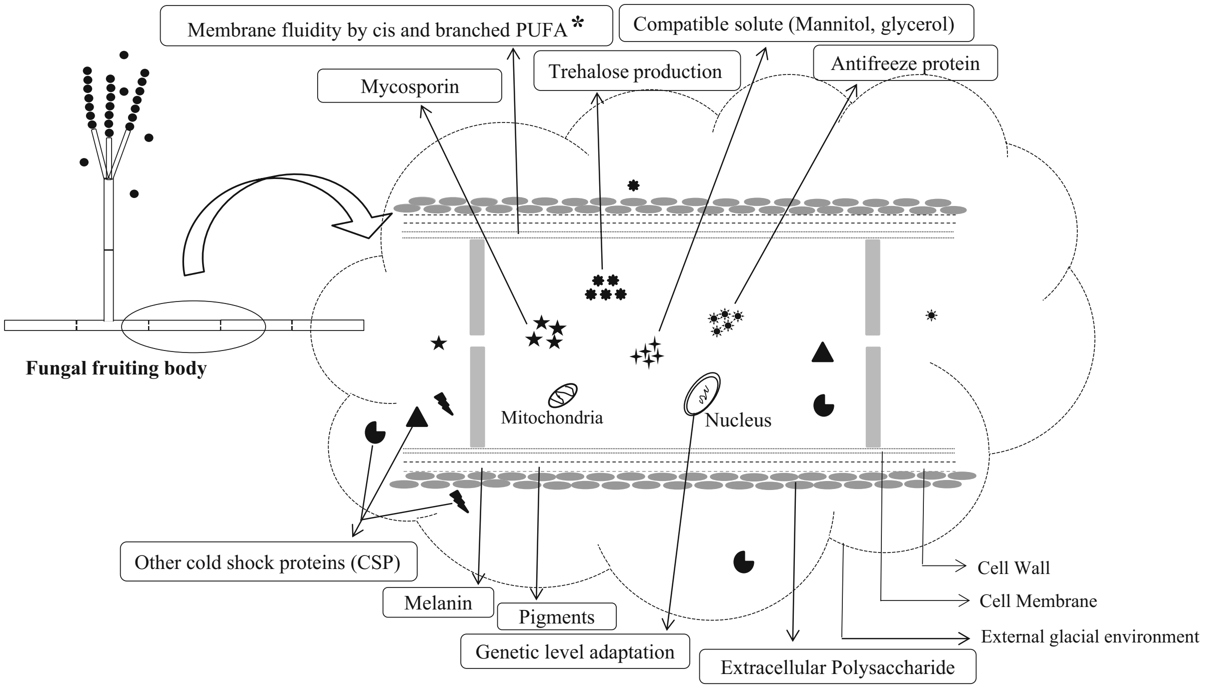

Fig. 2 A typical structure of psychrophilic and psychrotropic fungi and their adaptability mechanisms in low temperature environments, *Polyunsaturated fatty acids

frequently elevated (Nishiyama 1977), that produce similar consequence of osmotic disparity as caused by freezing (Gunde-Cimerman et al. 2003). UV-B is a solar spectrum's component that causes wide range of harmful effects (Kerr and McElroy 1993) on the environment due to which the whole productivity of ecosystems may be affected. The consequences of UV-B radiation (280–315 nm) have been observed on fungal growth (Gunasekera et al. 1997; Newsham et al. 1997). The significant detrimental effects of UV-B have also been observed on several Antarctic terrestrial fungi including *G. pannorum*, *Phoma herbarum*, *Mortierella parvispora*, *Pythium* and *Verticillium* species (Hughes et al. 2003).

4.1 Adaptation characteristics

To thrive under extreme conditions, fungi have adapted special mechanisms and features (Fig. 2). However, all the mechanisms in psychrophilic fungi are not completely known that allows them to survive at low temperature (Weinstein et al. 2000; Smith 1993; Snider et al. 2000; Russell 1990). To grow at low temperature, it is necessary that all the cell components of psychrophilic fungi must function properly (Russell 1990). Several tools of cold tolerance have been documented in fungi, as mentioned earlier.

4.1.1 *Plasma membrane fluidity maintenance*

The first line of defense is the cell membrane that faces the change coming from external environment. It is, therefore, important to be stable and function properly. Cell membrane consists of phospholipid bilayer and proteins organized in various coinciding domains with unlike fluidity features (Strancar et al. 2000; Simons and Toomre 2000). Hence, a minute change can considerably disturb membrane functions (Hazel and Williams 1990). It is well established that the Antarctic and other cold inhabitant microorganisms alter membrane lipid conformation as a strategy of cold-tolerance (Russell 1990). Extreme low temperature causes freezing and dehydration, damages cells by changing the cell membrane lipids from liquefied crystalline to gel phase and leads to disruption of membrane function (Crowe et al. 1987). This transition can be handled by an increase in fatty acids' unsaturation. Various strains isolated from Antarctic region including *Cadophora fastigiata*, *Mortierella alpine* and *Mortierella antarctica*, produce arachidonic and linoleic acid, when grown at low temperature and the change of fatty acid in cell membrane in reaction to cold temperature has even been scrutinized in *Geomyces vinaceus* and *G. pannorum* and in other Antarctic strains (Maggi et al. 1991; Finotti et al. 1993). In a similar study, the presence of fatty acids 'stearidonic acids' were also reported, in another fungi *Mortierella elongate* only, formerly described in psychrotrophic zygomycete, however the ergosterol were not detected (Weinstein et al. 2000). The increased membrane fluidity has been reported in psychrotolerant yeast *Rhodosporidium diobovatum* (Turk et al. 2011), indicating the role of unsaturation of fatty acids in maintaining integrity and functionality of plasma membrane at low temperature.

4.1.2 Compatible solute–polyols

Fungi produce various compatible solutes to overcome the increased dehydration and osmotic stress due to low temperature (Pascual et al. 2002). Glycerol is supposed to be the utmost important compatible solute (Brown 1978). Sugars, such as mannitol provides cryoprotective ability during freeze or desiccation (Feofilova et al. 1994). These solutes sustain the function and integrity of cell membrane to stabilize it. They can stabilize plasma membrane by sustaining their function and integrity and complete dehydration (Crowe et al. 1984, 1986). Grant (2004) observed an increase in the concentration of mannitol and glycerol to sustain the turgor pressure against heat mediated decrease in the external water potential i (Grant 2004). Mannitol might have role in cryoprotection (Weinstein et al. 1997), and is thought to be dynamic in water stress protection (Lewis and Smith 1967). Polyols are thought to act as buffering agents (Jennings 1984). The potential cryoprotectant role of polyols in fungi is revealed by comparing *Humicola marvinii* with *H. fuscoatra* (Weinstein et al. 1997). Polyols (acyclic sugar alcohols) are the principal soluble carbohydrates in fungi (Lewis and Smith 1967). Polyol's main function in fungi is in osmoregulation and coenzyme regulation (Jennings 1984) as well as protection against damage due to freezing by lowering the freezing point of intracellular fluid.

4.1.3 Trehalose

Trehalose is a disaccharide widely found in both reproductive and vegetative stages in fungi (Thevelein 1984). Trehalose plays a key role in enhancing the resistance in fungi to environmental stress conditions, like freezing, desiccation, dehydration and extreme temperature (Lewis et al. 1995; D'Amore et al. 1991). It has been documented that concentration of trehalose increases, when fungi is subjected to low temperature and such changes have been seen in excised alpine mycorrhizal roots (Niederer et al. 1992), *H. marvinii*, a psychrophile, (Weinstein et al. 2000) and *Hebeloma* species of the arctic and temperate regions (Tibbett et al. 1988a). Weinstein et al. (2000) documented the increase of cryoprotective carbohydrates at low temperature in *H. marvinii*, such as extracellular glycerol and intracellular trehalose, while in *Mortierella elongate*, only intracellular trehalose, in field soils of maritime Antarctica. It has also been documented that thermophilic fungus *Myceliophthora thermophila* (growth optimum at 42 °C) has also shown an increase in trehalose and mannitol content and a decrease in inositol content when exposed to low temperature stress (growth at 26 °C), suggesting a role for trehalose and mannitol in the fungal response to low temperature (Feofilova et al. 1994). Trehalose has been found to be the most effective cryoprotectant during desiccation or freezing and help in maintaining membrane integrity and function (Crowe et al. 1986).

4.1.4 Cold-active enzymes

The fungi and other microbial proliferation at extremely low temperature is extensively supported by cold-adapted enzymes as they provide high flexibility and active site complementarity for substrate, ensuing an increased specific activity at low energy cost (Weinstein et al. 2000; Kuddus et al. 2011). Such flexibility is accomplished by combining structural features including, increased surface residue charge, decreased ionic and electrostatic interactions and deterioration in core hydrophobicity (Weinstein et al. 2000). The tractability also comprise substitution of proline by glycines in surface loops, decreased in lysine–arginine ratio, low subunit and inter domain interaction and reduced aromatic interaction (Gerday 2000; Gianese et al. 2001).

Several Antarctic fungal species produce cold dynamic enzymes (Fenice et al. 1998) that may highlight the struggle of the fungi to flourish at low temperatures. Although, some Antarctic fungal species have wide enzymatic capabilities that intensify probability of persistence under hostile conditions (Fenice et al. 1997). Fungal strains isolated from Antarctic soil has been documented to have an enzymatic activity at low temperature e.g. psychrophilic fungal species, *H. marvinii*, *H. fuscoatra* and *H. marvinii*, responsible for production of extracellular protease and inorganic phosphate solubilization in solid media at 15 °C, have also been documented from Antarctic soil (Weinstein et al. 1997). Similarly, Fenice et al. (1997) reported different fungal strains including mitosporic fungi, yeast like fungi, Ascomycetes and sterile mycelial strains to produce various extracellular enzymes like DNase, protease, phosphatase, amylase glucose oxidase, lipases and polygalacturonase. The strains were isolated from diverse locations of Victoria Land (Antarctic continent). The ectomycorrhizal fungal strains belonging to genus *Hebeloma* have been screened for proteolytic and phosphatase activity (Tibbett et al. 1988a, b).

Enzymes can also act as a virulence factor in animals as well as in plants. One of such enzyme in plants is keratinase. Out of 72 positive samples (67.3 %), a total of seven genera with eleven species *Chrysosporium keratinophilum* (3.7 %), *Chrysosporium tropicum* (5.6 %), *Chrysosporium* state of *Ctenomyces serratus* (11.2 %), *G. pannorum* (2.8 %), *Malbranchea* sp. (0.9 %), *Microsporum gypseum* complex (20.6 %), *Microsporum nanum* (1.9 %), *Microsporum van-breuseghemii* (0.9 %), *Trichophyton ajelloi* (15 %), *Trichophyton terrestre* (2.8 %) and *Uncinocarpus reesii* (1.9 %) were isolated from soil at glacier banks of Gulmarg, Khilanmarg, Sonamarg and Tangmarg of Kashmir valley, and were able to utilize keratin, and are keratinophilic fungi and dermatophytes (Deshmukh 2002).

4.1.5 *Antifreeze proteins*

Production of Antifreeze protein (AFP) is one of the key strategies of prokaryotes and poikilothermic eukaryotes to persevere in low temperature environment (Duman and Olsen 1993). Antifreeze proteins adsorb to ice surface and avoid its growth and to attach to ice nucleators (Knight et al. 1993: Sicheri and Yang 1995). AFPs when bind to ice, lowers the freezing temperature of a solution, melting point remains same. This phenomenon is known as thermal hysteresis (Urrutia et al. 1992). The thermal hysteresis ranges from 2 to 6 °C in insects, in fish from 1 to 1.5 °C and in plants from 0.1 to 0.5 °C (Urrutia et al. 1992), in fungi it ranges from 0.3 to 0.35 °C in fungi (Snider et al. 2000) and 0.1 to 0.35 °C in bacteria (Duman and Olsen 1993). AFPs alter the ice crystal pattern, i.e. it changes the ice crystals from hexagonal to pyramid (Scotter et al. 2006). Antifreeze proteins' adsorption to ice crystals can lead to inhibition of recrystallization (Knight et al. 1984, 1988). Antifreeze proteins have been studied in fungi (snow molds) that are pathogenic to dormant plants under snow covers (Hoshino 2005; Hoshino et al. 2003; Snider et al. 2000). Snow molds consist of two key fungal taxa, Basidiomycetes and Ascomycetes and one pseudofungal taxon of oomycetes. However, among all three taxa, the AFPs have only been identified in *Coprinus psychromorbidus* belonging to basidiomycetes (Hoshino et al. 2003). The Ascomycetes isolated from Antarctica have been studied in detail among which seven strains were able to produce and modify ice crystal nature, although they were not recognized as Antifreeze proteins (Hoshino 2005). Xiao et al. (2010) recognized and purified a novel fungal antifreeze protein from Antarctic ascomycetes *Antarctomyces psychrotrophicus.*

4.1.6 *Mycosporines*

Mycosporines are renowned small secondary metabolites, which were initially revealed in spores of various terrestrial fungi and sporulating mycelia (Young and Patterson 1982; Bernillon et al. 1984). Mycosporine compound, like mycosporine glutaminol was found in *Trichothecium roseum* belonging to Deuteromycetes (Favre-Bonvin et al. 1987). The oxo-carbonyl chromophores are present in these compounds (absorbing radiation of UVB at 310 nm), are restricted to fungi that are found in terrestrial habitats (Shick and Dunlap 2002). In Basidiomycetous yeasts like *Rhodotorula minuta* and *Rhodotorula slooffiae*, the Mycosporine glutaminol glucoside (absorb UV at 310 nm) was studied for the first time (Sommaruga et al. 2004). Similarly, a non-melanized and predatory Antarctic fungus *Arthrobotrys ferox*, which feed on springtail, was capable of producing carotenoids and mycosporins that act as protecting agents against UV (Arcangeli et al. 1997; Arcangeli and Cannistraro 2000). In our knowledge, mycosporines have not been investigated in fungi from polar and non-polar origin, but the vast presence of mycosporines in other fungi use them to protect themselves from UV radiation, has clearly shown that these metabolites can exist in such fungi but it needs further exploration.

4.1.7 *Melanin*

Melanin is a distinctive and multifunctional pigment present in all biological kingdoms (Eisenman and Casadevall 2012; Gomez and Nosanchuk 2003). In fungi it provides protection against various environmental stresses like desiccation, ionizing radiation, oxidizing agent and UV light (Gorbushina 2003; Butler and Day 1998). It also plays a part in fungal pathogenesis. Several strains of Antarctic fungal taxa like having melanized strains that resist UV radiation including *Alternaria alternat*, *Stachybotrys chartarum* and *Ulocladium consortiale* (Domsch et al. 1980). Hughes et al. (2003) observed *P. herbarum*, isolated from Antarctica, was able to produce a brown pigment, probably melanin, within 24 h of disclosure to high radiation of UV-B. Similarly, many other investigators also reported the melanin in fungi (Kogej et al. 2004), which perhaps gives the idea that melanin is helping them to face the extreme conditions.

4.1.8 *Fungal adaptation to high pressure*

High pressure disturbs or inhibits the microbial activity such as growth, respiration and specific biochemical processes (Abe 2006). Effect of lethal pressures on yeast cells were studied by several groups (Iwahashi et al. 2003). Iwahashi et al. (2003) studied DNA microarrays of *S. cerevisiae* and analysed expression levels of ~6000 genes. The genome-wide expression profiles suggested that high pressure (180 MPa at 4 °C for 2 min) caused damage to cellular organelles as same as damage caused by detergents, oils, freezing and thawing (Raghukumar et al. 2010). It has been observed that the effects of pressure that cause growth inhibition in *S. cerevisiae* were different from those caused by lethal pressures (Abe 2004).

Pressure-inducible genes, to help in pressure acclimatization, have been studied in marine bacteria (Bartlett 1991). In case of bacteria, the pressure effects on DNA replication, growth (El-Hajj et al. 2009), gene expression, membranes, membrane proteins, DNA structure and function, cell division, protein and enzyme functions have been studied in detail while in case of fungi the studies have not been carried out except their detection in the deep-sea sediments and capability to grow under high pressure and yield extracellular enzymes active under raised hydrostatic pressure (Raghukumar and Damare 2008). In conclusion, none of the principle mechanism of adaptability has yet been explored. It needs to be further investigated to find out the factors involved in adaption of fungi in deep sea environment.

5 Applications

5.1 Cold active enzymes

Psychrophilic fungi are capable of providing a large number of biotechnological and pharmaceutical applications (Fig. 3). Psychrophilic fungi are capable of synthesizing secondary metabolites that are very unique to cold ecosystems (Margesin et al. 2008). They are an important source of cold-adapted enzymes which are economically important, as they work actively at low and moderate temperatures (Georlette et al. 2003). Fungi from cold habitats have the ability to be used as biofertilizers and production of pigments of medicinal value (Singh et al. 2011, 2014) (Table 3).

The psychrophilic enzyme that is active at low and moderate temperature provides probable cost-effective benefits (Cavicchioli et al. 2002). For instance, it works in low temperature set-up in winter season, provides high yields, increases stereospecificity, decreases undesirable reactions and saves significant energy in large scale process, which requires the heating of reactors. The thermophilic and mesophilic fungi have been investigated extensively for the production of extracellular enzymes (Sahai and Manocha 1993; Hankin and Anagnostakis 1975), however psychrophilic fungi are yet to be investigated in detail.

Cold active enzymes, polygalacturonases and alkaline proteases have been characterized from deep-sea yeast and fungi, respectively (Abe et al. 2006; Damare et al. 2006a, b). Alkaline, cold-tolerant proteases have been isolated from deep-sea fungi in the Central Indian

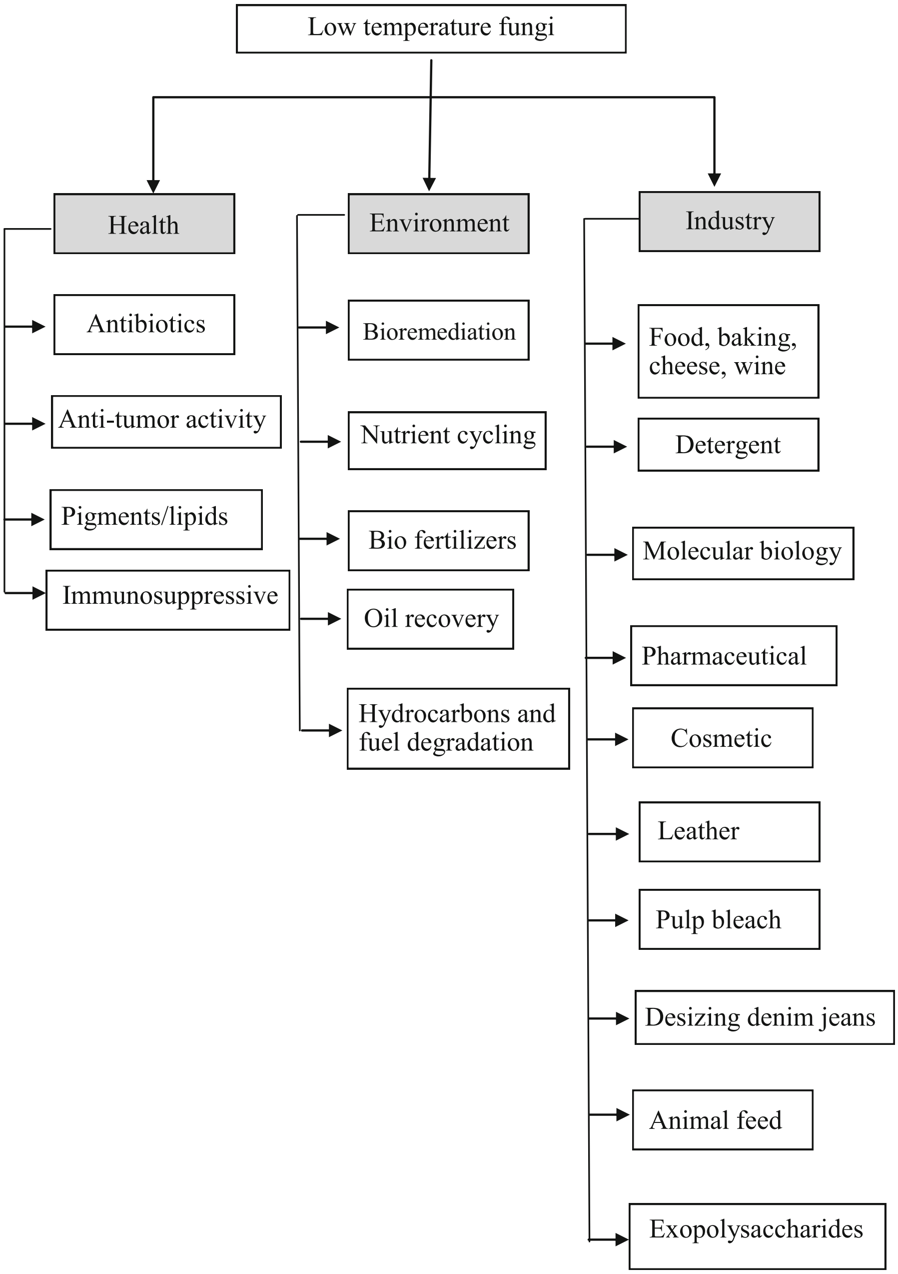

Fig. 3 Schematic representation of psychrophilic and psychrophilic fungal metabolites applications in different fields

Basin. Many of these grew and produced alkaline proteases at 5 and 30 °C and 1 bar pressure. *Aspergillus ustus* (NIOCC #20) produced the highest amounts of the enzyme. The fungus produced alkaline, cold-tolerant protease when grown at 30 °C and 1 bar pressure. The enzyme was active at combinations of 5, 30 and 50 °C with 300 bar pressure (Damare et al. 2006a, b). The presence of psychrophilic yeasts in supra- and sub-glacial sediments, ice and meltwater collected from two glaciers of the Italian Alps (Forni and Sforzellina—Ortles-Cevedale group) was investigated. A significant proportion of isolated yeasts exhibited one or more extracellular enzymatic activities (starch-degrading, lipolytic, esterolytic, proteolytic and pectinolytic activity) at 4 °C (Turchetti et al. 2008).

Table 3 Fungal species with various cold-active enzymes production and their applications in different fields

Enzymes	Temperature (°C)	Fungal species	Applications	References
α-amylases	4–20	*Thelebolus microsporus*, *Rhodotorula glacialis* and *Rhodotorula psychrophenolica*	1. Starch conversion 2. Detergent industry 3. Fuel alcohol production 4. Processed-food industry such as baking, brewing, preparation of digestive aids, production of cakes, fruit juices and starch syrups 5. Pulp and paper industry	Turchetti et al. (2008), Singh et al. (2014)
Cellulases	4	*Cladosporium oxysporum* and *Geomyces* sp.	1. Detergent industry 2. Fuel alcohol production 3. Textile industry 4. Bioremediation	Duncan et al. (2006)
Glucose oxidases	20–25	*Geomyces pannorum* and *Verticillium lecanii*	1. Food technology 2. Bioanalysis	Fenice et al. (1997)
Lipases	20–25	*Aspergillus versicolor*, *Alternaria* sp., *Cladosporium cladosporioides* and *Phoma* sp.	1. Production of fatty acids 2. Detergent industry	Fenice et al. (1997)
Phosphatases	10–30	*Aspergillus niger* and *P. citrinum*	1. Biofertilization	Singh et al. (2011), Gawas-Sakhalkar et al. (2012)
Polygalacturonases	0–60	*Sclerotinia borealis*, *Cryptococcus liquefaciens*, and *Aspergillus japonicus*	1. Food industry 2. Pectin hydrolysis	Takasawa et al. (1997), Abe et al. (2006)
Proteases	2–50	*Aspergillus ustus*, *Cryptococcus gilvescens*, *Mrakia gelida* and *Rhodotorula laryngis*	1. Detergent industry 2. Textile industry	Damare et al. (2006a, b), Turchetti et al. (2008)
Xylanases	4–20	*Criptococcus albidus*	1. Bioconversion of lignocellulosic materials 2. Higher-value products, such as fuel and other Chemicals 3. Production of oligosaccharides	Amoresano et al. (2000)

Zucconi et al. (1996) isolated psychrotolerant *G. pannorum* that hydrolyze starch and produce lipase, urease, extracellular chitinase, that are active at lower than 25 °C. Fenice et al. (1997) reported enzyme production by screening various strains of fungi, isolated from various locations of Victoria (continental Antarctica), including polygalacturonase, pectinase, amylase, cellulose, chitinase, cellulases, phosphatase, glucose oxidase, urease, protease, lipase, RNase, DNase. Takasawa et al. (1997) isolated polygalacturonase from *Sclerotinia borealis* psychrophilic fungi. Various other fungal strains including *G. pannorum* have been documented from Antarctica that produce keratinases (Marshall 1998). Similarly, the *Cadophora*, *Penicillium*, *Geomyces* and *Cladosporium* species were documented for production of extracellular endo-1, 4-β-glucanases at 15 and 4 °C (Duncan et al. 2006). Gawas-Sakhalkar et al.

(2012) analyzed fungal isolates from Arctic soils for the production of phosphatase enzyme, among all the isolates a *Penicillium citrinum* strain PG162 (a cold-tolerant fungus) was documented as best producer of intracellular acid phosphatase. Hassan (2015) screened 77 fungal strains, isolated from Batura, Passu and Siachen glaciers, Pakistan, were found to produce six extracellular enzymes including amylase, cellulase, deoxyribonuclease, lipase, phosphatase and protease. Fungal isolates were good in producing lipase and cellulose. *Sporobolomyces ruberrimus* was able to produce 5 enzymes except phosphatase. For instance, glucose oxidase has a significant application in food technology and bioanalysis is produced by species belonging to *Aspergillus*, *Penicillium*, *Pleurotus*, *Alaromyces* and *Phanerochaete*. However, only three strains like *Aspergillus niger*, *P. chrysogenum* and *Penicillium amagasakiense* are responsible for industrial scale production (Crueger and Crueger 1990).

For reduction of viscosity and clarification of fruit juices at low temperature, cold active pectinases can be used. Mukherjee and Singh (2011) documented that the α-amylase activity were maximum at 20 °C, signifying its use in food industry, in fabric treating and as a detergent additive, baking industry, pulp bleach, desizing denim jeans. Moreover, they can be used in industrial 'peeling' of leather, detergents, food industry, dough fermentation, cheese ripening, baking industry, wine industry, animal feed and molecular biology (Mayordomo et al. 2000).

5.2 Pharmaceutical products

The fungi from temperate and tropical habitats, have been reported for pharmaceutical products production (Schulz et al. 2002), although the metabolites isolated from psychrophilic and psychrotrophic fungi are quite rare. However, to some extent, this aspect of the psychrophilic fungi has been investigated by many researchers. Fungi have been found thriving in the Pacific Ocean floor, where the nutrient availability is low and the sediments are more than 100 million years old. This finding leads to the idea that life is present everywhere and at unusual places and it also creates an opportunity for pharmaceutical companies which are looking for new and more efficient antibiotics to counter the increasing problem of emergence of drug-resistant bacteria.

From point of view of pharmaceutical products, the *Penicillium* species are of a great interest. The *Penicillium* species such as *Penicillium lanosum* and *Penicillium soppii* found in permanently cold soils, can efficiently produce valuable secondary metabolites e.g. griseofulvin and cycloaspeptide A (both are antibiotic compounds with antimicrobial activity) (Frisvad et al. 2006). *Penicillium antarcticum*, a psychrotolerant to mesophilic and halotolerent species (McRae and Seppelt 1999), can produce patulin and asperentins. Several other species including *Penicillium ribium*, *Penicillium rivulorum* and *Penicillium algidum* can produce other secondary metabolites. For instance, *P. ribium* are able to produce a cyclic nitropeptide psychrophilin A as well as cycloaspeptide A and D (Frisvad et al. 2006: Dalsgaard et al. 2004a), while *P. rivulorum* can effectively produce communesin G and H and psychrophilin B and C (Dalsgaard et al. 2004b, 2005a). Similarly, *P. algidum* are capable of producing psychrophilin D and cycloaspeptide A and D (Dalsgaard et al. 2005b). Interestingly, these cyclic peptides are mostly produced by fungi harbor in low temperature habitat. The cyclic peptides have been found with varied biological activities, such as antibacterial activity, immunosuppressive activity, and anti-tumor activity (Joo 2012).

Brunati et al. (2009) revealed the antimicrobial activity of filamentous fungi belonging to fifteen diverse genera. Among 160 fungal strains, 47 fungi exhibit activity against *Staphylococcus aureus*, *E. coli*, *Cryptococcus neoformans* and *Candida albicans*, although, the activity against filamentous fungi and Enterobacteria was low. The skyrin and rugulosin isolated from the Antarctic *P. chrysogenum* are very fascinating and currently these are explored for insecticidal and medical applications (Sumarah et al. 2005).

An antifungal protein, AfAFPR9, was isolated from the *Aspergillus fumigatus* R9, isolated from the South Atlantic sediment sample that possessed antifungal activity against plant pathogenic *Fusarium oxysporum*, *Alternaria longipes*, *Colletotrichum gloeosporioides*, *Paecilomyces variotii* and *Trichoderma viride* (Rao et al. 2015). In an another study, a novel antifungal protein (Pc-Arctin) was purified from *P. chrysogenum* A096 isolated from an Arctic sediment that exhibited antifungal activity against *P. variotii*, *A. longipes* and *T. viride* (Chen et al. 2013).

Newly isolated fungal species, from Batura, Passu and Siachen glaciers, Pakistan, were checked for their antimicrobial activity against multi-drug resistant (MDR) clinically isolated bacterial and fungal strains such as *E. coli* (MDR), *Klebsiella pneumonia* (MDR), *S. aureus* (MDR), *Staphylococcus* sp., *Enterococcus* sp. (Vancomycin resistant *Enterococcus*), *C. albicans* and *A. niger*, respectively. The fungal strains showed good antimicrobial activity against Gram positive bacteria as compared to Gram negative bacterial and fungal strains (Hassan 2015).

5.3 Bioremediation potentials

It has been thought that psychrophilic microorganisms might remediate the waste water and polluted soils in winter season when the endogenous microbial degradative capability is reduced by low temperature. Although, not enough work has been done on the bioremediation potentials of the psychrophilic fungi but it is the need of the time that this aspect of cold-tolerant fungi should be considered for much better exploration. However, Hughes et al. (2007) have studied the Antarctic fungi comprising genera *Trichoderma*, *Phoma*, *Penicillium*, *Trichoderma*, *Mortierella* and *Mollisia* for hydrocarbons and fuel degradation. It was also observed that *Mortierella* species might be capable of using dodecane as sole carbon source. This work indicates the future use of Antarctic fungi for hydrocarbon degradation. According to Adams et al. (2006) fungi are important as decomposers in Antarctic environment. Yergeau et al. (2007) have described the genes responsible for decomposition through microarray survey of the Antarctic Peninsula and recommended that fungi are the prevailing decomposers in the Antarctica.

5.4 Pigment/lipid production

Pigment/lipids produced by cold-tolerant fungi, are usually used to tolerate and face the harsh temperature. Many of the investigators have reported lipids like polyunsaturated triglycerides and fatty acids from fungi that thrive at low temperature mostly (psychrotolerant and psychrophilic) in increased quantity (Weinstein et al. 2000; Weete and Gandhi 1999: Istokovics et al. 1998). Singh et al. (2014) reported a fungal strain, *Thelebolus microsporus*, as a cold tolerant fungus, which can be used for fatty acid and pigment production. Pigment was confirmed as carotenoid through complete analysis. The commercial application of such pigments/lipids is very vast. For instance the linolenic acid is used for enhancement of food for individuals suffering from diabetic neuropathy, eczema and cardiovascular diseases (Singh et al. 2014). Similarly, linoleic acid a key aromatic compound is precursor of 1-octen-3-ol, has been reported in most fungi including *T. microsporus* (Singh et al. 2011, 2014).

5.5 Exopolysaccharide (EPS) production

The Antarctic strain *P. herbarum* Westend CCFEE 5080 was examined and investigated for the production of exopolysaccharide (EPS) (Selbmann et al. 2002). The molecular structure of the EPS was characterized as a β 1–3, 1–6 glucan of 7.4×10^6 Dalton. Commonly, the production of EPS by fungi signifies as a response to harsh environmental condition i.e. it was found that embedded mycelium showed higher ability to grow than the unembedded one after exposing it to repeated freeze and thaw cycles (Selbmann et al. 2002). It has been documented that the meristematic black fungi from Antarctica produce EPS externally to the hyphae or adjacent to conidia, similar to *Friedmanniomyces endolithicus* (Selbmann et al. 2005). Different microbes can produce EPS which is independent of seasonal variations and EPS recovery and purification is relatively easy (Sutherland 1994). Due to their possible bioactive role (Cheung 1996) and rheological behavior (Sutherland 1994), EPS are of great applicability in cosmetic and pharmaceutical industries, food technology and oil recovery (Hisamatsu et al. 1997; Blaicher and Mackin 1995).

5.6 Bio-fertilization capabilities

Phosphorus is a significant nutrient that plays vital role in crop plant yields and development. In nature, phosphorus is present in both organic and inorganic forms. The insoluble inorganic phosphate present in soil is not significant to plants until converted to soluble form. The inorganic phosphorus converted to organic form due to solubilization can be used by plants upon mineralization. Numerous microorganisms are responsible for the conversion of insoluble phosphates to soluble form via chelation and exchange of reaction and acidification (Reyes et al. 2002; Narsian and Patel 2000). A number of bacteria, Actinomycetes and mesophilic fungi that are responsible for phosphate solubilization have been documented from High Arctic glacier, Kanchanaburi (Thailand) (Nenwani et al. 2010; Stibal et al. 2009; Nopparat et al. 2007). Fungi produce organic acid for phosphorus solubilization and have more solubilization efficiency than bacteria (Nenwani et al. 2010). Researchers have tried to encapsulate fungi that are responsible for solubilization of phosphate that have an agricultural and industrial importance (Vassileva et al. 1998). Various microfungal genera including *Aspergillus*, *Penicillium* and *Fusarium* are identified that produce phosphatase (Yoshida and Tamiya 1971; Nozawa et al. 1998; Vassileva et al. 1998; Haas et al. 1991). Similarly, species of Ectomycorrhizal *Hebeloma* (cold- tolerant fungi) has also been revealed to produce cold active acid phosphatases (Tibbett et al. 1998). The cold tolerant phosphate solubilizing fungi has been reported in Arctic soils for the first time by Singh et al. (2011).

6 Conclusions

Psychrophilic and psychrotrophic fungi grow well at low temperature. They have been extensively investigated in Antarctica and Arctic environments but less significantly in non-polar habitats. Various studies have shown that fungi are psychrotrophic in polar and non-polar habitats. They are naturally exposed and subjected to several extreme conditions of very low temperature, high UV-B radiations, frequent freeze and thaw cycles, low water and nutrient availability. The life of fungi is impossible without an active ecological niche constituting proper nutrient cycling among autotrophic and heterotrophic entities. Cold habitats are one of the most extreme environments for survival. The presence of fungus in cod habitats is quite interesting. The possibility of its presence on glaciers can be hypothesized as, ‘to overcome the extreme low temperature environment, fungi adopted all the necessary equipment needed for survival at such an extreme condition’. Under such circumstances, a most important question arises that from where they obtain their food? It can be explained by the fact that on the alpine glaciers, the main sources for nutrition are plants, bacteria, archaea and viruses, and their metabolites produced and released as a result of their interactive ecological cycles. Another point to consider in case of valley glaciers or mountain glaciers is that during summers there is vegetation on the mountain slopes or tops above the glacier valleys and these plants erode with wind and rain and flow down where they are embedded in the glacier body. The microorganisms utilize this plant material as carbon and energy source. Similarly, the rain drains the surface soil of the mountain containing different metals and trace elements down to the glacier, which is then used up by fungus and chemolithotrophs in their normal biochemical pathways. The most important possibility is the interactive ecology of fungi, bacteria, archaea and viruses, which creates an environment, helping in the growth of some microorganisms (including fungi). The viruses as well, in their lytic cycles produce nutrients, for the heterotrophic microorganisms (fungi) by killing other microbes (bacteria etc.). The fungi adapted themselves to harsh conditions of low nutrient and low temperature through various mechanisms. Although, all the physiological and ecological adaptive mechanisms still need more exploration but such adaptability mechanisms include alterations in membrane lipid or fatty acid configuration, an increase production of cold-active enzymes, compatible solutes, trehalose and synthesis of melanin and mycosporine. It is a fact that psychrophilic and psychrotrophic fungi have greater potential of applications in various biotechnological and pharmaceutical fields. They can provide the production of cold-active enzymes, pharmaceutical metabolites, EPS and having a good potential of bioremediation and biofertilization capabilities.

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