



## Fate of mitosporic soil fungi in cold deserts: A review

Skarma Nonzom<sup>1</sup> and Geeta Sumbali<sup>2</sup>

<sup>1,2</sup>Department of Botany, University of Jammu, B.R. Ambedkar Road,  
Jammu-180006 (J&K), INDIA.

**Abstract:** Deserts are apparently lifeless. Yet, they may consist of numerous minute and microscopic habitats and microenvironments that are inhabited by many microorganisms. These may adopt different lifestyles, for example saprotrophs, symbionts or parasites. Some species are cosmopolitan with a wide distribution, while others due to their ecological plasticity may adapt to harsh environments precluded to most of life forms. Since stress allows only the tolerant forms to grow, the microorganisms not only dominate such habitat but also grow sufficiently to impart special visible features to the habitat. In stressing conditions, their role is even more crucial for the recycling of organic matter and uptake of nutrients. When the conditions become extreme and competition is low, fungi focus on extremotolerance and evolve peculiar competences to exploit natural or xenobiotic resources in the particular constraints imposed by the environment. The study of fungi in the natural extreme environments may be of valuable biotechnological potential for the production of extremozymes, specific metabolites and for their exploitation in bioremediation programmes.

**Key words:** mitosporic soil fungi, cold desert, adaptations, importance

### I. Introduction

Mitosporic fungi represent more than half of the Ascomycota and are very important as parasites and saprophytes. This group of fungi produce their spores asexually (conidia or oidia) or by budding and generally fall in two groups: species that lack the morphology of sex altogether and make only mitospores or no spores at all, and those that can make sexual structures with meiospores, but only rarely. In nature, both groups are usually encountered only in their mitosporic states. They are commonly known as imperfect fungi (Deuteromycetes) because they do not fit into the commonly established taxonomic classifications of fungi that are based on biological species concepts or morphological characteristics of sexual structures. The Deuteromycota (Greek for "second fungi") was once considered as a formal phylum of the Kingdom Fungi. However, now it is used informally to denote species of fungi that are asexually reproducing members of the fungal Phyla Ascomycota and Basidiomycota. Initially, these organisms were segregated in the Fungi Imperfecti or Deuteromycota and generally assumed to be clonal with very widespread distribution. In the last decade, analysis of nucleic acid has shown that mitosporic fungi can be classified with their meiosporic relatives and can recombine in nature and show genetic differentiation and isolation as do meiosporic fungi. There are about 25,000 species that have been classified in the Deuteromycota and many of them are Basidiomycota or Ascomycota anamorphs.

Mitosporic fungi are generally easily dispersed and are able to colonize a wide variety of substrates and can withstand many different environmental conditions. They are particularly skilled in colonizing as they persist in novel environments, use novel resources and form novel associations, taking advantage of the suites of traits that they carry at the time of encountering new conditions. This process known as ecological fitting works very well with fungi due to their ecological, biological and morphological plasticity [1]. Fungi have many different functions in soils, which include both active roles, such as, degradation of dead plant material, and inactive roles where propagules are present in the soil as resting states. Fungi also play an important role in biogeochemical cycling of the elements (e.g., carbon, nitrogen, phosphorus, sulphur, etc.), which is interlinked with their ability to adopt a variety of growth, metabolic and morphological strategies, their adaptive capabilities to environmental extremes and their mutualistic associations with animals, plants, algae and cyanobacteria [2]. The saprobic fungi represent the largest proportion of fungal species in soil and they perform a crucial role in the decomposition of plant structural polymers, such as, cellulose, hemicelluloses and lignin, thus contributing to the maintenance of global carbon cycle [3]. Fungi are also major biodeteriorating agents of stone, wood, plaster, cement and other building materials, and it is now realized that they are important components of rock-inhabiting microbial communities with significant roles in mineral dissolution and secondary mineral formation [2]. In semidesert and desert environments, where primary production is greatly reduced, soil microorganisms experience not only physical stress, but also the harsh oligotrophic conditions. However, it is known that fungi are not only able to survive but are also able to propagate in various environmental extremes [4].

## II. Exploration of extreme environments by fungi

Most of the fungi exhibit a filamentous growth habit, which provides the ability to adopt both explorative and exploitative growth strategies and the formation of linear organs of aggregated hyphae for protected fungal translocation [2]. Some fungi are polymorphic, occurring as both filamentous mycelium and yeast-like cells, as in black meristematic or microcolonial fungi colonizing rocks [5-6]. Fungi can also grow inside their own parental hyphae, utilizing dead parts of the colony under the protection of parental cell walls [6]. This unique ability of fungi to translocate nutrients through the mycelial network is an important feature for exploring extreme environments [7-8].

Fungi may thrive in unusual environments, which range from extremely dry and cold deserts in the Antarctic and other very cold areas worldwide [9], highest mountain peaks [10] to deep permafrost soils [11-12], geothermal and humid soils in volcanic areas [13], acid mine drainages with sulphuric acid [10-14] or in the highly alkaline sites [15]. An extreme environment is defined as “one that differs considerably from the range of culture conditions that we believe is normal, either in natural settings or in the laboratory” [16]. Instead of calling these environments extreme, they preferred to call them “stressful” where certain abiotic factor(s) imposed a condition that restricts or prevents growth of most organisms. Environments with extreme physicochemical parameters were thought of as being hostile until microbiologists discovered that they are actually inhabited by a wide diversity of microorganisms [17]. Organisms that survive and thrive under conditions that are detrimental to the majority of other species have become a focus of increasing scientific attention over the last few years, with some ground breaking discoveries of stress tolerating mechanisms [17]. Extremophiles are promising models to further strengthen our understanding of the functional evolution of stress adaptation. Their biology widens our views on the diversity of terrestrial life and it has come as a surprise that not only prokaryotes but also eukaryotes have a great capacity to adapt to extreme conditions [17].

## III. Mitosporic fungi from cold deserts

Ice in nature has long been considered as only enclosing those microorganisms, which have been randomly deposited on its surface [18]. However, it is now known that different types of ice such as snow, glacial ice and sea ice provide environments that can support active microbial growth and reproduction [19-22]. In particular, several fungal species have been isolated in considerable numbers from subglacial ice of polythermal glaciers [4]. In cold deserts, for example, in the dry valleys of Antarctica, fungi are widely distributed in the soil but with low abundance [23]. Endemic fungi have been found associated with wood of historic expedition huts on Ross Island [24]. Similarly, in the dry polar desert soils, only yeasts have been found as endemic species [25]. In these extreme and isolated areas, endemic species showing physiological and morphological adaptations have locally evolved. It has been observed that 0°C is not in itself an extreme condition and that cold environments may be considered extreme only if another factor creates adverse conditions, for example, low water activity in arid Antarctic soil, low nutrient availability and high pressure in the deep sea [26].

Low temperature is the major stress factor that exerts a strong direct and indirect effect on microbial life processes by inducing different adaptation strategies and the establishment of psychrotrophic and psychrophilic forms. A psychrophile is defined as an organism capable of growth at or below 0°C but unable to grow above 20°C, whereas a psychrotolerant (also termed psychrotrophic) organism is capable of growth at around 0°C and can also grow above 20°C [27]. Under low temperature environments, the importance and distinction between psychrophiles and psychrotrophs or psychrotolerants have also been recognized [28]. Psychrotolerant microbes are important in high-altitude agroecosystems since they survive and retain their functionality at low temperature conditions, while growing optimally at warmer temperatures [29]. Low temperature creates other stress conditions, for example, water is biologically unavailable when frozen. It is also assumed that due to prevailing low nutrient conditions, fungi live in soil as dormant propagules that become active when fresh organic matter enters the ecosystem. Extremely low temperatures not only restrict microbial enzyme activity and membrane integrity [30-31], but also constrain the availability of liquid water for the hydration of biomolecules and as a medium for biochemical processes [32].

True psychrophilic microorganisms are restricted to permanently cold habitats, such as oceans, polar areas, alpine soils and lakes, snow and ice fields and caves as they have optimum temperatures of 16°C and a maximum growth temperature of 20°C, but they can also grow at 0°C. Psychrotolerant microorganisms, in contrast, have maximum growth temperatures above 20°C, although they can grow at 10°C. Well known psychrophilic and psychrotolerant fungi are found in genera such as *Alternaria*, *Cladosporium*, *Keratinomyces*, *Leptomit*, *Penicillium*, etc [26]. In polar regions, the occurrence of fungi is coupled to water availability, just like that in the warm desert ecosystems. Yeasts tend to predominate in the undisturbed areas of dry interior valleys of Antarctica. *Cryptococcus albidus* is one of the most prevalent psychrophilic species [33]. However, as research activity has increased at the poles, some previously unknown fungi have been detected. For example, Cameron [33] listed two species of Phycomycetes; two species of Ascomycetes; 27 species of mitosporic Ascomycetes, of which *Chrysosporium*, *Penicillium* and *Phialophora* represented the majority of the taxa. In addition, they also found 10 species of yeasts from the Antarctic soils. Species diversity of fungi isolated from

dry Arctic soils was similar to that from dry regions of Antarctica [34]. Onofri [35] reported that in Antarctica, 0.6% of the known fungal species were water molds (Kingdom Chromista) and 99.4% were composed of true fungi including yeasts (unicellular organisms) and filamentous fungi from the Phyla Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota. A key study that included Dry Valley sites revealed that some locations (e.g., Mt Fleming and Allan Hills) supported cultivable free living soil fungi including *Cryptococcus antarcticus*, *C. friedmannii*, *C. vishniacii* and *Candida parapsilosis* [36]. Most of the fungi recorded in the Antarctic continent are anamorphic forms. This may be attributed to the fact that the fungi gave up sexual reproduction as this simplification means that life cycles can be concluded in a shorter time and without metabolic costs.

There is evidence that as temperature falls, the changing strengths of different types of molecular interactions can cause proteins to denature [37] and even the enzymes that remain properly folded, may slow or halt the release of reaction products [38-39]. Many microbes exhibit optimization of turnover rate relative to substrate binding and increased thermolability, such as, lower denaturing temperatures [39]. There is also evidence that different extracellular enzymes with lower thermal maxima are expressed when fungal cells are chilled [40-41] and that membrane composition is altered at low temperature [42-44]. However, the physiological and ecological mechanisms in cold-tolerant fungi that permit low temperature growth are still not fully understood [30-46].

#### IV. Mitosporic fungi from cold desert soils of India

The cold desert area in India covers 12 out of 131 desert blocks in India and is spread over an approximate area of 74, 809 sq. kms. This includes regions of Leh and Kargil districts of Ladakh in Jammu & Kashmir and Lahaul and Spiti along with some parts of Chamba and Kinnaur districts of Himachal Pradesh. Only few studies have been conducted on the soil mycoflora in the cold deserts in India. Sagar [48] isolated 45 species of fungi from the rhizosphere of various plants of the cold desert areas of Himachal Pradesh. Also, Deshmukh [49] and Kotwal [50] isolated keratinophilic from selected soils of Ladakh. Recently, Nonzom [51] isolated 32 mitosporic fungi from the cold arid base soil of Moonland landscape, Ladakh. It must be emphasized that it is impossible to accomplish an exhaustive survey of the soil mycoflora. Due to different growth rates, it is very difficult to recover some of the fungal species. It is well known that the dilution plate method, which is widely used in soil mycological investigations, favours isolation of heavily sporulating fungi [52]. But in the highly stressful habitats, some fungi lose their dominant position, and the contribution of slower-reproducing but stress-selected micromycetes (such as most of melanin-containing species) in the community structure becomes much more significant.

#### V. Role of melanins in the survival of fungi inhabiting extreme environment

Sometimes single strategies are not specific for single stress factors but may allow the microorganisms to cope with more than one unfavourable condition. Many fungi constitutively synthesize melanin [53], which is likely to confer a survival advantage in the environment [54] by protecting against UV and solar radiation [55]. In fungi, melanin is an important protective factor against the adverse effects of environmental stresses, such as UV radiation, drying, high concentrations of salts, heavy metals, and radionuclides. The presence of melanin allows fungi to exist under the influence of high electromagnetic radiation, for example, in high mountain regions, desert soils, and on plant surfaces. Recently, the dominance of melanised fungi such as *Ulocladium*, *Alternaria*, *Cladosporium*, *Drechslera*, *Humicola* was observed in the cold deserts of moonland landscape, Ladakh [51]. Under extreme conditions, the proportion of melanized fungi in mycobiota usually increases, for example, in ecotopes contaminated with radionuclides [56-59]. It has been shown experimentally those dark colored spores of many fungi are resistant to UV irradiation [60-61]. The presence of melanin pigments ensures a high survival rate during high levels of UV radiation, while non-pigmented forms die within a few minutes. Melanised fungi also exhibit improved resistance to high concentrations of salts. *Hortaea werneckii*, *Phaeothea triangularis*, *Trimmatostroma salinum*, *Aureobasidium pullulans*, and *Cladosporium* species live in salters and are able to tolerate high (close to saturation) salt concentrations [62]. For some types of these fungi (*Hortaea werneckii*, *Phaeothea triangularis* and *Trimmatostroma salinum*), hypertonic sodium chloride solutions are their natural environment [63]. Further, it has been suggested that the presence of melanin in the cell wall of *H. werneckii* reduces the flow of salt into the cell [63].

The presence of melanin also ensures the survival of microscopic fungi under the conditions of technogenic pollution. In industrial and roadside areas, an increase in the proportion of dark colored melanin containing fungi, which were more resistant to contamination in urban areas by heavy metals and unsaturated hydrocarbons, was observed [64-65]. Similarly, in the air and snow samples of urban areas, representatives of the genera *Cladosporium* and *Alternaria* were dominant [66]. Radionuclide contamination led to a change in fungal communities, an increased proportion of melanised fungi, and a reduced diversity of species [58-67]. Most common in contaminated zones were the species of *Cladosporium*, *Ulocladium*, *Stachybotris* and *Humicola*. Some of the widely available species included *Cladosporium sphaerospermum*, *C. herbarum*, *C.*

*cladosporioides*, *Alternaria alternata*, and *Aureobasidium pullulans* [58-68]. Melanized fungi (mainly *Cladosporium* spp., *A. alternata*, *A. pululans*, and *Hormoconis resinae*) have been found even in environs of destroyed reactor in Chernobyl [68]. The distribution of melanized fungi in areas with high levels of radiation undoubtedly reflects their advantage over light colored fungal species. However, a majority of the basic mechanisms of radiation resistance of living organisms are not currently established [69].

There are three main types of melanins: eumelanins (black and dark colored polymers), pheomelanins (yellow and red polymers), and the most heterogeneous group of allomelanins, including soluble piemelanins [70]. In fungi, there are melanins of all three types [70-71]. Despite the difference in their origins, melanin pigments have a number of common characteristics that allow them to fulfill their protective function. Melanins are chemically stable compounds that are not soluble in water and organic solvents. They can form a solution in an alkaline medium and are discolored in the presence of strong oxidants. The presence of quinoid groups explains the presence of paramagnetic centers and the ability of melanin pigments to deactivate free radicals and peroxides and absorb heavy metals and toxic electrophilic metabolites. These pigments exhibit strong antioxidant properties [72-74]. Melanin containing cells are more resistant to H<sub>2</sub>O<sub>2</sub> and NO [75]. The gene expression of melanin synthesis enzymes increases the resistance of fungi to oxidants [76]. A hypothesis that melanins trap free radicals formed during the radiolysis of water by radiation was suggested for the mechanism of radioprotective action [77-78]. It was also assumed that melanin pigments participating in redox reactions are able to perceive the energy of radiation (UV, visible light, and radiation) and make it available for metabolic processes [58, 79-80]. Probably, this explains the activation of metabolic processes and the growth of fungal hyphae under the influence of different types of radiation, found in melanin containing fungi [79, 81]. It was also shown that irradiating melanin caused its oxidation, which was more expressed in the presence of reducing agents, such as ascorbate [82]. This confirms the possibility of participation of melanin in active electron transfer in living cells and the existence of a hypothetical mechanism of transfer of radiation energy for the maintenance of metabolic processes. Further research in this area can provide a better understanding of the nature of the radio and UV protective effect of melanin.

Melanized microorganisms inhabit some remarkably extreme environments including high altitude, Arctic and Antarctic regions with the latter habitats being characterized by the naturally occurring higher radiation levels than those at lower altitudes [83]. First reports on black fungi with aggregated micro-colonies in cold deserts of Antarctica were published by Friedmann [84] and Friedmann [85]. Black fungi share a number of universally present characters such as strong melanization, thick and multi-layered cell walls and production of exopolysaccharides, which result in an extraordinary ability to tolerate chemical and physical stress [86]. It is likely that such strategies allow fungi of both cold and hot deserts to withstand strong shifting in environmental conditions [87]. According to Ma [88], black fungi have a worldwide distribution especially in places where environmental conditions are extreme due to extreme temperature, low nutrient availability, high radiation and lack of water. Rocks inhabiting black fungi together with some lichens are today assumed to be the most stress resistant eukaryotic organisms known on the Earth [89]. Experiments have shown that their stress resistance against solar radiation, radioactivity, desiccation and oligotrophic conditions even allows them to survive in space [90]. For this reason, black fungi are now model organisms for Astrobiology [90].

The most extensive work on diversity and taxonomy of microcolonial fungi from the Antarctic environment was done by Onofri [91] and Selbmann [9] who isolated and described black fungal species from the Antarctic desert. Melanin is more prevalent in aerial fungi living on the leaves and rocks [92-93]. Infact, melanins produced by *Cladosporium* and *Oidiodendron* species protect against UV and gamma radiation [94] and also against artificial solar irradiation [95]. Similarly, Ursi [93] noted preponderance of black fungi on and within rocks sampled in Europe and proposed that this was because of the protective effects of melanin against UV, sunlight and desiccation. Melanin is also known to protect certain fungi against lysis in natural soils. For example, cell wall melanin of the conidia of *Cochliobolus sativus* is known to protect them against lysis in natural soils and by lytic enzyme preparations [96]. There are also some reports, which indicate that microbial melanin protects against extremes of temperature [97-98].

## VI. Soil factors affecting mitosporic fungi inhabiting cold deserts

The number and kind of microorganisms present in the soil depend on many environmental factors, such as, amount and type of available nutrients, available moisture, degree of aeration, pH, temperature, etc. Microorganisms respond to nitrogen [99-100], organic matter [101-102] and soil moisture [100-103]. Their abundance in soil varies spatially as well as temporally, and this pattern is related to temporal and spatial variations in the quantity and quality of nutrients [100, 104]. Among the various nutrients, organic carbon, nitrogen, phosphorous and potassium are very important for fungi. In the absence of any one of these, the growth and sporulation of fungi and other microorganisms gets hampered. Magnesium, manganese and iron though needed in very small quantities, are also essential [05]. The availability of other micro nutrients such as, Fe, Mn, Cu and Zn in 1–25 ppm concentration is also essential [106]. In addition, soil temperature, pH and moisture are some of the major factors affecting fungal population and diversity [107]. Onofri [108] observed a



strong influence of the amount of carbon source on the growth and antibiotic activity of fungi in Antarctic rocks and soil. Fernandez [109] showed temperature and moisture to be the dominant abiotic controls of soil respiration in the cold desert of southeastern Utah. In a recent study, Nonzom [110] observed that the soil physico-chemical properties such as electrical conductivity, texture, pH, also affect the soil mitosporic diversity in the cold desert of Ladakh. In addition, they also observed the influence of macronutrients such as nitrogen, carbon, organic matter, etc and micronutrients such as iron, zinc, manganese and copper on the diversity and distribution of mitosporic fungi [110].

## VII. Importance of mitosporic fungi inhabiting extreme cold environments

The beneficial effects of soil microorganisms are manifold and range from nitrogen fixation and organic matter decomposition to breakdown of metabolic byproducts and agrochemicals enhancing the bioavailability of nitrates, sulphates, phosphates and essential metals [111]. Fungi, together with bacteria, are responsible for most of the recycling, which returns dead material to the soil in a form in which it can be reused. Fungi are considered general manager in nutrient recycling department of nature without which the recycling activities would be seriously reduced. The fungal populations are correlated with the nitrogen levels and moisture of the soil [112]. Fungi have 40–55% carbon use efficiency so they store and recycle more carbon (C) compared to bacteria and help recycle both nitrogen (N) and phosphorus (P) to plants. Due to their smaller size and much greater surface area, fungi can efficiently scavenge for N and P better than plant root hairs and greatly increase the plant root nutrient extraction efficiency. Fungi perform enormous functions in various fields including ecological, pharmaceutical, industrial, agricultural, food and beverage industries, biocontrol, bioremediation, etc.

Apart from their disease causing nature [113], soil fungi have many beneficial effects including their role in the industrial area [114–116]. Fungi perform important services related to water dynamics, nutrient cycling and disease suppression. Along with bacteria, fungi are important as decomposers (Nature's recyclers) in the soil food web, converting hard to digest organic material into usable forms. As decomposers, they play most important role in our economy because fertility of soil greatly depends on microbial activity.

Fungi, particularly mitosporic fungi, are important producers of biologically active molecules, including cyclosporin A, the immune-suppressant drug used in organ transplant operations, lovastatin the cholesterol-reducing substance and a group of antibiotics, which include cephalosporin, griseofulvin, sordarin, fusidic acid, etc., that possess several antibacterial and antifungal activities.

Fungi serve as the source of commercially important enzymes and natural products ranging from abscisic acid to zymosterol that result in a billion dollar industry [117–118]. Therefore, fungal fermentation processes for a variety of enzymes such as protease, pectinase, cellulase, lipolase, amylase, etc., have been standardized on a large scale and several commercial scale plants established for their manufacture. They are increasingly used to ferment solid organic waste substrates into usable products such as methane and fertilizers [119] and are invaluable as substitutes for chemicals in the pulp and paper industry [120]. Fungal species screened for secondary metabolites using modern techniques are less than 1% of those that may exist [121]. Thus, the potential is enormous for the discovery of valuable natural products resulting from a directed search and screening of fungi from unexplored habitats.

## VIII. Conclusion

These findings provide important insights that aid our understanding of the diversity and distribution of mitosporic fungi in natural ecosystems and their adaptations in these extreme habitats. Information on fungal diversity and functions in extreme habitats might provide scope for bioprospecting of new source of drugs and other industrially important biomolecules and enzymes. Due to their enormous stress tolerance, desert fungi could also be a promising source for new biotechnological and medical adaptations, as for example protective agents against oxidative stress. Despite the severe conditions of cold deserts, the overall portrait shows a relatively rich mycoflora, more diversified than one might expect. They show a range of morphological and physiological adaptations, similar to those adopted by other taxa from different extreme environments. One such adaptation of considerable importance is melanisation, which confers significant survival advantage in such hostile environments. It is probable that these fungi have been possibly selected among a highly diversified mycoflora, originally present in such environments. These positively selected microfungi appear as the predominant group in these environments because they are benefited by their extremotolerance ability and the absence of faster growing competitors.

## Acknowledgements

The first author is grateful to University Grants Commission (UGC), New Delhi for the financial assistance in the form of Rajiv Gandhi National Fellowship (RGNF), which facilitated the study.

## References

- [1]. Agosta SJ and Klemens JA (2008). Ecological fitting by phenotypically flexible genotypes: Implications for species associations, community assembly and evolution. *Ecological Letters*, 11: 1123–1134.
- [2]. Fomina M, Burford EP and Gadd GM (2005). Toxic metals and fungal communities. In: "The Fungal Community: Its Organization and Role in the Ecosystem." (Eds: Dighton J, White JF and Oudemans P), CRC Press, Boca Raton, pp. 733–758.

- [3]. Saravanakumar K and Kaviyarasan K (2010). Seasonal distribution of soil fungi and chemical properties of Montane wet temperate forest types of Tamil Nadu. *African Journal of Plant Science*, 4: 190-196.
- [4]. Gunde-Cimerman N, Sonjak S, Zalar P, Frisvad JC, Diderichsen B and Plemenitas A (2003). Extremophilic fungi in Arctic ice: a relationship between adaptation to low temperature and water activity. *Physics and Chemistry of Earth*, 28: 1273-1278.
- [5]. Sterflinger K (2000). Fungi as geologic agents. *Geomicrobiology Journal*, 17: 97-124.
- [6]. Gorbushina AA, Whitehead K, Dornieden T, Niesse A, Schulte A and Hedges JI (2003). Black fungal colonies as units of survival: hyphal mycosporines synthesized by rock-dwelling microcolonial fungi. *Canadian Journal of Botany*, 81: 131-138.
- [7]. Boswell GP, Jacobs H, Davidson FA, Gadd GM and Ritz K (2003). Growth and function of fungal mycelia in heterogeneous environments. *Bulletin of Mathematical Biology*, 65: 447-477.
- [8]. Jacobs H, Boswell GP, Scrimgeour CM, Davidson FA, Gadd GM and Ritz K (2004). Translocation of carbon by *Rhizoctonia solani* in nutritionally-heterogeneous environments. *Mycological Research*, 108: 453-462.
- [9]. Selbmann L, de Hoog GS, Mazzaglia A, Friedmann EI and Onofri S (2005). Fungi at the edge of life: Cryptoendolithic black fungi from Antarctic deserts. *Studies in Mycology*, 51: 1-32.
- [10]. Selbmann L, de Hoog GS, Zucconi L, Isola D, Ruisi S and Gerrits van den Ende AHG (2008). Drought meets acid: Three new genera in a dothidealean clade of extremotolerant fungi. *Studies in Mycology*, 61: 1-20.
- [11]. Gilichinsky DA, Wilson GS, Friedmann EI, McKay CP, Sletten RS and Rivkina EM (2007). Microbial populations in Antarctic permafrost: Biodiversity, state, age, and implication for astrobiology. *Astrobiology*, 7: 275-311.
- [12]. Zucconi L, Selbmann L, Buzzini P, Turchetti B, Guglielmin M and Frisvad JC (2011). Searching for eukaryotic life preserved in Antarctic permafrost. *Polar Biology*, 5: 749-757.
- [13]. Appoloni S, Lekberg Y, Tercek MT, Zabinski CA and Redecker D (2008). Molecular community analysis of arbuscular mycorrhizal fungi in roots of geothermal soils in Yellowstone National Park (USA). *Microbial Ecology*, 56: 649-659.
- [14]. Baker BJ, Lutz MA, Dawson SC, Bond PL and Banfield JF (2004). Metabolically active eukaryotic communities in extremely acidic mine drainage. *Applied and Environmental Microbiology*, 70: 6264-6271.
- [15]. Nagai K, Suzuki K and Okada G (1998). Studies on the distribution of alkalophilic and alkali-tolerant soil fungi II: Fungal flora in two limestone caves in Japan. *Mycoscience*, 39: 293-298.
- [16]. Zak JC and Wildman HG (2004). Fungi in stressful environments. In: "Biodiversity of fungi: inventory and monitoring methods." (Eds: Mueller GM, Bills GF and Foster MS), New York: Elsevier Academic Press, pp. 303-315.
- [17]. Gostincar C, Grube M, De Hoog S, Zalar P, Gunde-Cimerman N (2009). Extremotolerance in fungi: Evolution on the edge. *Fems microbiology ecology*, 71 (2-11).
- [18]. Ma LJ, Rogers SO, Catranis CM and Starmer WT (2000). Detection and characterization of ancient fungi entrapped in glacial ice. *Mycologia*, 92: 286-295.
- [19]. Christner BC, Mosley-Thompson E, Thompson LG, Zagorodnov V, Sandman K and Reeve JN (2000). Recovery and identification of viable bacteria immured in glacial ice. *Icarus*, 144: 479-485.
- [20]. Price PB and Sowers T (2004). Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proceedings of the National Academy of Science USA*, 101: 4631-4636.
- [21]. Rohde RA and Price PB (2007). Diffusion-controlled metabolism for long-term survival of single isolated microorganisms trapped within ice crystals. *Proceedings of the National Academy of Science USA*, 104: 16592-16597.
- [22]. Price PB (2009). Microbial genesis, life and death in glacial ice. *Canadian Journal of Microbiology*, 55: 1-11.
- [23]. Vishniac HS (1996). Biodiversity of yeasts and filamentous microfungi in terrestrial Antarctic ecosystems. *Biodiversity and Conservation*, 5: 1365-1378.
- [24]. Blanchette RA, Held BW, Jurgens JA, Mcnew DL, Harrington TC, Duncan SM and Farrell RL (2004). Wood-destroying soft rot fungi in historic expedition huts of Antarctica. *Applied and Environmental Microbiology*, 70: 1328-1335.
- [25]. Vishniac HS (1993). The microbiology of Antarctic soils. In: "Antarctic Microbiology." (Ed: Friedmann EI), Wiley-Liss Inc, New York, USA, pp. 297-342.
- [26]. Gounot AM (1986). Psychrophilic and psychrotrophic microorganisms. *Experientia*, 42: 1192-1197.
- [27]. Cavicchioli RK, Siddiqui S, Andrews D and Sowers KR (2002). Low temperature extremophiles and applications. *Current Opinion in Biotechnology*, 13: 1-9.
- [28]. Margesin R (2009). Effect of temperature on growth parameters of psychrophilic bacteria and yeasts. *Extremophiles*, 13: 257-262.
- [29]. Mishra PK, Bisht SC, Bisht JK and Bhatt JC (2012). Cold-tolerant PGPRs as bioinoculants for stress management." In: "Bacteria in Agrobiological: Stress Management." (Ed: Maheshwari DK), Springer, Berlin, Germany, pp. 95-118.
- [30]. Russell NJ (1990). Cold adaptation of microorganisms. *Philosophical Transactions of the Royal Society, London B*, 326: 595-611.
- [31]. Crowe JH, Hoekstra FA, Crowe LM (1992). Anhydrobiosis. *Annual Review of Physiology*, 54: 579-599.
- [32]. Wynn-Williams DD and Edwards HGM (2000). Antarctic ecosystems as models for extraterrestrial surface habitats. *Planet Space Science*, 48: 1065-1075.
- [33]. Cameron RE, Honour RC and Morelli FA (1976). Antarctic microbiology- preparation for Mars life detection, quarantine and back contamination. In: "Extreme Environments: Mechanisms of Microbial Adaptation." (Ed: Heinrich MR), Academic Press, New York, pp. 57-84.
- [34]. Bergero R, Girlanda M, Varese GC, Intili D and Luppi AM (1999). Psychrooligotrophic fungi from Arctic soils of Franz Joseph Land. *Polar Biology*, 21: 361-368.
- [35]. Onofri S, Selbmann L, Zucconi L and Pagano S (2004). Antarctic microfungi as models for exobiology. *Planetary and Space Science*, 52: 229-237.
- [36]. Arenz BE, Held BW, Jurgens JA, Farrell RL and Blanchette RA (2006). Fungal diversity in soils and historic wood from the Ross sea region of Antarctica. *Soil Biology and Biochemistry*, 38: 3057-3064.
- [37]. Franks F, Mathias SF, Hatley RHM, Baust JG, Hvidt A, Chapman D and Jaenicke R (1990). Water, temperature and life (and discussion). *Philosophical Transactions of the Royal Society of London B*, 326: 517-533.
- [38]. Feller G, Arpigny JL, Narinx E and Gerday C (1997). Molecular adaptations of enzymes from psychrophilic organisms. *Comparative Biochemistry and Physiology Part A: Physiology*, 118: 495-499.
- [39]. Gerday C, Aittaleb M, Arpigny JL, Baise E, Chessa JP, Garsoux G, Petrescu I and Feller G (1997). Psychrophilic enzymes: a thermodynamic challenge. *Biochimica et Biophysica Acta*, 1342: 119-131.
- [40]. Tibbett M, Grantham K, Sanders FE, Cairney JW, 1998. Induction of cold active acid phosphomonoesterase activity at low temperature in psychrotrophic ectomycorrhizal *Hebeloma* spp. *Mycological Research* 102: 15330-1539.
- [41]. Tibbett M, Sanders FE, Cairney JW, Leake JR, 1999. Temperature regulation of extracellular proteases in ectomycorrhizal fungi (*Hebeloma* spp.) grown in axenic culture. *Mycological Research* 103: 707-714.
- [42]. Kerekes R and Nagy G (1980). Membrane lipid composition of a mesophilic and psychrophilic yeast. *Acta Alimentaria*, 9: 93-98.

- [43]. Hammonds P and Smith SN (1986). Lipid composition of a psychrophilic, a mesophilic and a thermophilic *Mucor* species. Transactions of the British Mycological Society, 86: 551-560.
- [44]. Weinstein RN, Montiel PO and Johnstone K (2000). Influence of growth temperature on lipid and soluble carbohydrate synthesis by fungi isolated from fellfield soil in the maritime Antarctic. Mycologia, 92: 222-229.
- [45]. Smith D (1993). Tolerance to freezing and thawing. In: "Stress Tolerance of Fungi." (Ed: Jennings DH). Marcel Dekker Inc, New York, USA, pp. 145-171.
- [46]. Cairns AJ, Howarth CJ and Pollock CJ (1995). Submerged batch culture of the psychrophile *Monographella nivalis* in a defined medium, growth, carbohydrate utilisation and responses to temperature. New Phytologist, 129: 299-308.
- [47]. Snider CS, Hsiang T, Zhao G and Griffith M (2000). Role of ice nucleation and antifreeze activities in pathogenesis and growth of snow molds. Phytopathology, 90: 354-361.
- [48]. Sagar A, Raghwa S, Bhallan T and Lakhanpal T (2007). Studies on the mycoflora of cold desert area of Himachal Pradesh. Indian Phytopathology, 60: 35-41.
- [49]. Deshmukh SK, Verekar SA and Shrivastav A (2010). The occurrence of keratinophilic fungi in selected soils of Ladakh (India). Natural Science, 2: 1247-1252.
- [50]. Kotwal S and Sumbali G (2011). Incidence of myco-keratinophiles in cold arid soil at high altitude khardung village of Ladakh, India. Journal of Mycology and Plant Pathology, 41: 72-76.
- [51]. Nonzom S and Sumbali G (2015). Incidence and diversity spectrum of mitosporic fungi from the cold arid base soil of Moonland landscape (Ladakh), India. International Journal of Pharma and Biosciences, 6: 252-261.
- [52]. Andrews JH (1992). Fungal life-history strategies. In: "The fungal community, its organization and role in the ecosystem." (Eds: Carroll GW and Wicklow DT), Marcel Dekker, New York, pp. 119-145.
- [53]. Jacobson ES (2000). Pathogenic roles for fungal melanins. Clinical Microbiology Reviews, 13: 708-717.
- [54]. Steenbergen JN, Shuman HA and Casadevall A (2001). *Cryptococcus neoformans* interactions with amoebae suggest an explanation for its virulence and intracellular pathogenic strategy in macrophages. Proceedings of the National Academy of Sciences USA, 98: 15245-15250.
- [55]. Nosanchuk JD, and Casadevall A (2003). The contribution of melanin to microbial pathogenesis. Cell Microbiology, 5: 203-223.
- [56]. Zhdanova NN and Vasilevskaya AI (1988). Melanin Containing Fungi under Extreme Conditions, Kiev: Naukova Dumka.
- [57]. Zhdanova NN, Zakharchenko VA and Hasel Wandter K (2005). In: "The Fungal Community, Its Organization and Role in the Ecosystem." (Eds: Dighton J, White JF and Oudemans P), Baton Rouge: CRC Press, pp. 759-768.
- [58]. Dighton J, Tugay T and Zhdanova, N (2008). Fungi and ionizing radiation from radionuclides, FEMS Microbiology Letters, 2: 109-120.
- [59]. Grishkan I (2011). Ecological stress: Melanization as a response in fungi to radiation. In: "Extremophiles Handbook." (Ed: Horikoshi K), Tokyo: Springer Verlag, pp. 1135-1146.
- [60]. Rast DM, Stussi H, Hegnauer H and Nyhlen LE (1981). In: The Fungal Spore: Morphogenetic Controls. (Eds: Turian G and Hohl HR), London: Academic Press, pp. 507-531.
- [61]. Mirchink TG (1988). Pochvennaya mikologiya (Soil Mycology), Moscow: Izd. Mosk. Gos. Univ.
- [62]. Gunde Cimerman N, Zalar P, de Hoog S and Plemenitas (2000). Hypersaline waters in salterns-natural ecological niches for halophilic black yeasts. FEMS Microbiology Ecology, 32: 235-240.
- [63]. Kogej T, Stein M, Volkman M and Gorbushina AA, Galinski EA and Gunde Cimerman N (2007). Osmotic adaptation of the halophilic fungus *Hortaea werneckii*: role of osmolytes and melanization. Microbiology, 153: 4261-4273.
- [64]. Kul'ko AB and Marfenina OE (2001). The distribution of microscopic fungi along Moscow roads. Microbiology (Moscow), 70: 709-713.
- [65]. Marfenina OE, Kul'ko, AB, Ivanova AE and Sogonov MV (2002). Fungi in Urban Environments. Mikologia Fitopatologia, 36: 22-32.
- [66]. Kul'ko AB and Marfenina OE (1998). Microbiology (Moscow), vol. 67, no. 4, pp. 470-472.
- [67]. Zhdanova NN, Tugay T, Dighton J, Zheltonozhsky V and McDermott P (2004). Ionizing radiation attracts soil fungi. Mycological Research, 108: 1089-1096.
- [68]. Karpenko YuV, Pavlichenko AK, and Zhdanova NN (2006). In: "Uspekhi meditsinskoi mikologii (Advances in Medical Mycology)". (Ed: Sergeev YuV) Moscow: Nats. Akad. Mikol. 7: 46-47.
- [69]. Gwin KR and Battista JR (2012). Extremophiles: Microbiology and Biotechnology. (Ed: Anitori RP) Norfolk: Caister Academic Press, pp. 25-52.
- [70]. Plonka PM and Grabacka M (2006). Melanin synthesis in microorganisms-biotechnological and medical aspects. Acta Biochimica Polonica, 53: 429-443.
- [71]. Singh S, Malhotra AG, Pandey, A, and Pandey KM (2013). Computational model for pathway reconstruction to unravel the evolutionary significance of melanin synthesis. Bioinformation, 9: 94-100.
- [72]. Korytowski W, Kalyanaraman B, Menon IA, Sarna T and Sealy RC (1986). Reaction of superoxide anions with melanins: electron spin resonance and spin trapping studies Biochimica et Biophysica Acta, 882: 145-153.
- [73]. Rozanowska M, Sarna T, Land E and Truscott T (1999). Free radical scavenging properties of melanin interaction of eu and pheo-melanin models with reducing and oxidising radicals. Free Radical Biology and Medicine, 26: 518-525.
- [74]. De Cassia R and Pombeiro Sponchiado SR (2005). Antioxidant activity of the melanin pigment extracted from *Aspergillus nidulans*. Biological and Pharmaceutical Bulletin, 28: 1129-1131.
- [75]. Cunha MM, Franzen AJ, Seabra SH, Herbst MH Vugman NV, Borba LP, de Souza W and Rozental, S (2010). Melanin in *Fonsecaea pedrosoi*: a trap for oxidative radicals. BMC Microbiology, 10: 80.
- [76]. Yang Y, Fan F, Zhuo R, Ma F, Gong Y, Wan X, Jiang M and Zhang X (2012). Expression of the laccase gene from a white rot fungus in *Pichia pastoris* can enhance the resistance of this yeast to H<sub>2</sub>O<sub>2</sub>-mediated oxidative stress by stimulating the glutathione-based antioxidative system. Applied and Environmental Microbiology, 78: 5845-5854.
- [77]. Mosse I, Kostrova L, Subbot S, Maksimenya I and Molophei V (2000). Melanin decreases clastogenic effects of ionizing radiation in human and mouse somatic cells and modifies the radioadaptive response. Radiation and Environmental Biophysics, 39: 47-52.
- [78]. Kudryashov YB (2004). Radiatsionnaya biofizika (ioniziruyushchie izlucheniya) (Radiation Biophysics (Ionizing Radiation)), Moscow: FIZMATLIT.
- [79]. Dadachova E, Bryan RA, Huang X, Moadel T, Schweitzer AD, Aisen, P, Nosanchuk JD and Casadevall A (2007). Ionizing radiation changes the electronic properties of melanin and enhances the growth of melanized fungi. Plos One, 2: 457.
- [80]. Dadachova E and Casadevall A (2008). Ionizing radiation: how fungi cope, adapt and exploit with the help of melanin Current Opinion in Microbiology, 11: 525-531.

- [81]. Tugai TI, Zhdanova NN, Zheltonozhskii VA and Sadovnikov LV (2007). Development of radioadaptive properties for microscopic fungi, long time located on terrains with a heightened background radiation after emergency on Chernobyl NPP. *Radiatsionnaia Biologiya Radioecologia*, 47: 543-549.
- [82]. Turick CE, Ekechukwu AA, Milliken CE, Casadevall A and Dadachova E (2011). Gamma radiation interacts with melanin to alter its oxidation-reduction potential and results in electric current production *Bioelectrochemistry*, 82: 69-73.
- [83]. Robinson CH (2001). Cold adaptation in Arctic and Antarctic fungi. *New phytologist*, 151: 341-353.
- [84]. Friedmann EI (1982). Endolithic microorganisms in the Antarctic cold desert. *Science*, 215: 1045-1053.
- [85]. Friedmann EI, McKay CP and Nienow JA (1987). The crypto endolithic microbial environment in the Ross Desert of Antarctica: satellite-transmitted continuous nano-climate data. *Polar Biology*, 7: 273-287.
- [86]. Sterflinger K (2005). Black yeasts and meristematic fungi: ecology, diversity and identification. In: "The Yeast Handbook. Biodiversity and Ecophysiology of Yeasts." (Ed: Seckbach J), Springer-Verlag Berlin and Heidelberg GmbH and Co, pp. 501-514.
- [87]. Gorbushina AA and Krumbein WE (1999). Poikilotroph response of micro-organisms to shifting alkalinity, salinity, temperature and water potential. In: "Microbiology and biogeochemistry of hypersaline environments". (Ed: Oren A). Boca Raton, FL CRC Press, LLC, pp. 75-86.
- [88]. De Hoog GS and Grube M (2008). Black fungal extremes. *Studies in Mycology*, 61: 198.
- [89]. Onofri S, Barreca D, Selbmann L, Isola D, Rabbow E, Horneck G, Vera JPP, de Hatton JL (2008). Resistance of Antarctic black fungi and cryptoendolithic communities to simulated space and Mars conditions. *Studies in Mycology*, 61: 99-109.
- [90]. Ma LJ, Rogers SO, Catranis CM and Starmer WT (2000). Detection and characterization of ancient fungi entrapped in glacial ice. *Mycologia*, 92: 286-295.
- [91]. Onofri S, Pagano S, Zucconi L and Tosi L (1999). *Friedmanniomyces endolithicus* (Fungi, Hyphomycetes), anam. gen. and sp. nov., from continental Antarctica. *Nova Hedwigia*, 68: 175-181.
- [92]. Mirchink TG, Kashinka GB and Abaturon YD (1968). Resistance of the dark coloured fungi *Stemphylium botryosum* (WALLR) and *Cladosporium cladosporioides* (Fries) de Vries to gamma irradiation. *Mikrobiologiya*, 37: 865-869.
- [93]. Ursi C, Wollenzien U, Criseo G and Krumbein WE (1997). Biodiversity of the rock inhabiting microbiota with special reference to black fungi and black yeasts. In: "Microbial diversity and ecosystem function." (Eds: Allsopp D, Colwell RR, and Hawkszworth DL), CAB International Publishers, Wallingford, Oxon, U.K, pp. 289-302.
- [94]. Zhdanova NN, Gavryushina AL and Vasilevskaya AI (1973). Effect of gamma and UV-irradiation on survival of *Cladosporium* sp., and *Oidiodendron cerealis*. *Mikrobiologicheskii Zhurnal* (Kiev), 35: 449-452.
- [95]. Zhdanova NN, Vasilevskaya AI, Antonenko AL and Udobenko VF (1981). Resistance of some melanin containing hyphal fungi to artificial solar light. *Mikrobiologicheskii Zhurnal* (Kiev), 43: 178-182.
- [96]. Old KM and Robertson WM (1970). Effects of lytic enzymes and natural soil on the fine structure of conidia of *Cochliobolus sativus*. *Transactions of the British Mycological Society*, 54: 343-350.
- [97]. Zhdanova NN, Melezhik AV and Vasilevskaya AI (1980). Thermostability of some melanin-containing fungi. *Biology Bulletin of the Academy of Sciences of the USSR*, 7: 305-310.
- [98]. Rosas AL and Casadevall A (1997). Melanization affects susceptibility of *Cryptococcus neoformans* to heat and cold. *FEMS Microbiology Letters*, 153: 265-272.
- [99]. Jenkins MB, Virginia RA and Jarrel WM (1988). Depth distribution and seasonal populations of mesquite-nodulating rhizobia in warm desert ecosystems. *Soil Science of Society American Journal*, 52: 1644-1650.
- [100]. Wardle DA (1992). A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Reviews*, 67: 321-358.
- [101]. Hussey MR, Skinner QD, Adams JC and Harvey AJ (1985). Denitrification and bacterial numbers in riparian soils of a Wyoming mountain watershed. *Journal of Range Management*, 38: 492-496.
- [102]. Lynch JM and Whipps JM (1990). Substrate flow in the rhizosphere. *Plant and soil*, 128: 1-10.
- [103]. Botterner P (1985). Response of microbial biomass to alternate moist and dry conditions in a soil incubated with <sup>14</sup>C- and <sup>15</sup>N labeled plant material. *Soil Biology and Biochemistry*, 17: 329-337.
- [104]. Nedwell DB and Gray TRC (1987). Soils and sediments as matrices for microbial growth. In: "Ecology of microbials, communities." (Eds: Fletcher M, Gray TRG and Jones JG), Cambridge. University press, Cambridge, pp. 21-54.
- [105]. Saksena SB (1955). Ecological factors governing the distribution of soil microfungi in some forest soils of Sagar. *Journal of Indian Botanical Science*, 34: 267-297.
- [106]. Alexander M (1986). *Soil Microbiology*. John Wiley and Sons Publishers, New York.
- [107]. Song FQ, Tian XJ, Li ZQ, Yang CL, Chen B, Hao JJ and Zhu J (2004). Diversity of filamentous fungi in organic layers of two forests in Zijin Mountain. *Journal of Forest Research*, 15: 273-279.
- [108]. Onofri S (2000). Ecology and biology of microfungi from Antarctic rocks and rocks and soils. *Ital. J. Zool, Supplement*: 163-167.
- [109]. Fernandez DP, Neff JC, Belnap J and Reynolds RL (2006). Soil respiration in the cold desert environment of Colorado Plateau (USA): abiotic regulators and threshold. *Biogeochemistry*, 78: 247-267.
- [110]. Nonzom S and Sumbali G (2014). Impact of some ecological factors on the occurrence and distribution of mitosporic fungi in the cold deserts of Ladakh (India). *International Journal of Pharmaceutical Science Invention*, 3: 32-40.
- [111]. Bridge P and Spooner B (2001). Soil fungi: diversity and detection. *Plant and Soil*, 232: 147-154.
- [112]. Lorgio EA, Julio RG and Peter LM (1999). Variation in soil organisms and nutrients underneath and outside the canopy of *Adesimia bedwilli* (papilionaceae) shrubs in arid coastal Chile following drought and above average rainfall. *Journal of Arid Environments*, 42: 61-70.
- [113]. Wainwright M (1995). *An Introduction to Fungal Biotechnology*. Wiley, Chichester.
- [114]. Henriksson G, Johansson G and Pettersson G (2000). A critical review of cellobiose dehydrogenases. *Journal of Biotechnology*, 78: 93-113.
- [115]. Bergquist P, Te'o V, Gibbs M, Curach N and Nevalainen K (2003). Recombinant bleaching enzymes from thermophiles expressed in fungal hosts. In: "Applications of Enzymes to Lignocellulosics." (Eds: Mansfield SD and Saddler JN), American Chemical Society Symposium Series, 855: 435-445.
- [116]. Nevalainen H and Te'o V (2003). Enzyme production in industrial fungi- role of molecular genetics. In: "Applied Mycology and Biotechnology Vol. 3." (Ed: Arora DK), Elsevier Science, pp. 241-259.
- [117]. Lambert PW (1983). Industrial enzyme production and recovery from filamentous fungi. In: "The Filamentous Fungi." (Eds: Smith JE, Berry DR, and Kristiansen B), Fungal Technology Arnold, London, 4: 210-237.
- [118]. Edwards MJ (1988). *ATCC microbes and cells at work. An index to ATCC strains with special applications*. American Type Culture Collection, Rockville, Maryland.



- [119]. Fox FM (1993). Tropical fungi: their commercial potential. In: "Aspects of Tropical Mycology." (Eds: Isaac S, Frankland JC, Watling R and Whalley AJS), Cambridge University Press, Cambridge, pp. 253-263.
- [120]. Kirk TK, Burgess RR and Koning JW Jr (1993). Use of fungi in pulping wood: an overview of biopulping research. In: "Frontiers in Industrial Mycology." (Ed: Leatham GF), Chapman and Hall, New York. pp. 99-111.
- [121]. Nisbet LJ and Fox FM (1991). The importance of microbial biodiversity to biotechnology. In: "The biodiversity of microorganisms and invertebrates: its role in sustainable Agriculture." (Ed: Hawksworth DL), CAB International., Wallingford, pp. 224-229.