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Environments influence the psychrophily of fungi and oomycetes in the cryosphere.

TAMOTSU HOSHINO and NAOYUKI MATSUMOTO

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Cryophilic fungi are defined by the physiological characteristics of their different life stages. Abiotic and biotic environmental factors influence physiological characteristics of cryophilic fungi and oomycetes. The relationships between fungal psychrophily and their habitat is discussed.

Key words: cryosphere, psychrophile, psychrophily, life cycle, *Sclerotinia nivalis*, snow moulds, *Typhula*

Tamotsu Hoshino, Biomass Refinery Research Center (BRR), National Institute of Advanced Industrial Science and Technology (AIST), 739-0046 Higashi-hiroshima, Japan; e-mail: tamotsu.hoshino@aist.go.jp

Naoyuki Matsumoto, Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan; e-mail: nowmat@a011.broada.jp

What are cryophilic fungi ?

Fungi normally have different cells in their life cycle and fungal thermal dependence varies according to their life cycle stages and is thus completely different from that of bacteria. Various examples show that the concept of psychrophily in bacteria by Morita (1975) does not apply to fungi. Hence, we proposed the term “cryophilic fungi” to denote the organisms adapted to the cryosphere (Hoshino & Matsumoto 2012). Cryophilic fungi include not only saprophytes but also parasites, as well as symbionts (Hoshino et al. 2013a). Some groups of cryophilic organisms attack overwintering plants and other living organisms including fungi on/in/under snow. In this review, we discuss the diversity and eco-physiological characteristics of these fungi. The concept of cryophilic fungi is defined as fungi that are present in the cryosphere, complete their lifecycles (sexual and/or asexual reproductions), and grow under subzero temperature where wa-

ter remains in the solid state such as snow and ice. The concept of cryophilic fungi also applies to unculturable fungi such as mycorrhizal fungi.

Research history

Fungi in the cryosphere have been less studied than those in temperate conditions. However, these organisms and their activities were recorded two centuries ago. The first observation was probably from rotted winter barley under snow cover in Toyama, Japan in 1788 (Hori 1934). Eriksson (1879) published a scientific report on winter injury of winter crops in Sweden. Rostrup (1888) was the first to publish an overview of the fungi of Greenland. In his review, he listed phytopathogenic fungi from Flora Danica (Hornemann 1836). Fischer (1888) was probably the first to report that an unidentified fungus grew at 0°C. Fungi in Antarctica have been surveyed since the beginning of the 20th century

(e.g. Bommer & Rousseau 1900). Cooke (1944) reported mushrooms in melted snowbanks in the alpine region of North America. Berry & Magoon (1934) and Morita (1966) summarized early studies of microorganisms, including fungi that grew at low temperatures.

Diversity

Snow fungi associate with snow algae in cryoseston which is defined as the community of organisms living on the snow (Nedbalová et al. 2008). Kol (1968) listed 82 species of snow fungi and fungi incertae sedis: *Chionaster nivalis* (Bohlin) Wille, *C. bicornis* Kol, and ascomycetous *Selenotila nivalis* Lagerh are among typical snow fungi.

The term snow moulds refers to pathogenic fungi under snow. They attack dormant plants such as forage crops, winter cereals, and conifer seedlings at low temperatures under snow cover (e.g. Smith 1989, Hsiang et al. 1999, Hoshino et al. 2009). Snow cover maintains darkness, humidity, and low temperatures and protects plants from cold and desiccation (Matsumoto & Hoshino 2008). “Snow moulds” or “snow mould fungi” is a generic name including diverse taxonomic groups of pathogenic organisms. Bruehl et al. (1966) found 55 taxa including unidentified species from winter wheat in early spring, and Årsvoll (1975) described 33 taxa from forage grasses just after snowmelt. However, most of these organisms are considered not pathogenic, or simply remained inactive under snow.

Matsumoto isolated 47 taxa from sclerotia of *T. incarnata* Lasch, and *T. ishikariensis* S. Imai, (Matsumoto 1989). Among these isolates a traditional zygomycete *Mucor hiemalis* Wehmer was found. Ascomycetes found included *Clonostachys rosea* f. *rosea* (Link) Schroers, Samuels, Seifert & W. Gams (syn. *Gliocladium roseum*), *Hormonema* sp., *Lecanicillium lecanii* (Zimm.) Zare & W. Gams (syn. *Verticillium lecanii*), *Paraconiothyrium minitans* (W.A. Campb.) Verkley (syn. *Coniothyrium minitans*), *Trichoderma harzianum* Rifai, *Trichoderma pseudokoningii* Rifai. All these had parasitic activities to sclerotia of *Typhula* spp. Basidiomycete *Cylindrobasidium parasiticum* D.A. Reid is a mycoparasite of sclerotia of *T. incarnata* in Scotland (Woodbridge et al. 1989), and ascomycetes

Episclerotium sclerotium (Rostr.) L.M. Kohn, and *Episclerotium sclerotipus* (Boud.) L.M. Kohn are also parasites of sclerotia of *Typhula phacorrhiza* (Reuchard) Fr. and *Sclerotinia* spp (Kohn & Nagasawa 1984).

Snowbank fungi are mushrooms emerging after snowmelt. Snowbanks linger till spring and summer in heavily timbered areas of the high Rocky Mountains. The snow bank fungi are comprised of ecologically diverse groups that belong to both Ascomycetes and Basidiomycetes. They are adapted to the unique microclimate provided by remnant snow in high elevation conifer forests (Cripps 2009). This set of fungi was subsequently called the “Snowbank flora” by Smith (1975). Moser (2004) described the snowbank “fungi” unique to North America. Subsequently, Cha et al. (2010) found snowbank fungi also in Hokkaido, northern Japan.

Effect of abiotic factors on thermal dependence

Most studies on the relationship between microorganisms and temperature have focused on physiological characteristics for its own sake and did not consider biological interactions, despite the fact that fungi in nature interact with various organisms in different environments. Wolf & Wolf (1949) stated that conceivably, the temperature differential might be an important factor when two or more species were competing for substrata but that it may not necessarily constitute the controlling factor.

In Norway, the basidiomycetous snow mould fungus, *Typhula ishikariensis* was divided into three groups (I, II and III) based on their mating reaction (Matsumoto & Tronsmo 1995, Matsumoto et al. 1996). *T. ishikariensis* group III is prevalent in the northernmost part of Norway (Matsumoto & Tronsmo 1995, Matsumoto et al. 1996), Greenland (Hoshino et al. 2006), and Svalbard (Hoshino et al. 2003). The distribution pattern of this fungus indicates that group III is more adapted to low temperatures than groups I and II. Isolates of groups I and II grow normally at 10°C on PDA, whereas group III isolates show irregular growth at this temperature (Matsumoto et al. 1996, Hoshino et al. 1997), and hyphal growth stops at 15°C. However, mycelia of group III isolates showed normal growth

at 10°C when PDA cultures were covered with water (Hoshino et al. 2008).

The ascomycetous snow mould, *Sclerotinia borealis* Bubák & Vleugel prevails where soil freezing is severe (Tomiyaama 1955, Röed 1960, Nissinen 1996). Tomiyama (1955) cultured *S. borealis* and *Typhula incarnata* on both frozen and unfrozen potato dextrose agar (PDA) plates that were kept outside in Sapporo, northern Japan. Mycelial growth of *T. incarnata* was inhibited on frozen plates, but *S. borealis* grew faster on frozen plates than on unfrozen ones. His experiments were not made under controlled conditions and have not been reproduced by others. Under controlled conditions, we confirmed his results that *S. borealis* grew on frozen PDA (Hoshino et al. 2009, 2010). *S. borealis* showed normal mycelial growth under the frozen condition, and mycelial growth rate on frozen plates at -1°C was faster than that on unfrozen PDA at its optimal growth temperature of 4–10°C. *S. borealis* can grow at low water potential on plates containing twice the concentration of medium ingredients (Tomiyaama 1955), sucrose and KCl (Bruehl & Cunfer 1971) as well as D-mannitol (Namikawa et al. 2004). An increase in intracellular osmosis enhanced mycelial growth and shifted the optimal mycelial growth temperature from 10–15°C to 4°C. However, mycelial growth of other snow moulds such as *Sclerotinia nivalis* I. Saito and *Sclerotinia trifoliorum* Erikss was inhibited at low water potential (Hoshino et al. 2009, 2010). Therefore, osmophilism of *S. borealis* was probably a unique feature to adapt to severe freezing. These results suggested that the cardinal temperature range of cryophilic fungi varies with cultural conditions.

Effect of biotic factors on thermal dependence

Mycelial growth of *T. ishikariensis* group I on PDA at 0°C was half that of its optimal growth at 10°C. However, when cultures were covered with unsterile soil to introduce natural microbial antagonists, mycelial growth was much less at 10°C than at 0°C (Matsumoto & Tajimi 1988, Hsiang et al. 1999). These facts indicate that *T. ishikariensis* group I is unable to develop mycelia at 10°C in nature

The ascomycetous snow mould, *Sclerotinia nivalis* is psychrotolerant and its optimal mycelial growth temperature is 20°C (Saito 1997). However, the fungus could infect *santonica* (*Artemisia cina*) and carrot at 0 or 3°C but not at 15°C (Saito 2001). Sclerotia germinated rapidly on unsterilised soil at 0°C, producing abundant mycelia to invade carrot roots. In contrast, at 20°C, myceliogenic germination failed to occur, and consequently carrot roots escaped from infection. Germination of sclerotia and mycelial growth were probably affected by suppressive activities of soil microorganisms (Saito 2001). This fungus may be considered as “psychrophile” (Morita 1975) from its ecological view point. These facts suggest that environmental factors are one of the important factors, determining cardinal temperature range of cryophilic fungi. Fig. 1 illustrates the concept of cryophilic fungi and the relationship with fungal psychrophily and environmental factors.

Ecophysiology of eurythermal cryophilic fungi

Snow moulds are unique in that they prevail when their hosts lie dormant during the winter. However, not all of them prevail exclusively under snow. Matsumoto (1994) divided them into obligate and facultative snow moulds. Facultative snow moulds are relatively fast-growing and occur under moist environmental conditions when plants are not necessarily covered with snow or even in summer; e.g. *Sclerotinia trifoliorum* encourages clover rot in damp winter (Lester & Large 1958), and *Microdochium nivale* (Fr.) Samuels & I.C. Hallett causes leaf blotch of wheat in summer (Asuyama 1940).

Mesophilic ascomycetes *Gremmeniella abietina* var. *abietina* (Lagerb.) M. Morelet and *Gremmeniella abietina* var. *balsamea* Petrini, L.E. Petrini, Lafl. & Ouell. cause scleroderma canker of conifers (Lijia et al. 2010). Plants with diseased needles are often found below the snowline, and winter temperatures influence infection rate; those overwintering at -7 and -3°C were more seriously diseased than those kept at 0°C (Petäistö & Laine 1999). These fungi can grow at subzero temperatures (Yokota et al. 1974). These findings suggest that *G. abietina* is active in a

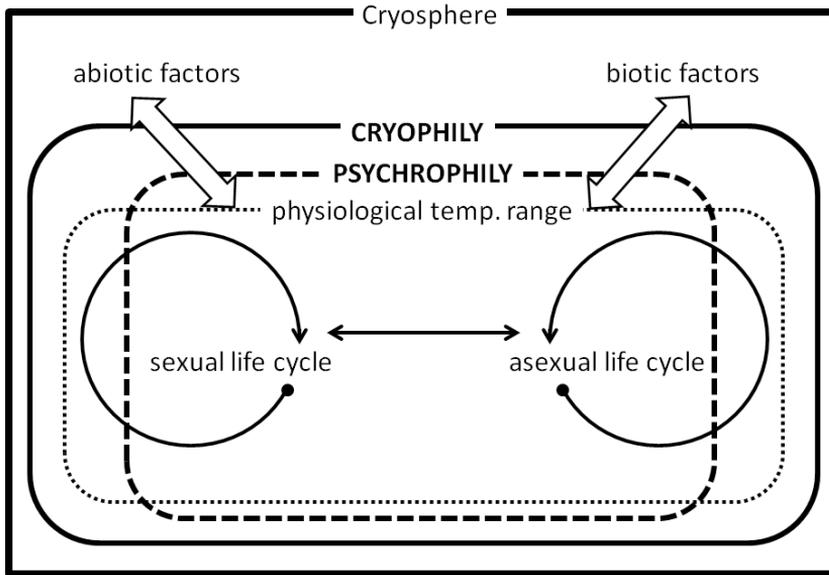


Figure 1. The concept of cryophilic fungi and its relationship with psychrophily and environmental factors.

wide temperature range between subzero to summer air temperatures in the cryosphere. A similar life cycle occurs in the ascomycetes among *Microsphaeropsis* sp., causing canker on *Cornus controversa* (Akimoto 1992).

Evolution of cryophilic fungi

Fungal fossil diversity increased throughout the Paleozoic Era with all modern classes reported in the Pennsylvanian Epoch (320–286 Ma) (Taylor et al. 1994). Present climatic zones on earth were formed from the Cretaceous period (145–66 Ma), then plants adapted in cold environment (Sakai 1995). Cryophilic fungal saprophytes probably evolved from mesophilic saprophytes, and consequently some species of cryophilic fungi acquired pathogenicity against overwintering plants (Matsumoto 1997). *Pythium*, *Sclerotinia* and *Typhula* are typical genera of snow moulds, and species of mesophiles and psychrotolerants are greater in number than psychrophiles. Pathogenicity and cold-adaptation are essential factors for fungi to become cryophilic phytopathogens, and these factors co-evolved in *Typhula* (Hoshino 2005).

Pathogenicity is strongly correlated with freezing resistance in oomycetous snow moulds

(Hoshino et al. 2009, 2013b). Fungi in permafrost are characterized by both the presence of natural cryoprotectants such as plant substrates or derivatives in these ecotopes and the ability to utilize their inherent mechanisms of protection (Ozerskaya et al. 2009). Stakhov et al. (2008) demonstrated that ancient seeds of higher plants constituted a specific habitat for microorganisms in frozen ground, which favoured their survival for millennia. Cold-accumulated plants also store cryoprotectants in their cytosol, and *Pythium* spp. in infected tissues, probably utilize host cryoprotectants to tolerate freezing.

Snow moulds are invariably stress tolerant, but their level of tolerance differs from organism to organism. They are either airborne or soilborne, or both. Airborne pathogens are ruderal or *r*-selected, reaching new habitat through spores before snow cover, and different strains of the same species share plant tissues to develop. Though not airborne, *Pythium* spp. have the same strategy. Soilborne snow moulds, except *Pythium* spp., exploit plant tissues nearby and excludes other strains through intraspecific antagonism. *T. ishikariensis* is, in this context, a typical *K*-strategist among snow moulds (Matsumoto 1992). The mode of epidemiology does not coincide with cold-tolerance in snow moulds and divides them into two categories, i.e., facultative and obligate

snow moulds (Matsumoto 1994). *S. borealis*, *T. incarnata* and *T. ishikariensis* are obligate snow moulds that prevail exclusively under snow and are tolerant to cold with different mechanisms. *Pythium* spp. and *Microdochium nivale* are facultative snow moulds and can develop without snow, even in summer during cool and damp periods. They are moderately tolerant of cold. Though fungal pathogens are less frequently recorded from the cryosphere than from the temperate zone, their diversity in adaptation strategy is significant and needs further investigations to reveal the complex ecosystem of the cryosphere.

Conclusions

The concept of cryophilic fungi is defined as fungi that are present in the cryosphere, complete their lifecycles, and grow under subzero temperatures where water remains in the solid state such as snow and ice. Their psychrophily is defined by physiological characteristics at each stage of their lifecycle. Environmental features (abiotic and biotic factors) also influence the physiological characteristics of cryophilic fungi.

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