available at www.sciencedirect.com

SciVerse ScienceDirect

journal homepage: www.elsevier.com/locate/funeco

# Snow moulds in polar environments

*Motoaki TOJO*[a,*], *Kevin K. NEWSHAM*[b]

[a]*Graduate School of Life and Environmental Sciences, Osaka Prefecture University, Sakai, Osaka 599-8531, Japan*
[b]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom*

ARTICLE INFO

*Article history:*
Received 29 September 2011
Revision received 30 November 2011
Accepted 20 December 2011
Available online 17 February 2012
*Corresponding editor:*
Lynne Boddy

*Keywords:*
Antarctic
Arctic
Ascomycetes
Basidiomycetes
Bipolar distribution
Oomycetes
Opportunistic parasites
Psychrophiles
Psychrotrophs
*Pythium*

ABSTRACT

Snow moulds are fungi and fungal-like microbes that occur frequently as pathogens of moss and vascular plant species in the Arctic and Antarctic, chiefly in maritime areas with permanent snow cover for several months of each year. Here, we review the environments inhabited by polar snow moulds, their distribution and the macroscopic features of infections, such as the sclerotia that form on the leaves of higher plants, or the more frequently encountered concentric rings found in moss stands. The microscopic features of infections are described, as are the taxa of snow moulds found in polar habitats, such as the ascomycetes *Thyronectria antarctica* var. *hyperantarctica* and *Sclerotinia borealis*, the basidiomycete *Typhula ishikariensis* and the oomycete *Pythium*. Recent research, also reviewed here, indicates that a heterothallic species of *Pythium* apparently has a bipolar distribution. The adaptations of snow moulds to polar environments, such as their growth at low temperatures, are covered, as are avenues for future research on these microbes.



## Introduction

Snow moulds are fungi and fungal-like micro-organisms that are pathogens of plants in cool temperate environments (Iriki *et al.* 2001; Hoshino *et al.* 2009). They are essentially opportunistic parasites that attack their hosts under snow cover when plant resistance is lowered by interrupted photosynthesis and the eventual exhaustion of reserve materials (Nakajima & Abe 1994; Hoshino *et al.* 2009). Snow moulds occur not only in cool temperate zones but are also frequent in Antarctic and Arctic habitats, where they cause distinctive infection patterns in moss and higher plant tissues (Longton 1973; Fenton 1983; Hoshino *et al.* 2003, 2004, 2006a; Bridge *et al.* 2008). In this review, we describe the environments inhabited by polar snow moulds, the macro- and microscopic features of infections, the different taxa causing snow mould infections in polar habitats, and their adaptations and responses to low temperatures. Finally, we suggest avenues for future research on these microbes.

## Environments inhabited by polar snow moulds

Snow moulds are frequently encountered in polar regions in stands of plants in damp or wet habitats (Longton 1973). They usually occur in maritime areas on level ground at the bases of cliffs where snowdrifts form during spring, or in rills and moist stream beds (Hoshino *et al.* 2001a), although they have also been recorded in high alpine areas of Greenland and

* *Corresponding author*. Tel.: +81 72 254 9411; fax: +81 72 254 9918.
E-mail address: tojo@plant.osakafu-u.ac.jp (M. Tojo).
1754-5048/$ – see front matter 
doi:10.1016/j.funeco.2012.01.003

Spitsbergen (Wilson 1951). Snow moulds typically infect plants that are covered with snow and ice for several months of each year. As noted in many studies, sub-nival environments are relatively stable in temperature. For example, at Barrow (71° 17′ N, 156° 46′ W), on the shores of the Arctic Ocean, the temperature of plants under snow of 260 mm depth was constant at −7 °C in late spring, until meltwater percolated through the snow shortly before complete snowmelt (Tieszen 1974). At Rothera Point on Adelaide Island close to the western Antarctic Peninsula (67° 34′ S, 68° 07′ W), at which infections caused by snow moulds occur in the moss *Sanionia uncinata*, the temperatures of plants under snow and ice during spring and autumn have been measured at between 0 °C and −7 °C, with temperatures only falling to −20 °C and occasionally −30 °C during winter (Newsham 2010). At Signy Island (60° 42′ S, 45° 35′ W) in the South Orkneys in the maritime Antarctic, at which snow moulds have been frequently reported (Longton 1973; Fenton 1983; Bridge *et al.* 2008), temperatures of *S. uncinata* under >500 mm of snow cover have been similarly measured at between −1 °C and −6 °C during spring and autumn (Davey *et al.* 1992). During the summer, however, the temperatures of plants at Rothera Point and at Signy Island can frequently reach 15–20 °C at solar noon under cloudless skies, and routinely fall to freezing point at night (Davey *et al.* 1992; Newsham 2010). Thus, although the sub-nival environment provides a relatively thermally stable habitat for snow moulds, these microbes are adapted to survive wide variations in temperature in polar habitats after emergence from snow and ice cover.

Plant tissues under snow in polar habitats are frozen and desiccated (Wasley *et al.* 2006), but water availability will rise rapidly as ice- and snow-melt occurs. Plants, in which photosynthesis has been interrupted for several months, and from which reserve materials have been exhausted, thus frequently emerge from snow and ice cover with water contents of several hundred percent (Newsham, unpubl. data), favouring the development of snow moulds in their tissues. This is consistent with the view that the development of snow mould infections, which occur frequently in hydrophilous species of moss in both Arctic and Antarctic habitats (Fenton 1983; Hoshino *et al.* 1999; Yamazaki *et al.* 2011), is associated with water availability (Tronsmo *et al.* 2001). However, precipitation in polar habitats is typically low, with annual precipitation of <350 mm per annum in southern maritime Antarctic habitats, the majority of which falls as snow (Smith 1984). Similarly, in Kongsfjorden (79° 57′ N, 11° 29′ E) on Spitsbergen in the high Arctic, at which snow moulds occur in colonies of *S. uncinata*, annual precipitation is 200–300 mm water equivalents per annum (Fleming *et al.* 1997), and daily rainfall only exceeds 5 mm on 15–20 d each year (Tojo & Nishitani 2005). Thus, unless fed by permanent sources of fresh water, plants can rapidly become desiccated after emergence from snow and ice-cover, presenting a further challenge to the survival of snow moulds.

## Distribution and macroscopic features

Snow mould infections are frequent throughout the Arctic and the maritime and sub-Antarctic (Fig 1). Some snow moulds, such as *Typhula ishikariensis* (speckled snow mould), *T. incarnata* (grey snow mould) and *Sclerotinia borealis* (snow scald) form sclerotia

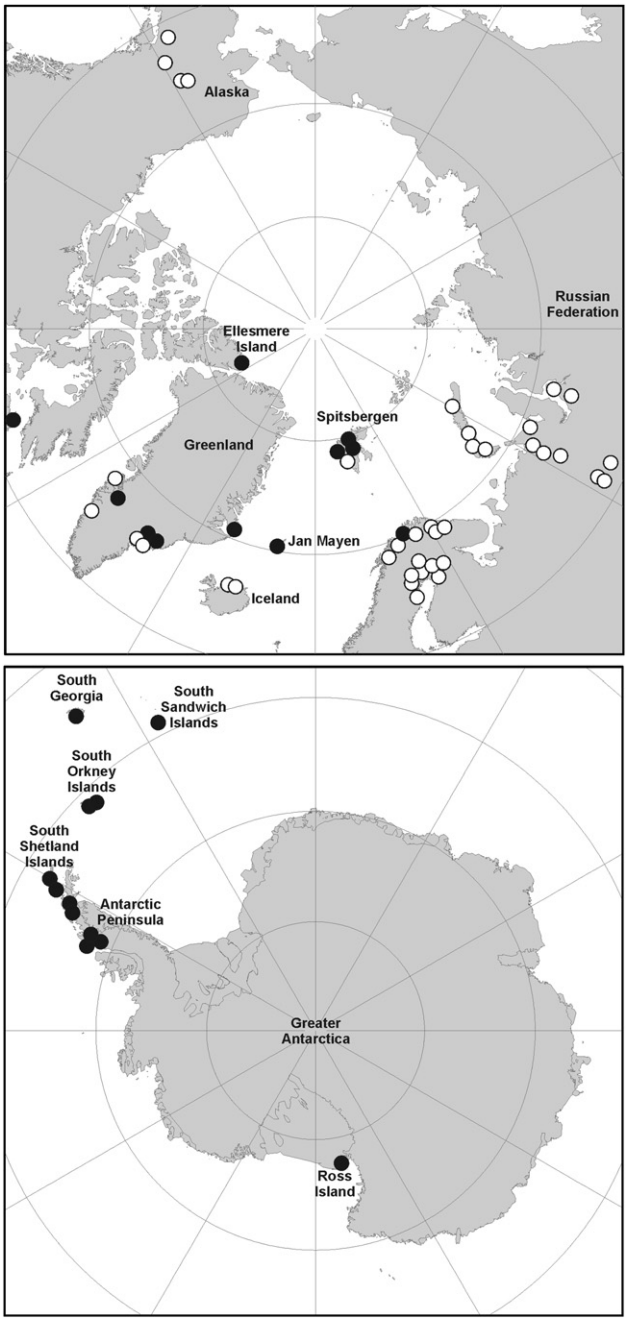


**Fig 1 – Locations at which snow mould infections have been recorded in the Arctic (top) and Antarctic (bottom). Open circles mark the positions at which sclerotial infections, caused by *Typhula* spp. and *Sclerotinia borealis*, have been recorded, and filled circles mark the positions of ring infections. Data from Wilson (1951), Ekstrand (1955), Jamalainen (1957), Lebeau & Logsdon (1958), Hawksworth (1973), Longton (1973), Arsvoll (1975), Kristinsson & Gudleifsson (1976), Ridley *et al.* (1979), Fenton (1983), Greenfield (1983), Smith (1982, 1994), Matsumoto & Tronsmo (1995), Hoshino *et al.* (1997, 1999, 2000, 2001a, 2001b, 2002, 2003, 2004, 2006a, 2006b); Shiryayev (2004, 2006, 2008), Tojo & Nishitani (2005), Bridge *et al.* (2008) and Yamazaki *et al.* (2011). Note that the numerous records of *Typhula* spp. infections recorded by Jamalainen (1957) in southern Finland are not shown.**