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Minireview

Snow Molds: A Group of Fungi that Prevail under Snow

NAOYUKI MATSUMOTO[1]*

[1]*Department of Planning and Administration, National Agricultural Research Center for Hokkaido Region, 1 Hitsujigaoka, Toyohira-ku, Sapporo 062–8555, Japan*

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Snow molds are a group of fungi that attack dormant plants under snow. In this paper, their survival strategies are illustrated with regard to adaptation to the unique environment under snow. Snow molds consist of diverse taxonomic groups and are divided into obligate and facultative fungi. Obligate snow molds exclusively prevail during winter with or without snow, whereas facultative snow molds can thrive even in the growing season of plants. Snow molds grow at low temperatures in habitats where antagonists are practically absent, and host plants deteriorate due to inhibited photosynthesis under snow. These features characterize snow molds as opportunistic parasites. The environment under snow represents a habitat where resources available are limited. There are two contrasting strategies for resource utilization, i.e., individualisms and collectivism. Freeze tolerance is also critical for them to survive freezing temperatures, and several mechanisms are illustrated. Finally, strategies to cope with annual fluctuations in snow cover are discussed in terms of predictability of the habitat.

Key words: snow mold, snow cover, low temperature, *Typhula* spp., *Sclerotinia borealis*

Introduction

In northern regions with prolonged snow cover, plants often suffer from damage due to overwintering problems. However, the process itself cannot be observed because it occurs under snow and, consequently, realize the damage only by the death and poor regrowth of plants after snowmelt. The phenomenon is referred to as winterkill (in Japanese, "toson" for winter cereals and "fuyugare" for forage crops) which does not define the cause and is ambiguous. Such damage is mostly ascribed to diseases caused by fungi, i.e., snow molds. Field and laboratory experiments using 12 cultivars of orchardgrass, *Dactylis glomerata*, in Sapporo, Hokkaido revealed that survival was most strongly correlated to resistance to *Typhula* spp. (1). Direct evidence comes from experiments with turfgrass sprayed with fungicides in late fall to control snow molds; plants were green just after snowmelt in plots treated with chemicals, while untreated control plots remained brown.

Snow mold fungi are taxonomically diverse and vary ecologically. Not all snow molds prevail exclusively under snow, and several species can thrive even on plants during the growing season in summer. Matsumoto (43) divided them into obligate and facultative snow molds (Table 1). Obligate snow molds grow exclusively in winter with or without snow, whereas facultative snow molds can damage growing plants. Facultative snow molds tend to have higher optimum growth temperatures than obligate snow molds, which explains their relative ubiquity in time and space. Cook (11) showed that the pink snow mold fungus *Microdochium nivale* was associated with every growth stage of winter cereals.

* Corresponding author. E-mail: nowmat@affrc.go.jp; Tel: +81–11–857–9257; Fax: +81–11–859–2178.

Typical snow molds have a distinct life cycle, i.e., an active phase under snow and a dormant phase from spring to fall. This life cycle is as follows; 1) spring to fall: Dormancy mostly in the form of sclerotia. Sclerotia are attacked by mycoparasites (48) and arthropods (25); 2) late fall: Sclerotia germinate to resume growth by producing sporocarps. Ascospores of the Sclerotinia snow mold fungus, *Sclerotinia borealis* and basidiospores of the gray snow mold fungus, *T. incarnata* are effective as propagules, whereas those of the speckled snow mold fungus, *T. ishikariensis* are not infective. The former two pathogens are epidemic as compared to *T. ishikariensis* since they have airborne propagules; 3) early winter: Infection occurs normally under snow (59), but *T. incarnata* monokaryons derived from basidiospores are obtained from plants before snow cover develops (45). Mycelia developed from overmature sporocarps after sporulation can infect host plants when plants are pressed against

Table 1. Obligate and facultative snow molds[a]

Obligate snow molds[b]	Facultative snow molds[b]
low-temperature basidiomycetes (=*Coprinus psychromorbidus*)	*Ceratobasidium gramineum*
Phacidium abietis	*Microdochium nivale*
Pythium iwayamai	*Pythium graminicola*
Racodium therryanum	*Pythium paddicum*
Sclerotinia borealis	*Rhynchosporium secalis*
Sclerotinia nivalis	*Sclerotinia trifoliorum*
supponuke fungus (=*Athelia* sp.[c])	
Typhula incarnata	
Typhula ishikariensis	
Typhula trifolii	

[a] After Matsumoto (43) with modifications.
[b] Obligate snow molds prevail exclusively in winter, while facultative snow molds can thrive during the growing season of hosts.
[c] Inferred from molecular data (A. Kawakami, unpublished data).

them by snow (13); and 4) winter: Snow molds attack dormant plants under snow to propagate. Plants resist fungal invasion using reserve material accumulated before winter. Sclerotia are produced before snowmelt.

Snow molds are, as a whole, endemic, but unusual winter climates often result in outbreaks. *S. borealis* badly affected orchardgrass in eastern Hokkaido in 1975, resulting in a serious shortage of cattle feed (4). Of 15,000 ha of damaged grasslands, 62% were reseeded, 28% renovated, and 10% planted with other crops. The 1974–75 winter favored an outbreak because of the following unusual climatic conditions: 1) persistent snow cover started much later than usual, and plants were predisposed to the disease, and 2) snow cover was deeper, and snowfall in late March prolonged thawing of persistent snow cover and extended the active phase of *S. borealis*. The outbreak motivated farmers to grow cold-tolerant (resistant to *S. borealis*) timothy, *Phleum pretense*, instead of productive orchardgrass. *T. ishikariensis* is a typical endemic pathogen, and its occurrence does not usually fluctuate. However, in 1988, the early onset of persistent snow cover in mid-November in the Abashiri area hindered the spraying of fungicides on winter wheat. Surveys made the following spring revealed that 30% of the fields were abandoned (55).

Several reviews on snow molds have been published with regard to the evolutionary ecology of *Typhula* spp. (42), Typhula snow molds on turfgrass (32), and biological control (44). The present article overlaps to some extent with a previous paper (43), which also referred to mechanisms of adaptation by snow molds, but the emphasis here is on recent findings, including roles in natural ecosystems, the freeze tolerance of snow molds, and adaptations to the predictability of the habitat under snow.

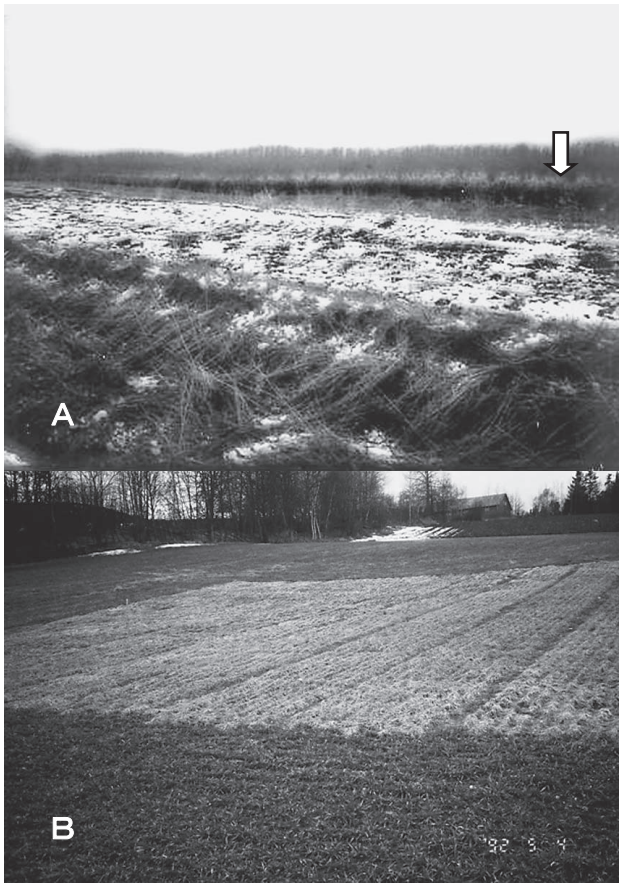

Fig. 1. Freeze damage of conifers (A) and perennial ryegrass (B). Snow cover insulates against freezing air temperatures. Plant tops (arrow) remained uncovered with snow and had freeze damage (A). Difference in freeze tolerance between perennial ryegrass and timothy (B). Perennial ryegrass died due to freezing damage (rectangle in the center), while timothy planted around the rectangular survived.

The habitat under snow

Snow molds as opportunistic parasites. Snow cover insulates against freezing temperatures and protects plants from freezing damage (Fig. 1A and B). The under-snow environment is characterized by constant low temperatures, darkness, and high moisture. The psychrophily of snow molds is used to monopolize plant resources in a habitat where antagonists are practically absent. Matsumoto and Tajimi (49) demonstrated stress tolerance of *T. ishikariensis* using plate cultures covered with unsterile field soil at 0°C, the ambient temperature under snow, and at 10°C, the optimal growth temperature. The mycelial growth rate of the fungus at 0°C was *ca*. half that at 10°C; however, the fungus failed to grow at 10°C when cultures were covered with unsterile soil to introduce microbial antagonism despite that growth was not affected at 0°C. Thus, snow molds are thought to avoid antagonism by escaping to the under-snow habitat. They are stress-tolerant strategists that prevail under snow with high stress and low disturbance (17).

Since the low temperature under snow restricts species diversity, the mycoflora is poor. For example, Bruehl *et al.* (9) found 55 fungi, including unidentified species from winter wheat in winter and early spring. Årsvoll (6) described 33 fungi from forage grasses just after snowmelt. These fungi were, however, mosophiles and unlikely to have been actively growing under snow. Inventories of plant diseases indicate that the low temperature under snow does restrict diversity; 40 fungi are described as pathogenic to wheat, but only five species are recognized as snow mold pathogens (71). Orchardgrass has 29 fungal pathogens, and four kinds of snow molds are incited by seven fungi (3). In Hokkaido, winter crops are grown even in areas where persistent snow cover lasts for 140 days or more. The habitat of snow molds is also characterized by the fact that only a few fungal species monopolize host plants for such a long time.

Darkness under snow inhibits photosynthesis. Reserve materials are depleted by respiration, and plants are predisposed to attack by snow molds. Nakajima and Abe (56) demonstrated the decrease in resistance of winter wheat varieties to *M. nivale* coupled with depletion of reserve materials under controlled conditions. Varietal difference in disease resistance coincided with the rate of nutrient depletion.

Their growth in the absence of antagonists and with physiologic decline of host plants under snow characterizes snow mold fungi as opportunistic parasites, allowing them to monopolize plant resources for a long period of time.

Snow molds in the ecosystem. Like ordinary plant parasites, snow molds are involved in succession in the ecosystem as decomposers. However, their significance is little

studied. Examples may be found in snow molds of forest trees such as *Racodium therryanum* and *Phacidium abietis* (=*Ph. infestans* var. *abietis*). *R. therryanum* exists where the A0 layer is thick under the canopy (37) and starts to prevail on plant litter when snow cover of 20–30 cm lasts for 7–10 days before attacking seeds and seedlings (63). This is why the natural regeneration of *Picea jezoensis* occurs exclusively on dead trees and not on the forest floor. Other fungi not recognized as snow molds also play an important role in seed viability under snow; *Rhizoctonia solani* and *Cylindrocarpon magnusisnum* cause the seeds of *Fagus crenata* to decay (33), and *Colletotrichum dematium* kills current-year *F. crenata* seedlings (62). Acorns of *Quelcus* spp. are attacked by *Ciboria batshiana* to decay (34). In polar regions, mosses are important primary colonizers and have disease patches (Tojo, M., *et al.* 2002. Abstracts for XXV Symposium on Polar Biology. p. 64, Tokyo, in Japanese; Tojo, M., *et al.* 2002. Abstracts for XXV Symposium on Polar Biology. p. 65, Tokyo, in Japanese) caused by the snow rot fungi, *Pythium* spp. These fungi are pathogenic but do not cause serious damage to the hosts. Rejuvenation of moss colonies occurs in disease patches, or patches provide secondary colonizers with foot holds for establishment (22).

Recent molecular techniques demonstrated microbial diversity in an alpine dry meadow soil under snow (41). Its mycoflora included a variety of undescribed ascomycetes, which contrasted with forest soil mycoflora consisting of many basidiomycetes (64). Elucidating the function of these novel fungi should provide further insights into ecosystems under snow.

Survival strategies

Individualism vs. collectivism. Ordinary plant pathogens that grow during the growing season of hosts can migrate to healthy plant tissues or plants to cause secondary infections when plant resources are exhausted. However, this does not apply to snow molds. Snow cover not only prevents long distance migration but limits the increase in plant biomass: the under-snow habitat represents an environment where resources are limited. Strategies of obligate snow molds are divided into individualism and collectivism. In individualistic fungi, genetically distinct strains antagonize each other and do not coexist in the same substrate; however, fungal collectivism is characterized by the coexistence of genetically different strains. Facultative snow molds extend their activity to summer, and their strategy is collectivism.

Årsvoll (7) inoculated timothy plants with four isolates each of *T. ishikariensis*, *T. incarnata*, *M. nivale*, and *S. borealis*, individually or as a mixture (Table 2). Inoculation with single isolates invariably caused severe plant damage, and a mixture of four isolates each of *M. nivale* and *S. borealis* resulted in the same extent of damage. In the case of *T. ishikariensis* and *T. incarnata*, however, disease severity was much decreased. The phenomenon was described as "antagonism" but was not discussed in an ecological context as it was by Matsumoto and Tajimi (47). The same phenomenon was reported in the low-temperature basidiomycete (38).

Intraspecies antagonism may be recognized in paired cultures of basidiomycetes, including *Typhula* spp. (Fig. 2).

Table 2. Disease severity of timothy plants inoculated with four isolates of snow mold pathogens, individually or in a mixture

Pathogen	Isolate				Mixture 1+2+3+4
	1	2	3	4	
Typhula ishikariensis	96.1	99.0	98.7	93.7	<5.0
Typhula incarnata	96.2	70.6	94.9	88.3	46.0
Micridocium nivale	75.9	82.9	96.5	86.8	87.8
Sclerotinia borealis	89.6	81.9	78.4	89.3	87.1

After Åsvoll (7)

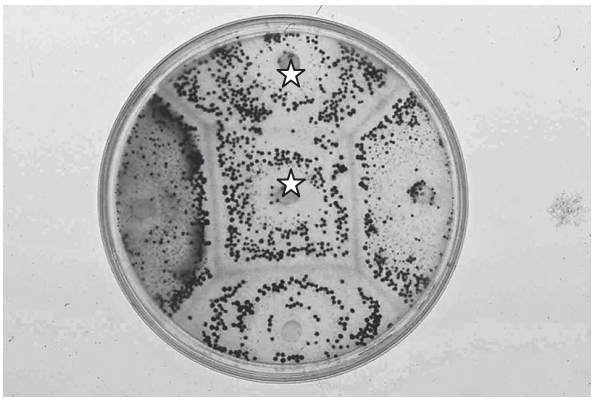

Fig. 2. Recognition of individuals of *Typhula ishikariensis* biotype B in paired cultures. Five different isolates are grown on oatmeal agar. Isolates differing in genetic background produce dark demarcation lines between colonies and are regarded as different individuals. If there is no line along the colony junction of two isolates (asterisked), they are regarded as the same.

Hyphal fusion results in the formation of a dark demarcation line produced along the colony junction between vegetatively incompatible isolates. Such isolates are defined as different individuals. Thus, intraspecific antagonism is a means of separating individual mycelia within natural populations based on heterogenic incompatibility (68). Vegetative hyphal fusions are a feature found generally in fungi. In basidiomycetes, intraspecies antagonism is a dikaryotic phenomenon, functioning as a barrier to the exchange of nuclei and cytoplasm. Intraspecies antagonism between dikaryons maintains the integrity and genetic uniqueness of the individual and consequently reserves genetic variability in the population. As outbreeders, basidiomycetes such as *Typhula* spp. and wood-decaying fungi share limited resources through intraspecies antagonism. Individuals of *T. ishikariensis* biotype B occur in single disease patches on the turf (Fig. 3). Turfgrass plants often survive infection along the junction of patches which corresponds to the dark demarcation line in paired cultures.

Ascomycetous snow molds, most typically in *S. borealis*, spread airborne propagules before winter, and genetically distinct strains often colonize the same spots. They do not directly antagonize each other. Their strategy for the utilization of resources is collectivism.

Freeze tolerance. Snow molds exist in north Atlantic regions such as Iceland (28), Greenland (29), Svalbard (26), and northern Norway (54), as well as in maritime Antarctica (8), where lands are arid and not suitable for agriculture. The maritime climate in these localities has rainfall even in win-

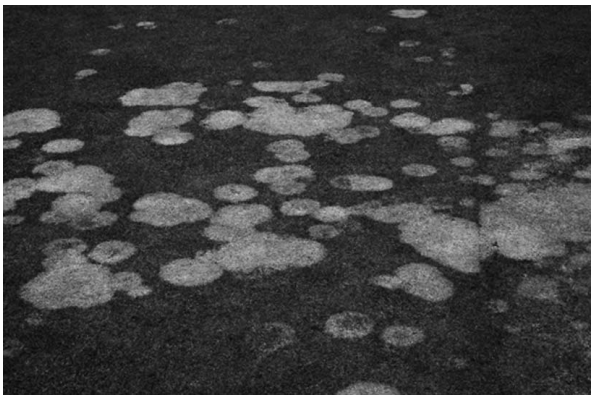

Fig. 3. Disease patches on turfgrass caused by *Typhula ishikariensis* biotype B. Each individual of *T. ishikariensis* biotype B occupies each patch.

ter when the temperature rises, and then snow cover thaws. Thawed water subsequently freezes to cause damage to plants (5, 12). Snow molds are also found in inland regions in Alaska (39), Canada (65), and Russia (23), where soil freezes deep in the ground. What are the mechanisms by which they survive a freezing environment? Hodkinson and Wookey (18) illustrated ecophysiologic features of soil organisms that thrive in tundra, i.e., capacity to dehydrate, production of antifreeze, escape to the under-snow habitat, resistance to anoxia, etc. In fungi, freeze tolerance mechanisms include increases in intracellular trehalose and polyol concentrations and unsaturated membrane lipids as well as the secretion of antifreeze proteins (AFPs) and enzymes active at low temperatures (61). Different snow molds developed different mechanisms to protect them from freeze damage and to prevail at subfreezing temperatures (31).

Mycelia of snow molds were frozen at −20°C for 24 h and then incubated at −1°C to observe their growth (Hoshino, T., unpublished data). All the facultative snow molds and the supponuke fungus failed to survive the −20°C treatment, while obligate snow molds such as *T. incarnata*, *T. ishikariensis*, *S. borealis*, and *R. therryanum* resumed growth after the treatment. These results indicate that snow mold fungi differ in freeze tolerance and that the differences reflect differences in survival strategy during winter.

In the coastal region of northern Norway, the most prevalent taxon in the *T. ishikariensis* complex is group III (54). Mycelia of *T. ishikariensis* groups I and III were frozen to −40°C at a rate of 20°C/h and thawed gradually for 16 h to 2°C (20). They were then incubated at their respective optimum growth temperatures at 10 (group I) and 2°C (group III) to compare mycelial regrowth; regrowth was retarded in group I, but normal in group III. The freezing point in the latter ranged from −9.8 to −6.1°C, and the amount of antifreeze protein was higher than that in group I. Group III isolates from Siberia where soil freezes to a depth of 3 m showed the same level of freeze tolerance (23).

Growth inhibition of ice crystals through antifreeze protein (AFP) production is a common freeze tolerance mechanism in many organisms. AFPs show heat hysteresis. Hysteresis manifests itself in a state of transition when melting temperature and freezing temperature do not agree: water thaws at 0°C but freezes at subzero temperatures when AFP is present. Fungi also produce AFPs (14). Among snow molds (27, 66), AFP production is known in basidiomycetous fungi such as *Coprinus psychromorbidus* (=the low-temperature basidiomycete), *T. ishikariensis*, *T. incarnata*, and *T. phacorrhiza*, but not in the ascomycetous *M. nivale* or *S. borealis* as well or in oomycetes, *Pythium* spp. AFPs produced outside and inside the cell inhibit the growth of ice crystal to facilitate survival at subzero temperatures, but their involvement in pathogenesis is considered unlikely. However, AFPs must function at the host-parasite interface; since extracellular enzymes are involved in the absorption of nutrients from host cells, nutrition uptake by snow molds may be inhibited if the ambient environment is totally frozen. Of AFPs reported from a wide range of organisms (15), fungal AFPs are unique in that they do not have any similarity with known proteins (27) and in their presence, ice crystals grow into "Stone Age arrow knives (27)." Other AFPs form hexagonal ice crystals (16).

Sclerotinia borealis is distributed in areas with severe winters where soil freezes deep in the ground before snowfall (58, 69). Tomiyama (69) designated eastern Hokkaido a Sclerotinia area. Amano and Ozeki (2) revealed a relationship between resistance to *S. borealis* and freeze tolerance in winter wheat cultivars. However, freeze tolerance differs among plant species, with some plants more susceptible to freeze damage and Sclerotinia snow mold. The distribution of *S. borealis* is dependent on the freeze tolerance of its hosts. Soil freezing is not a criterion determining its occurrence. Perennial ryegrass, *Lolium perenne*, which is much less freeze tolerant than timothy (Fig. 1B), is damaged by the fungus in snowy, northern and central areas of Hokkaido with little soil freezing (59). Perennial ryegrass plants with freeze damage are predisposed to the attack from Sclerotinia snow mold even in these areas. These findings indicate that freeze tolerance is the physiological factor most critical to host-*S. borealis* interactions and to the fungus itself.

Ascospores of *S. borealis* can tolerate −22.2°C when deposited on grass leaves (59). *S. borealis* tolerates freezing through a mechanism different from that basidiomycetous snow molds have. The latter fungi produce AFPs to survive freezing, while *S. borealis* is considered to tolerate freezing through osmophily. Tomiyama (69) kept PDA cultures of *S. borealis* and *T. incarnata* outdoors in winter to freeze them. Mycelial growth of *T. incarnata* was inhibited on the frozen medium, while *S. borealis* grew faster on frozen than unfrozen media. *S. borealis* grows well on media fortified with sucrose or KCl (10), and D-mannitol (57). High osmotic pressure improves mycelial growth of the fungus and alters growth-temperature relations (Hoshino, T., *et al.*, unpublished data). The strategy of *S. borealis* seems analogous to that of bacteria in permafrost (permanently frozen soil). Bacteria from Siberian permafrost are osmophylic and able to survive and grow, utilizing the solute in unfrozen water even at −20°C (60).

The facultative snow mold *M. nivale* adapts to low temperatures with an increase in fatty acid content and change in its composition (35). When the incubation temperature was reduced from 25°C to 10°C, linolenic acid (18:3) markedly increased at the expense of lonoleic acid (18:2) and oleic acid

(18:1). The change helped to maintain membrane fluidity. A further decrease in incubation temperature to 4°C did not result in any appreciable change in fatty acid content, but the amount of triacylglycerol, the sole major component of the neutral lipid fraction of the fungus, increased. Triacylglycerol constitutes the main reserve material in *M. nivale*. In conclusion, under snow, *M. nivale* shifts its metabolism to accumulate reserve materials but does not increase production of unsaturated fatty acids to adapt to low temperatures. This partially explains the relatively poor freeze tolerance of *M. nivale*.

Few studies have been conducted on freeze tolerance in oomycetes. *Pythium* spp. are important to winter cereals grown in rotational paddy fields in Japan (67) and to winter wheat in low-lying areas of Washington, USA (40). They also occur on mosses in Greenland (30), Svalbard (21), and Antarctic (8), and in these regions, freeze tolerance is critical for survival. They can grow at 0–5°C (24). *P. iwayamai* mycelia fail to survive at −20°C (Hoshino *et al.*, unpublished data), and *Pythium* spp. from polar regions can not tolerate −20°C, either. While the −20°C treatment kills propagules such as oospores and hyphal swellings, surviving propagules are conditioned to germinate (Tojo, M., personal communication). Though their propagules are mostly unable to tolerate freeze damage, *Pythium* spp. are considered to use freezing as a signal to resume growth through the germination of surviving propagules.

Predictability of snow cover. Snow cover is essential for snow molds, providing them with favorable environmental conditions. Endemic snow molds such as *Typhula* spp. show adaptations to local environments. Examples may be found in *T. ishikariensis* and *T. incarnata*. The duration of persistent snow cover is most critical; however, even in snowy regions, snow cover does not occur regularly but fluctuates annually. Sclerotia of *Typhula* spp. germinate in response to low temperature and high humidity (36, 53) in fall on the assumption that snow cover will occur subsequently. The assumption is risky in that snow cover does not always occur as anticipated or may thaw just after it occurs.

Predictability of snow cover, in fact, varies even within localities with the same mean annual number of days with snow cover. An example is illustrated by the four localities of *T. ishikariensis* biotype B (Table 3). They have ca. 120 days with snow cover per annum, but annual fluctuations differ greatly with a coefficient of variation ranging from 6.9 to 18.7. Matsumoto and Tajimi (51) devised a snow over index (mean annual number of days with snow cover/annual fluctuation, CV) to denote the predictability of each locality. Of these localities, it is much harder to predict when snow cover starts and ends in Oomagari than in Yakumo.

Isolates of *T. ishikariensis* biotype B were collected from seven localities, including the four above (51). The snow cover index varied from 1.2 in Sendai to 17.2 in Hamatonbetsu (Table 3). Sclerota became significantly smaller as values for the index decreased. Whereas the Hamatonbetsu population from the locality with the most constant snow cover showed extensive variability in the size of sclerotia, populations from localities with less persistent snow cover showed much less variability. There were differences in the carpogenic germination of sclerotia according to predictability; the

Table 3. Snow cover conditions in localities of *Typhula ishikariensis* biotype B

Locality	Snow cover conditions		
	Mean no. days with sow cover	CV (%)[a]	Index[b]
Hamatonbetsu	146.1	8.5	17.2
Yakumo	117.8	6.9	17.1
Abashiri	120.5	9.3	13.0
Sapporo	122.2	10.2	12.0
Oomagari	119.6	18.7	6.4
Morioka	95.7	20.6	4.7
Sendai	41.5	34.0	1.2

[a] annual fluctuation.
[b] No. days with snow cover per annum/CV.
After Matsumoto and Tajimi (51)

populations from Hamatonbetsu and Yakumo produced sporocarps readily, whereas those from Abashiri, Sapporo, Oomagari, and Morioka were slow in germinating. The Sendai population mostly failed to develop sporocarps and was practically asexual. Though there was no overall correlation between snow cover conditions and virulence, isolates from Sendai were highly virulent.

A reliable habitat exists where a constant cover of snow is maintained for long periods and the duration of snow cover is quite uniform year after year. Where snow cover lasts, the fungus can allocate abundant energy to sclerotia, and large sclerotia develop large sporocarps (52). In contrast, in a habitat with ephemeral snow cover, snow cover occurs intermittently and lasts for short periods. On the Sendai plain, the small sclerotium form of *T. ishikariensis* biotype B (52) (formerly referred to as biotype C) is an entire soilborne pathogen, attacking underground plant parts to cause damping off (19). There, the habitat in soil is much more stable than the habitat under snow. The local population is considered to be selected for small sclerotia and high virulence to survive unpredictable habitats. The small sclerotium form can attack plants without waiting for the physiologic deterioration of hosts with strong virulence, and its small sclerotia, which mature rapidly without external stimuli (49), have a selective advantage in an unstable habitat like the Sendai plain.

Typhula incarnata is highly sexual (50, 70) and versatile (46), and its ubiquity is ascribed to these features. Populations of *T. incarnata* from four localities with contrasting winter snow cover conditions did not vary in mycelial growth rate, sclerotium size, or virulence but differed in readiness for carpogenic germination (53); when sclerotia of medium size ranging from 1 to 2 mm were kept outdoors in the shade at temperatures ranging from −4 to 14°C for 45 days, percent germination of sclerotia for populations from Yamaguchi (annual number of days with snow cover, 10–20 days) and Toyama (60–90 days) was *ca*. 20 and 40%, respectively, whereas it was 50 and 55% for Sapporo (120 days) and Nayoro (150 days) populations, respectively. This is the only variability detected among populations of *T. incarnata*. There was, however, no population difference when sclerotia were incubated under controlled conditions. Sclerotia started to germinate in ca. two weeks, and a half of them germinated 23 days after incubation in every population. These results indicate that the threshold for germination differs among

populations. In less snowy areas, the threshold is high so that local populations do not respond to faint signals for germination. There, suitable climatic conditions for the pathogen are highly unpredictable; high temperature and low humidity may interrupt sclerotium germination, and germinated sclerotia are not likely to function as propagules. Genotypes whose sclerotia germinate readily may not survive in such a changeable habitat.

Conclusions

Winter climate largely affects the incidence and severity of snow molds. Individual snow mold fungi react differently to environmental conditions, and this governs their distribution and year-to-year occurrence. The recent tendency towards global warming has certainly changed snow mold mycoflora. In the Sclerotinia area in eastern Hokkaido, *S. borealis* is no longer a problem due to the early onset of snow cover and warm winters. The supponuke fungus seldom occurs in this area, either. *T. ishikariensis* biotype A has replaced these fungi. We need to revise the agriculture system, according to the change in snow mold mycoflora. If the tendency of warm winters continues, more productive but less winter hardy plants and cultivars will be selected. In other words, the impact of snow molds should remain the same, and winter wheat will still need to receive chemicals to control snow molds. Hokkaido may be the only place in the world where chemical control of snow molds is essential to support wheat production. Accumulated knowledge on the ecology of snow molds, along with physiological studies of plants, should provide clues for developing countermeasures to climate change.

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