Biology and Management of Typhula Snow Molds of Turfgrass

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Snow mold diseases are caused by fungi that grow and attack dormant plants at low temperatures under snow cover (42). These psychrophilic or "cold-loving" organisms are opportunistic parasites that can damage perennial plants or overwintering annual crops when plant disease resistance is lowered due to depletion of plant carbohydrate reserves (59). In addition, low temperatures limit the activity and number of competitors and antagonists of snow mold fungi, and allow these pathogens to monopolize the nutrient-rich but weakened plant tissues (42).

Most snow mold fungi that have been investigated are pathogens of economically important plants such as conifers and grasses. Some important snow mold pathogens on conifers include *Neopeckia coulteri* on pine (6), *Herpotrichia juniperi* on juniper (6,72), *Phacidium infestans* on pine (38), and *P. abietis* on various conifers (22). Sage brush (*Artemisia dentata*) is also susceptible to an unidentified snow mold disease (60). The major snow mold diseases of turfgrasses and winter cereals are caused by psychrophiles such as *Coprinus psychromorbidus*, *Myriosclerotinia borealis*, *Typhula ishikariensis*, *T. incarnata*, and low-temperature-tolerant organisms such as *Microdochium nivale* (78).

Fungi adapted to low temperatures can be found in polar (91), temperate (78), and mountainous regions (72) all over the world; but how many fungal species can actually grow under snow cover? The effects of low temperature are reflected in the low diversity of fungi active under snow cover. In some areas, dormant foliage is covered by snow for over half the year, yet only a few pathogenic fungi exploit these resources (42,65). Among conifer diseases, few demonstrate observable pathogenic activity under snow cover (28). Approximately 40 fungal species have been described as pathogens of wheat seedlings, but only five have been found to be pathogenic under snow (84). Eighty-nine fungal species were found on winter wheat seedlings and other plants collected in winter and early spring (13), and 33 species were found on forage crops just after snowmelt (3), but most were mesophiles and likely dormant during winter. This low diversity of active fungal species under snow cover is one of the factors that facilitates the use of biocontrol agents.

Duration of snow cover plays an important role in the biology of overwintering plants and low-temperature organisms. The cold environment limits biological activity, but snow mold fungi can thrive under these protected conditions. Turfgrasses and winter cereals survive harsh winters partly because of the protection and moisture provided by snow (24). However, if snow cover is prolonged, snow mold damage can occur. Snow cover not only retards the growth of host plants, but also predisposes them to attack by snow mold fungi by increasing the contact of soilborne inoculum to plant tissues (79), by exhausting plant carbohydrate reserves (36,59), and by creating a stable dark environment near 0°C (81). Increased disease severity or decreased disease resistance was directly correlated with duration of snow cover for *Myriosclerotinia borealis* on *Dactylis glomerata* (68) or *Microdochium nivale* on winter wheat (59). Typhula snow molds show greatest disease severity in years with long duration of snow cover (64) and in regions subjected to heavy snowfall (57).

Many perennial plants that normally are covered by snow during the winter are able to avoid damage from snow molds because they translocate reserve materials to roots and retain few green tissues aboveground

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through winter (14). However, intensively managed turfgrasses are usually required to stay green until snowfall, and the grass plants may not be properly prepared for winter dormancy, particularly if fertilized with soluble nitrogen in the late fall (4,85). Typhula snow molds are more damaging during winters when snow falls on unfrozen ground and also if the turfgrass sward is lush going into winter (83).

Typhula Snow Mold Fungi

In areas with long duration of snow cover, the most important winter diseases of perennial grasses and winter cereals are caused by species of *Typhula*. Typhula snow molds occur from cool temperate to boreal regions of the Northern Hemisphere (78). In a survey of golf course superintendents, these molds were the second most damaging turfgrass disease of the Great Lakes Region and the fifth overall in the United States (1). In Canada, snow mold diseases of turfgrasses are prevalent and may account for half of the fungicide used on turfgrass (T. Hsiang, *unpublished*). In northern Japan, the damage due to *Typhula* species has been the major concern of golf course keepers (N. Matsumoto, *unpublished*).

The Typhula snow molds are also known as gray snow mold, snow scald, speckled snow mold, and Typhula blight. For clarity, we refer to *T. incarnata* as the causal agent of gray snow mold, *T. ishikariensis* as the causal agent of speckled snow mold, and both species collectively as causing Typhula blight. A third species, *T. phacorrhiza*, which is antagonistic to *T. ishikariensis* and *T. incarnata* (15,53,90), has also been found to be weakly pathogenic to winter wheat (70) and is associated with patches on golf course fairways in Wisconsin (57).

The basidiomycetous genus *Typhula* has been assigned to different taxonomic families over time. In the most recent edition of the authoritative text, *Dictionary of the Fungi*, the genus *Typhula* was assigned to Cantharellales, which also contains other clavarioid fungi (26). Previously, it was placed in the Clavariaceae of the Aphyllophorales (27). In the GenBank taxonomy web page (www3.ncbi.nlm.nih.gov), *Typhula* is assigned to the Thelephorales. Recent ribosomal DNA sequencing placed *T. phacorrhiza* alongside agarics and separated it from other clavarioid fungi (29,30).

Variation in *T. ishikariensis* has led to taxonomic confusion, and the nomenclature of different species, varieties, biotypes, or groups differs among researchers (Table 1). *Typhula idahoensis* was named for a snow mold pathogen found in the Pacific Northwest on cereal and turfgrasses (69). However, based on morphological similarities, MacDonald (40) synonymized *T. idahoensis*, *T. borealis*, and *T. ishikariensis*, giving *T. ishikariensis* priority. On the basis of pathogenicity, distribution,

Fig. 1. Snow mold patches on *Lolium perenne* caused by *Typhula incarnata*. Sclerotia of *T. incarnata* were found in the patches.

Fig. 2. Snow mold patches on *Agrostis palustris* caused by *Typhula ishikariensis* (left) and *Microdochium nivale* (right) are very similar, except for the presence of sclerotia with *T. ishikariensis*. Small white balls are fertilizer pellets.

Table 1. Classification of the *Typhula ishikariensis* complex by different researchers[a]

Bruehl and Cunfer, 1975 (10)	Årsvoll and Smith, 1978 (5)	Matsumoto et al., 1982 (47)	Matsumoto and Tajimi, 1991 (52)	Matsumoto et al., 1996 (55)	Matsumoto, 1997 (43)
T. ishikariensis	var. *ishikariensis*	Biotype A	Biotype A	Group I	Biological species I
T. idahoensis	var. *idahoensis*	Biotype B	Biotype B	Group III	Biological species I
T. ishikariensis	var. *canadensis*	Biotype C	Biotype Bss[b]	Group II	Biological species II

[a] Taxa in each row do not show absolute equivalence, but they are similar in many aspects.
[b] Small sclerotial form of biotype B.

basidiocarp size (10), and mating experiments (12), *T. idahoensis* was split from *T. ishikariensis* (Table 1). However, based on genetic evidence and morphological characters, Årsvoll and Smith (5) regarded them as conspecific and reduced *T. idahoensis* to a variety of *T. ishikariensis*, as well as designating *T. ishikariensis* var. *canadensis* to accommodate a variant widely distributed in Canada (Table 1). Bruehl and Machtmes (11) conducted more extensive mating experiments between *Typhula* isolates and maintained that *T. ishikariensis* and *T. idahoensis* were distinct species. They also rejected *T. ishikariensis* var. *canadensis* as a distinct variety. Matsumoto (43) divided the *T. ishikariensis* complex into two biological species (Table 1): var. *ishikariensis* from turfgrass in North America belongs to biological species I, but Japanese biotype A, also belonging to biological species I, did not attack turfgrass under natural conditions; and biological species II, which seemed more specialized to monocots and caused snow mold on turf (43), includes var. *canadensis* in North America and biotype B in Japan (54). More recent work using genetic markers has found that *T. phacorrhiza*, *T. incarnata*, and *T. ishikariensis* are distinct species, and that the varieties of *T. ishikariensis* in North America do not show genetic differences at a species level (30).

Symptoms and Signs

Circular straw-colored patches caused by snow molds are visible as the snow melts in late winter or early spring (Fig. 1). These patches are usually less than 1 m across but can coalesce to form large areas of blighted turfgrass (18). In addition to Typhula blight, pink snow mold, caused by *Microdochium nivale*, may also be present on turfgrass after snowmelt. Symptoms of pink snow mold may be similar to those of Typhula blight (Fig. 2); however, *M. nivale* requires little or no snow cover to cause disease, and it does not produce sclerotia.

Symptoms caused by *T. incarnata* and *T. ishikariensis* may be difficult to distinguish, except that *T. ishikariensis* requires much longer periods of snow cover for disease development. *T. ishikariensis* is common in areas with snow cover lasting for more than 100 days (3,81); and *T. incarnata* is found in areas with snow cover of more than 65 days (N. Matsumoto, *unpublished*). Mild symptoms caused by *T. incarnata* may appear without snow cover in the late fall and early spring as small, circular, water-soaked or straw-colored patches up to 15 cm across (32). After a mild winter, low levels of disease are seen as 5-cm-diameter light yellow areas. Sometimes a line of surviving green plants occurs between patches because each patch is occupied by a single strain which is antagonistic to other strains (54).

Symptoms are more severe after several months of snow cover, with individual patches up to 60 cm across and plants covered with mycelium at the patch margins (Fig. 3) or across the entire patch right after snowmelt. The mycelium is white, but can become covered by dust and assume a gray-white appearance (hence the name "gray snow mold" (32; Fig. 4). Plants within patches may be matted and appear slimy with mycelium and sclerotia (Fig. 5). At spring thaw, sclerotia may be found in the leaves and crowns of infected plants.

As the patch dries, a thin crust of mycelium can develop over the affected area, giving it a bleached appearance. Usually, only the leaves are killed and the crown survives to produce new leaves in the spring. However, the disease can become quite severe if the pathogen invades the crown tissue, and reseeding or resodding may be required in the spring. If left untreated, patches will persist well into the growing season (Fig. 6). Where damage is

Fig. 3. Snow mold patch on *Agrostis palustris* caused by *Typhula ishikariensis* taken 1 week after snowmelt. Sclerotia are visible in the dried mycelium near the patch margin, and small white balls are fertilizer pellets.

Fig. 5. Center of a snow mold patch during snowmelt appearing slimy with matted grass and sclerotia of *Typhula ishikariensis*.

Fig. 4. Grayish white mycelium of *Typhula ishikariensis* covering the surface of a patch right after snowmelt.

Fig. 6. Snow mold patches may still be apparent on turfgrass several months after snowmelt.

not severe, diseased plants resume growth after winter and soon become indistinguishable from healthy plants.

Although *T. incarnata* and *T. ishikariensis* cause similar disease symptoms and can be found together in complexes associated with *T. phacorrhiza* (57), there are distinct differences between these species that aid in correct diagnosis. In culture, the mycelia have different characteristics (Fig. 7), and each species is distinguishable by features of the sclerotia (Fig. 7, Table 2).

Sclerotia of *T. ishikariensis* are small (<2 mm across), generally spherical, and loosely attached to leaves or embedded in tissues. They are usually observed as small black spots on plant tissues in the field, but when soaked with water, they become light to dark brown. On turf that is cut at a putting green height (<7.5 mm), masses of sclerotia may be visible on the patch surface (Fig. 5). On longer cut turf, the sclerotia often drop off from leaf blades and may not be obvious even right after snowmelt. The cells of the outer rind of sclerotia show variations in pattern from rounded to lobate (Fig. 7), but these patterns cannot be used as the sole basis of differentiating subgroups within the *T. ishikariensis* complex (55).

Sclerotia of *T. incarnata* are initially light colored (pink, yellow, or brown) and darken with age and drying to a reddish brown. They are irregularly shaped (spherical to subglobose) and up to 5 mm in diameter but usually less than 3 mm. They often remain attached to plant tissues, and the rind cells are moderately interlocked (Fig. 7). *T. phacorrhiza* has large pyriform to irregularly shaped, pedicellate sclerotia, often up to 7 mm in diameter, which are reddish to dark brown and firmly attached to plant debris by a well-developed stalk. The rind cell patterns are heavily digitate and conspicuous (Fig. 7).

Characteristics of spore-producing structures also differ among these species. *T. incarnata* produces pink clavate sporocarps, up to 20 mm long (Fig. 8), which can occasionally be observed on turf in the fall. *T. ishikariensis* has white clavate sporocarps, usually less than 15 mm long (Fig. 8), which are very rarely observed on turf. Sporocarps of *T. phacorrhiza* are filiform and dark when mature, and up to 100 mm long, but seldom observed in the field. In culture, the long, sterile, yellowish brown sporocarps of *T. phacorrhiza* develop

Table 2. Sclerotial characteristics of *Typhula* species associated with grasses

	T. ishikariensis	***T. incarnata***	***T. phacorrhiza***
Color	Dark brown to black	Pink to hazel brown	Light to dark brown
Diameter	0.2 to 2 mm	0.5 to 5 mm	1 to 7 mm
Shape	Spherical	Irregular	Pyriform to irregular
Relative numbers	Abundant	Many	Few
Rind cell patterns	Not lobate	Lobate	Digitate
Attachment	Usually loose	Usually embedded	Pedicellate

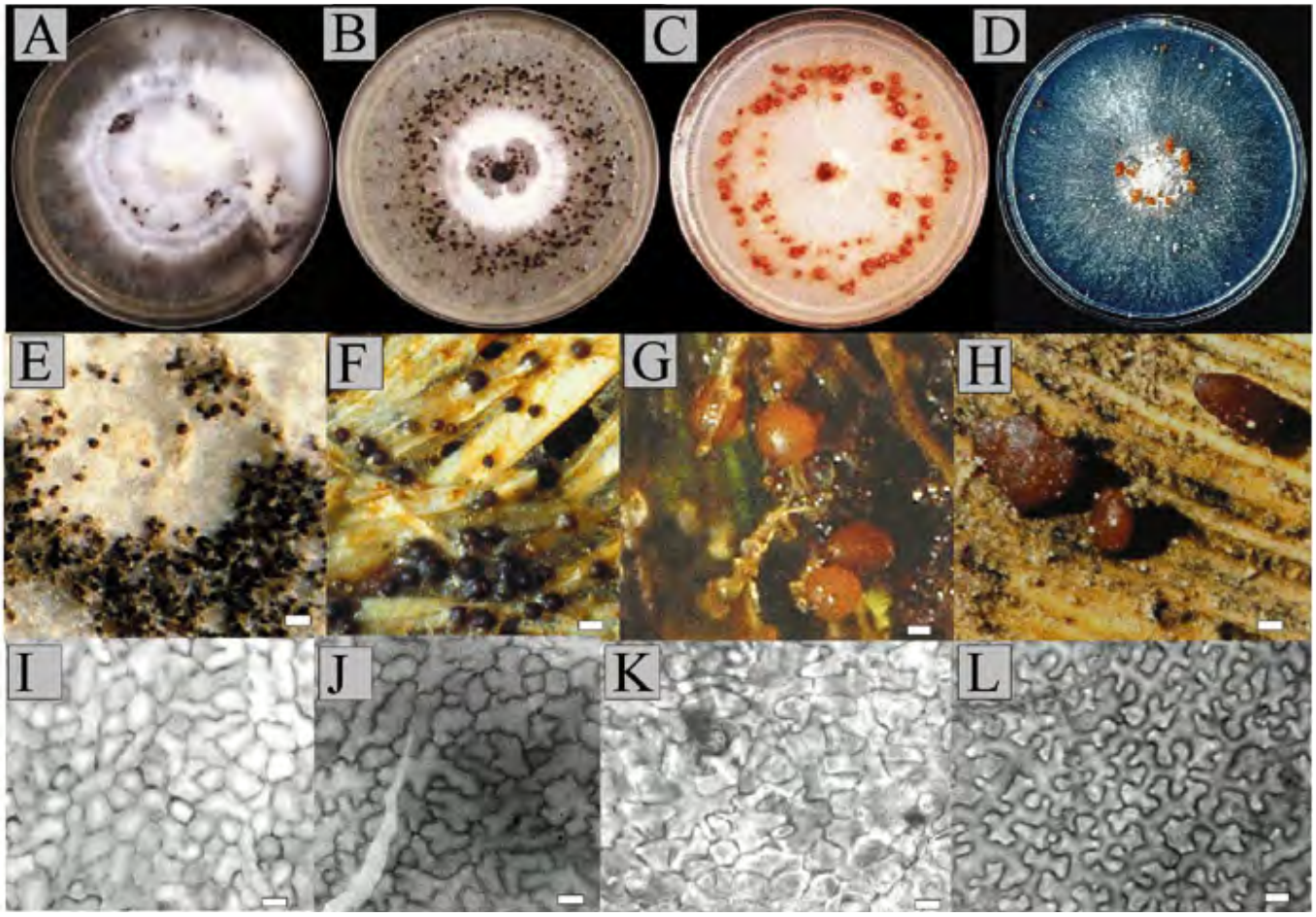

Fig. 7. Cultural morphology (A to D), sclerotia (E to H), and sclerotial rind patterns (I to L) of *Typhula ishikariensis* var. *canadensis* (A,E,I), *T. ishikariensis* var. *ishikariensis* (B,F,J), *T. incarnata* (C,G,K), and *T. phacorrhiza* (D,H,L). Cultures were grown on potato dextrose agar for up to 6 weeks at 10°C (A to D), and sclerotial rind patterns (E to H) were obtained by photomicroscopy of thin slices of the outer surfaces of water-soaked sclerotia. Scale bars at the bottom right of the sclerotia pictures (E to H) represent 1 mm, while those of the rind cells (I to L) represent 10 µm.

abundantly from either sclerotia or mycelium (69).

Other phenotypic differences of *Typhula* species associated with turfgrasses and cereals include cultural morphology (11), field survival of sclerotia (48), pectic zymograms (86), sclerotial polypeptides (62), temperature effects on growth and polypeptide composition (63), and fungicide efficacy in the field (83; I. Saito, *personal communication*).

Generalized disease cycle. In late autumn, the cool, wet weather (10 to 18°C) and diffuse UV light favor sclerotial germination (78) (Fig. 9). Spore-producing structures called clavula arise from sclerotia (often just one per sclerotium for *T. ishikariensis*), and basidia develop. Except for *T. incarnata* (32), the sexual stage is seldom observed in nature, and the primary inoculum is believed to be the mycelium originating from sclerotia rather than basidiospores (19). Particularly in years that are dry and warm just prior to snowfall, sclerotia germinate under snow cover and produce mycelia (83). Under snow cover, mycelia spread, produce infection cushions, and penetrate plant tissues directly or through stomata (20,66). After snowmelt, sclerotia are usually visible on or in infected tissues (Figs. 3 and 5). Fluffy, light-colored mycelium may also be present (Fig. 4). The colonized dead plant tissues decompose and disintegrate, and the sclerotia fall to the thatch and soil where they oversummer. During summer, sclerotia of *T. incarnata* are heavily parasitized by fungi, and germination rates can be reduced by 90% (48), while sclerotia of *T. ishikariensis* are relatively unaffected by mycoparasites. The effects of summer fungicide use and cultural practices on the survival of sclerotia are uncertain.

Ecology and Pathogenicity

T. ishikariensis, *T. incarnata*, and *T. phacorrhiza* are adapted for low-temperature growth. All three species show greater growth at 0°C than at 20°C (Fig. 10). In pure culture, their growth temperature optima range from 7 to 15°C (78); however, under field conditions, they are not active at these optimal growth temperatures. The inability of *T. incarnata* and *T. ishikariensis* to cause disease at their optimal temperature under field conditions can be attributed to microbial antagonism (50). In one experiment, radial mycelial growth of *T. ishikariensis* on potato dextrose agar (PDA) at 0°C was half that at the optimal temperature, 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 (Fig. 11). These three *Typhula* species are ubiquitous in regions with prolonged snow cover. The incidence and dominance of these fungi are thought to be intimately related to climate (64,81).

T. incarnata. *T. incarnata* has been reported from northern Europe, Canada, the northern United States, and Japan (78). In mild maritime climates, winters are seldom long or severe enough to cause extensive low-temperature injury or prolonged grass dormancy, and hence this facultative parasite is unable to establish sufficiently as a saprotroph to cause disease problems (32). Although *T. incarnata* is generally found in areas with more than 65 days of snow cover, it is uncommon in areas of extreme winter temperatures (76). In Canada, *T. incarnata* is found in the Great Lakes Region, the Maritimes, and British Columbia, but is rare on the Prairies (76). The wide geographic range of this fungus is ascribed to its ecological versatility (45). Within local populations, there is not much variation in mycelial growth rates (45). Sclerotia of *T. incarnata* from areas of long-lasting and heavy snowfall germinate faster than those from areas of less persistent snow cover (45).

T. incarnata utilizes a broad range of substrates, from live tissues to dead organic matter, and is a weak pathogen with a major saprotrophic phase (42). It is less virulent than *T. ishikariensis* but has a higher competitive saprotrophic ability (42). *T. incarnata* is common on winter cereals and turfgrasses in areas of abundant snow cover (78).

T. ishikariensis. *T. ishikariensis* has been reported from northern Japan, northern Scandinavia, Canada, and the northern United States (78), as well as Russia (73). It is restricted to areas with greater than 50 cm of snow cover for more than 60 days (46), or greater than 90 days of snow cover (3,81). *T. ishikariensis* has evolved strains that are adapted to different conditions. This diversity and specialization in *T. ishikariensis* may be one reason for the resulting taxonomic controversies over *T. ishikariensis* varieties. In Japan, *T. ishikariensis* biotype A is restricted to regions of heavy and long-lasting snowfall. It can attack both dicots and monocots, thus promoting its chances of survival in a limited area (54). Biotype B in Japan is more widely distributed but is restricted to monocots. For biotype B, size variation in sclerotia is positively correlated with the duration of snow cover, and virulence is negatively correlated with duration of snow cover (51).

T. ishikariensis is usually soilborne, and the fungus spreads mainly by vegetative growth under snow, with mycelium from sclerotia as the primary inoculum. Sclerotia of *T. ishikariensis*, although smaller than those of *T. incarnata*, can survive

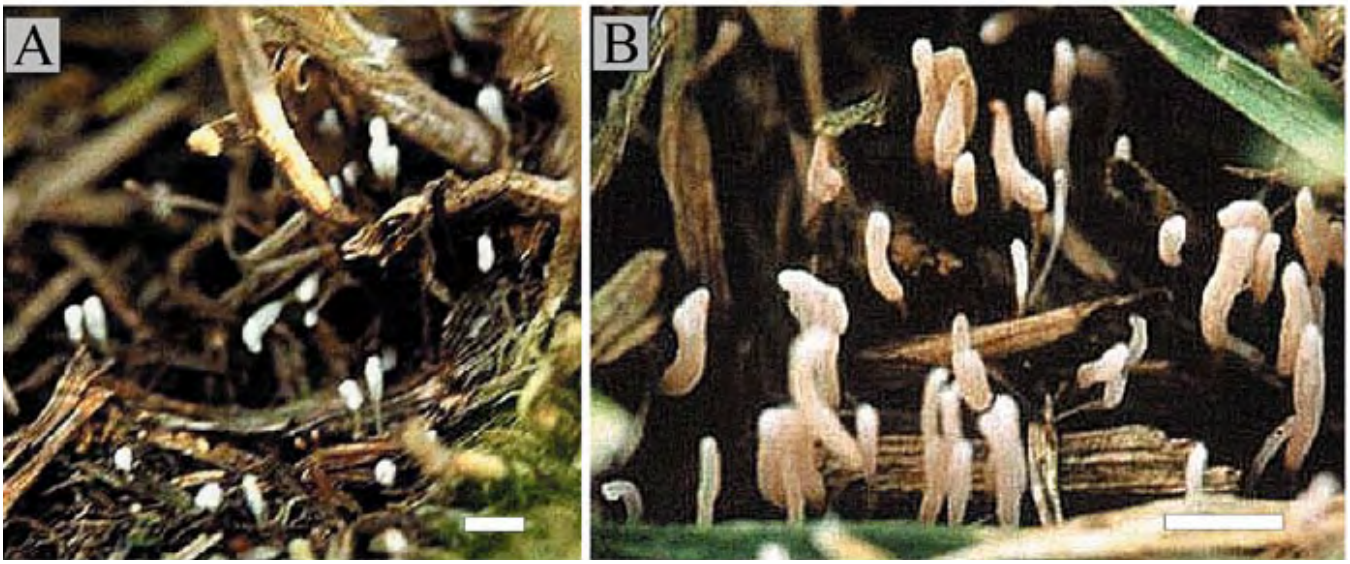

Fig. 8. Sporocarps of *Typhula ishikariensis* (A) and *T. incarnata* (B) observed during a wet period in late fall. Scale bars at the bottom right of each picture represent 10 mm.

better through summer (48) and are often produced on roots as well as leaves. *T. ishikariensis* attacks graminaceous plants but has also been found in clover, alfalfa, winter turnip, rape, sugar beets, and bulbs of iris and tulip (33). *T. ishikariensis* is almost always parasitic, with only one record of saprotrophism (41).

T. phacorrhiza. *T. phacorrhiza* has been found in Japan (53), northern Europe (8,69), India (35), Ontario (70), New York (69), Wisconsin (57), Washington (17), and Iceland (N. Matsumoto, *unpublished*). Early work on *T. phacorrhiza* (69) reported that it is widely distributed in temperate climates and is saprotrophic, colonizing leaf debris of grasses and deciduous plants. In Ontario, Burpee et al. (15) first observed *T. phacorrhiza* on necrotic foliage of *Poa pratensis*, but it is most commonly seen on overwintered corn stubble (90). In Wisconsin, it has been found on foliage of *Agrostis palustris*, *P. annua*, *P. pratensis*, and unidentified grasses adjacent to golf course fairways, and in the litter of *Acer saccharinum*, *Ulmus* sp., *Quercus rubra*, and *Chenopodium alba*. Schneider and Seaman (70,71) reported *T. phacorrhiza* as a pathogen of winter wheat (*Triticum aestivum*) in Ontario, Canada, based on controlled environment studies and a field study with a single *T. phacorrhiza* isolate. However, Burpee et al. (15) found that *T. phacorrhiza* was nonpathogenic to *A. palustris* and significantly suppressed speckled snow mold. Matsumoto and Tajimi (53) also described isolates of *T. phacorrhiza* that suppressed speckled snow mold of *Lolium perenne* in field tests in Japan. Wu et al. (90) confirmed that *T. phacorrhiza* isolates from cornfields across southern Ontario could suppress gray and speckled snow mold of *A. palustris* in field experiments. Using their five most suppressive isolates, Wu and Hsiang (90) found that *T. phacorrhiza* did not induce disease symptoms in winter field trials on 12 different turfgrass species or varieties and two winter wheat varieties in Ontario.

Recently, Millett and Maxwell (57) found *T. phacorrhiza* sclerotia in Wisconsin golf courses associated with diseased patches that were bleached white and mainly on top of existing patches caused by *T. incarnata*, *T. ishikariensis*, or a combination of both. However, *T. phacorrhiza* was found alone in some patches, and these were almost always whiter than the surrounding patches caused by *T. incarnata* or *T. ishikariensis*. Also, there were cracks in the dried turfgrass crust that resembled dried, bleached algal masses. On top of the white patches, there were often a few distinctive, large, reddish brown sclerotia of *T. phacorrhiza* with a stipe attaching it to the debris. The extent to which Wisconsin

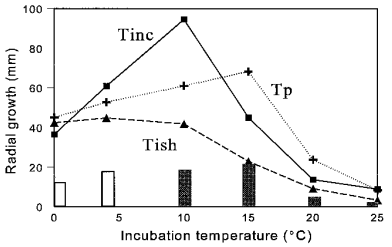

Fig. 10. Influence of temperature on mycelial growth on potato agar of three *Typhula* species (Tinc = *T. incarnata*, Tp = *T. phacorrhiza*, Tish = *T. ishikariensis*). Radial growth was measured after 39 days at 10°C. Each point is the mean of four isolates per species, with four replicates per isolate. The bars above the x-axis represent the least significant difference between means at *P* = 0.05, and shaded bars indicate significant differences between species in an analysis of variance (*P* = 0.05). From Wu and Hsiang (89).

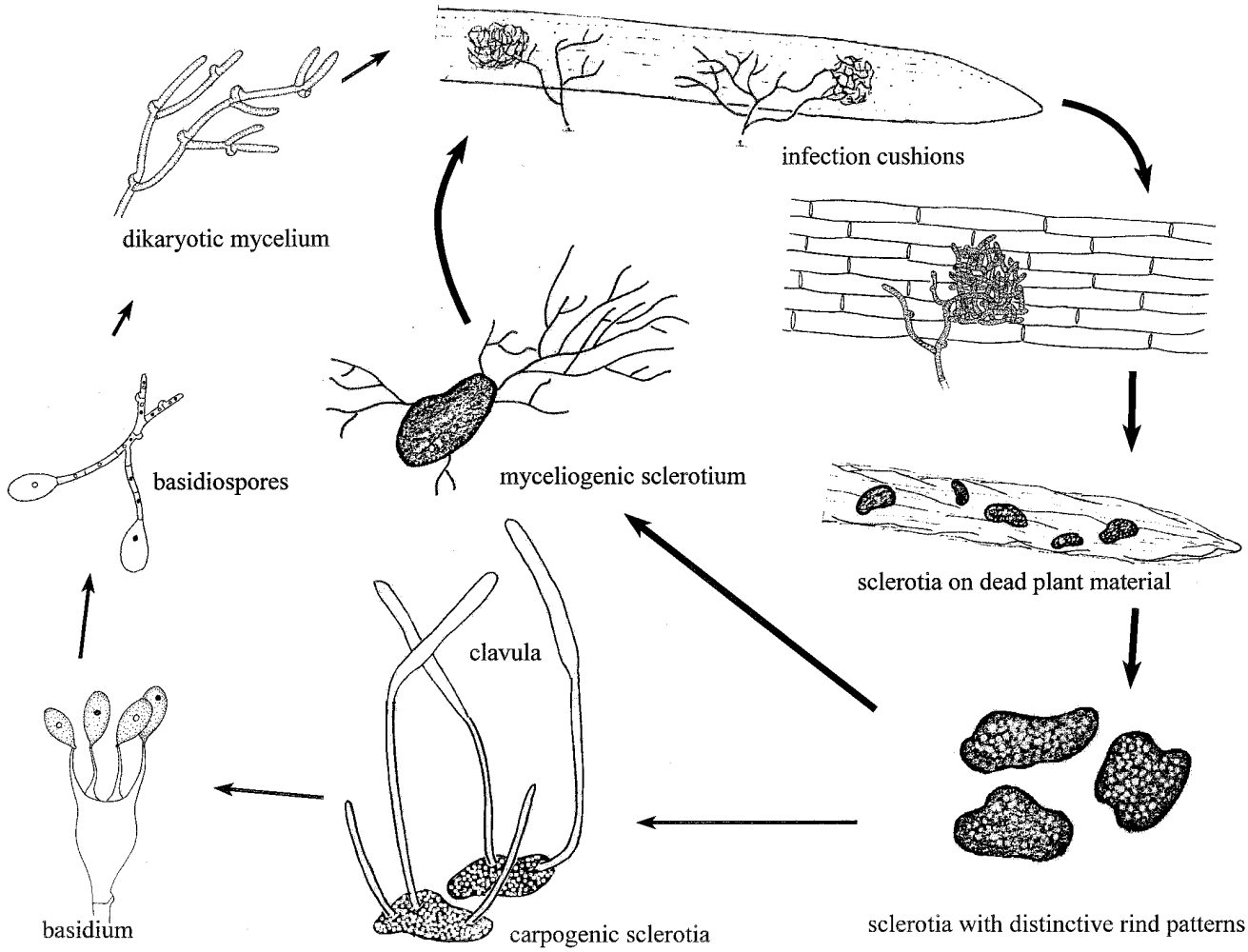

Fig. 9. Generalized disease cycle of Typhula snow molds. Full details are provided in the text.

turfgrass isolates of *T. phacorrhiza* are pathogenic, saprotrophic, or disease suppressive is uncertain. Schneider and Seaman (71) found that *T. phacorrhiza* demonstrated a low saprotrophic ability on winter wheat tissue compared with both *T. incarnata* and *T. ishikariensis*. In growth chamber experiments at 5 and 10°C with Wisconsin isolates on unhardened seedlings of *A. palustris*, the pathogens *T. ishikariensis* and *T. incarnata* were more aggressive than *T. phacorrhiza* (S. M. Millett, *unpublished data*).

Management

Winter injury to plants may be caused by biotic sources such as snow mold pathogens, but there are also abiotic sources such as desiccation, frost injury, and freezing damage. Comparison of winter injury on plants treated with a general protectant fungicide versus untreated can reveal the extent of abiotic and biotic winter injury. Depending on the amount or duration of snow cover, fungicide-treated plants may show less injury than untreated plants (Fig. 12).

Our understanding of Typhula snow molds has increased over the years, but control of these diseases in intensively managed turf still relies heavily on fungicide applications supplemented by cultural approaches. In addition, pink snow mold caused by *Microdochium nivale* (an ascomycete) frequently occurs along with Typhula blight on turfgrass (16,83). Some fungicides that are effective against pink snow mold are ineffective against Typhula blight and vice versa. Sound management practices integrate cultural practices and consider the occurrence of different snow mold diseases. Monteith and Dahl (58) may have been among the first to comment on integrated disease management when they wrote, "The control of turf diseases essentially involves three principles of plant disease control: the use of disease resistant grasses, the employment of correct cultural practices, and the judicious use of fungicides."

Fig. 11. Mycelial growth of *Typhula ishikariensis* at 0°C (left) or 10°C (right) on potato dextrose agar (bottom) or field soil (top).

Fig. 12. Turfgrass treated prior to snowfall with fungicide (left center) or untreated (right center), viewed after snowmelt.

Fungicides. Currently used fungicides to control snow mold diseases include quintozene, chlorothalonil, iprodione, chloroneb, propiconazole, benomyl, triadimefon, vinclozolin, azoxystrobin, flutolanil, fenarimol, cyproconazole, thiram, and—surprisingly—mercury. Mercurial fungicides were banned in the United States in 1970 due to concerns with chronic toxicity (21), but the ban was reversed in 1976 to allow the use of mercury for control of winter diseases on golf course greens, tees, and approaches (87). Since 1994, mercury fungicides have no longer been available for sale in the United States (83). In Canada, the registration for mercurial fungicides on turfgrass was removed in 1995. Mercurial fungicides have not been used on turfgrass in Japan since the 1970s. Although no longer registered in North America, mercurial compounds are still applied for control of snow molds on turfgrass because they are much cheaper than other fungicides (one-third to one-tenth the cost on an area basis) and are highly efficacious against Typhula blight and other snow molds (32,87). Some negative aspects of mercurial fungicides are that they do not degrade to nontoxic components, they remain persistent in golf course soils (23), and they may contaminate nearby aquatic ecosystems (56).

Fungicides are applied once just prior to snowfall to protect the grass against Typhula blight throughout the winter. The application rate can be five times higher for the single snow mold treatment compared with an application for a summer turfgrass disease. If applied too far in advance of permanent snow cover, rainfall and continued leaf growth may dilute the effectiveness of the fungicide. Depending on the type of fungicide, applications over a light covering of snow may still provide protection (87). Some fungicides are better able to persist and provide protection throughout long winters, but even with the proper conditioning of turfgrass for winter and the use of normally efficacious fungicides, abundant snow mold disease may still occur (87).

Turfgrass fungicides are typically applied in volumes ranging from 5 to 20 liters per 100 m^2. This is equivalent to 0.05 to 0.2 mm of precipitation. Thus, the effective coverage is only on the foliage. Furthermore, these applications may select

for soilborne genotypes (N. Matsumoto, *unpublished*). This is one reason that fungicides may need to be reapplied every year to locations where disease was fully controlled the previous year and no sclerotia were observed in the spring. Inoculum can arise from sclerotia produced on roots to cause disease in later years. Dependable control of snow molds may require mixtures of fungicides, since several different fungal pathogens may be active (16,83). Snow mold incited by *T. ishikariensis* is considered to be harder to control than that caused by *T. incarnata* (80,83,87). However, Couch (18) points out that *T. ishikariensis* is found primarily in regions where snow cover persists, and disease severity may be greater because plant carbohydrate reserves are depleted, increasing their susceptibility.

Resistance. *L. perenne* is considered the most susceptible to Typhula blight, followed by *Festuca arundinacea*, *A. palustris*, and then *P. annua* and *P. pratensis*, with *F. rubra* the least susceptible of the major northern turfgrasses (83,88). However, within each species, there can be very large differences in susceptibility among cultivars (39,83), and a major determining factor in snow mold resistance is the depletion of carbohydrate reserves as affected by duration of snow cover (9,59). Wu and Hsiang (88) found that susceptibility of 12 turfgrass species or varieties to *T. ishikariensis* and *T. incarnata* was strongly correlated. Other turfgrasses, such as *A. tenuis*, seem to have high resistance to snow mold diseases; however, they may be more susceptible to other diseases (83).

The National Turfgrass Evaluation Program (NTEP) coordinates evaluation of turfgrass varieties at sites in the United States and Canada. One of the characteristics measured in these multiyear trials is disease resistance. Although the trials depend on natural inoculum, they provide a multisite view of disease resistance. For example, one report gives Typhula ratings for 27 *A. palustris* varieties from 24 sites, showing a wide range in the amount of Typhula blight observed on different varieties (2). Studies like these can allow selection of varieties that show greater resistance to Typhula blight, particularly since heritability estimates for resistance to snow molds in grasses are high (24).

The physiological condition of the turfgrass plant has the strongest influence on its ability to resist attack by Typhula blight (9,59). If plants are not winter-hardened, they will suffer freeze damage with subzero temperatures or upon snowfall (14). Freeze-injured plants are more susceptible to pathogenic attack (24). Even if the plant becomes cold-hardy prior to snowfall, basal metabolism will use up carbohydrate reserves during periods of long snow cover, and the plant may become sufficiently weakened to be overwhelmed by pathogen attack.

Biocontrol. Many attempts have been made to examine biological control of snow mold diseases as an alternative to fungicides (25,31,34,48,75,77). In a biological control program for Typhula blight, there are two potential points of attack: one is during winter activity and the other is during summer dormancy (44). The use and timing of the biological control treatments may depend on the vulnerability of the pathogen at different stages, and also on the necessity of protecting the crop when it is most susceptible to attack. During summer, sclerotia of *T. incarnata* are heavily parasitized, and viability can be greatly reduced (48). However, reduction of sclerotial inoculum in a specific area may not necessarily result in lower disease pressure, since airborne infection from other areas is possible with *T. incarnata*. Sclerotia of *T. ishikariensis* are relatively unaffected by mycoparasites during summer dormancy, but establishment of sclerotial parasites of *T. ishikariensis* during summer is difficult because of the intense competition among microorganisms during the summer (48).

Promising results have come from the use of *T. phacorrhiza* as an antagonist of Typhula blight applied before snowfall. Burpee et al. (15) and Matsumoto and Tajimi (53) explored biological control of speckled snow mold with *T. phacorrhiza*. They found isolates that could inhibit disease caused by *T. ishikariensis* on *A. palustris* (15) and on *D. glomerata* or *L. perenne* grown as forage (53). Wu et al. (90) screened a larger number of *T. phacorrhiza* isolates and found a large variation in ability to suppress gray snow mold on *A. palustris*. After three seasons of field testing, they found several isolates that provided statistically significant control equal to a standard fungicide treatment (90). Aside from the possible pathogenicity of *T. phacorrhiza* to grasses, another concern with the use of *T. phacorrhiza* as a biocontrol agent is that it may not control other snow mold diseases that often coexist with Typhula blight.

Matsumoto and Tajimi (49) obtained antagonistic antibiotic-producing fluorescent pseudomonad bacteria from sclerotia and leaves infected by Typhula species. A culture filtrate of *Pseudomonas fluorescens* was inhibitory to mycelial growth of *T. ishikariensis*, and bacterial suspensions applied in late fall were able to reduce snow mold damage (67). Sudate and Fujiwara (discussed in 44) found an isolate of *Humicola grisea* Traaen var. *grisea* from turfgrass that strongly inhibited growth of several snow mold fungi in field tests, with disease control equivalent to that of an organic copper fungicide.

Introduction and establishment of antagonists have been the largest problems in practicing biocontrol. The harsh winter environment under prolonged snow cover dictates that any potential biological control agent aimed at reducing Typhula blight must also be low-temperature tolerant and active under those conditions. Because of the low diversity of active species under snow, antagonists that are low-temperature tolerant may become established more easily. Matsumoto (44) has discussed the feasibility of snow mold biocontrol on turfgrass and concludes that the necessity for annual applications of a biocontrol agent may result in costs even greater than fungicide use; however, environmental risks and societal concerns may justify these costs as long as the efficacy is acceptable.

Compost-amended topdressings have also been found to significantly reduce Typhula blight. One effect of composts is to improve growth in early spring and promote recovery just because of their nitrogen content. However, composts also contain microorganisms that may show antagonism to turf pathogens. In one test, some compost-amended topdressings significantly decreased Typhula blight damage compared with the untreated control or the conventional fungicide, but others significantly increased disease (61). Although some of these topdressings have efficacy, their removal in spring may be a significant obstacle for turfgrass managers. Furthermore, miscellaneous debris, such as twigs, within some composts can significantly damage delicate greens mowers.

Cultural practices. Cultural practices including fertilization and snow removal have been used to manage Typhula blight. Fertilizers are applied to turfgrasses to maintain their aesthetic value, performance, and quality. Disease resistance can be altered through physiological and biochemical processes that are intimately connected with the nutritional status of the turfgrass.

Nitrogen fertility plays an important role in the ability of grasses to overwinter. Excessive nitrogen fertilization near the end of the growing season promotes lush growth (83) and prevents grasses from developing winter hardiness (78). However, nitrogen fertilization in the fall after the growth of the leaf blades has stopped may promote rapid growth and recovery in the spring (18,78,83). Tyson (82) demonstrated that the application of inorganic fertilizers, especially calcium nitrate, reduced snow mold disease severity on *Agrostis* species compared with organic sources such as cottonseed meal, dried blood, and Milorganite. Unfortunately, calcium nitrate has the potential to induce foliar burn on most turfgrasses (7). Recommendations for dealing with snow mold damage in the spring include promoting rapid drying and warming, improving drainage, replanting or resodding, or lightly fertilizing affected areas (74). However, nitrogen fertilization soon after snowmelt may predispose the grass to other diseases (37).

Because Typhula blight requires prolonged snow cover, attempts have been made to reduce snow mold severity by removing snow from the grass surface. Snow removal can reduce snow mold damage, but also allows for increased damage by winter desiccation (87). Snow removal as a management option for gray snow mold is more important in areas that have more than 3 months of snow cover. Snowmelt in the spring can be enhanced by applications of dark materials such as topdressings or fertilizers (78). Strategic placement of windbreaks or snow fences may help to reduce snow accumulation from drifts (18). Cultural techniques may reduce the severity of snow mold diseases, but cannot prevent them entirely (87).

Future Research

Typhula snow molds are very important as pathogens in cold regions; however, many aspects of their ecology, biology, and pathology are not known. These organisms have highly specialized niches and can cause great devastation under a narrow range of conditions. As climatic patterns change worldwide, the distribution and relative abundance of snow mold fungi may also be altered. Aside from their importance as plant pathogens, they can also be very useful as research organisms in cryobiology and fungal ecology. Investigation of adaptation mechanisms to low temperatures can provide insights in biology and may also lead to commercial uses. The genetic variation and high degree of specialization in *T. ishikariensis* may reflect incipient speciation, and the relationship of *T. ishikariensis* isolates from around the world needs to be tested. More information is also needed on the population biology of *Typhula* species and how they reproduce, establish populations, and survive over summer.

Just as with most turfgrass diseases, many of the management recommendations for snow molds derive from limited or indirect experimental evidence, and more direct research is needed. With changes in the availability and use of mercurial and other older synthetic fungicides in North America, more information on these organisms will be required to effectively manage them. Although *T. phacorrhiza* has been found to suppress Typhula blight, it has also been associated with patches on turfgrass, and more research is needed to clarify its disease-suppressive and phytopathological properties. We hope this article stimulates scientists working on other plant pathogenic fungi and may motivate them to study these fascinating Typhula snow molds.

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Mr. Millett expects to complete all requirements this year for his Ph.D. in the Department of Plant Pathology at the University of Wisconsin at Madison. His thesis work has focused on the distribution and characterization of *Typhula* species pathogenic to turfgrasses of Wisconsin golf courses. In 1998, he participated in the National Science Foundation's Summer Institute in Japan, where he studied with Dr. Matsumoto. In 1997, Mr. Millett received the Dr. James Watson Graduate Fellowship Award from the Golf Course Superintendents Association of America, mainly for helping establish the Turfgrass Disease Diagnostic Laboratory at the University of Wisconsin. He received an M.S. degree in plant pathology from Clemson University under the direction of Dr. Bruce Martin and a B.S. in botany from Truman State University. His M.S. degree focused on the effects of herbicides on Rhizoctonia blight of warm-season turfgrasses.

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