Aggressiveness of *Typhula ishikariensis* Isolates to Cultivars of Bentgrass Species (*Agrostis* spp.) Under Controlled Environment Conditions

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ABSTACT

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Speckled snow mold, caused by *Typhula ishikariensis*, is one of the most important Typhula snow molds in subarctic zones of the Northern Hemisphere. Nine isolates of three *T. ishikariensis* varieties (var. *ishikariensis*, var. *canadensis*, and var. *idahoensis*) isolated from infected turfgrasses on golf course fairways throughout Wisconsin were evaluated for their aggressiveness toward nine cultivars of three bentgrass species (three creeping, three colonial, and three velvet cultivars) under controlled environmental conditions. Speckled snow mold severity increased as inoculum concentration of *T. ishikariensis* was increased. In general, bentgrass susceptibility increased between 9 and 11 weeks after seeding but gradually decreased thereafter, suggesting expression of age-related resistance as plants matured. Significant differences in aggressiveness were detected within and among *T. ishikariensis* varieties. Significant interactions between *T. ishikariensis* varieties or isolates and bentgrass species were detected, but there was no interaction between pathogen isolates and bentgrass cultivars. Disease severity evaluations showed significant differences among bentgrass cultivars and species in their response to *T. ishikariensis*. Since bentgrass species exhibit differential responses to *T. ishikariensis* varieties, representative isolates of each variety should be employed for screening of bentgrass germplasm for resistance to speckled snow mold.

Typhula ishikariensis Imai, the causal agent of speckled snow mold, is an important pathogen of winter cereals and perennial grasses in subarctic zones of the Northern Hemisphere (14,24,25,28). The pathogen has been documented in alfalfa, clover, conifer, timothy, and winter turnip in addition to graminaceous plants (14,16,28). There are three varieties of *T. ishikariensis*: var. *ishikariensis*, var. *canadensis*, and var. *idahoensis* (3). *T. ishikariensis* var. *ishikariensis* favors a less fluctuating habitat and has faster growth ability than var. *canadensis* and var. *idahoensis* (7,9,20).

Most cool-season turfgrasses, including bentgrass (*Agrostis* spp.), Kentucky bluegrass (*Poa pratensis* L.), creeping red fescue (*Festuca rubra* L.), and perennial ryegrass (*Lolium perenne* L.) have been reported as hosts of *T. ishikariensis* (1,25,28). Bentgrass species are commonly used on golf course tees, greens, and fairways, and often sustain severe damage from *T. ishikariensis* infections during winter (15). Of the bentgrass species, creeping (*A. stolonifera* L.), colonial (*A. capillaries* L.), velvet (*A. canina* L.), redtop (*A. gigantean* L.), and dryland (*A. castellana* L.), creeping bentgrass is used most frequently for golf course turf, but interest is increasing in the development of colonial and velvet bentgrass varieties for golf course use (4,26,32).

The symptoms of speckled snow mold on turfgrasses appear after snowmelt in late winter or early spring as circular, water-soaked or straw-colored patches. Individual patches are usually less than 1 m across but can coalesce to form large areas (30). Plants in diseased patches are typically matted, slimy, and covered with mycelium and sclerotia of the pathogen. During the spring thaw, *T. ishikariensis* produces numerous brown or black sclerotia, which serve as oversummering structures and become a source of primary inoculum when temperatures become more favorable for pathogen germination in late fall (15).

The severity of snow mold damage is generally governed by environmental conditions such as temperature, humidity, snow cover duration, and availability of primary inoculum (5,6,10). In particular, snow cover duration and air temperature during winter have the greatest impact on the ecological distribution of *Typhula* species (9). Extended periods of continuous snow cover and low temperatures reduce the photosynthetic and metabolic rate of the host plants, thereby increasing their susceptibility to infection and colonization by the pathogen (22).

The spatial distribution of *T. ishikariensis* varieties may be caused by their adaptation to harsh conditions, such as long snow cover period, low temperature, and host nutrient status (9,19,21). *T. ishikariensis* var. *ishikariensis* is frequently found in areas with reduced snow cover duration compared to var. *canadensis* and in areas with lower temperature than the other *T. ishikariensis* varieties (9).

The most environmentally sound means of disease control is through the use of resistant cultivars. Currently, snow mold diseases are managed with a combination of cultural practices and preventative fungicide applications in the fall (8,33). The use of pathogen-resistant cultivars has been limited by our knowledge of the relative susceptibility of bentgrass species and cultivars to snow mold diseases. Characterization of the pathogenic variation within and among *T. ishikariensis* varieties has provided valuable information for breeding programs aimed at improving resistance to speckled snow mold (31). Therefore, in the present study, we examined the effect of inoculum concentration and plant age on the susceptibility of bentgrass species and cultivars by *T. ishikariensis* under controlled environmental conditions, and also evaluated the variation in aggressiveness within and among varieties of *T. ishikariensis*.

MATERIALS AND METHODS

Plant materials. Four creeping bentgrass cultivars (L-93, Penncross, Pennlinks, and Providence), three colonial bentgrass cultivars (Bardot, SR 7100, and Tiger), and three velvet bentgrass cultivars (Barvaria, Greenwich, and Vesper) were used for this study. Cultivars of creeping and colonial bentgrass (0.056 g of seeds) and velvet cultivars (0.035 g of seeds) were evenly sown into plastic pots (5.3 × 5.3 × 5.1 cm) containing commercial potting soil mixture (Metro Mix 366-P, Scott's Company, Marysville, OH). The plants were grown in the greenhouse at 18 to 28°C with light and dark cycle of 16 and 8 h, respectively. The plants were mown weekly with scissors to a height of 0.6 cm beginning 2 weeks after germination until

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the onset of hardening for acquisition of snow mold resistance of tested plants (2,13). The fertilizer (SunGrow Company, Austin, TX) at 0.02-0.005-0.02 g of actual N-P-K per pot was applied biweekly from 4 weeks after germination to 2 weeks prior to hardening.

Plants were transferred to a controlled environment chamber for hardening 21 days prior to their scheduled inoculation. Hardening conditions were 10°C and 10-h day length for 7 days; 5°C and 8-h day length for 7 days; and 2°C and 6-h day length for 7 days. The pots were placed into plastic trays containing distilled water to assure constant moisture.

Fungal isolates and inoculum. Three isolates of each of three *T. ishikariensis* varieties were randomly selected from a collection of isolates previously collected in Wisconsin (Table 1) (9). Inoculum was prepared using a procedure modified from Wang et al. (31). In brief, five 5-mm-diameter plugs were taken from the edge of colonies growing on potato dextrose agar (PDA) and transferred to 20 ml of potato dextrose broth (PDB) in 250-ml flasks and grown for 20 days at 10°C ± 1°C with no light. For each isolate, four to six flasks of mycelium were harvested and mixed, then air-dried for 30 min under a laminar flow hood. Residual water in air-dried mycelia was finally removed by vacuum-filtration for 3 min under 21 psi (1.5 kg/cm^2) of pressure through cheesecloth. Mycelium weights were recorded and the mycelium was homogenized in a blender with sterile distilled water for 30 s. The mycelial suspensions were then adjusted to the desired concentration using sterile distilled water.

Inoculation procedure. Sterile pipettes were used to deliver 1 ml of mycelium suspension directly to the soil surface in the center of each pot. Immediately after inoculation, distilled water was applied to the foliage until runoff with a hand sprayer. Inoculated pots were then arranged in a randomized complete block design in a plastic box (70 × 40 × 15 cm, Rubbermaid, Wooster, OH); approximately 30% of the total volume of the box was filled with moist potting soil (1 soil:1 distilled water, vol/vol). The box was covered to maintain the high humidity required for disease development and was transferred to a controlled environment chamber maintained at 2°C and 0-h day length for 21 days, 5°C and 6-h day length for 7 days, and 10°C and 8-h day length for 10 days. The boxes were completely randomized and arranged in the growth chamber.

Experiment 1 was conducted to evaluate the effect of inoculum concentration on disease development. For this experiment, 11-week-old plants after seeding were inoculated with mycelial suspensions containing 0.1, 0.2, 0.3, and 0.4 g mycelium/ml from two *T. ishikariensis* var. *ishikariensis* isolates (no. 2 and no. 3). Six bentgrass cultivars, L-93, Penncross, Pennlinks, and Providence (creeping), Tiger (colonial), and Greenwich (velvet), were inoculated with each inoculum concentration.

Experiment 2 was conducted to evaluate the effect of plant age on disease development. The same six cultivars used in the first experiment were inoculated 9, 11, 13, and 15 weeks after seeding with a 0.3 g/ml mycelial suspension of *T. ishikariensis* var. *ishikariensis* isolate 3, var. *canadensis* isolate 4, or var. *idahoensis* isolate 9.

Experiment 3 was conducted to evaluate variation in pathogenicity/aggressiveness of nine isolates representing three *T. ishikariensis* varieties (Table 1) and also evaluate the speckled snow mold susceptibility of nine cultivars representing each of three bentgrass species. Creeping bentgrass cultivars L-93, Penncross, and Providence, colonial bentgrass cultivars Bardot, SR7100, and Tiger, and velvet bentgrass cultivars Barvaria, Greenwich, and Vesper were inoculated 15 weeks after seeding using a 0.3-g/ml mycelial suspension.

Disease evaluation and statistical analysis. Disease severity for all three experiments was assessed at 38 days after inoculation by visually estimating the percentage of pot surface area exhibiting speckled snow mold symptoms. The rating at 38 days postinoculation was chosen based on previous inoculations (unpublished data) because this rating was the most reliable under the infection and colonization conditions used in this study. Data are analyzed using mean values of two runs since no significant difference between the runs ($P < 0.01$) was detected.

All statistical analyses were conducted using general linear models procedure (PROC GLM) in SAS 7.1 (27). An analysis of variance was used to evaluate the effects of inoculum concentration or plant age on disease development of four creeping bentgrass cultivars. Mean comparisons were done by using the least significant difference (LSD, $P = 0.05$).

Speckled snow mold severity for nine cultivars of three bentgrass species inoculated with nine isolates of three *T. ishikariensis* varieties were also analyzed by the ANOVA. Differences among inoculum concentrations, plant ages, or cultivars were compared using Fisher's protected least significant difference (LSD) at $P = 0.05$.

For experiment 3, the source of variation for bentgrass species was partitioned into two orthogonal contrasts: diploid (velvet) versus tetraploid genomes (creeping and colonial), and the two tetraploid genomes (creeping versus colonial) according to the procedures of Steel et al. (29). Specifically, the contrast between diploid and tetraploid genomes was performed in order to test for differences in speckled snow mold reaction between bentgrass species having diploid (velvet with A_1A_1) and tetraploid genomes (colonial with $A_1A_1A_2A_2$ and creeping with $A_2A_2A_3A_3$) (17). Likewise, the contrast between the two tetraploid genomes served to test for differences between bentgrass species having different tetraploid genomes ($A_1A_1A_2A_2$ and $A_2A_2A_3A_3$). Cultivars within species comprised the remainder of the variability among the nine cultivars. The method of contrasts was used to partition the interactions of the bentgrass species contrasts with isolates within each *T. ishikariensis* variety. All treatments were assumed to be fixed and blocks were assumed to be random in all ANOVAs (27). Mixed models analysis was used to compute standard errors of least squares treatment means.

RESULTS

Experiment 1: Effect of inoculum concentration on disease development. Typical symptoms of speckled snow mold, circular and water-soaked infections, were observed on inoculated plants. Initial disease symptoms appeared 2 weeks after inoculation using the highest inoculum concentration (0.4 g mycelium/ml) and 3 weeks after inoculation with the lowest concentration (0.1 g mycelium/ml). ANOVA of disease severity detected a significant inoculum concentration effect (Table 2). Disease severity on bentgrass plants progressively increased as inoculum concentration increased from 0.1 to 0.4 g mycelium/ml (Fig. 1).

A cultivar effect ($P < 0.0001$) was detected among the four creeping bentgrass cultivars. Overall, 'L-93' creeping bentgrass was the least susceptible to concentrations tested, while 'Pennlinks' was the most susceptible. The disease severity of colonial bentgrass 'Tiger' was similar to

Table 1. Nine isolates of *Typhula ishikariensis* varieties tested for aggressiveness on cultivars of creeping, colonial, and velvet bentgrass species and the site of collection

No.	Classification	Site of collection
1	*T. ishikariensis* var. *ishikariensis*	Lanark Links, WI
2	*T. ishikariensis* var. *ishikariensis*	Botten's Green Acres, Douglas, WI
3	*T. ishikariensis* var. *ishikariensis*	Spider Lake Golf Resort, Sawyer, WI
4	*T. ishikariensis* var. *canadensis*	Botten's Green Acres, Douglas, WI
5	*T. ishikariensis* var. *canadensis*	Sioux Creek Golf Course, Barron, WI
6	*T. ishikariensis* var. *canadensis*	Tahkodah Hills Golf Course, Bayfield, WI
7	*T. ishikariensis* var. *idahoensis*	Four Seasons Golf Course, Marinette, WI
8	*T. ishikariensis* var. *idahoensis*	Homestead Golf Course, Wood, WI
9	*T. ishikariensis* var. *idahoensis*	Spread Eagle Golf Course, WI

that of cultivars of creeping bentgrass; however, velvet bentgrass 'Greenwich' was more susceptible than creeping and colonial cultivars. A significant interaction ($P < 0.0127$) between isolates and inoculum concentrations was detected (Table 2).

Experiment 2: Effect of plant age on disease development. Significant effects of plant age, isolate, and cultivar ($P < 0.0001$) and interaction between isolate and plant age within cultivar ($P < 0.0001$) were detected (Table 3). Disease severity was greatest at the 11-week-old stage and lowest at the 15-week-old stage (Fig. 2). Interestingly, 9-week-old plants showed reduced disease severity compared with 11-week-old plants. A similar trend was noted in most cultivars of the three bentgrass species (Fig. 2), but was most evident in Penncross and Pennlinks cultivars of creeping bentgrass.

Experiment 3: Aggressiveness of *T. ishikariensis* varieties to bentgrass species. Significant differences ($P < 0.0001$) among varieties of *T. ishikariensis* were detected on nine cultivars of three bentgrass species (Table 4). Isolates of var. *ishikariensis* were more aggressive than isolates of the other varieties (Fig. 3). In addition, significant interactions such as variety × creeping and colonial versus velvet cultivars, isolate (variety) × creeping and colonial versus velvet cultivars, and isolate (variety) × creeping versus colonial cultivars were observed (Table 4). Var. *idahoensis* was more aggressive to velvet bentgrass cultivars than to cultivars of the other bentgrass species. Significant differences in aggressiveness were observed among isolates within each *T. ishikariensis* variety (Table 4 and Fig. 3).

Speckled snow mold severity was significantly lower on cultivars of creeping and colonial bentgrasses than on velvet bentgrass, whereas no differences were detected between cultivars of creeping and colonial bentgrass (Table 4 and Fig. 3).

DISCUSSION

In the present study, aggressiveness of isolates of three *T. ishikariensis* varieties was evaluated on cultivars of three bentgrass species under controlled environmental conditions. In the inoculated plants, the mycelium of *T. ishikariensis* invaded the crown tissue and the upper portion of the plants, which resulted in circular, water-soaked patches in the infected plants. The infected plants were matted with mycelium and sclerotia. Eventually, the plants were killed.

All bentgrass cultivars tested were susceptible to *T. ishikariensis*, with an observation of no hypersensitive reaction, but there was a quantitative variation in susceptibility. These findings support a previous study (31) where the existence of quantitative resistance in creeping bentgrass clones to *Typhula* species was described. Further, Wang et al. (31) reported

Table 2. Analysis of variance for speckled snow mold severity for four cultivars of creeping bentgrass inoculated with two isolates of *Typhula ishikariensis* var. *ishikariensis* at four inoculum concentrations (0.1, 0.2, 0.3, and 0.4 g mycelium/ml) under controlled environment conditions

Source of variation	df	Mean square	*F* value	*P*
Experiment	1	61.9	1.14	0.2880
Replication (experiment)	4	87.4	1.61	0.1757
Isolate	1	317.8	5.84	0.0169
Inoculum concentration (cultivar)	12	5,815.0	106.81	<0.0001
Cultivar	3	450.0	9.18	<0.0001
Isolate × cultivar	3	69.0	1.27	0.2877
Isolate × inoculum concentration (cultivar)	12	121.4	2.23	0.0127
Error	155	54.4		

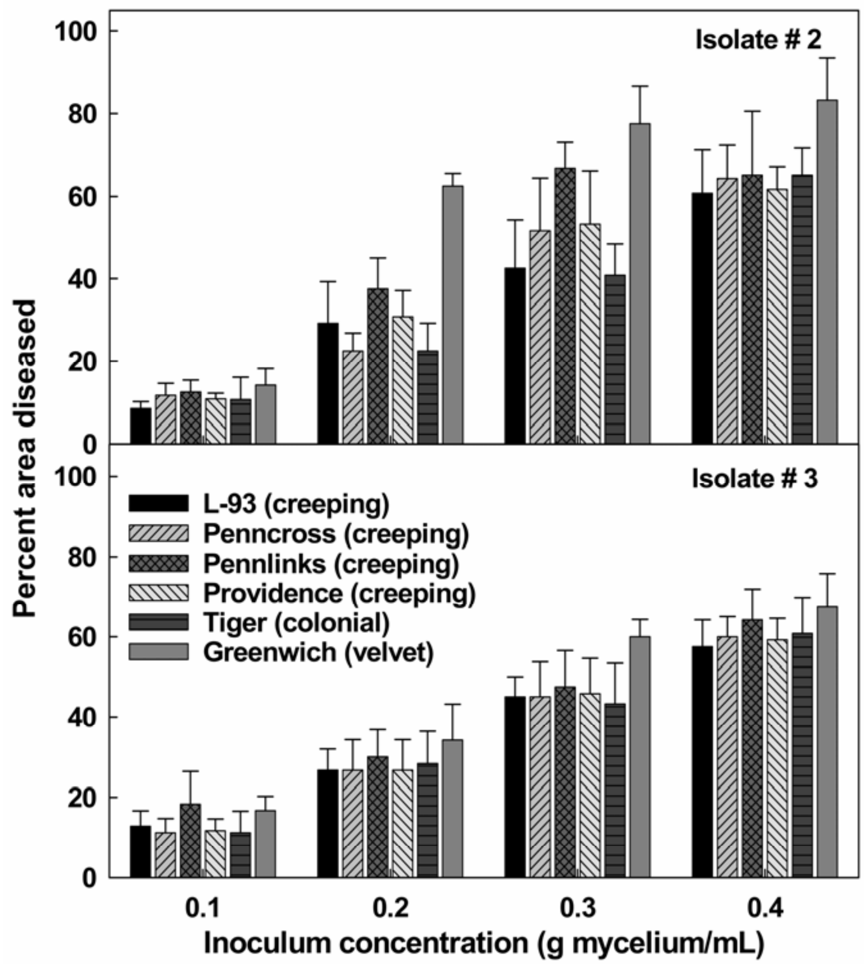

Fig. 1. Disease severity of six cultivars of three bentgrass species inoculated with two isolates of *Typhula ishikariensis* var. *ishikariensis* at four inoculum concentrations under controlled conditions. Disease severity was based on mean percent area diseased averaged over three replicates of two experiments. Bars represent standard error of the mean.

Table 3. Analysis of variance for speckled snow mold severity for four cultivars of creeping bentgrass inoculated with three isolates of *Typhula ishikariensis* at 9, 11, 13, and 15 weeks after seeding under controlled conditions

Source of variation	df	Mean square	*F* value	*P*
Experiment	1	215.3	1.47	0.2262
Replication (experiment)	4	59.3	0.41	0.8047
Cultivar	3	4,435.7	30.33	<0.0001
Plant age (cultivar)	12	2,850.7	19.49	<0.0001
Isolate	2	5,464.9	37.37	<0.0001
Isolate × cultivar	6	276.4	1.89	0.0833
Isolate × plant age (cultivar)	24	831.7	5.69	<0.0001
Error	235	146.2		

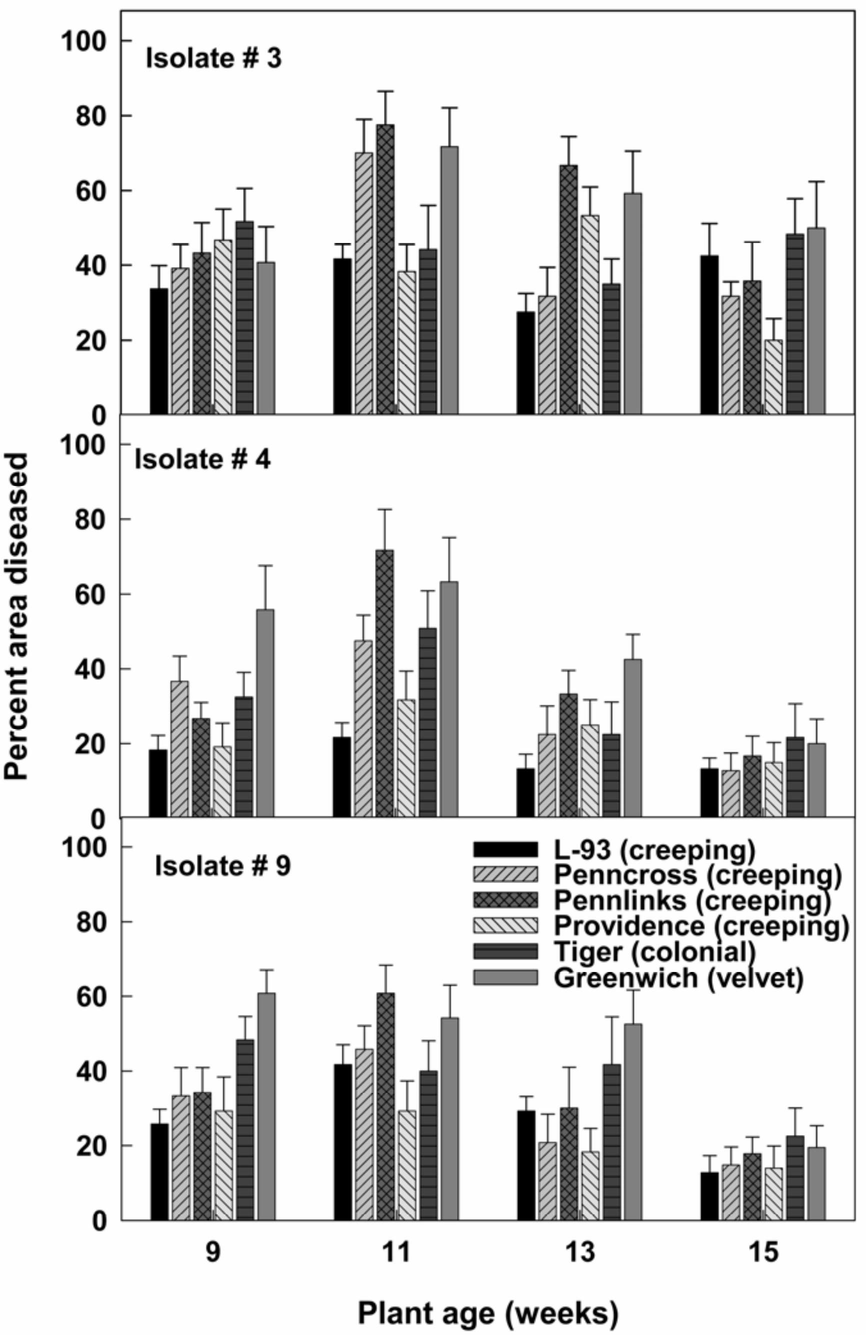

Fig. 2. Disease severity of six cultivars of three bentgrass species inoculated with three isolates of *Typhula ishikariensis* varieties (isolate 3: var. *ishikariensis*, isolate 4: var. *canadensis*, isolate 9: var. *idahoensis*) at four plant ages (9, 11, 13, and 15 weeks after seeding) under controlled conditions. Disease severity was based on percent area diseased averaged over three replicates of two experiments. Bars represent standard error of the mean.

that Typhula snow mold resistance in clones of creeping bentgrass is a generalized form of resistance, most likely non-race-specific. This phenomenon also has been recognized in wheat–snow mold pathogen systems (5,12), where snow mold resistance is expressed quantitatively and resistant cultivars exhibit higher survival and yield compared with susceptible cultivars.

Analysis of variance of disease severity showed an interaction effect ($P < 0.0127$) between isolates and inoculum concentrations within cultivar. It is likely due to a variation in the mycelium concentrations used for the inoculation, because the significant interactions occurred only at the low concentrations (0.1 and 0.2 g mycelium/ml) (Fig. 1). Based on this result, 0.3 g mycelium/ml seemed to be the optimum inoculum concentration for bentgrass germ plasm or cultivar screening under controlled conditions. However, field inoculations should also be performed to verify disease resistance under field conditions.

We observed an increase in susceptibility between 9 and 11 weeks in some cultivars, which may be due to the increase in plant density that occurs during this time. The significant effect of plant age on disease susceptibility indicated that some cultivars of bentgrasses become less susceptible to speckled snow mold over time. These results indicate that bentgrass plants express age-related resistance to *T. ishikariensis* as they mature, similar to other snow mold pathogen–host interactions (2,10,11,23). Nakajima and Abe (23) reported that older, hardened winter wheat plants were more resistant to snow mold than young plants similarly hardened under controlled conditions. This age-related resistance is believed to be associated with the more rapid accumulation of carbohydrates during hardening and slower metabolization of the carbohydrates in older plants (5,18,34). Therefore, we suggest that 15-week-old bentgrass plants are required for proper screening of speckled snow mold susceptibility under controlled conditions.

The increased susceptibility of 9- to 11-week-old bentgrass may be induced by changes in canopy density. Reduced canopy density in immature stands may initially hinder spread of the pathogen from plant to plant. As the stand matures and the canopy becomes more dense, susceptibility may increase until the age-related resistance mechanisms are expressed. The susceptibility of L-93, Providence, and Tiger did not change significantly over the course of 15 weeks. These cultivars may have the capability to express age-related resistance earlier than the cultivars Penncross, Pennlinks, and Greenwich. These cultivars expressing early resistance might be beneficial in the field because it would allow one to plant later in the fall without increasing snow mold susceptibility. Cultivar-dependent snow mold resistance might be enabled at different times during the maturation process, further supporting results of Gaudet et al. (13), which indicated that earlier and higher accumulation of physiologically active substances was involved with snow mold resistance in winter wheat resistant cultivars.

Cultivars of creeping and colonial bentgrasses were less susceptible to *T. ishikariensis* than velvet bentgrass cultivars, and no significant differences were noted between creeping and colonial bentgrass cultivars. This supports the NTEP (National Turfgrass Evaluation Program) data (2001 WI, published online) collected under field conditions, showing that the creeping and colonial bentgrass cultivars were more resistant to snow molds than velvet bentgrass cultivars. It appears that polyploid bentgrass species (creeping with $A_2A_2A_3A_3$ and colonial with $A_1A_1A_2A_2$ genomes) are less susceptible to *T. ishikariensis* than diploid bentgrass species (velvet with A_1A_1 genome). The resistance genes to *T. ishikariensis* may be contained in the A_2A_2 genome, which is common to creeping and colonial bentgrasses.

Table 4. Analysis of variance for speckled snow mold severity for nine cultivars of three bentgrass species, creeping, colonial, and velvet, inoculated with nine isolates of three *Typhula ishikariensis* varieties under controlled conditions

Source of variation	df	Mean square	*F* value	*P*
Experiment	1	14.9	0.28	0.5979
Replication (experiment)	4	100.5	1.88	0.1125
Variety	2	1,001.4	18.77	<0.0001
Isolates (variety)	6	1,231.1	23.07	<0.0001
Creeping and colonial vs. velvet cultivars	1	18,978.4	355.64	<0.0001
Creeping vs. colonial cultivars	1	13.0	0.24	0.6213
Cultivar (species)	6	107.2	2.01	0.0634
Variety × creeping and colonial vs. velvet cultivars	2	1,705.3	32.00	<0.0001
Variety × creeping vs. colonial cultivars	2	30.6	0.57	0.5637
Variety × cultivar (species)	12	57.8	1.08	0.3724
Isolate (variety) × creeping and colonial vs. velvet cultivars	6	709.6	13.30	<0.0001
Isolate (variety) × creeping vs. colonial cultivars	6	268.3	5.03	<0.0001
Cultivar (species) × isolate (variety)	36	57.9	1.09	0.3428
Error	400	53.4		

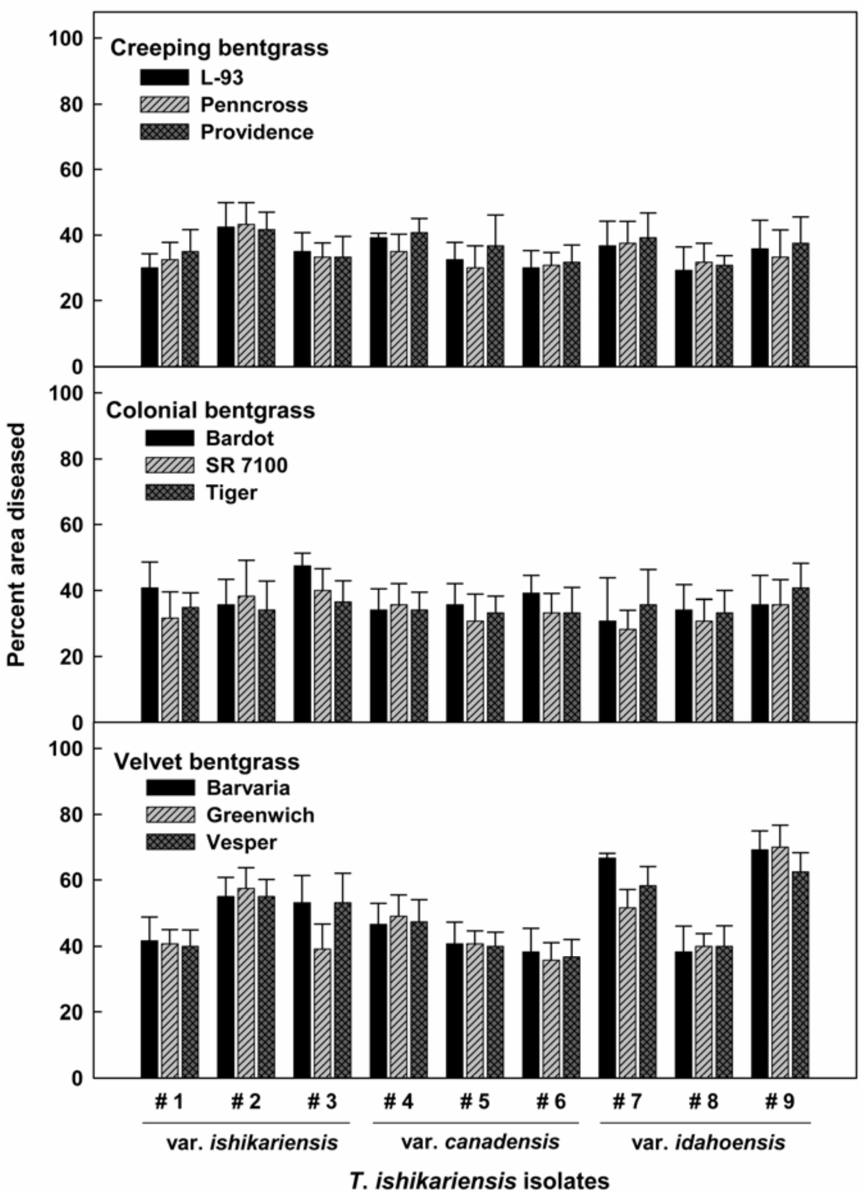

Fig. 3. Disease severity of nine bentgrass cultivars inoculated with three isolates of three *Typhula ishikariensis* varieties under controlled conditions. Disease severity was based on percent area diseased averaged over three replicates of two experiments. Bars represent standard error of the mean.

Significant differences in aggressiveness among isolates within and among *T. ishikariensis* varieties and the lack of isolate and cultivar interaction are very useful information for breeders. This will streamline the process of selecting and breeding *Typhula*-resistant cultivars within a given bentgrass species because inoculations may be conducted with a single virulent isolate. However, significant interactions between isolates within variety and bentgrass species suggest that a range of isolates representing *T. ishikariensis* varieties should be tested when evaluating clones or cultivars of different bentgrass species.

In summary, when screening for snow mold resistance under growth chamber conditions, inoculum concentration and plant age should be carefully considered. More importantly, varieties and isolates of *T. ishikariensis* should be selected specifically for each bentgrass species. Further studies under natural field conditions are required to better understand the interactions between isolates of *T. ishikariensis* varieties and bentgrass species.

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