Mycoscience (2007) 48:365–372
DOI 10.1007/s10267-007-0374-4

FULL PAPER

Yoshie Terashima · Azusa Fujiie

Comparison of conditions for mycelial growth of *Lepista sordida* causing fairy rings on *Zoysia matrella* turf to those on *Agrostis palustris* turf

Received: January 15, 2007 / Accepted: July 10, 2007

Abstract Symptoms of fairy rings caused by *Lepista sordida* have been reported on Zoysiagrass (*Zoysia* spp.) turf maintained at fairway height (2 cm), but not on bentgrass (*Agrostis* spp.) maintained at putting green height (0.5 cm). The mycelia of this fungus inhabit primarily the upper 0–2 cm layer of the soil extending into the thatch. To compare conditions for the mycelial growth in *Z. matrella* turf to those in *A. palustris* turf, we examined the effects of nutrients, temperature, water potential, and pH in the field as well as in the laboratory. Greater growth of the mycelia was observed in medium that included hot water extracts from soil of the 0–1 cm zone in *Z. matrella* turf compared to that from *A. palustris*. The upper soil layer in *Z. matrella* turf contained more organic matter from clippings than that in *A. palustris*. The temperature and water potential of the 0–2 cm soil zone in *Z. matrella* turf were also more favorable for the mycelial growth. The soil pH values of this zone in *Z. matrella* turf were less favorable compared to *A. palustris* but within the range for accelerating mycelial growth.

Key words *Agrostis palustris* · Fairy rings · *Lepista sordida* · *Zoysia matrella*

Introduction

Turfgrasses used for golf courses in Japan consist mainly of two types: warm-season Zoysiagrasses, such as *Zoysia matrella* Merr., and cool-season bentgrasses, such as *Agrostis palustris* Huds. *Zoysia matrella* is used mostly for fairways, while *A. palustris* usually is used for putting greens because of its tolerance for low mowing heights.

Fairy rings are caused by at least 54 species of mushroom-forming fungi that colonize soil (Couch 1995). Fairy ring development has one or a combination of three effects on turfgrasses: (1) the turfgrass is ultimately killed or badly damaged, (2) the grass is only stimulated, or (3) the fairy rings do not influence the growth of the grass (Shantz and Piemeisel 1917). The symptoms associated with *Marasmius oreades* (Bolt.: Fr.) Fr., a common pathogen causing the most damaging fairy rings in North America, Europe, and the South Pacific, have been summarized by Smith et al. (1989). Grass death was caused by a combination of complex phenomena, including hydrogen cyanide production by *M. oreades* mycelia, parasitism of the grass by the mycelia (Filer 1965), and hydrophobic soil induced by its mycelial growth (Filer 1965, 1966).

Fairy rings on turf caused by *Lepista sordida* (Schum.: Fr.) Sing. [=*L. subnuda* Hongo] have been reported only in Japan. The occurrence of sporophores and symptoms associated with the presence of this fungus, such as the formation of a dark green belt caused by stimulated turfgrass growth and a withered zone of dead grass, have been reported only in turfs of *Z. matrella* and *Z. japonica* Steud. (Tahama 1973, 1978, 1982; Tani 1991; Terashima and Fujiie 2005). This pathogen and symptoms have not been reported on *A. palustris* turf.

We have previously observed fairy rings of *L. sordida* with a radius up to 6 m and reported that the outward movement of the concentric ring associated with mycelial growth was 125 cm/year on *Z. matrella* turf at the Chiba Prefectural Agriculture Research Center, Chiba City, Japan (Terashima and Fujiie 2005). Dense mycelia were located beneath the outer edge of the dead grass belt, below the dead grass belt itself, and beneath the inner dark green grass belt. The visible mycelia existed primarily within a range of 0–2 cm of the upper soil with no mycelia observed at depths of 3 cm or more (Terashima and Fujiie 2005). This 0–2 cm zone included a thatch layer, which is defined as "a tightly inter-

Y. Terashima (✉)
Chiba Prefectural Forest Research Center, 1887-1 Haniya, Sanmu, Chiba 289-1223, Japan
Tel. +81-475-88-0505; Fax +81-475-88-0286
e-mail: y.trshm2@ma.pref.chiba.lg.jp

A. Fujiie
Former Chiba Prefectural Agriculture Research Center, Chiba, Japan

Part of this study was presented orally at the 46th meeting of the Mycological Society of Japan in 2002

mingled layer of dead and living stems and roots that develop between the zone of green vegetation and the soil surface" (Beard 1973).

Given that the fungus did not cause any direct damage to the seedlings of the Zoysiagrass in laboratory experiments, we assumed that the reason for turfgrass death could be attributed to the thick mycelial mat that developed and rendered the thatch layer impervious to water (Terashima and Fujiie 2005). Consequently, the question arose as to why the mycelia of this fungus grew on turfs of *Z. matrella* but not on *A. palustris* in the field. The aim of this study was therefore to characterize the conditions conducive for *L. sordida* mycelial growth on *Z. matrella* turf in the field and to compare these against conditions on *A. palustris* turf. We examined nutrition, as well as temperature, water potential, and pH of the soil beneath the turfs based on laboratory experiments, and compared these parameters between *Z. matrella* and *A. palustris*.

Materials and methods

Study site and turf management

The study site comprised a 7000-m^2 sward of *Zoysia matrella* turf and a 2300-m^2 area of *Agrostis palustris* turf that were examined in a previous study (Terashima and Fujiie 2005). The *Z. matrella* turf was laid on loam and clay soil in 1990 and was maintained at golf fairway conditions; it was mowed to a height of 2 cm every 2 or 3 days, fertilized with nitrogen at a rate of 15 g/m^2/year, and only watered during drought conditions in summer. As with fairway turf, cut grass was not removed, and a thatch layer accumulated to a depth of 1.5–2.0 cm. The *A. palustris* turf was laid on a sand-based soil following United States Golf Association specifications, to represent putting green turf. It was mowed to a height of 0.5 cm every day, fertilized at a rate of 16 g/m^2/year nitrogen, and irrigated artificially almost every day. The grass clippings were gathered and removed, and thatch accumulated only to a depth of approximately 0.5 cm.

Temperature measurement in soil layers

Soil temperatures were measured in both types of turf at four different soil depths. The measurement was conducted at the soil surface (0 cm), as well as at 0.5, 2.0, and 4.0 cm below the soil surface using thermistors (Hobo H8, Onset Computer) from April 1999 to March 2001.

Sampling of turfgrass and soil for laboratory experiments

Analysis of major nutritional components in turfgrass leaves

The two types of turf were grown in Wagner pots (diameter, 14 cm). One hundred grams of fresh leaves from both turfs were collected separately in July and August 1998. The leaves were dried at 70°C for 2 days. Neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) were assayed; cellulose was determined by subtracting ADL from ADF, hemicellulose was determined by subtracting ADF from NDF, lignin was taken as ADL, and total nitrogen was analyzed using the Kjeldahl method (Horii 1975).

Pretreatment of materials for mycelial growth and pH measurement

For the mycelial growth experiment using hot water extracts of leaves and soil, 100 g fresh tissue of both grasses was collected from the Wagner pots in July 2000. Fresh soil samples in flat block shape (width, thickness, and depth: 9, 1, and 10 cm) were collected at the same time from both types of turf with a cup cutter. The soil samples were then cut horizontally into ten 1-cm-deep layers (width, thickness, and depth: 9, 1, and 1 cm) from which the roots were removed. The pH values of the soil samples were measured after mixing in four times the soil weight of distilled water.

Cylindrical core samples for assessing mycelial growth

To determine which soil layer was colonized by mycelia, three cylinder-shaped core samples (diameter and depth: 9 and 10 cm) were taken using a cup cutter from both types of turf. Care was taken not to disrupt the soil structures of the samples.

Measurement of water potential and water content of soil

Two sets of soil samples collected in a flat block shape (width, thickness, and depth: 9, 1, and 10 cm) were cut horizontally into ten layers and the roots were removed. One set of the ten layers was subjected to water potential measurements using a vapor-pressure osmometer (Aqualab CX-2; Nihon-Zeneraru, Tokyo, Japan) at 25°C, and the means of duplicate measurements were analyzed. The other set was then used to measure water content, after being dried to constant weight at 95°C.

Mycelial growth experiments under different conditions

Fungal isolate and inoculum

The fungal isolate was obtained from *L. sordida* sporophore tissue from the study site in 1996. For the experiments in liquid media, inocula of the mycelia on agar (diameter, 4 mm) cultured on the medium described below on plates (diameter, 90 mm) were used. In the experiments using soil samples, a mixture of a 50% (w/w) commercial bark compost (Sumirin-yuki; Sumirin Agro-products, Aichi, Japan) and 50% dried wheat bran were added to give a 20% concentration of basal medium with a water content of 65% in a polypropylene pot (diameter and height: 8 and 13 cm) and

autoclaved for 60 min. The mycelia grown on this bark-wheat medium were used as inoculum.

Basal medium, culture conditions, and mycelial measurements

Modified Czapek and Dox medium was used as the basal medium (pH 6.0). This medium contained 15 g glucose, 15 g sucrose, 5 g yeast extract (Difco), 5 g polypepton (Nihon Pharmaceuticals, Japan), 1 g KH_2PO_4, 0.5 g $MgSO_4 \cdot 7H_2O$, 0.5 g KCl, 0.01 g $FeSO_4 \cdot 7H_2O$, and distilled water added to a final volume of 1 l. For maintenance and inoculation, the basal medium with 1.5% (w/v, the same hereafter) agar was used, and the liquid medium was used in all the experiments.

The experiments in liquid media were conducted as follows, unless otherwise mentioned. Ten 100-ml replicate flasks containing 10 ml medium were autoclaved at 121°C for 5 min. The mycelia were incubated during the stationary phase in the dark at 25°C for 7 days. The cultured mycelia were collected using a nylon cloth (125 mesh), rinsed with distilled water, dried to constant weight at 95°C, and weighed. Each experiment was repeated at least two times.

Periodic change in mycelial growth and effect of media with different C/N ratios

Glucose and sucrose concentrations of the basal medium were substituted with 2% glucose, and 20 ml medium was poured into 90 flasks. The mycelia were incubated at increments of 7 days for 7 to 63 days. After incubation, the media were filtered using a membrane filter (pore size, 0.4 µm). Glucose concentrations of the media with the basal medium were determined using the enzymatic bioassay method for D-glucose (F-Kit, Boehringer Mannheim, Mannheim, Germany) with a UV spectrophotometer (UV-150; Shimadzu, Kyoto, Japan) following the manufacturer's instructions.

Yeast and polypepton in the basal medium were changed to 1 g yeast. Instead of adding glucose and sucrose, different concentrations of glucose were added to the basal medium in five increments of C/N ratio between 0 and 50.

Effect of carbon sources and nutrients from turfgrasses and soils

Effect of media with different carbon sources

Instead of adding glucose and sucrose, 16 different carbon sources were added separately to the basal medium at 3% (see Fig. 3). Medium without a carbon source was used as a control.

Effect of media from hot water extracts of turfgrass and soil

The samples of turfgrass leaves and soils described earlier were dried at 70°C for 24 h, added to 50 and 10 times distilled water to give 2% and 10% concentrations of solutions, respectively, and heated for 60 min. The hot water extracts thus obtained were filtered using a nylon cloth, Dacron cloth (230 mesh), and then filter paper. The extracts from the turfgrasses were diluted further with distilled water to give concentrations of 0.2% and 0.02%. These 10-ml turfgrass and soil extracts from the two types of turf were then poured into ten 100-ml Erlenmeyer flasks.

Mycelial growth in core soil samples from turfs

The three cylindrical soil core samples taken from both types of turf described earlier were brought to the laboratory. A hole (diameter and depth: 2 and 10 cm) was made in the vertical direction in the center of the sample. The single sample was then placed into a 1000-ml glass beaker, and the beaker was placed into a polypropylene bag and autoclaved for 60 min after the inner temperature of the sample reached 121°C. The inoculum was then placed into the hole and the bag was heat-sealed. After 9 days of mycelial incubation, the samples were cut in half vertically, the inocula were removed, and the extent of mycelial growth was examined.

Effect of temperature

The mycelia were incubated in the basal medium at increments of 5°C, between 5° and 40°C.

Effect of media with different water potentials

Water potentials of the media were changed by adding different concentrations of polyethylene glycol (PEG) 6000 (Brownell and Schneider 1985) as an osmotizing agent: 0%, 2%, and 5% to 50% (w/w) in increments of 5%. The water potential of the media was measured using a vapor pressure osmometer as already described.

Effect of initial medium pH

For the medium preparation, carbon sources and other components were separately autoclaved. The media with pH values ranging from 4 to 10 were then adjusted with autoclaved 1 N KOH or 1 N HCl solutions.

Results

Effect of incubation period and C/N ratio of media on mycelial growth

The mycelial growth rate of *L. sordida* was fastest between days 7 and 14 in media supplemented with 2% glucose (Fig. 1). The glucose content in the medium began to decrease rapidly after 14 days and was almost 0 by day 42.

Mycelial growth was observed in media with C/N ratios ranging from 0 to 50 (Fig. 2). The mycelial weight increased in proportion with the C/N ratio until the ratio reached 30. Based on these findings (Figs. 1, 2), we selected an incuba-

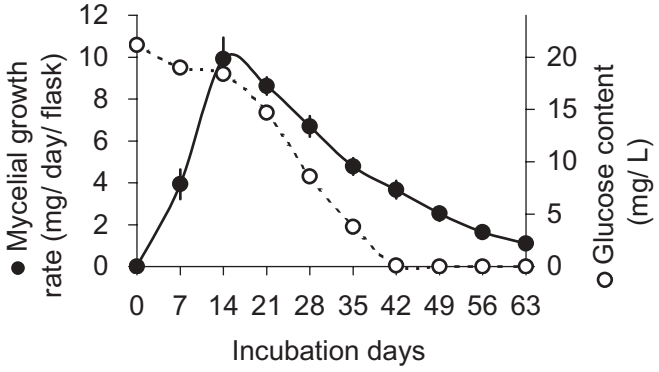

Fig. 1. Change in mycelial growth rate of *Lepista sordida* and glucose content in media over a 63-day period. *Bars* indicate standard deviations

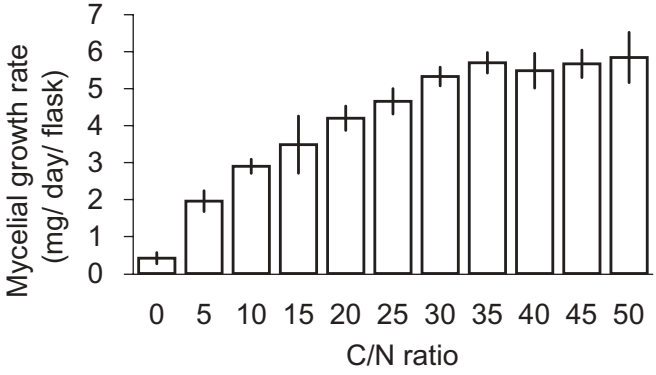

Fig. 2. Mycelial growth rate of *L. sordida* for different C/N ratios from 0 to 50. *Bars* indicate standard deviations

Table 1. Composition of major components of *Zoysia matrella* and *Agrostis palustris* turfgrass leaves

Material	Composition as dry basis %				
	Moisture	Cellulose	Hemicellulose	Lignin	Nitrogen
Z. matrella					
July	7.4	27.6	52.3	6.6	3.1
Aug.	7.0	31.2	49.1	7.2	2.3
A. pulstris					
July	8.3	18.8	37.3	4.1	4.6
Aug.	7.8	18.9	38.6	5.0	3.1

Cellulose, ADF-ADL; hemicellulose, NDF-ADF; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin

tion period of 7 days and a C/N ratio of 30 for the following experiments.

Effect of carbon source on mycelial growth and major nutritional components of turfgrass leaves

Table 1 shows the composition of the major nutritional components of *Z. matrella* and *A. palustris* turfgrass leaves. The average concentrations of cellulose, hemicellulose, and lignin for *Z. matrella* turfgrass in July and August were 1.6-, 1.3-, and 1.5 fold higher than those of *A. palustris*, respectively. Conversely, the concentration of nitrogen was 0.7 times lower in *Z. matrella* turfgrass than in *A. palustris*.

Figure 3 depicts the mycelial growth in media containing different carbon sources (3%) with the initial pHs. The mycelia were observed to grow better in the media containing amylose, CM-cellulose, mannose, galactan, xylose, dextrin, starch, maltose, arabinose, and galactose, in order of increasing growth, than in the medium with glucose. No statistically significant differences were observed among the mycelial growth in the four most optimal media containing amylose, CM-cellulose, mannose, or galactan by Sheffe's *F* post hoc test at the 5% level. The initial pH values of the media with pectin and pectic acid were exceptionally low, 4.2 and 3.1, respectively. The pH of the medium containing lignin was 6.9; the remainder ranged between 4.8 and 6.0.

In media produced from the hot water extracts of turfgrasses or soils, the mycelia grew best with 2% extract of *A. palustris* turfgrass leaves, 10% extract of the 0–1 cm soil layer from *Z. matrella* turf, and 2% extract of *Z. matrella* turfgrass leaves (Fig. 4). Conversely, the mycelia showed inferior growth in the medium containing the extract of the 0–1 cm layer from *A. palustris* turf.

Of the core samples from *Z. matrella* turf, the mycelia were observed to grow both on the upper turf surface surrounding the hole into which the inocula were placed, as well as on the inside walls of the holes (Fig. 5A,C). However, in the core samples from *A. palustris* turf, mycelia only grew on the upper surface and did not grow on the hole walls (Fig. 5B,D).

Effect of temperature on mycelial growth and temperature in soil layers

Figure 6 shows that mycelial growth occurred in the medium at temperatures ranging from 10° to 30°C, with an optimal temperature of 25°C. The equation for the linear relationship between 10° and 25°C could be described by

$$y = 0.4867x - 4.2693$$

where y was the mycelial growth and x the temperature. The developmental zero (predicted minimum temperature

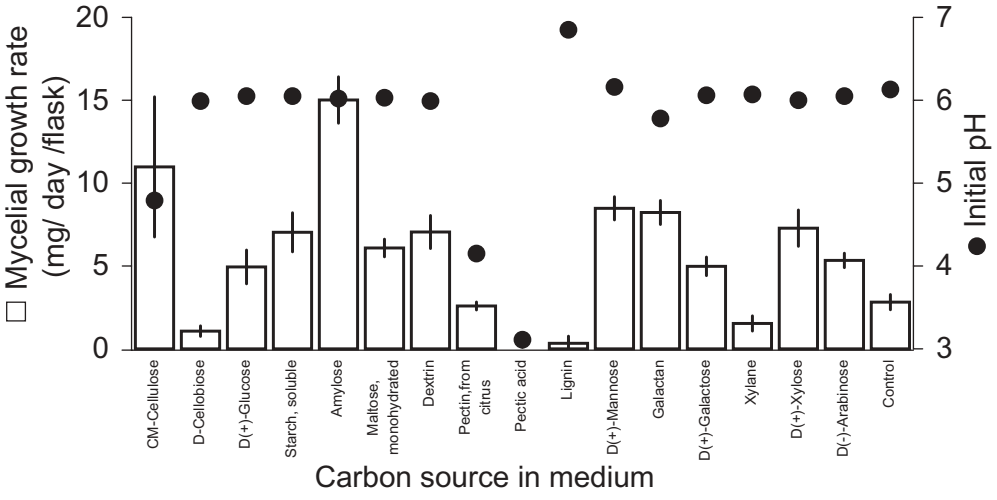

Fig. 3. Mycelial growth rate of *L. sordida* and initial pH in media with 16 different carbon sources. *Bars* indicate standard deviations

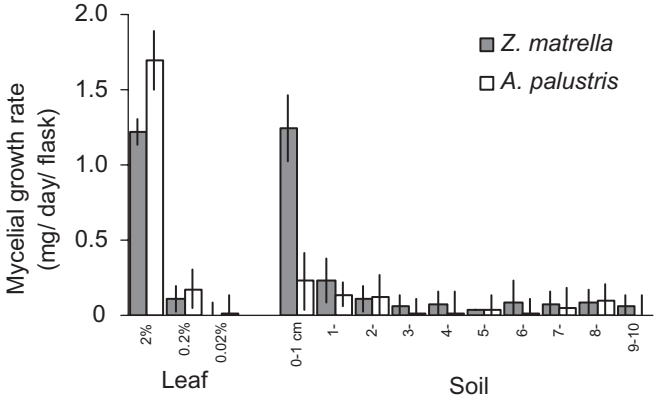

Fig. 4. Mycelial growth rate of *L. sordida* in media produced from hot water extracts of leaves and soil layers from *Zoysia matrella* and *Agrostis palustris* turfs. Extract concentrations of leaves were 2%, 0.2%, and 0.02%, and those for the soil layers were 0.1%. *Bars* indicate the standard deviations

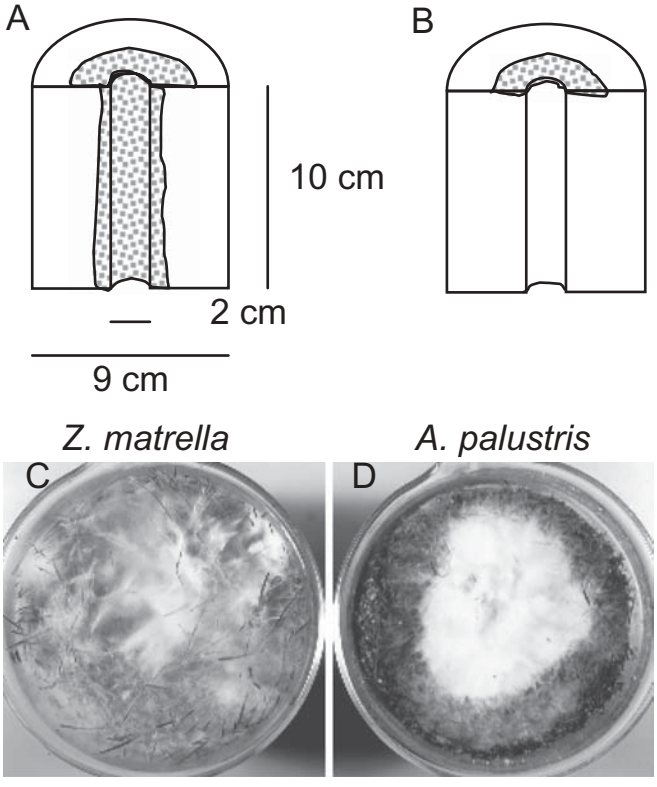

Fig. 5. Illustrated vertical cross sections of core samples from *Z. matrella* (**A**) and *A. palustris* (**B**) turfs, and photographs of soil surfaces of *Z. matrella* (**C**) and *A. palustris* (**D**) turfs. *Dotted areas* in **A** and **B** show the presence of mycelia

for growth) was 8.8°C, because $x = 8.8$ where $y = 0$ (Terashima and Fujiie 2006); this means that mycelial growth was accelerated between 8.8° and 25°C.

Figure 7 shows that the cumulative average temperatures of every 5 days between 8.8°C and 25°C in the field from April 1999 to March 2001. The temperatures of the soil layers of 0.5, 2.0, and 4.0 cm depth beneath *Z. matrella* turf were higher than those beneath *A. palustris* turf. However, the cumulative average temperature at the soil surface (0 cm) of the *Z. matrella* turf was slightly lower than that of *A. palustris*. The cumulative temperature in the 0.5–2.0 cm layer beneath *Z. matrella* turf, where the mycelia might be affected, was higher than that beneath *A. palustris*. The lowest monthly average temperature of 2.6°C was observed at the –0.5 cm soil layer in January 2001, with the highest of 29.5°C observed at the –2.0 cm soil layer in August 2000 beneath *Z. matrella* turf. Beneath *A. palustris* turf, the lowest average monthly temperature of 2.1°C was at the –0.5 cm soil layer in January 2001, and the highest temperature, 28.6°C, was observed at the –2 cm soil layer in August 2000.

Effect of water potential on mycelial growth and water potential in soil

Figure 8 shows the mycelial growth according to the different water potentials in media adjusted with PEG at concentrations ranging from 0 to 50%. Water potential indicates the available water content that mycelia can use. The water potentials in the medium with 0% PEG was –0.7. The mycelia grew best in the media at water potentials of –0.8,

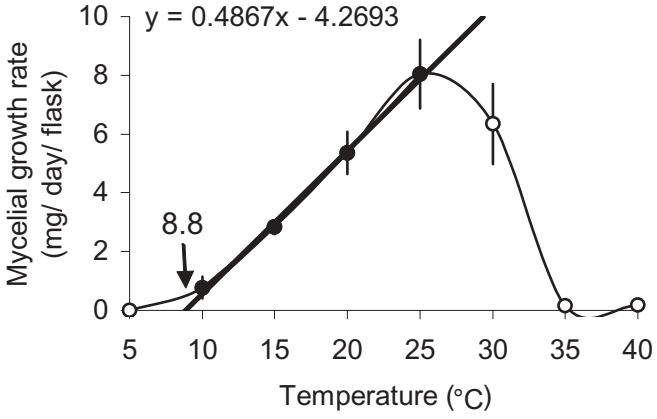

Fig. 6. Mycelial growth rate of *L. sordida* at temperatures ranging from 5° to 40°C. The equation for the linear relationship between 10° and 25°C is $y = 0.4867x - 4.2693$, where y is the mycelial growth and x is the temperature. The developmental zero was 8.8°C. *Bars* indicate standard deviations

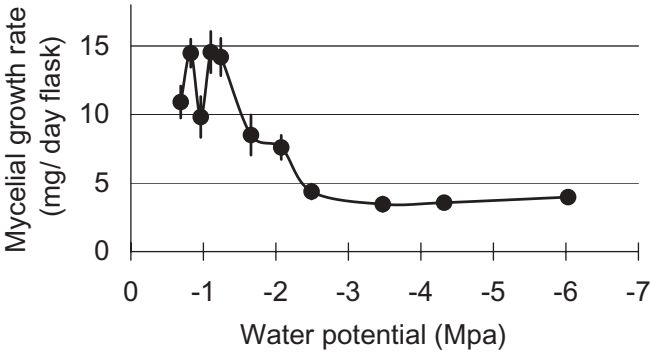

Fig. 8. Mycelial growth rate of *L. sordida* in response to changes in water potentials. The water potentials in liquid media were adjusted with polyethylene glycol (PEG) 6000. *Bars* indicate standard deviations

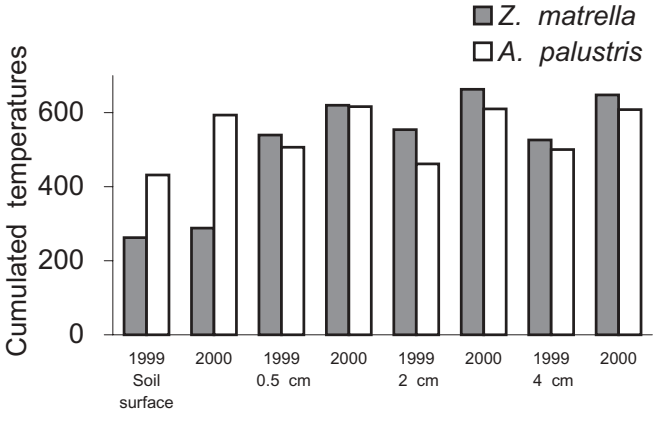

Fig. 7. Cumulative temperatures above the developmental zero (8.8°C) at the soil surface and –0.5, –2.0, and –4.0 cm soil layers beneath *Z. matrella* and *A. palustris* turfs in 1999 and 2000

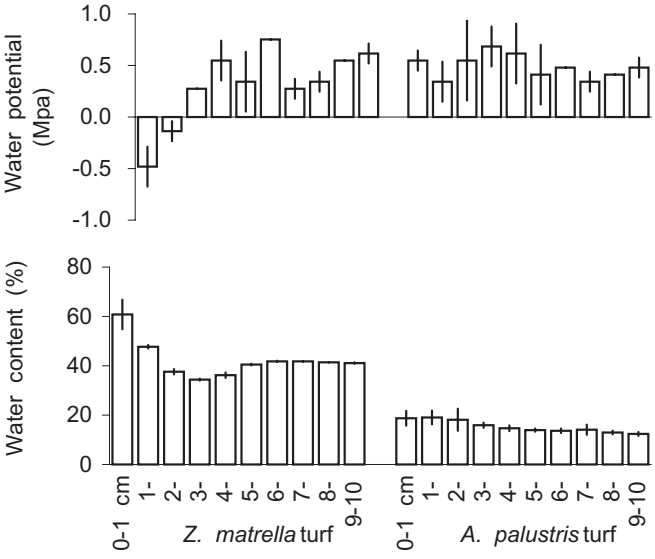

Fig. 9. Water potentials and water content of soil layers from *Z. matrella* and *A. palustris* turfs. *Bars* indicate standard deviations

–1.1, and –1.2 Mpa emended with 2%, 10%, and 15% PEG, respectively. Their growth rates were reduced according to the decline of the water potential until –6.0 Mpa in the medium with 50% PEG with the exception of the decline at water potential of –1.0 Mpa with 5% PEG concentration.

Figure 9 shows the water potentials and water contents of the soil samples. The water potential of the 0–1 cm layer from *Z. matrella* turf was –0.5 Mpa and that of the 1–2 cm layer was –0.2 Mpa. The remaining layers from *Z. matrella* turf ranged between 0.3 and 0.8 Mpa and those from *A. palustris* turf between 0.3 and 0.7 Mpa. The water potential in the upper soil layer beneath *Z. matrella*, where the mycelia might grow, was the closest to the optimal condition. The water content in any soil layer from *Z. matrella* turf was higher than that from the *A. palustris* counterpart.

Effect of medium pH for mycelial growth and soil pH

The mycelia grew in the media with pH ranging from 4.0 to 8.7 with an optimum pH of 6.0 (Fig. 10). The pH of the soils sampled from *Z. matrella* turf ranged from 7.3 to 7.7 whereas those from *A. palustris* turf ranged between 5.6 and 6.4 (Fig. 11).

Discussion

Hot water extracts made from the 0–1 cm soil layer taken from *Zoysia matrella* turf in the field were more favorable for the growth of *Lepista sordida* mycelia than those prepared from *Agrostis palustris*. The growth of the mycelia

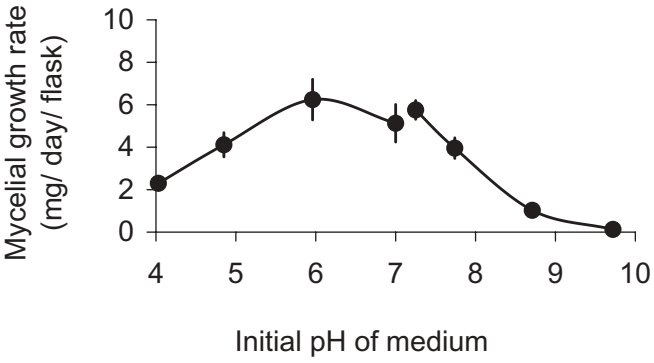

Fig. 10. Mycelial growth rate of *L. sordida* in media with different initial pH (4–10). *Bars* indicate standard deviations

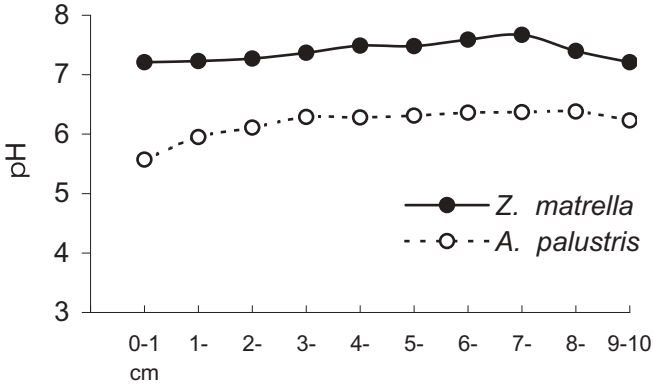

Fig. 11. pH values of the soil layers from *Z. matrella* and *A. palustris* turfs

on the cylindrical soil core samples supported this finding; i.e., the improved mycelial growth on the samples from *Z. matrella* turf compared to the samples from *A. palustris* turf. This difference was assumed to occur because the upper soil layer beneath *Z. matrella* turf contained more clippings and thatch, which provided more nutrition for mycelial growth than that found beneath *A. palustris* turf. The principal difference in soil structure between *Z. matrella* and *A. palustris* turfs is the thickness of the thatch. In fairways, as a general rule, clippings are returned to the turf surface because they are not a problem so long as they do not form obstacles for ball-roll by forming clumps on the surface. Conversely, clippings are removed from putting greens on golf courses because they interfere with play (Turgeon 1999). Clippings are a source of plant nutrients; they contain 3%–5% nitrogen (Hanson and Juska 1969), as shown in the result from the analysis of the two types of turfgrass here; they also contain 0.5% phosphorus and 2.0% potassium (Hanson and Juska 1969). Because of the clippings, among other possible reasons, *Z. matrella* turf at fairway height possesses a thicker thatch layer of 1.5–2.0 cm than *A. palustris* (0.5 cm) grown at greens height. Clipped leaves of *A. palustris* were removed and hence did not accumulate as thatch.

Although the mycelia grew better in the extracts from the 0–1 cm layer beneath *Z. matrella* turf, the hot water extract from 2% *Z. matrella* turfgrass leaves was less effective at promoting mycelial growth compared to the extracts produced from *A. palustris*. The differences in the composition of major components between *Z. matrella* and A. *palustris* were that *Z. matrella* leaves contained more carbohydrates, cellulose, and hemicellulose and less nitrogen than *A. palustris* leaves. In spite of higher cellulose and hemicellulose content in *Z. matrella* leaves, the mycelia showed less growth in the extract from nitrogen-poor *Z. matrella* leaves. Cellulose is the main structural component of the cell walls in most plants, followed by hemicelluloses, that are closely associated with cellulose and also occur in the matrix of the plant cell walls.

From the mycelial growth experiment in the liquid media with the 16 different carbon sources, the mycelia grew well on amylose, CM-cellulose, mannose, and galactan, which are related to the structural components of plants. Amylose is a component of starch, which is an abundant storage carbohydrate in higher plants. CM-cellulose is a type of cellulose. Mannose is found in mannans, which is a polysaccharide found in certain plants as hemicellulose, and galactan is a galactose polymer and a type of hemicellulose. Lignin is a major component of the vascular tissue of terrestrial plants. Higher lignin content in *Z. matrella* turfgrass leaves might also contribute to the accumulation of thicker thatch. Higher lignin content is found in plant tissue that is more resistant to decomposition, and thatch is composed primarily of the plant matter that is most resistant to decay (Waddington et al. 1992). From this experiment, mycelia of this fungus showed superior ability to utilize the polysaccharides contained in higher plants. Soil beneath *Z. matrella* turf accumulated more thatch, which contained the polysaccharides as nutrient for the fungus, than that beneath *A. palustris*. Therefore, the soil beneath *Z. matrella* provided better nutritional conditions for mycelial growth.

In the field, the cumulative average temperatures above 8.8°C were higher for *Z. matrella* turf in the soil layer of 0.5–2.0 cm, where the mycelia might exist, compared to those for *A. palustris*, meaning that the duration of suitable temperatures for mycelial growth above 8.8°C and below 25.0°C in the 0.5–2.0 cm layer beneath *Z. matrella* was longer than that beneath *A. palustris*. The results from the field measurements and laboratory experiments showed that the temperature conditions for the mycelia were more favorable for the growth in soils beneath *Z. matrella* turf compared to *A. palustris*.

According to the results from the mycelial growth experiment in liquid media with PEG, the mycelia grew well in the media with water potentials ranging between –0.7 and –1.2 Mpa. The water potential in the 0–1 cm layer beneath *Z. matrella* turf in the field was –0.5 Mpa, the nearest value to the optimum for the growth of the mycelia obtained from the experiment. From these results, the water potentials of the 0–1 cm soil layer beneath *Z. matrella* turf were more favorable for the mycelial growth compared to the condition in any other layer for either type of turf.

In this experiment, the control medium without PEG had a water potential of –0.7 Mpa, and no differences in the

optimal mycelial growth were observed in the media with water potentials of –0.8, –1.1, and –1.2 Mpa. The mycelial growth declined as the water potential decreased until it reached –3.4 Mpa. For *Armillaria mellea* (Whiting and Rizzo 1999) and *A. gallica* (Whiting and Rizzo 1999) isolates in media amended with KCl or sucrose, mycelia grew well at between –0.5 and –1.5 Mpa and declined below –1.5 Mpa. For rhizomorphs of *A. luteobubalina* (Pearce and Malajczuk 1990) in soil, the maximum growth occurred at –0.6 Mpa, the minimal growth occurred at –7.0 Mpa, and no growth occurred at –0.01 Mpa (field capacity) and –0.0001 Mpa (water-holding capacity). The results from this experiment are in agreement with these reports.

The pH values of the soil layers observed for *Z. matrella* in the field were 7.3 to 7.7 and those for *A. palustris* were 5.6 to 6.4. These data were in agreement with the observation that Zoysiagrass grows well in soils with pH of 6.0–7.0 and that creeping bentgrass grows well in soils with pH of 5.5–6.5 (Beard 1973). The soil pH in any layer beneath *A. palustris* turf, 5.6 to 6.4, was closer to the optimal value, 6.0, for the mycelial growth obtained from the experiment. However, the pH values 7.2 and 7.3 of the soil from 0–1 and 1–2 cm layers beneath *Z. matrella* turf gave 79% and 76% of the maximum mycelial growth, respectively, which means that the pH value of the 0–2 cm soil layer beneath *Z. matrella* turf was also within the range for supporting the mycelial growth.

The findings indicated that the mycelia favored the soil beneath *Z. matrella* turf more than that beneath *A. palustris* because of the organic-rich thatch layer that resulted from clippings being allowed to remain. However, the mycelia preferred the hot water extracts of *A. palustris* leaves, which contained less cellulose and hemicellulose but more nitrogen compared to *Z. matrella* leaves. The mycelia grew better in higher cumulative average temperature above 8.8°C and below 25°C in the 0–2 cm soil layer beneath *Z. matrella* compared to that beneath *A. palustris*. The water potential of the 0–2 cm layer beneath *Z. matrella* was more favorable for mycelial growth than any other sampled layer beneath either type of turf. Soil pH in the 0–2 cm layer beneath *Z. matrella* was not optimal for mycelial growth but still supported 76% of maximal growth.

We conclude that the reason why *L. sordida* mycelia is favored by the 0–2 cm soil layer environment beneath *Z. matrella* turf was the increased utilization of the nutrient from the organic-rich soil, plus favorable temperatures and water potential.

Acknowledgments The authors express sincere thanks to Dr. Tom Hsiang, of the University of Guelph, Canada, for his technical comments on this manuscript.

References

Beard JB (1973) Turfgrass: science and culture. Prentice-Hall, New Jersey

Brownell KH, Schneider RW (1985) Roles of matric and osmotic components of water potential and their interaction with temperature in the growth of *Fusarium oxysorum* in synthetic media and soil. Ecol Epidemiol 75:53–57

Couch HB (1995) Diseases of turfgrasses, 3rd edn. Krieger, Melbourne, FL, pp 181–186

Filer HJ (1965) Damage to turf grasses caused by cyanogenetic compounds produced by *Marasmius oreades*, a fairy ring fungus. Plant Dis Rep 49:571–574

Filer HJ (1966) Effect on grass and cereal seedlings of hydrogen cyanide produced by mycelium and sporophores of *Marasmius oreades*. Plant Dis Rep 50:264–266

Hanson AA, Juska FV (1969) Turfgrass science. American Society of Agronomy, Madison, WI

Horii S (1975) Quality judgment of grass and forage crops (in Japanese). In: Committee for Analytical Methods for Cultivated Plants (ed) Analysis and measurement methods of cultivated plants for the diagnosis of nutrient condition. Yokendo, Tokyo, pp 494–500

Pearce MH, Malajczuk N (1990) Factors affecting growth of *Armillaria luteobubalina* rhizomorphs in soil. Mycol Res 94:38–48

Shantz HL, Piemeisel RL (1917) Fungus fairy rings in Eastern Colorado and their effect on vegetation. J Agric Res 11:191–245

Smith JD, Jackson N, Woolhouse AR (1989) Fungal diseases of amenity turf grasses, 3rd edn. Spon, London, pp 339–353

Tahama Y (1973) On the main disease of turfgrass (in Japanese). J Jpn Soc Turfgrass Sci 2(2):27–32

Tahama Y (1978) On the fairy rings of turfgrass, *Zoysia matrella* L. (in Japanese). J Jpn Soc Turfgrass Sci 7:111–114

Tahama Y (1982) Ecological studies on the fairy rings of turfgrass, *Zoysia matrella* L. (in Japanese). J Jpn Soc Turfgrass Sci 11:161–167

Tani T (1991) Color atlas of diseases of turfgrasses (in Japanese). Softscience, Tokyo, pp 84–91

Terashima Y, Fujiie A (2005) Development of a fairy ring caused by *Lepista sordida* on Zoysiagrass over an eight-year period. Int Turfgrass Soc Res J 10:251–257

Terashima Y, Fujiie A (2006) Influence of temperature on fruit body emergence of the basidiomycetes, *Bovista dermoxantha*, *Vascellum curtisii* and *Conocybe lactea*, on turf of bentgrass, Zoysiagrass and bluegrass in summer. J Jpn Soc Turfgrass Sci 35:19–24

Turgeon AJ (1999) Turfgrass management, 5th edn. Prentice Hall, New Jersey

Waddington DV, Carrow RN, Shearman RC (1992) Turfgrass. American Society of Agronomy, Madison, WI

Whiting EC, Rizzo DM (1999) Effect of water potential on radial colony growth of *Armillaria mellea* and *A. gallica* isolates in culture. Mycologia 91:627–635