The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates

Markus N. Thormann, Randolph S. Currah, and Suzanne E. Bayley

Abstract: Nine species from a suite of 55 microfungi isolated from living and decomposing *Sphagnum fuscum* were selected for studies of in vitro decomposition of tannic acid, cellulose, and starch. In vitro decomposition of *S. fuscum* plants and spruce wood chips was also examined. *Oidiodendron maius* and *Oidiodendron scytaloides* degraded tannic acid, giving a positive reaction for polyphenol oxidases. Most taxa degraded cellulose and starch via the synthesis of cellulases and amylase, respectively. Mass losses of spruce wood chips generally exceeded those of *S. fuscum*. A basidiomycete, similar to *Bjerkandera adusta*, caused the greatest mass losses in spruce wood chips (10.2%), while *O. scytaloides* caused the smallest mass losses (3.4%) after 8 weeks. For *S. fuscum*, *Sordaria fimicola* caused the greatest (5.1%) and *Mucor hiemalis* the smallest (0.1%) mass losses after 8 weeks. Filamentous microfungi have considerable potential to decompose a variety of carbon substrates of bryophilous residues in peatlands.

Key words: microfungi, *Sphagnum fuscum*, peatlands, carbon, decomposition.

Résumé : Neuf espèces d'un cortège de 55 champignons microscopiques isolés de *Sphagnum fuscum* vivants et en décomposition ont été sélectionnées pour l'étude de la décomposition in vitro de l'acide tannique, du cellulose et de l'amidon. La décomposition in vitro de plants de *S. fuscum* et de copeaux d'épinette a également été étudiée. *Oidiodendron maius* et *Oidiodendron scytaloides* ont dégradé l'acide tannique, signe de l'activité de polyphénol oxidases. La plupart des taxons ont dégradé le cellulose et l'amidon par la synthèse de cellulases et d'une amylase, respectivement. Les pertes de masse de copeaux d'épinette étaient généralement supérieures à celles de *S. fuscum*. Un basidiomycète semblable à *Bjerkandera adusta* a occasionné les plus importantes pertes de masse dans les copeaux de bois (10,2 %), alors que *O. scytaloides* a entraîné les plus petites pertes (3,4 %) après 8 semaines. Dans le cas de *S. fuscum*, *Sordaria fimicola* a occasionné la plus importante (5,1 %) et *Mucor hiemalis* la moins importante (0,1 %) perte de masse après 8 semaines. Les champignons filamenteux microscopiques bénéficient d'une potentiel considérable pour la décomposition d'une foule de substrats de carbone contenus dans les résidus de mousses dans les tourbières.

Mots clés : champignons microscopiques, *Sphagnum fuscum*, tourbières, carbone, décomposition.

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Introduction

Peatlands cover approximately 14% of Canada's (National Wetlands Working Group 1988) and approximately 16% of Alberta's land surface, of which 4.9% are bogs and the remainder are fens (Vitt et al. 1996). Bogs are ombrotrophic peatlands that receive nutrients only from precipitation and are dominated by *Sphagnum* species, *Picea mariana* (Mill.) BSP., and members of the Ericaceae. Fens are minerotrophic peatlands that receive water from precipitation and ground water sources and are dominated by sedges, shrubs, and (mostly) non-*Sphagnum* moss species (Szumigalski and Bayley 1996*b*; Thormann and Bayley 1997*b*). *Sphagnum* species are of great importance to many northern peatlands because of their ability to acidify their surroundings and hold large quantities of water in their hyaline cells (Vitt and Andrus 1977). Moreover, *Sphagnum* litter exhibits slow decomposition rates. *Sphagnum fuscum* (Schimp.) Klinggr. is the dominant hummock-forming bryophyte species in Canadian bogs (Vitt and Andrus 1977) and can also occur, although less abundantly, in fens.

Peatlands accumulate peat, a heterogeneous assemblage of partially decomposed plant materials (approximately 50% carbon), annually (Thormann et al. 1999*b*). Gorham (1990) estimated that northern peatlands store between 180 and 277 Gt (1 Gt = 10^9 t) of carbon, which represents approximately 10–16% of the total global terrestrial detrital carbon, indicating their importance to the global carbon cycle. In light of the dominance of *S. fuscum* in bogs and their large contribution to the annual accumulation of carbon in peatlands (Thormann et al. 1999*b*), it is surprising that little is known about the microbes inhabiting living and decomposing *S. fuscum* plants. It has been suggested that fungi are the principal decomposer microbes in many acidic ecosystems and assume a more dominant role than bacteria (Latter et al. 1967; Williams and Crawford 1983). However, the majority of recent studies investigating carbon dynamics in peatlands concentrate on bacterial populations and their role in the mineralization of carbon to produce the greenhouse gas methane (CH_4) (Bubier et al. 1993; Roulet et al. 1993; Yavitt

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M.N. Thormann,[1] R.S. Currah, and S.E. Bayley. Biological Sciences Department, University of Alberta, Edmonton, AB T6G 2E9, Canada.

[1]Corresponding author (e-mail: mthorman@ualberta.ca).

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et al. 1993). Furthermore, some studies do not consider fungi to be involved in the decomposition of plant litters (e.g., Gilbert et al. 1998).

In a related study, we isolated and identified 55 microfungi from living and decomposing gametophytic tissues of *S. fuscum* (Thormann et al. 2001*b*). The objectives for this study were to select a subset (nine) of those taxa and assess their ability to decompose a variety of carbon substrates as an initial determination of their potential contribution to the decomposition of bryophyte remains and hence their role in the accumulation of peat in peatlands.

Methods

Study area and site description

Mild summers and cold, snowy winters characterize the climate of southern boreal Alberta. The mean annual temperature is 1.7°C and the total mean precipitation is approximately 500 mm (Environment Canada 1982). The Perryvale bog (54°28′N, 113°16′W) lies within the Subhumid Low Boreal ecoclimate region of Canada (Ecoregions Working Group 1989) and is dominated by *P. mariana*, *Vaccinium vitis-idaea* L., *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *S. fuscum*. A more detailed site description with respect to vegetation composition and surface water chemistry is in Thormann et al. (1999*a*, 2001*a*).

Cultural techniques and isolation of microfungi from living and decomposing *Sphagnum fuscum*

The top 3 cm of approximately 20 individual living, healthy *S. fuscum* plants were collected in early May, July, and September 1997 and processed as outlined below. A decomposition study using nylon mesh bags was initiated that fall. Briefly, between five and eight individual living *S. fuscum* plants (top 3 cm) were placed into each of 18 decomposition bags. These bags were returned to the bog and placed horizontally approximately 2 cm below the moss surface to mimic natural decomposition conditions. Subsets of triplicate decomposition bags with decomposing *S. fuscum* were retrieved after 20 and 50 days in 1997, after 250 and 365 days in May and September 1998, respectively, and after 456 and 730 days in May and September 1999, respectively.

Each of 10 randomly selected, cleaned segments of live (May–September 1997 samples) and dead (20–730 day decomposed samples, September 1997 – September 1999) *S. fuscum* were cut with a flame-sterilized scalpel into 10–12 smaller segments. These were surface-sterilized for 5 min in 10% H_2O_2 and washed with sterilized, distilled water (dH_2O). Of these, five randomly selected *S. fuscum* segments were placed on each of three plates of potato dextrose agar (PDA, 39.0 g Difco Laboratories (Detroit, Mich.) potato dextrose agar, 1.0 L dH_2O), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (MYC, containing cycloheximide, 35.6 g Difco mycobiotic agar, 1.0 L dH_2O) (n = 3 for each of the four primary isolation media at each of the ten sampling events). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth. Plates were incubated at room temperature (approximately 20°C) in the dark and fungi were subcultured onto malt extract agar (MEA, 15.0 g Difco malt extract agar, 20.0 g Difco agar, 1.0 L dH_2O) as soon as they grew from the plant material. For identification purposes, slide cultures (Sigler 1993) on mixed cereal agar (Pablum®, H.J. Heinz Company of Canada Ltd., 100.0 g mixed cereal, 15.0 g Difco agar, 1.0 L dH_2O) were prepared, mounted in polyvinyl alcohol, and photographed using an Olympus BX-50 microscope with a PM-10AK photosystem.

Representative cultures or slides were deposited at the University of Alberta Microfungus Collection and Herbarium (UAMH) and (or) the University of Alberta Cryptogamic Herbarium (ALTA) and (or) the Centraalbureau voor Schimmelcultures (CBS).

Selection of fungi for the decomposition studies

Among 262 records of fungi from living and decomposing *S. fuscum*, Fungi Imperfecti, zygomycetes, ascomycetes, and basidiomycetes were all represented (Thormann et al. 2001*b*). Fifty-five fungi (three ascomycetes, three basidiomycetes, 11 zygomycetes, 28 Fungi Imperfecti, 10 unnamed Mycelia Sterilia) were described. Thirty-six species represented new records from *Sphagnum* and 45 species were new records for *S. fuscum* (Thormann et al. 2001*b*). For an initial assessment of their enzymatic abilities, we selected a single strain of each of five hyphomycetes, two teleomorphic ascomycetes, one zygomycete, and one basidiomycete (Table 1). These included *Oidiodendron maius* Barron (ericoid mycorrhizal fungus) and *Oidiodendron scytaloides* Gams & Söderström; an unusual species of *Acremonium* similar to *Acremonium curvulum* W. Gams; two common soil and phylloplane species, *Penicillium thomii* Maire and *Trichoderma viride* Pers.:Fr.; two ascomycetes generally regarded as being coprophilous, *Sordaria fimicola* (Roberge ex Desmaz.) Ces. & De Not. and *Sporormiella intermedia* (Auersw.) Ahmed & Cain; the common zygomycete *Mucor hiemalis* Wehmer; and a basidiomycete similar to *Bjerkandera adusta* (Willd.:Fr.) P. Karst.

These nine fungi accounted for 80 of the 262 records (31%) obtained from *S. fuscum*, thus, they constituted a significant portion of all fungal records from this bryophyte (Thormann et al. 2001*b*). Despite the frequent variability in physiological profiles among strains of the same fungus, we chose to examine the physiological variability of fungi belonging to substantially different taxonomic affinities, i.e., different divisions or different families within the same division. Hence, only one strain of each of the nine taxa was examined in this study.

Enzymatic degradation of selected carbon sources

Cellulose degradation was tested using the cellulose–azure method (Smith 1977) with modified Melin-Norkrans medium (MMN, 1.0 g D-glucose anhydrous, 2.0 g Difco malt extract agar, 1.0 g yeast extract, 10.0 g KH_2PO_4, 5.0 g $(NH_4)_2HPO_4$, 3.0 g $MgSO_4 \cdot 7H_2O$, 1.0 g $CaCl_2$, 0.5 g NaCl, 12.0 g Difco agar, and 1.0 L dH_2O) substituted for the nutrient medium. Approximately 20 mL of MMN were added to 50-mL Pyrex culture tubes; these were autoclaved, and the medium was allowed to solidify. A 2% (w/v) cellulose–azure preparation in MMN was autoclaved separately, and approximately 1.5–2.0 mL of the suspension was transferred into each Pyrex culture tube. For each species, three Pyrex culture tubes with cellulose–azure medium were inoculated with small plugs of mycelium and stored in the light at room

Table 1. Accession numbers and isolation information of the nine fungal taxa isolated from living and decomposing *Sphagnum fuscum* from a bog in southern boreal Alberta, Canada.

Fungi (accession No.)	Substrate (no. of isolates)
Acremonium cf. *curvulum* (CBS 102853)	Decomposing (2) *S. fuscum*
cf. *Bjerkandera adusta* (ALTA 10853)	Living (3) *S. fuscum*
Mucor hiemalis (ALTA 10697)	Living (10) and decomposing (27) *S. fuscum*
Oidiodendron maius (ALTA 10700, UAMH 9749)	Decomposing (1) *S. fuscum*
Oidiodendron scytaloides (UAMH 9750)	Living (1) and decomposing (1) *S. fuscum*
Penicillium thomii (ALTA 10860)	Living (3) and decomposing (13) *S. fuscum*
Sordaria fimicola (ALTA 10705, UAMH 9475)	Living (4) *S. fuscum*
Sporormiella intermedia (ALTA 10706)	Living (1) *S. fuscum*
Trichoderma viride (ALTA 10713)	Living (4) and decomposing (11) *S. fuscum*

Note: ALTA, University of Alberta Cryptogamic Herbarium; CBS, Centraalbureau voor Schimmelcultures; and UAMH, University of Alberta Microfungus Collection and Herbarium.

temperature. Degradation of cellulose was indicated by the release of the azure dye from the cellulose agar and its diffusion into the lower, clear layer of MMN.

The presence of polyphenol oxidases (PPO) was tested using tannic acid medium (TAM, 5.0 g tannic acid (Baker analyzed), 15.0 g Difco malt extract agar, 20.0 g Difco agar, and 1.0 L dH_2O) (Davidson et al. 1938). For each species, three petri plates of TAM were inoculated and stored in the dark at room temperature. A positive reaction was the formation of a dark brown pigment surrounding the point of inoculation generally within 4 days after inoculation.

Starch degradation was tested by adding 2.0 g of soluble starch (BDH Chemicals Canada Ltd., Toronto, Ont.) to 1.0 L MMN (Hutchison 1990). Once the individual colonies covered approximately 75% of the petri plates, they were flooded with an iodine solution (5.0 g KI, 1.5 g I, 100.0 mL dH_2O). After 5 min, the solution was decanted and a clear zone around the colony in an otherwise purple plate indicated that amylase was produced and starch was degraded.

Visual comparative qualitative and quantitative evaluations (+++, ++, +, and –, indicating decreasing quantities of degraded carbon source) were made based on the amount of azure dye released in the cellulose–azure assay and the amount of discoloration on the top and reverse of the TAM petri plates in the tannic acid assay. The width of the clear zone around colonies on the starch plates was used to assess the degree of amylase synthesis. These physiological tests are widely used and have been used often as indicators of taxonomic relationships among fungal taxa (Hutchison 1990; Untereiner and Malloch 1999; Rice and Currah 2001).

Cladosporium herbarum (Pers.:Fr.) Link, which is known to degrade cellulose (Marsh et al. 1949), tannic acid (Minoura and Okazaki 1968), and starch (Domsch 1960), was used as a positive control. This taxon was isolated from living *S. fuscum* as well, but it was not used in the decomposition experiments.

Decomposition of *Sphagnum fuscum* plants and spruce wood chips

For each of the nine fungal taxa, 40 mL of peptone broth agar (20.0 g Difco agar, 1.0 g Difco bacto-peptone broth, 1.0 L dH_2O) was poured into each of six 100 × 80 mm glass petri dishes. These dishes were inoculated with one of the nine fungal taxa. One 2.5 × 3.0 cm, 65-µm gauge polyester mesh pouch (to minimize plant material losses during handling) containing the top 3 cm of four *S. fuscum* plants was placed into each petri dish. Filled pouches were dried at 48°C to constant weight, weighed to the nearest 0.01 g, and autoclaved at 121°C (liquid cycle) for 15 min prior to placement into the petri dishes. After 4 and 8 weeks, the pouches were removed from three petri dishes and surficial fungal mycelium was carefully removed from the surface. The pouches were dried at 48°C to constant weight, weighed to the nearest 0.01 g, and the mass loss was determined by subtracting the final mass from the initial mass for each pouch. Mass losses, as indicators of decomposition, were expressed as percentages of the initial masses.

This experimental design was duplicated using ten 8 × 8 × 4 mm (approximate dimensions) spruce wood chips per petri dish instead of *S. fuscum*. The wood chips were autoclaved at 121°C (liquid cycle) for 20 min prior to placing them directly onto the medium. Mass losses were determined as outlined above. Twelve petri dishes served as controls and were not inoculated with any fungi. Mass losses due to leaching of nutrients from the bryophyte litter and spruce wood chips were determined after 4 and 8 weeks. Leaching accounted for 1.6 and 2.0% mass losses from *S. fuscum* after 4 and 8 weeks, respectively. Mass losses due to leaching were 0.3 and 0.4% for the wood chips after 4 and 8 weeks. These mass losses were subtracted from the measured mass losses prior to statistical analyses.

Statistical analyses

An extended Kruskal–Wallis test (factors were Substrates and Time) was used to determine significant differences between mass losses after 4 and 8 weeks decomposition for each natural substrate and between natural substrates (spruce wood chips versus *S. fuscum*) for each fungal taxon. This analysis was chosen because of (*i*) the low number of replicates for each treatment (n = 3) and (*ii*) deviations in the data from normality and homogeneity of variances (Zar 1984).

Results and discussion

Enzymatic degradation of tannic acid, cellulose, and starch

Most of the taxa were able to effectively degrade cellulose (eight of nine) and starch (seven of nine) (Table 2). Several *Acremonium* species other than *A.* cf. *curvulum* synthesize

amylase (Franz 1975), and this enzyme has been shown previously to be synthesized by *T. viride*, *P. thomii*, and *M. hiemalis* (Domsch et al. 1980). Although it has been shown by Jefferys et al. (1953) and Domsch (1960) that *S. fimicola* can utilize cellulose as a carbon source, cellulase synthesis among *Acremonium* species is variable. The cellulolytic capability of *O. maius* has been suggested by Hambleton and Currah (1997), while the ability of *S. intermedia* and *O. scytaloides* to degrade cellulose has not been reported previously. The cellulolytic abilities of *T. viride*, *P. thomii*, and *M. hiemalis* have been shown in the past and our results concur (Domsch et al. 1980).

Synthesis of polyphenol oxidases, necessary for lignin degradation, was found in both species of *Oidiodendron*, but not in the other fungal taxa (Table 2). The synthesis of polyphenol oxidases among fungi is less common compared with cellulases and amylases (Domsch et al. 1980). Utilization of lignin by *Oidiodendron* species has been demonstrated previously (Haselwandter et al. 1990). It must be noted though that we used the colour change on the tannic acid medium as an indicator of polyphenol oxidase synthesis. Lignin is structurally different from tannic acid, and although some fungi utilized tannic acid in this study, they may not be able to utilize lignin directly as a carbon source.

Enzymatic degradation of *Sphagnum fuscum* and spruce wood chips

Generally, mass losses of spruce wood chips exceeded those of *S. fuscum* ($p < 0.05$) (Table 3). Mean mass loss differences between these two substrates for the nine fungi combined after 4 and 8 weeks of decomposition were 2.3 and 3.1%, respectively (Table 3). Cf. *Bjerkandera adusta* caused the greatest (10.2%) and *O. scytaloides* caused the smallest (3.4%) mass losses of spruce wood chips after 8 weeks. *Sordaria fimicola* and *M. hiemalis* caused the greatest and smallest mass losses of *S. fuscum* after 8 weeks (5.1 and 0.1%, respectively) (Table 3). The remaining fungal taxa caused intermediate mass losses (Table 3). Generally, mass losses of either substratum were similar after 4 and 8 weeks of decomposition (13 of 18 treatments, $p > 0.05$).

Concentrations of lignin or lignin-like substances and cellulose in gymnosperm wood (40–50% cellulose, 25–35% lignin) (Rayner and Boddy 1988) and *S. fuscum* (<4.5% starch, 38% cellulose, 30% lignin-like substances) (Yavitt et al. 1997; Turetsky et al. 2000) are similar, therefore, it was surprising that their mass losses differed substantially. In decomposition studies, litter quality (tissue concentrations of nitrogen, phosphorus, phenolic and tannic compounds, lignin, cellulose, and hemicellulose) has been implicated to influence mass losses of herbaceous and woody plant litter (Clymo 1965; Johnson and Damman 1991; Kasai et al. 1995; Tsuneda and Thorn 1995; Szumigalski and Bayley 1996*a*; Thormann and Bayley 1997*a*, 2001*a*). For example, carbon to nitrogen (C:N) quotients of living and decomposing *S. fuscum* are generally <100 (Szumigalski and Bayley 1996*a*; Thormann et al. 2001*a*). Conversely, C:N quotients of wood are usually >1000 and can be as high as 2500 (Rayner and Boddy 1988), indicating significantly lower concentrations of nitrogen in wood. These differences should have contributed to lower decomposition rates for the wood chips compared with the bryophyte. Previous studies have shown that mass losses of woody plant tissues exceed those of bryophyte tissues after 1 year (Bartsch and Moore 1985; Szumigalski and Bayley 1996*a*). Johnson and Damman (1991, 1993) showed that inherent, physiological characteristics of *Sphagnum* species, such as the cell wall composition, controls the decay of this bryophyte in peatlands. The decay of wood has been ascribed primarily to basidiomycetes, and it has been shown that some basidiomycetes have the ability to parasitize bacteria (Barron 1988) and yeasts (Hutchison and Barron 1996) or trap nematodes (Barron and Thorn 1987) to obtain nitrogen. Thus, despite the high C:N quotient of wood compared with those of many other substrates, its decomposition rate may be similar to substrates with lower C:N quotients, such as *S. fuscum*, because some of the fungi primarily associated with wood decay have alternate strategies to obtain crucial elemental nutrients, such as nitrogen and phosphorus.

Peptone, a source of nitrogen, was added to the base medium in the glass petri dishes to assure growth of the fungi prior to colonization of the plant material. This nitrogen supply may have affected the growth rates of the fungi and their ability to colonize and ultimately degrade these two plant materials; however, other sources of nitrogen and other elemental nutrients are available to fungi in situ. Therefore, our base medium did not provide any sources of nutrients to these fungi that they would not have access to in nature. Furthermore, this study examined the relative mass losses of these two natural substrates incurred by nine fungi in vitro. In situ conditions differ significantly and results would likely be different. In situ mass losses of *S. fuscum* were 14 and 17% after 4 and 8 weeks, respectively (Thormann et al. 2001*a*). Not surprisingly, those mass losses substantially exceed the single taxon in vitro mass losses reported here due to large and diverse microbial (fungi and bacteria) and invertebrate populations that combine to decompose plant materials in nature.

Decomposition of carbon substrates by fungi

Northern peatlands store a significant portion of the world's terrestrial carbon as peat (Gorham 1990). With increasing atmospheric CO_2 concentrations and subsequent temperature increases, these peatlands may change from carbon sinks to carbon sources (Hilbert et al. 2000), whereby some of the stored carbon is mineralized and released as CO_2 (aerobic decomposition) or CH_4 (anaerobic decomposition). Most recent studies using carbon fluxes from peatlands as indicators of rates of decomposition concentrate on the production of CH_4 by bacterial populations (Bubier et al. 1993; Roulet et al. 1993; Yavitt et al. 1993), because CH_4 has a 7.5× higher global warming potential per molecule than CO_2 (Houghton 1997). Fungi generally are not addressed or are ignored altogether as important components of mineralization processes (Gilbert et al. 1998). However, in acidic ecosystems, such as bogs, fungi may assume a more dominant role than bacteria, and the majority of cellulolytic organisms may be fungi (Latter et al. 1967). Furthermore, Williams and Crawford (1983) showed that fungi were more diverse in their abilities to utilize a variety of carbon sources and that they play an important role in the decomposition of lignin and cellulose in peatlands.

Table 2. Enzymatic degradation of tannic acid, cellulose, and starch by nine fungal taxa isolated from living and decomposing *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada (n = 3 per treatment).

Fungal taxa	Tannic acid	Cellulose	Starch
Acremonium cf. *curvulum*	–	+++	++
cf. *Bjerkandera adusta*	–	++	–
Mucor hiemalis	–	+	+++
Oidiodendron maius	+++	+	+
Oidiodendron scytaloides	+	++	++
Penicillium thomii	–	++	+++
Sordaria fimicola	–	+	–
Sporormiella intermedia	–	–	+
Trichoderma viride	–	+++	+++

Note: +++, strong reaction; ++, intermediate reaction; +, weak reaction; –, no reaction.

In a related study, 262 records of fungi representing 55 different species were derived from living and decomposing *S. fuscum* between May 1997 and September 1999 (Thormann et al. 2001*b*). Of these, we selected nine species for the current study (Table 1). None of these nine taxa has been reported previously from *S. fuscum*, although some of these species have been isolated previously from peat (McLennan and Ducker 1954; Thrower 1954; Christensen and Whittingham 1965; Dooley and Dickinson 1971; Dal Vesco 1974–75; Nilsson et al. 1992). These nine fungi had varying abilities to utilize different carbon sources (Table 2) and caused varying mass losses of *S. fuscum* and spruce wood chips in vitro (Table 3). Our results suggest that fungi are involved in the decomposition of peat, and thus the mineralization of carbon, supporting results by Williams and Crawford (1983). Therefore, it is important to consider the roles of fungi in the decomposition of carbon substrates, especially in northern peatlands with their significant carbon deposits.

Caution is required when interpreting these data, because they are only indications of the relative abilities of these nine fungi to degrade tannic acid, cellulose, and starch or cause mass losses of *S. fuscum* and spruce wood chips. Also, the ability of a fungus to utilize a particular substrate in vitro does not necessarily imply the same ability in situ; however, it does indicate the potential ability of this fungus to utilize a particular substrate. These fungi compete for resources with other organisms in situ, i.e., in their realized niche, which may lead to the suppression of some of the abilities expressed in vitro, i.e., in their fundamental niche. The fundamental niche of an organism is always larger than its realized niche because of the absence of competition in the former. This study did not determine if these taxa have similar enzymatic abilities in the presence of other organisms or in situ, and additional studies are needed to investigate these aspects. Furthermore, histological examinations of decomposed plant material are necessary to confirm and refine these results. Nonetheless, these data indicate that microfungi have considerable potential to decompose various carbon substrates of bryophilous and lignicolous residues in bogs.

Table 3. Mass losses of spruce wood chips and *Sphagnum fuscum* by nine fungal taxa from living and decomposing *Sphagnum fuscum* from a bog in southern boreal Alberta (n = 3 per treatment).

	Mass losses (% ± SE)	
Fungal taxa and sustrata	4 weeks	8 weeks
Acremonium cf. *curvulum*		
Spruce wood chips	4.5 (0.6)*a1*	4.6 (0.1)*a1*
S. fuscum	3.3 (0.4)*a1*	3.9 (0.8)*a1*
cf. *Bjerkandera adusta*		
Spruce wood chips	4.8 (0.3)*a1*	10.2 (1.1)*b1*
S. fuscum	1.6 (0.6)*a2*	1.7 (0.7)*a2*
Mucor hiemalis		
Spruce wood chips	4.3 (0.2)*a1*	4.9 (0.2)*b1*
S. fuscum	0.3 (0.0)*a2*	0.1 (0.0)*a2*
Oidiodendron maius		
Spruce wood chips	4.4 (0.2)*a1*	4.6 (0.2)*a1*
S. fuscum	1.5 (0.4)*a2*	2.5 (0.5)*a2*
Oidiodendron scytaloides		
Spruce wood chips	3.3 (0.1)*a1*	3.4 (0.5)*a1*
S. fuscum	3.2 (0.3)*a1*	3.6 (1.2)*a1*
Penicillium thomii		
Spruce wood chips	4.2 (0.3)*a1*	5.1 (0.3)*b1*
S. fuscum	0.5 (0.1)*a2*	1.8 (0.2)*b2*
Sordaria fimicola		
Spruce wood chips	5.2 (0.3)*a1*	5.2 (0.6)*a1*
S. fuscum	4.2 (1.2)*a1*	5.1 (0.7)*a1*
Sporormiella intermedia		
Spruce wood chips	3.5 (0.3)*a1*	5.1 (0.3)*b1*
S. fuscum	3.4 (0.4)*a1*	3.2 (0.3)*a2*
Trichoderma viride		
Spruce wood chips	4.3 (0.1)*a1*	5.6 (0.2)*b1*
S. fuscum	0.4 (0.0)*a2*	0.5 (0.0)*a2*

Note: Italic letters indicate significant differences in mass losses between decomposition periods for each substratum, while italic numbers indicate significant differences in mass losses between the substrata at each decomposition period for each fungal taxon. In situ mass losses of *S. fuscum* were 14 and 17% after 4 and 8 weeks, respectively (Thormann et al. 2001*a*).

Species ecology

Some *Oidiodendron* species, such as *O. maius*, are mycorrhizal with members of the Ericaceae, such as *Rhododendron* and *Vaccinium* species common to peatlands (Barron 1962; Stoyke and Currah 1991; Hambleton and Currah 1997). The ability to degrade cellulose and tannic acid by *Oidiodendron* species may be necessary for the successful colonization of the root cortical cells of members of the Ericaceae. Tsuneda et al. (2001) showed that *O. maius* has the ability to degrade cell walls of *S. fuscum* by simultaneously degrading all cell wall components, such as amorphous cell wall components and microfibrillar elements. *Oidiodendron scytaloides* is common to soils of oak and coniferous forests in Europe (Gams and Söderström 1983), but it is less common in North America. Its enzymatic abilities have not been tested in the past; however, the presence of this fungus in roots of dying *Abies* sp. (Sigler and Flis 1998) and decomposing *S. fuscum* suggests that it is a saprophyte with substantial cellulolytic and lignolytic qualities.

The ascomycetes *S. fimicola* and *S. intermedia* are classical coprophilous fungi that have been isolated frequently from herbivore and carnivore dung in the past (Iftikhar and Cain 1972; Lundqvist 1972). It has generally been assumed that coprophilous fungi are restricted to the dung of specific animals because of the complex nature of dung (Lundqvist 1972). For example, *S. fimicola* grows preferentially on dung of herbivores (horses, hares, rabbits) (Lundqvist 1972), possibly because of the coarse nature of the cellulosic materials prevalent in the dung of these animals. This ascomycete was able to degrade cellulose effectively (Table 2) and was deemed a "cellulose-eater" by Dal Vesco et al. (1967). *Sordaria fimicola* has been isolated repeatedly from peat (McLennan and Ducker 1954; Thrower 1954) and may be more involved in the decay of plant residues than has been assumed previously. Many herbivorous animals, such as moose, deer, and rabbits, frequent bogs to forage on herbs, shrubs, and lichens. Thus, the spores of these coprophilous fungi may be consumed and dispersed by these herbivores, thereby meeting the suggested spore germination requirements (acidity) outlined by Bell (1983). Nonetheless, we suggest that some coprophilous fungi may have an alternate life strategy and can act as plant saprophytes under certain conditions. The pH of bogs is between 3.8 and 4.1 (Szumigalski and Bayley 1996*b*; Thormann and Bayley 1997*b*; Thormann et al. 2001*a*) and may be low enough to induce germination of the ascospores. We isolated both ascomycetes from living *S. fuscum* in July 1997, indicating that they may be saprophytic on plants following the germination of the discharged ascospores on nearby plants or peat and prior to consumption by herbivores, a theory first suggested by Webster (1970).

Acremonium cf. *curvulum* is strongly cellulolytic but not lignolytic (Table 2). We isolated this species from several decomposing *S. fuscum* segments in 1998. *Acremonium curvulum* is uncommon in continental North America (CBS databases) and has been isolated principally from soils and leaves of plants (Gams 1971). Our isolate may be an important cellulose degrader of *S. fuscum* in this bog, as indicated by the mass losses of *S. fuscum* incurred over the first 8 weeks of decomposition in vitro (Table 3). This species degrades cell wall components of *S. fuscum* in a preferential mode, first by fragmenting and removing the amorphous outer cell wall layer and then by attacking the microfibrils of the central cell wall layer, thereby producing voids within the leaf tissues (Tsuneda et al. 2001). Gams (1971) indicated that only a few *Acremonium* species are saprophytes or parasites of specific plant species, whereas the majority are generalists and can be isolated from a variety of substrates. Both of our records came from a cycloheximide-amended medium, indicating *A.* cf. *curvulum*'s resistance to this growth inhibitor.

The basidiomycete similar to *B. adusta* caused the greatest mass losses of the spruce wood chips (10.2%) (Table 3), despite a limited enzymatic profile (Table 2). Many basidiomycetes are efficient wood saprophytes and contribute to nutrient cycling within ecosystems (Lumley et al. 2001). Our isolates shared some morphological characteristics, such as arthroconidial and hyphal morphology and colony characteristics, with some of these, for example, *B. adusta* (Stalpers 1978). *Bjerkandera adusta* occurs primarily on angiosperms and is less commonly isolated from conifers, such as species of *Picea* (Stalpers 1978). Although we did not isolate fungi from spruce wood, black spruce (*P. mariana*) is common to western continental bogs and the presence of this basidiomycete in our bog would not be unusual. Conversely, our basidiomycete isolates also were similar to the mycoparasite *Geotrichopsis mycoparasitica* Tzean & Estey (Tzean and Estey 1991). This mycoparasite has been shown to parasitize a variety of hyphomycetes (Tzean and Estey 1992), including some that were isolated during our investigation of the filamentous microfungus communities of living and decomposing *S. fuscum*. More extensive cultural, physiological, and (or) molecular techniques are necessary to identify the basidiomycete isolates.

Penicillium thomii and *T. viride* are frequently isolated from a variety of living and decomposing organic substrates (see Domsch et al. 1980). Both taxa utilized cellulose and starch as carbon sources (Table 2) and are thought to cause the largest mass losses of decomposing plant litters by decomposing cellulose and hemicellulose (Deacon 1984). Although generally isolated from the surfaces of plant materials, they have the ability to invade and colonize deeper plant tissues and play significant roles in the degradation of organic materials. Furthermore, *T. viride* is a mycoparasite and has the ability to decrease interspecific competition for nutrients by parasitizing other fungi within the same substrate.

Mucor hiemalis is one of the most common soil fungi and the most frequent representative of the Mucorales (Domsch et al. 1980). It has a worldwide distribution and has been isolated from a variety of habitats, including peatlands (McLennan and Ducker 1954; Thrower 1954). It is considered a "sugar fungus", readily utilizing simple organic materials that leach naturally out of plant materials (Deacon 1984). Leaching accounted for most of the mass losses from *S. fuscum* litter and spruce wood chips inoculated with *M. hiemalis*.

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