

Patterns of distribution of microfungi in decomposing bog and fen plants

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

Abstract: The microfungal assemblages from the litter of the dominant vegetation of a forested bog and a riverine, sedge-dominated fen in southern boreal Alberta, Canada, were investigated over a 2-year period. Canonical correspondence analyses showed distinctly different fungal communities associated with litter of the dominant plant species of this bog (*Sphagnum fuscum* (Schimp.) Klinggr.) and fen (*Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots). Plant tissue quality variables, including total phosphorus and total nitrogen tissue concentrations, correlated most strongly with the fungal communities. In contrast, site-specific environmental (surface water chemical variables) and physical (peat and water temperatures, water level) variables were not correlated with the fungal communities of these five decomposing fen and bog plant litters. Of 93 identified fungal taxa, 25% occurred exclusively in the bog and 56% occurred exclusively in the fen. Eighteen species (19%) were common to the materials examined from both peatlands. Several species of (i) *Aspergillus*, *Mortierella*, and *Oidiendron* were restricted to the *Sphagnum* litter in the bog, and species of (ii) *Phialophora*, *Phialocephala*, *Fusarium*, *Dimorphospora foliicola*, *Monocillium constrictum*, and several basidiomycetes were restricted to the *Carex* and *Salix* plant litters in the fen. These taxa constitute components of the bog and fen fungal communities, respectively.

Key words: fungal communities, decomposition, bog, fen, canonical correspondence analysis (CCA).

Résumé : Pendant une période de 2 ans, les auteurs ont examiné les assemblages microfongiques des litières de la végétation dominante d'une tourbière haute arborée ainsi que d'une tourbière basse à carex riveraine, dans le sud de la forêt boréale en Alberta, au Canada. Les analyses par correspondances canoniques montrent des communautés nettement distinctes, associées à la litière de l'espèce de plante dominante de la tourbière haute (*Sphagnum fuscum* (Schimp.) Klinggr.) et de la tourbière basse (feuilles du *Carex aquatilis* Wahlenb. et rhizomes du *Salix planifolia* Pursh). Les variables de la qualité des tissus végétaux, incluant les teneurs totales en phosphore et en azote dans les tissus, montrent une forte corrélation avec les communautés fongiques totales. Au contraire, les variables environnementales spécifiques au site (variables chimiques de l'eau de surface) et variables physiques (températures de la tourbe et de l'eau, niveau de l'eau) ne montrent pas de corrélation avec les communautés fongiques de ces cinq litières en décomposition, venant des tourbières hautes et basses. Parmi les 93 taxons fongiques identifiés, 25 % se retrouvent exclusivement dans la tourbière haute et 56 % exclusivement dans la tourbière basse. Dix-huit espèces (19 %) sont communes à des matériaux provenant des deux tourbières. Plusieurs espèces (i) d'*Aspergillus*, *Mortierella* et *Oidiendron* sont limitées à la litière des *Sphagnum* de la tourbière haute, et les espèces de (ii) *Phialophora*, *Phialocephala*, *Fusarium*, *Dimorphospora foliicola*, *Monocillium constrictum*, ainsi que plusieurs basidiomycètes, sont restreints aux litières de *Carex* et de *Salix* de la tourbière basse. Ces taxons constituent des composantes des communautés fongiques des tourbières haute et basse, respectivement.

Mots clés : communautés fongiques, décomposition, tourbière haute, tourbière basse, analyses par correspondances canoniques (CCA).

[Traduit par la Rédaction]

Introduction

Peatlands cover approximately 4% of the world's and 14% of Canada's landscape (National Wetlands Working Group

1988) and play a significant role in the global carbon cycle (Gorham 1991) by virtue of their significant peat deposits (approx. 50% carbon). The fungal assemblages in a variety of peatlands have been examined in Antarctica (Baker 1970;

Received 17 June 2003. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 18 May 2004.

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

¹Corresponding author (e-mail: mthorman@nrcan.gc.ca).

²Present address: Canadian Forest Service, Northern Forestry Centre, 5320-122 St., Edmonton, AB T6H 3S5, Canada.

Wynn-Williams 1980), Asia (Hiroki and Watanabe 1996), Australia (McLennan and Ducker 1954; Thrower 1954), Europe (Latter et al. 1967; Dooley and Dickinson 1971; Dal Vesco 1974–1975; Nilsson et al. 1992), and North America (Christensen and Whittingham 1965; Christensen and Cook 1970; Williams and Crawford 1983a; Thormann et al. 2003). These studies have investigated the fungal assemblages of hummocks and hollows of bogs, fens, swamps, moors, muskeg, and anthropogenically altered wetlands. Christensen and Cook (1970), Williams and Crawford (1983a, 1983b), Hiroki and Watanabe (1996), and Fisher et al. (1998) examined physiological traits of microbial communities (bacteria and fungi) in peat. The fungal assemblages of specific peatland plant species throughout the process of decomposition have rarely been investigated (e.g., Thormann et al. 2003). Christensen and Cook (1970) and Nilsson et al. (1992) examined the fungal assemblages of peat at different depths, a proxy for different stages of the decomposition process of peat; however, the age and degree of decomposition of peat samples were not reported in their studies.

Despite the abundance of peatlands in Canada, only two studies have investigated the fungal communities of Canadian peatlands (Christensen and Cook 1970; Thormann et al. 2003), both incidentally in Alberta in western continental Canada. Clearly, additional studies are needed, given the importance of fungi to peatland biogeochemical processes (Thormann et al. 2001b) and the prevalence of peatlands in Canada (National Wetlands Working Group 1988). This is especially true when considering the potential impacts of rising atmospheric temperatures on peatlands (Gorham 1991) and their fungal communities under a global warming scenario. Changes in the fungal communities of peatlands may result in different enzymatic profiles of the fungal communities and thus could have profound effects on ecosystem processes, including decomposition, nutrient cycling, and plant production dynamics.

The objectives of the present study were to isolate and identify filamentous microfungi from decomposing bog and fen plants in southern boreal Alberta, Canada, and to determine if environmental variables influenced the composition of their assemblages. *Sphagnum fuscum* (Schimp.) Klinggr. plants from a bog and *Carex aquatilis* Wahlenb. leaves and rhizomes and *Salix planifolia* Pursh leaves and roots from a fen were selected because of their significant contribution to the total net primary production (Szumigalski and Bayley 1997; Thormann and Bayley 1997a) and accumulation of peat in peatlands of western continental Canada (Kuhry and Vitt 1996; Thormann et al. 1999a). *Carex* accounts for nearly 100% of the total aboveground plant production in the fen interior (Thormann and Bayley 1997b), and *Salix* predominates the plant community of the fen margin (M.N. Thormann, personal observation). *Sphagnum* accounts for 55% of the total aboveground plant production in Alberta bogs (see Thormann and Bayley 1997b), hence *Sphagnum* spp. are the dominant plants in this wetland class. Consequently, peat in both peatlands consists primarily of remains of these plant species (M.N. Thormann, personal observation). The two peatlands of the present study are representative of many peatlands in western continental Canada with respect to their plant community composition and surface water chemical and physical characteristics (e.g., Vitt 1994).

We hypothesized that the fungal assemblages associated with litters of the dominant bog and fen plants would differ significantly because of the differing quality of the plant tissues examined (Thormann et al. 2001a), as well as significantly different pH and alkalinity-related variables and different water levels between bogs and fens (Vitt 1994; Szumigalski and Bayley 1997; Thormann et al. 2001a).

This paper focuses on components of the bog and fen microfungal assemblages based on the microfungi we isolated from selected plant remains.

Materials and methods

Study area and site descriptions

The riverine sedge fen (54°28'N, 113°18'W) and Perryvale bog (54°28'N, 113°16'W) lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). The fen is dominated by *Carex aquatilis*, *Carex lasiocarpa* Ehrh., and *Salix planifolia*. The bryophyte stratum is discontinuous and consists primarily of *Brachythecium mildeanum* (Schimp.) Schimp. ex Milde. The bog is dominated by *Sphagnum fuscum*, *Picea mariana* (Mill.) BSP., and members of the Ericaceae. Vegetation composition, surface water chemistry, and physical parameters of both sites are provided in more detail in Thormann et al. (1999b, 2001a).

Isolation of microfungi from decomposing plant tissues

Plant material was collected in the bog (*Sphagnum fuscum* plants, upper 30 mm) and fen (*Carex aquatilis* leaves, upper 100 mm; *Carex aquatilis* rhizomes, 100-mm segments; *Salix planifolia* leaves, entire; *Salix planifolia* roots, 100-mm terminal segments) in early September 1997. We collected only senesced or dead leaves (yellow to pale brown in colour, from *Carex* and *Salix*) and rhizomes (soft and dark brown to black in colour, from *Carex*). The *Salix* root material consisted of a mixture of fine roots and roots with secondary growth (all with a diameter of 2 mm or less). *Sphagnum* material consisted of the stems, branches, all associated leaves, and the capitulum of apparently healthy plants. This plant material was used in a 2-year decomposition study, which was initiated in mid-September 1997. Briefly, between five and eight individual, randomly selected segments of each plant tissue were placed separately into each of 18 decomposition bags. Therefore, a total of 90 decomposition bags were deployed in both peatlands. These bags were placed horizontally approximately 20–50 mm below (bryophyte, root, and rhizome tissues) or on top of the peat surface (both leaf tissues) to mimic natural conditions of decomposition for these plant tissues. Sets of triplicate decomposition bags were retrieved after 20 and 50 d in 1997, after 250 and 365 d in May and September 1998, and after 456 and 730 d in May and September 1999. Day 0 samples represented “undecomposed” plant litters.

Microfungi were isolated from plant tissues at various stages of decomposition ($t = 0\text{--}730$ d; see previous paragraph). The decomposed plant tissues were cleaned and cut into 10 smaller segments. These were surface sterilized for 5 min in 10% hydrogen peroxide and washed repeatedly with sterile distilled water prior to placing them on four media selected for the isolation of a broad spectrum of filamentous

tous microfungi. These were potato dextrose agar (PDA; 39.0 g potato dextrose agar (Difco Laboratories, Detroit, Michigan), 1.0 L distilled water), PDA with rose bengal (0.03%), PDA with benomyl (0.0002%), and Mycobiotic agar® (containing cycloheximide, 35.6 g Mycobiotic agar (Difco), 1.0 L distilled water). Plates were incubated at room temperature (approx. 23 °C) in the dark, and emerging fungi were subcultured onto malt extract agar (15.0 g malt extract (Difco), 20.0 g agar (Difco), 1.0 L distilled water) for subsequent manipulation and maintenance. Plates were examined for emerging hyphae daily for the first 2 weeks, weekly for the following 6 months, and monthly for the following 2 years of incubation to maximize the isolation of different microfungi. Microfungi were identified using a combination of morphological and physiological characters.

Only fungi that produced distinctive diagnostic colony and morphological characters were enumerated in the present investigation. Nonsporulating and nondescript fungi represented less than 15% of all isolates and, along with chytridiomycetes and yeasts, were excluded from the present study. Isolation frequencies for all fungal taxa were determined by expressing the number of isolates of each taxon as a percentage of the total number of isolates obtained from the respective plant tissue (Table A1). More detailed descriptions of the decomposition study and microfungi isolation and identification approaches are provided in Thormann et al. (2003).

Statistical analyses

Canonical correspondence analysis (CCA) of the bog and fen plant tissues was done using CANOCO (ter Braak 1992). This analysis ordines communities and environmental variables, such that the relative position of the communities reflect their similarity and (or) dissimilarity, and the environmental variables are represented by vectors overlying the positions of the individual communities. The relative significance of the vectors is indicated by their length and direction from the axes origin. Variables included in the analyses were (i) plant tissues, (ii) length of time deployed in the field, (iii) surface water chemistry (nitrate, ammonium, total dissolved nitrogen, soluble reactive phosphorus, total dissolved phosphorus, total phosphorus, pH, conductivity, alkalinity, bicarbonate, dissolved organic carbon, calcium, and potassium), (iv) plant tissue quality (total carbon [TC], total nitrogen [TN], total phosphorus [TP], and TC/TN quotients), and (v) physical variables (peat temperature, water temperature, depth of the acrotelm (oxygenated peat horizon)) (Thormann et al. 1999b; 2001a). Pearson's correlation coefficients among all variables and the first and second CCA axes were generated from the ordinations. Ordination vectors were multiplied by 5 for a clearer representation in the biplot.

Differences in tissue quality variables between the bog and fen were analyzed using Student's *t* tests. Tissue quality data are presented as means ± SE.

Results and discussion

Differences in the fungal assemblages in the bog and fen litters

Substantially different microfungi were associated with

the decomposing plant tissues in the bog and fen. We identified 41 different microfungi from *Sphagnum fuscum*. In the fen, decomposing *Carex aquatilis* leaves and rhizomes yielded 33 and 30 taxa, respectively, while 33 and 34 micro-fungal taxa were isolated from decomposing *Salix planifolia* leaves and roots, respectively (Table A1). Overall, a total of 93 different fungal taxa were identified from the decomposing bog (one litter type, 41 different taxa) and fen (four litter types, 71 different taxa) plant litters. Twenty-three taxa were specific to the *Sphagnum* litter, and 52 taxa were specific to the *Carex* and *Salix* litters, with an overlap of 18 species between the single bog and at least one of the four fen litters (Table A1). Isolation frequencies of microfungi taxa from all five litters were similar, with few taxa occurring frequently (isolation frequencies of greater than 5%, 10%–21% of all isolates) and most occurring infrequently (isolation frequencies of less than 5%, 79%–90% of all isolates; Table A1).

Mitosporic ascomycetes (reproducing asexually only, but with putative ascomycete affinities) dominated the micro-fungal assemblages of the *Carex* and *Salix* litters, constituting a mean of 95% of all isolates. Zygomycetes were isolated more frequently from the *Sphagnum* litter (49% of bog isolates vs. mean of 13% of fen isolates), where their occurrence was similar to that of the mitosporic ascomycetes (50%). Basidiomycetes, and ascomycetes that formed ascocmata (sexual fruiting structures) in culture, were recovered infrequently in both peatlands (0%–15.3% isolation frequency), but were more prominently isolated from the *Carex* and *Salix* litters (means of 1.1% and 15.3% vs. 0.5% and 0.0% for ascomycetes and basidiomycetes in the four fen and one bog litters, respectively). Isolation frequencies of the five most common fungal taxa ranged from 3.2% to 14.3% in the fen (*Phialocephala dimorphospora* Kendrick and *Phialophora* cf. *alba*, respectively) and from 6.0% to 13.5% in the bog (*Mortierella minutissima* van Tieghem and *Mucor hiemalis* Wehmer, respectively; Table 1). Species of *Trichoderma* were common in all five plant litters and represented between 0.6% and 12.1% of all isolates depending on litter type and *Trichoderma* species (mean of 3.6% for all *Trichoderma* spp. of the five litter types; Table A1). Similarly, *Mucor hiemalis* was one of the five most common species in four of the five plant litters and represented between 4.1% and 17.1% of all isolates (mean of 10.5% for the five litter types; Table A1). Isolation frequencies of all fungal species from each plant litter are presented in Table A1.

Several studies have investigated the fungal assemblages of peatlands in the past (McLennan and Ducker 1954; Thrower 1954; Christensen and Whittingham 1965; Latter et al. 1967; Dooley and Dickinson 1971; Dal Vesco 1974–1975; Nilsson et al. 1992). However, none of these studies investigated the fungi specifically associated with plants whose remains constitute the bulk of the accumulated peat. An examination of their microfungi communities reveals a similar preponderance of species of *Penicillium*, *Trichoderma*, and *Mucor*. Comparing species lists from previous studies to that of the present study, there is an overlap of 11%–23%, suggesting that some microfungi species are isolated consistently from peatlands around the world. These species may be tolerant of low pH, low temperatures, and water-logged soil conditions. Furthermore, they may be able

Table 1. Isolation frequencies of the five most commonly isolated filamentous microfungi from different litter types at two peatlands in southern boreal Alberta, Canada.

Peatland classes	Microfungal taxa	Isolation frequencies (%)
Bog (<i>Sphagnum</i>)	<i>Mucor hiemalis</i>	13.5
	<i>Penicillium thomii</i>	10.0
	<i>Mortierella elongata</i>	8.5
	<i>Trichoderma viride</i>	6.5
	<i>Mortierella minutissima</i>	6.0
Fen (<i>Carex</i> and <i>Salix</i>)	<i>Phialophora</i> cf. <i>alba</i>	14.3 (0.7–45.5)
	<i>Mucor hiemalis</i>	9.7 (4.1–17.1)
	<i>Trichoderma viride</i>	5.9 (1.6–12.1)
	<i>Phialophora alba</i>	7.7 (3.3–11.4)
	<i>Phialocephala dimorphospora</i>	3.2 (0.0–8.9)

Note: Isolation frequencies represent the sum of individual isolation frequencies from each of the seven sampling dates (0–730 d decomposition; see the Table A1 for raw data) for each of the taxa. Fen frequencies represent means based on the four fen litter types (ranges).

to decompose relatively undecomposed plant materials (Christensen and Whittingham 1965), although an analysis of the physiological profiles of fungi from decomposing *Sphagnum fuscum* indicated a generally broad spectrum of enzymatic abilities, enabling them to utilize such carbon sources as pectin, cellulose, gelatin, and starch (Thormann et al. 2001b). However, these fungal assemblages had a limited ability to utilize complex polyphenolic polymers, including tannic acid (Thormann et al. 2001b), which constitute a significant portion of peat (Turetsky et al. 2000).

Dooley and Dickinson (1971) recognized two distinct fungal communities in naturally revegetated and bare, cut-away peat: a “cosmopolitan” community and an “indigenous” community. Their cosmopolitan community consisted of species common to soils around the world, including species of *Penicillium*, *Trichoderma*, and *Mortierella*. In contrast, *Oidiodendron griseum* Robak, *Phialophora* sp., and *Torulomyces lagena* Delitsch were some of Dooley and Dickinson’s (1971) indigenous fungi, which were restricted to specific soil types. Their classification was based on previous records of those fungi. While their use of the terms “indigenous” and “cosmopolitan” was useful to indicate the pattern of specificity they observed, out of context they are problematic, especially in light of the large variation of peat chemistry and peat composition among different peatland classes. In the present study, distinct communities were identified, with fungi originating exclusively from decomposing *Sphagnum fuscum* in the bog as part of the bog fungal community and those from decomposing *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots as part of the fen fungal community. For example, several species of *Oidiodendron* and *Mortierella* occurred exclusively in the bog litter, while species of *Phialophora* and *Phialocephala*, *Monocillium constrictum* W. Gams, and *Dimorphospora foliicola* Tubaki were isolated exclusively from the fen litters. Several species of *Trichoderma* and *Penicillium*, as well as *Mucor hiemalis*, occurred in both peatlands and represent part of the shared fungal community (Table 2).

Variables correlating with the microfungal assemblages of the bog and fen litters

A clear separation of the microfungal assemblages of the

bog (*Sphagnum*) and fen (*Carex* and *Salix*) plant litters was apparent along axis 1 (Fig. 1). CCA revealed that the *Sphagnum* fungal assemblages showed a strong correlation with the TC/TN quotient. The *Sphagnum* litter had a significantly higher TC/TN quotient than the *Carex* and *Salix* litters (68 ± 10 vs. 36 ± 19 in the bog and fen, respectively; $p < 0.05$). In contrast, the *Carex* and *Salix* fungal assemblages were more influenced by TN and TP tissue nutrient concentrations (Fig. 1). The *Carex* and *Salix* litters were significantly richer in TN (fen: 16.3 ± 6.5 mg·g⁻¹; bog: 6.9 ± 1.1 mg·g⁻¹; $p < 0.05$) and TP (fen: 1.40 ± 1.03 mg·g⁻¹; bog: 0.44 ± 0.22 mg·g⁻¹; $p < 0.05$) tissue concentrations than the *Sphagnum* tissue. Plant tissue quality variables were the only variables that correlated significantly with axes 1 and 2 (Table 3).

The occurrence of specific fungi in peatlands versus other ecosystems has been attributed most often to pH, water logging, and temperature (Christensen and Whittingham 1965; Latter et al. 1967; Nilsson et al. 1992). None of these environmental variables accounted for the variation of the fungal assemblages of these two peatlands (Fig. 1), despite significant differences in 12 of 17 surface water chemical and physical variables between these two sites, including water levels and pH (Thormann et al. 2001a). Instead, plant tissue quality variables significantly correlated with axes 1 and 2 (Table 3) and separated the fungal assemblages of the bog and fen litters (Fig. 1). Our results are similar to those of Pugh and Mulder (1971), who determined that the distribution of some fungi in their *Typha latifolia* L. tissue was affected by the nutrient status of the plant tissues at various stages of decay.

To our knowledge, this is the first attempt to identify the components of microfungal communities of different peatlands using the litter of the dominant plant species. Our results show that the microfungal communities associated with the decomposing dominant plant species in this bog and fen differ substantially, thereby supporting our hypothesis. However, we cannot separate the bog and fen from a mycological perspective with our data, since we examined only a small selection of plants from both sites. An impediment of this type of study is the general lack of common dominant plant species in bogs and fens due to the significantly different hy-

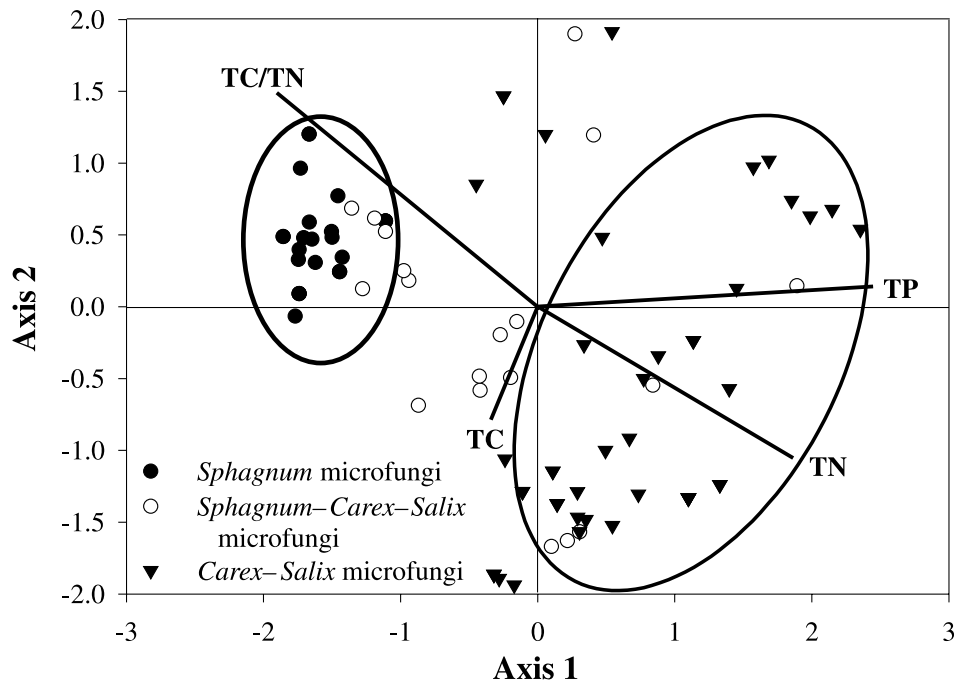
Table 2. Microfungal assemblages associated with the dominant litters at two peatlands in southern boreal Alberta, Canada.

Bog assemblage (<i>Sphagnum</i>)	Shared assemblage	Fen assemblage (<i>Carex</i> and <i>Salix</i>)
<i>Aspergillus niger</i>	<i>Botrytis cinerea</i>	<i>Aureobasidium pullulans</i>
<i>Aspergillus versicolor</i>	<i>Cladosporium herbarum</i>	Basidiomycete spp. 2–8
<i>Mortierella horticola</i>	<i>Mortierella elongata</i>	<i>Cladosporium cladosporioides</i>
<i>Mortierella ramanniana</i>	<i>Mortierella isabellina</i>	<i>Dimorphospora foliicola</i>
<i>Mortierella renispora</i>	<i>Mucor hiemalis</i>	<i>Monocillium constrictum</i>
<i>Oidiodendron maius</i>	<i>Penicillium funiculosum</i>	<i>Phialocephala dimorphospora</i>
<i>Oidiodendron scytalooides</i>	<i>Penicillium thomii</i>	<i>Phialocephala fortinii</i>
<i>Penicillium montanense</i>	<i>Trichoderma harzianum</i>	<i>Phialophora alba</i>
<i>Pochonia bulbillosa</i> ^a	<i>Trichoderma koningii</i>	<i>Phialophora</i> cf. <i>alba</i>
<i>Verticillium psalliotae</i>	<i>Trichoderma viride</i>	<i>Verticillium balanoides</i>

Note: Only the 10 most frequently isolated fungal taxa for each assemblage are listed.

^aPreviously reported as *Acremonium* cf. *curvulum* in Thormann et al. (2001b, 2003).

Fig. 1. Canonical correspondence analyses of microfungal assemblages in two peatlands in southern boreal Alberta, Canada. Symbols represent microfungal taxa isolated from the decomposing bog (*Sphagnum fuscum* plants) and fen (*Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots) plant tissues. Each symbol represents an individual fungal taxon; however, two or more taxa may occupy the same position on the biplot and may appear as a single symbol. Ellipses group most of the microfungal taxa that comprise components associated with the dominant bog and fen plant litters. TC, total carbon; TN, total nitrogen; TP, total phosphorus. Eigenvalues for axes 1 and 2 were 0.568 and 0.392, respectively.



drological and surface water chemical and physical characteristics of bogs and fens (e.g., Vitt 1994). Hence, direct comparisons of microfungal communities from the same dominant plant species (living and decomposing) from a bog and fen is unlikely. Additional living and decomposing above- and below-ground plant tissues and more peatlands need to be investigated to obtain a clearer picture of the distributional differences associated with microfungi in these two distinctive peatland classes. The inclusion of chytridiomycetes, conspicuous epigeous sporocarp-forming fungi, yeasts, and nonsporulating and nondescript microfungal taxa

may elucidate peatland class differences from a mycological perspective.

Acknowledgements

We thank Trevor Lumley and Richard Summerbell for assistance with the identification of some microfungi and Colleen Prather for assistance with the CCA analysis. Comments from two anonymous reviewers and the associate editor improved this paper, and their efforts were greatly appreciated. Funding for this project was provided by Natu-

Table 3. Pearson's correlation coefficients among the canonical correspondence axes and plant tissue quality variables of (i) decomposing *Sphagnum fuscum* from the Perryvale bog and (ii) *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots from the riverine sedge fen in Alberta, Canada.

	Axis 1	Axis 2	TC	TN	TC/TN	TP
Axis 1	—					
Axis 2	—	—				
TC	-0.122	-0.286	—			
TN	0.698**	-0.053	0.263	—		
TC/TN	-0.707**	0.539*	-0.251	-0.939***	—	
TP	0.919***	0.382	-0.21	0.754**	-0.723**	—

Note: TC, total carbon; TN, total nitrogen; TC/TN, total carbon to total nitrogen quotient; TP, total phosphorus. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

ral Sciences and Engineering Research Council of Canada (NSERC) grants to R.S.C. and S.E.B., and a Canadian Circumpolar Research Institute (C/BAR) research grant, a Challenge Grants in Biodiversity (jointly sponsored by the University of Alberta and the Alberta Conservation Association) research grant, three Society of Wetland Scientists research grants, and a Killam Memorial Scholarship research grant to M.N.T.

References

- Baker, J.H. 1970. Quantitative study of yeasts and bacteria in a Signy Island peat. *Br. Antarct. Surv. Bull.* **23**: 51–55.
- Christensen, P.J., and Cook, F.D. 1970. The microbiology of Alberta muskeg. *Can. J. Soil Sci.* **50**: 171–178.
- Christensen, M., and Whittingham, W.F. 1965. The soil microfungi in open bogs and conifer swamps in Wisconsin. *Mycologia*, **57**: 882–896.
- Dal Vesco, G. 1974–1975. Funghi del suolo di un pianoro acquitrinoso in valle di cogne (Aosta). *Allionia*, **20**: 81–92. [In Italian.]
- Dooley, M., and Dickinson, C.H. 1971. The ecology of fungi in peat. *Ir. J. Agric. Res.* **10**: 195–206.
- Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Canada Committee on Ecological Land Classification, Ecological Land Series No. 23, Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection, Environment Canada, Ottawa, Ont.
- Fisher, M.M., Graham, J.M., and Graham, L.E. 1998. Bacterial abundance and activity across sites within two northern Wisconsin *Sphagnum* bogs. *Microb. Ecol.* **36**: 259–269.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* **1**: 182–195.
- Hiroki, M., and Watanabe, M.M. 1996. Microbial community and rate of cellulose decomposition in peat soils in a mire. *Soil Sci. Plant Nutr.* **42**: 893–903.
- Kuhry, P., and Vitt, D.H. 1996. Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology*, **77**: 271–275.
- Latter, P.M., Cragg, J.B., and Heal, O.W. 1967. Comparative studies on the microbiology of four moorland soils in the northern Pennines. *J. Ecol.* **55**: 445–464.
- McLennan, E.I., and Ducker, S.C. 1954. The ecology of the soil fungi of an Australian heathland. *Aust. J. Bot.* **2**: 220–245.
- National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series No. 24, Sustainable Development Branch, Environment Canada and Poly Science Publications Inc., Ottawa, Ont.
- Nilsson, M., Bååth, E., and Söderström, B. 1992. The microfungal communities of a mixed mire in northern Sweden. *Can. J. Bot.* **70**: 272–276.
- Pugh, G.J.F., and Mulder, J.L. 1971. Mycoflora associated with *Typha latifolia*. *Trans. Br. Mycol. Soc.* **57**: 273–282.
- Szumigalski, A.R., and Bayley, S.E. 1997. Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. *Ecoscience*, **4**: 385–393.
- ter Braak, C.J.F. 1992. CANOCO — A FORTRAN program for canonical community ordination [computer program]. Microcomputer Power, Ithaca, N.Y.
- Thormann, M.N., and Bayley, S.E. 1997a. Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecol.* **131**: 1–16.
- Thormann, M.N., and Bayley, S.E. 1997b. Aboveground net primary production along a bog–fen–marsh gradient in southern boreal Alberta, Canada. *Ecoscience*, **4**: 374–384.
- Thormann, M.N., Szumigalski, A.R., and Bayley, S.E. 1999a. Aboveground peat and carbon accumulation potentials along a bog–fen–marsh wetland gradient in southern boreal Alberta, Canada. *Wetlands*, **19**: 305–317.
- Thormann, M.N., Currah, R.S., and Bayley, S.E. 1999b. The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. *Wetlands*, **19**: 438–450.
- Thormann, M.N., Bayley, S.E., and Currah, R.S. 2001a. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. *Can. J. Bot.* **79**: 9–22.
- Thormann, M.N., Currah, R.S., and Bayley, S.E. 2001b. Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. *Bryologist*, **104**: 548–559.
- Thormann, M.N., Currah, R.S., and Bayley, S.E. 2003. Succession of microfungal assemblages in decomposing peatland plants. *Plant Soil*, **250**: 323–333.
- Thrower, L.B. 1954. The rhizosphere effect shown by some Victorian heathland plants. *Aust. J. Bot.* **2**: 246–267.
- Turetsky, M.R., Wieder, R.K., Williams, C.J., and Vitt, D.H. 2000. Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. *Ecoscience*, **7**: 379–392.
- Vitt, D.H. 1994. An overview of factors that influence the development of Canadian peatlands. *Mem. Entomol. Soc. Can.* **169**: 7–20.
- Williams, R.T., and Crawford, R.L. 1983a. Microbial diversity of Minnesota peatlands. *Microb. Ecol.* **9**: 201–214.

- Williams, R.T., and Crawford, R.L. 1983*b*. Effects of various physiochemical factors on microbial activity in peatlands: aerobic biodegradation processes. *Can. J. Microbiol.* **29**: 1430–1437.
- Wynn-Williams, D.D. 1980. Seasonal fluctuations in microbial activity in Antarctic moss peat. *Biol. J. Linn. Soc.* **14**: 11–28.

Appendix A

Appendix appears on the following page.

Table A1. Isolation frequencies (%) of fungi from decomposing *Sphagnum fuscum* plants from a bog and *Carex aquatilis* leaves and rhizomes and *Salix planifolia* leaves and roots from a fen in southern boreal Alberta, Canada.

Classification ^a	Fungal taxa	Decomposition periods (d)							Totals
		0	20	50	250	365	456	730	
<i>Sphagnum fuscum</i> plants									
Aa	<i>Acremonium chrysogenum</i> (Thisum. & Sukop.) W. Gams					0.5			0.5
Aa	<i>Acremonium strictum</i> W. Gams					0.5			0.5
Aa	<i>Aspergillus niger</i> van Tieghem		0.5						0.5
Aa	<i>Aspergillus versicolor</i> (Vuill.) Tiraboschi		0.5						0.5
Aa	<i>Botrytis cinerea</i> Pers. ex Pers.		0.5						0.5
Aa	<i>Cladosporium herbarum</i> (Pers.) Link ex Gray	0.5							0.5
At	<i>Kernia retardata</i> Udagawa & Muroi					0.5			0.5
Z	<i>Mortierella alpina</i> Peyronel		0.5			1			1.5
Z	<i>Mortierella elongata</i> Linnem.	2.5	3	1		1.5		0.5	8.5
Z	<i>Mortierella horticola</i> Linnem.	0.5	1		0.5				2
Z	<i>Mortierella humilis</i> Linnem.	0.5							0.5
Z	<i>Mortierella isabellina</i> Oudem. & Koning				1	1.5	1		3.5
Z	<i>Mortierella minutissima</i> van Tieghem	1	0.5	1	0.5	2	1		6
Z	<i>Mortierella ramanniana</i> var. <i>angulispora</i> (Möller) Linnem.	1.5	0.5			2	2		6
Z	<i>Mortierella ramanniana</i> var. <i>ramanniana</i> (Naumov) Linnem.	0.5		0.5	1	1		0.5	3.5
Z	<i>Mortierella renispora</i> Dixon-Stewart	0.5	1			0.5		0.5	2.5
Z	<i>Mortierella verticillata</i> Linnem.	0.5			0.5				1
Z	<i>Mucor hiemalis</i> Wehmer	0.5	2.5	2	4	2	2.5		13.5
?	<i>Mycelium sterilium</i> 10						1		1
?	<i>Mycelium sterilium</i> 4				0.5				0.5
?	<i>Mycelium sterilium</i> 5							0.5	0.5
?	<i>Mycelium sterilium</i> 6				1				1
?	<i>Mycelium sterilium</i> 8						0.5		0.5
?	<i>Mycelium sterilium</i> 9						0.5		0.5
Aa	<i>Nodulisporium</i> sp.						0.5		0.5
Aa	<i>Oidiodendron maius</i> Barron			0.5					0.5
Aa	<i>Oidiodendron scytaloides</i> Gams & Söderström							0.5	0.5
Aa	<i>Penicillium funiculosum</i> Thom	1		1	1				3
Aa	<i>Penicillium montanense</i> Christensen & Backus				0.5		0.5		1
Aa	<i>Penicillium odoratum</i> Christensen & Backus				1	0.5	0.5		2
Aa	<i>Penicillium purpurogenum</i> Stoll	0.5							0.5
Aa	<i>Penicillium thomii</i> Maire	0.5	2.5	0.5	1.5	3	1.5	0.5	10
Aa	<i>Pochonia bulbillosa</i> (W. Gams & Malla) Zare & W. Gams ^b	1	2.5	1	1	1			6.5
Aa	<i>Sporothrix</i> sp. 1					0.5		1.5	2
Aa	<i>Sporothrix</i> state of <i>Ophiostoma stenoceras</i> (Robak) Melin & Nannf.							1.5	1.5
Aa	<i>Trichoderma aureoviride</i> Rifai							1	1
Aa	<i>Trichoderma harzianum</i> Rifai		1						1
Aa	<i>Trichoderma polysporum</i> (Link ex Pers.) Rifai			1					1
Aa	<i>Trichoderma viride</i> Pers. ex Gray	0.5	0.5		1	3		1.5	6.5
Aa	<i>Verticillium lecanii</i> (Zimm.) Viégas			0.5					0.5
Aa	<i>Verticillium psalliotae</i> W. Gams	1	1	1	1.5	1.5			6
	Totals	13	18	10	16.5	22.5	11.5	8.5	100
<i>Carex aquatilis</i> leaves									
Aa	<i>Acremonium butyri</i> (van Beyma) W. Gams							1.09	1.09
Aa	<i>Acremonium</i> state of <i>Nectria rishbethii</i> Booth			1.03					1.03
Aa	<i>Acremonium strictum</i>		1.09	1.09					2.18
B	<i>Armillaria sinapina</i> Bérubé & Dessur.		0.89				1.19		2.08

Table A1 (continued).

Classification ^a	Fungal taxa	Decomposition periods (d)							Totals
		0	20	50	250	365	456	730	
Aa	<i>Aureobasidium pullulans</i> var. <i>melanogenum</i> (de Bary) Arn.	1.28							1.28
B	Basidiomycete sp. 2		1.19						1.19
B	Basidiomycete sp. 3					1.19	4.06	1.09	6.34
B	Basidiomycete sp. 4					1.28		2.87	4.15
B	Basidiomycete sp. 5			1.19					1.19
B	Basidiomycete sp. 7		1.19						1.19
B	Basidiomycete sp. 8			1.19					1.19
Aa	<i>Botrytis cinerea</i>	1.28	1.69						2.97
Aa	<i>Cladosporium cladosporioides</i> (Fres.) de Vries	1.09							1.09
Aa	<i>Cladosporium herbarum</i>	4.06		1.69					5.75
Aa	<i>Dimporphospora foliicola</i> Tubaki				1.19		4.06		5.25
Aa	<i>Epicoccum purpurascens</i> Ehrenb. ex Schlecht.	1.19							1.19
Aa	<i>Monocillium constrictum</i> W. Gams				1.19		7.03	1.19	9.41
Aa	<i>Monocillium nordinii</i> (Bourchier) W. Gams				1.19		1.39		2.58
Z	<i>Mortierella elongata</i>		1.49	0.89					2.38
Z	<i>Mortierella minutissima</i>			0.89					0.89
Z	<i>Mucor hiemalis</i>		1.79	2.28					4.07
Aa	<i>Nodulisporium</i> sp.					2.28			2.28
Aa	<i>Penicillium chrysogenum</i> Thom						2.87		2.87
Aa	<i>Penicillium funiculosum</i>			2.87					2.87
Aa	<i>Penicillium odoratum</i>					1.09			1.09
Aa	<i>Penicillium thomii</i>				1.09				1.09
Aa	<i>Phialophora alba</i> van Beyma		2.09		2.87		1.15	1.19	7.3
Aa	<i>Phialophora</i> cf. <i>alba</i>				1.69		3.56	2.28	7.53
Aa	<i>Stagonospora caricis</i> (Oud.) Sacc.	1.69							1.69
Aa	<i>Trichoderma harzianum</i>		1.69		2.87		2.28		6.84
Aa	<i>Trichoderma koningii</i> Oud.						1.69		1.69
Aa	<i>Trichoderma viride</i>		2.09		2.09				4.18
Aa	<i>Verticillium lecanii</i>							2.09	2.09
Totals		10.59	15.2	13.12	14.18	5.84	29.28	11.8	100
Carex aquatilis rhizomes									
Aa	<i>Acremonium strictum</i>		0.81						0.81
B	<i>Armillaria sinapina</i>	0.81							0.81
Aa	<i>Arthrimum</i> state of <i>Apiospora montagnei</i> Sacc.					0.81			0.81
B	<i>Bjerkandera adusta</i> (Willd.: Fr.) Karst.				0.81				0.81
Aa	<i>Fusarium aquaeductuum</i> var. <i>medium</i> Wollenw.	0.81							0.81
Aa	<i>Fusarium oxysporum</i> Schlecht.	0.81							0.81
Z	<i>Mortierella elongata</i>			0.81					0.81
Z	<i>Mortierella isabellina</i>				0.81				0.81
Z	<i>Mortierella minutissima</i>			0.81					0.81
Z	<i>Mucor hiemalis</i>			4.07		0.81	1.63	0.81	7.32
Aa	<i>Penicillium chrysogenum</i>					0.81			0.81
Aa	<i>Penicillium funiculosum</i>			3.25					3.25
Aa	<i>Penicillium purpurogenum</i>	0.81							0.81
Aa	<i>Penicillium thomii</i>				0.81	0.81			1.63
Aa	<i>Phialocephala dimorphospora</i> Kendrick	0.81		2.44	1.63	0.81	3.25		8.94
Aa	<i>Phialocephala fortinii</i> Wang & Wilcox	0.81				1.63			2.44
Aa	<i>Phialophora alba</i>	1.63					1.63		3.25
Aa	<i>Phialophora</i> cf. <i>alba</i>	2.44	7.32	2.44	4.88	4.88	15.4	8.13	45.53
?	Pycnidial sp. 1			0.81					0.81
?	Pycnidial sp. 2				2.44				2.44
?	Pycnidial sp. 5			0.81					0.81
Aa	<i>Scopulariopsis brevicaulis</i> (Sacc.) Bain.		0.81						0.81
Aa	<i>Trichoderma aureoviride</i>		0.81						0.81

Table A1 (continued).

Classification ^a	Fungal taxa	Decomposition periods (d)							Totals
		0	20	50	250	365	456	730	
Aa	<i>Trichoderma harzianum</i>							0.81	0.81
Aa	<i>Trichoderma koningii</i>		2.44				1.63		4.07
Aa	<i>Trichoderma piluliferum</i> Webster & Rifai							0.81	0.81
Aa	<i>Trichoderma polysporum</i>		2.44			0.81			3.25
Aa	<i>Trichoderma pseudokoningii</i> Rifai							1.63	1.63
Aa	<i>Trichoderma viride</i>							1.63	1.63
Aa	<i>Verticillium lecanii</i>			0.81					0.81
	Totals	8.94	14.63	16.26	11.38	11.38	23.58	13.82	100
<i>Salix planifolia</i> leaves									
Aa	<i>Acremonium</i> state of <i>Nectria rishbethii</i>	1.06							1.06
Aa	<i>Alternaria alternata</i> (Fr.) Keissler	3.28	1.61	1.61					6.5
B	<i>Armillaria sinapina</i>						1.06	2.17	3.23
Aa	<i>Arthrimum</i> state of <i>Apiospora montagnei</i>		1.61	1.06					2.67
Aa	<i>Aureobasidium pullulans</i> var. <i>melanogenum</i>	2.17							2.17
Aa	<i>Aureobasidium pullulans</i> var. <i>pullulans</i> (de Bary) Arn.	1.06							1.06
B	Basidiomycetes sp. 4					1.61			1.61
B	Basidiomycetes sp. 6				1.06				1.06
Aa	<i>Botrytis cinerea</i>	1.06	1.61	1.06					3.73
Aa	<i>Cladosporium cladosporioides</i>	1.61	1.06						2.67
Aa	<i>Cladosporium herbarum</i>	3.28	1.61	2.17	3.28				10.34
Aa	<i>Dimorphospora foliicola</i>					2.17	3.84	1.06	7.07
Aa	<i>Fusarium chlamyosporum</i> Wollenw. & Reink.		1.06						1.06
Z	<i>Mortierella elongata</i>						2.17		2.17
Z	<i>Mortierella isabellina</i>			1.06					1.06
Z	<i>Mucor hiemalis</i>	1.61	1.61	1.06	3.28		1.06	1.61	10.23
Aa	<i>Nodulisporium</i> sp.					1.61			1.61
Aa	<i>Penicillium funiculosum</i>			1.61					1.61
Aa	<i>Phialocephala dimorphospora</i>				1.06				1.06
Aa	<i>Phialophora alba</i>	1.06			1.61	1.06	1.61	3.28	8.62
Aa	<i>Phialophora</i> cf. <i>alba</i>					1.61		1.61	3.22
Aa	<i>Polyscytalum</i> cf. <i>hareae</i>		1.06	1.61	1.06				3.73
Aa	<i>Scopulariopsis brevicaulis</i>		1.06						1.06
At	<i>Sordaria fimicola</i> (Rob.) Ces. & de Not.				1.06				1.06
Aa	<i>Stagonospora</i> sp.	1.06							1.06
Aa	<i>Trichoderma aureoviride</i>				1.67				1.67
Aa	<i>Trichoderma harzianum</i>		0.56		1.61	1.61	1.67	1.61	7.06
Aa	<i>Trichoderma koningii</i>						0.56		0.56
Aa	<i>Trichoderma piluliferum</i>					1.06		1.11	2.17
Aa	<i>Trichoderma pseudokoningii</i>				0.58			0.56	1.14
Aa	<i>Trichoderma viride</i>		1.67		1.11	0.56	1.67	0.56	5.57
Aa	<i>Ulocladium botrytis</i> Preuss					0.56			0.56
Aa	<i>Verticillium balanoides</i> (Drechsler) Dowsett, Reid & Hopkin				0.56				0.56
	Totals	17.25	14.52	11.24	17.94	11.84	13.64	13.57	100
<i>Salix planifolia</i> roots									
Aa	<i>Acremonium strictum</i>	0.71							0.71
Aa	<i>Cladosporium herbarum</i>		0.71	0.71					1.43
Aa	<i>Fusarium chlamydosporum</i>			1.43					1.43
Aa	<i>Fusarium sporotrichioides</i> Sherb.			1.43					1.43
Aa	<i>Monocillium constrictum</i>				2.14				2.14
Aa	<i>Monocillium nordinii</i>	0.71			0.71				1.43
Z	<i>Mortierella alpina</i>						0.71		0.71
Z	<i>Mortierella elongata</i>			0.71					0.71
Z	<i>Mortierella ericetorum</i>	1.43							1.43

Table A1 (concluded).

Classification ^a	Fungal taxa	Decomposition periods (d)							Totals
		0	20	50	250	365	456	730	
Z	<i>Mortierella minutissima</i>		0.71	0.71					1.43
Z	<i>Mucor cf. mucedo</i>					1.43			1.43
Z	<i>Mucor hiemalis</i>	2.14	2.86	0.71	1.43	0.71	3.57	5.71	17.14
Aa	<i>Penicillium commune</i>			0.71					0.71
Aa	<i>Phialocephala dimorphospora</i>				2.14	0.71			2.86
Aa	<i>Phialocephala fortinii</i>			0.71	2.14	0.71	2.86		6.43
Aa	<i>Phialophora alba</i>	1.43		1.43	2.86	2.86		2.86	11.43
Aa	<i>Phialophora cf. alba</i>				0.71				0.71
Aa	<i>Phialophora cyclaminis</i> van Beyma	0.71							0.71
Aa	<i>Phialophora melinii</i> (Nannf.) Conant				0.71				0.71
Aa	<i>Polyscytalum cf. hareae</i>			0.71					0.71
?	Pycnidial sp. 3	0.71							0.71
?	Pycnidial sp. 6							0.71	0.71
?	Pycnidial sp. 7				0.71				0.71
B	<i>Rhizoctonia</i> sp.					1.43			1.43
Aa	<i>Sporothrix</i> sp. 2	0.71							0.71
Aa	<i>Trichoderma aureoviride</i>						0.71		0.71
Aa	<i>Trichoderma harzianum</i>			0.71	0.71			0.71	2.14
Aa	<i>Trichoderma koningii</i>	1.43		2.14			1.43	0.71	5.71
Aa	<i>Trichoderma longibrachiatum</i>	0.71							0.71
Aa	<i>Trichoderma piluliferum</i>	0.71	1.43	1.43	0.71		0.71		5
Aa	<i>Trichoderma polysporum</i>	2.14		2.14	0.71	0.71	0.71	0.71	7.14
Aa	<i>Trichoderma pseudokoningii</i>	2.14	1.43		0.71				4.29
Aa	<i>Trichoderma viride</i>		2.14	2.14	3.57	2.14	1.43	0.71	12.14
Aa	<i>Verticillium balanoides</i>	1.43		0.71					2.14
Totals		17.14	9.29	18.57	20	10.71	12.14	12.14	100

^aAa, ascomycete anamorph; At, ascomycete teleomorph; B, basidiomycete; Z, zygomycete; ?, unknown taxonomic affinity.

^bPreviously reported as *Acremonium cf. curvulum* in Thormann et al. (2001b, 2003).