Diversity and function of fungi in peatlands: A carbon cycling perspective

Markus N. Thormann

Canadian Forest Service, Northern Forestry Centre, 5320-122 St., Edmonton, Alberta, Canada T6H 3S5 (e-mail: mthorman@nrcan.gc.ca). *Received 5 October 2004, accepted 14 March 2005.*

Thormann, M. N. 2006. **Diversity and function of fungi in peatlands: A carbon cycling perspective**. Can. J. Soil Sci. **86**: 281–293. Peatlands are a dominant landform in the northern hemisphere, accumulating carbon in the form of peat due to an imbalance between decomposition and plant production rates. Decomposer (saprobes) and mycorrhizal fungi significantly influence carbon dynamics by degrading organic matter via the synthesis of extracellular enzymes. As organic matter decomposes, litter quality variables figure most prominently in the succession of fungi. Hence, litters composed primarily of complex polymers decompose very slowly. Surprisingly, recalcitrant polymer degraders (mostly basidiomycetes) are rarely isolated from peat, which may explain the accumulation of complex polymers in peat profiles. While enzymatic profiles of mycorrhizal fungi and other root endophytes may be more limited compared with saprobes, many of these fungi can degrade polymers of varying complexity as well and hence may also be significant decomposers of organic matter. To date, anamorphic ascomycetes and zygomycetes are the most frequently isolated fungi from peatlands (63 and 10% of all taxa, respectively), and chytridiomycetes, teleomorphic ascomycetes, and basidiomycetes appear to be less common (11% of all taxa). The remaining 16% of taxa remain unidentified or are sterile taxa. How disturbances affect peatland microbial communities and their roles is virtually unknown. This aspect of peatland microbial ecology requires immediate attention. The objective of this paper is to review the current state of knowledge of the diversity of fungi and their roles in carbon cycling dynamics in peatlands.

Key words: Peatlands, fungi, carbon dynamics, diversity, functions, saprobes, mycorrhizas

Thormann, M. N. 2006. **La diversité et le rôle des champignons dans les tourbières vus sous l'angle du cycle du carbone**. Can. J. Soil Sci. **86**: 281–293. Les tourbières figurent parmi les principales formes de relief dans l'hémisphère nord. Elles accumulent du carbone sous la forme de tourbe, produit du déséquilibre entre le taux de décomposition et le taux de production des végétaux. Les microorganismes décomposeurs (saprobiontes) et les champignons des mycorhizes ont une action considérable sur la dynamique du carbone, car ils dégradent la matière organique par la synthèse d'enzymes extracellulaires. Lorsque la matière organique se décompose, ce sont les paramètres qualitatifs des détritus végétaux qui commandent le plus la succession de champignons. C'est pourquoi les débris essentiellement composés de polymères complexes se décomposent très lentement. Pourtant, il est surprenant qu'on isole si rarement les saprobiontes des polymères récalcitrants (surtout des basidiomycètes) de la tourbe, ce qui expliquerait l'accumulation de polymères complexes dans cette dernière. Bien que le profil enzymatique des champignons des mycorhizes et d'autres endophytes des racines soit plus étroit que celui des saprobiontes, bon nombre de ces champignons dégradent aussi des polymères de complexité variable. Ils pourraient donc être d'importants décomposeurs de la matière organique. Jusqu'à présent, les champignons qu'on retrouve le plus souvent dans les tourbières sont des ascomycètes anamorphes et des zygomycètes (63 % et 10 % des taxons, respectivement), les chytridiomycètes, les ascomycètes téléomorphes et les basidiomycètes semblant moins fréquents (11 % des taxons). Les taxons restants (16 %) n'ont pu être identifiés ou sont des taxons stériles. On ne sait presque rien sur la manière dont les perturbations affectent la microflore des tourbières et en modifient le rôle. Il conviendrait de se pencher immédiatement sur cet aspect de la micro-écologie des tourbières. L'article fait le point de nos connaissances sur la diversité des champignons et de leur rôle dans la dynamique du cycle du carbone dans les tourbières.

Mots clés: Tourbières, champignons, dynamique du carbone, diversité, fonctions, saprobiontes, mycorhizes

Wetlands cover about 4% of the world's and 14% of Canada's landscape (National Wetlands Working Group 1988). The Canadian Wetland Classification System recognizes five distinct wetland classes: bog, fen, marsh, swamp, and shallow open water (National Wetlands Working Group 1988). Of these, bogs and fens are the dominant wetland classes, globally and in Canada, and are of particular importance to the global carbon (C) cycle (Gorham 1991).

Bogs are ombrotrophic ecosystems that receive water and nutrients solely from precipitation. They are dominated by species of *Sphagnum* mosses, *Picea mariana* (Mill.) BSP, and members of the Ericaceae, including species of *Rhododendron*, *Andromeda*, and *Vaccinium*. Fens are minerotrophic ecosystems that receive water and nutrients from precipitation and ground and/or surface water flow. Fens can be subdivided into poor and rich fens. Poor fens are characterized by low mineral ion concentrations in the surface water and few moss indicator species, most of which are species of *Sphagnum* (Vitt 1994). Rich fens are characterized by high mineral concentrations in the surface water and an

Abbreviations: **DSE**, dark septate endophyte; **MRA**, *Mycelium radicis atrovirens*; **PPO**, polyphenol oxidases; **TC**, total carbon; **TN**, total nitrogen; **TP**, total phosphorus; **VAM**, vesicular-arbuscular mycorrhizas

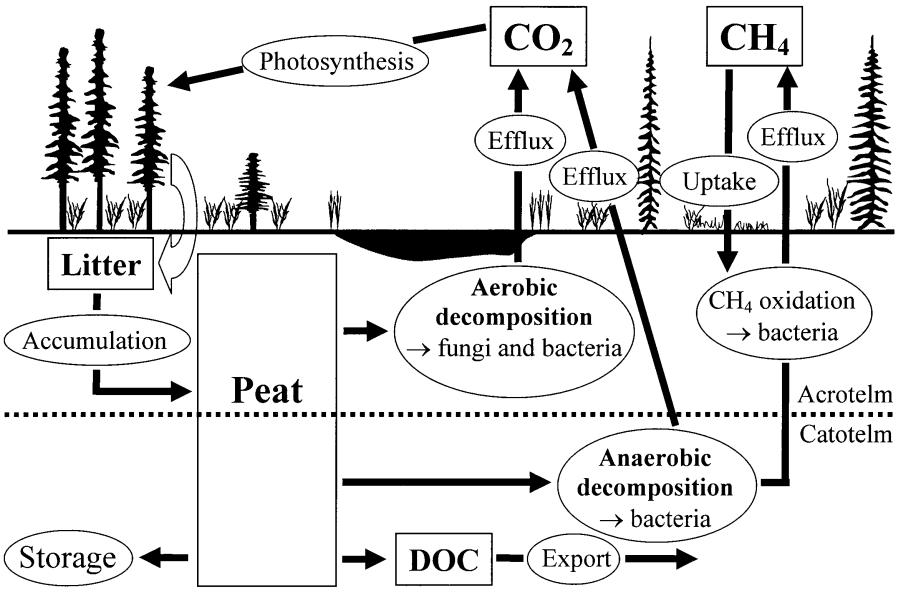

Fig. 1. Major carbon pathways in peatlands and the microbial groups (fungi, bacteria) responsible for the dominant biogeochemical processes.

increasing number of moss indicator species, including species of *Drepanocladus*, *Scorpidium*, and *Aulacomnium* ("brown" mosses; Vitt 1994). Additionally, shrubs, such as species of *Salix* and *Betula*, herbaceous plants, such as species of *Carex*, and trees, including species of *Larix* and *Picea*, occur in poor and rich fens (Vitt 1994; Szumigalski and Bayley 1996; Thormann and Bayley 1997a).

Peatlands accumulate peat, a heterogeneous assemblage of partially decomposed plant materials (about 45–50% C; Clymo 1984; Clymo et al. 1998). Gorham (1991) estimated that northern peatlands store between 180 and 277 Gt C (1 Gt = 10^9 t), which represents about 10 to 16% of the total global terrestrial detrital C, emphasizing their importance to the global C cycle. Peat accumulates because of an imbalance between plant production and organic matter decomposition (Clymo 1965; Malmer 1986; Vitt 1990). Photosynthetically fixed C accumulates annually in the acrotelm (oxygenated peat horizon) following leaf abscission, root and rhizome turnover, and bryophyte vertical growth (litter production; Fig. 1). The highest rates of decomposition, carried out by fungi and bacteria, occur in the acrotelm and result in CO_2 efflux into the atmosphere; however, most of the litter is only partially decomposed and is "buried" by litter produced the following year(s). It ultimately enters the catotelm (anaerobic soil horizon; Fig. 1), where decomposition rates are very slow and organic matter is decomposed only by anaerobic bacteria (Clymo 1984). This results in CH_4 production, which subsequently enters the atmosphere or is oxidized by aerobic methanotrophic bacteria as it diffuses vertically through the acrotelm (Fig. 1; Dedysh 2002; Wartiainen et al. 2003).

Despite the prevalence of peatlands in the northern hemisphere and their importance to the global C cycle, little is known about the microbial diversity and roles in these ecosystems. It has long been suggested that fungi are the principal decomposer microbes in many acidic ecosystems, such as many peatlands, and assume a more dominant role than bacteria (Kox 1954; Latter et al. 1967; Williams and Crawford 1983). Several recent studies focused on the mineralization of C to produce CH_4 (Bubier et al. 1993; Roulet et al. 1993), likely because CH_4 has greater global warming potential than CO_2 (Intergovernmental Panel on Climate Change 2001); however, CO_2 fluxes quantitatively far exceed CH_4 fluxes from peatlands (Blodau 2002; Blodau and Moore 2003). The objectives of this paper are to (1) summarize the current knowledge of fungal species richness in peatlands, (2) address the major roles of fungi in peatlands, (3) and indicate gaps in our understanding of fungal communities and their influence on C dynamics and stocks in peatlands.

FUNGAL SPECIES RICHNESS IN PEATLANDS

Microfungal communities (mycota) have been examined in a variety of peatlands in Europe and North and South America, investigating the mycota of hummocks and hollows of bogs, fens, swamps, moors, muskeg, anthropogenically altered wetlands, and individual wetland plants (Table 1). From a taxonomic perspective, in excess of 860 individual records of microfungi from peatlands have been reported, representing 648 different species. These were 408 anamorphic species with putative ascomycete affinities (reproduce asexually only), 22 teleomorphic ascomycetes (reproduce sexually), 25 basidiomycetes, 67 zygomycetes, 28 chytridiomycetes, and 106 taxa with unknown taxonomic affinities, yeasts, and *mycelia sterilia* (sterile isolates; Table 2).

Anamorphic ascomycetes were by far the largest group of fungi isolated from peatlands (408 species, or 63% of all

Table 1. Studies of microfungi in peatlands

Continent	Author(s)	Location	Peatland, substrate
North America	Bisby et al. (1935)	Manitoba, Canada	Fen, soil
	Christensen and Whittingham (1965)	Wisconsin, USA	Bogs, soil
	Christensen and Cook (1970)	Alberta, Canada	Bog and fens, soil
	Sparrow and Lange (1977)	Michigan, USA	Bog, soil
	Hurley (1981)	New Brunswick, Canada	Bog, soil
	Zattau (1981)	North Carolina, USA	Bog, soil
	Cormier et al. (1988)	Quebec, Canada	Peat moss samples
	Croft et al. (2001)	Quebec, Canada	Bog and fen, soil
	Thormann et al. (2001a, 2003)	Alberta, Canada	Bog, *Sphagnum fuscum*; Fen, *Carex aquatilis* leaves and rhizomes, *Salix planifolia* leaves and roots
South America	Searles et al. (2001)	Argentina	Bog, *Nothofagus antarctica* leaves; Fen, *Carex decidua* leaves
	Robson et al. (2004)	Argentina	*Sphagnum* sp. capitula
Europe	Stenton (1953)	UK	Fen, soil
	Boswell (1955)	UK	Bogs, soil
	Thornton (1956)	UK	Fen, soil (podzol)
	Sewell (1959a, b)	UK.	Heathland, soil
	Latter et al. (1967)	UK.	Fens (*Juncus*-dominated, *Calluna-Eriophorum*-dominated, bare peat), soil
	Dickinson and Dooley (1967, 1969)	Ireland	Bog, soil (undisturbed and cut-away)
	Dooley and Dickinson (1971)	Ireland	Bog, soil (undisturbed and cut-away)
	Maciejowska-Pokacka (1971)	Poland	Fen, soil
	Dal Vesco (1974–75)	Italy	Peatlands, soil
	Zvyagintsev et al. (1991)	Russia	Bog and fen, soil
	Nilsson et al. (1992)	Sweden	Bog, hummock and hollow peat, *Sphagnum* spp.; Fen, *Sphagnum* spp.
	Czeczuga (1993)	Poland	Bogs, water samples
	Beyer (1994)	Germany	Bog, *Eriophorum angustifolium* leaves
	Gilbert et al. (1998a, b)	France	Peatland, soil

Table 2. Taxonomic profile of fungi from peatlands

Fungal group	No. of records	Different taxa	Unidentified taxa
Ascomycetes - anamorphic	566	408	170
Ascomycetes - teleomorphic	23	22	6
Basidiomycetes	25	25	12
Chytridiomycetes	30	28	7
Zygomycetes	118	67	15
Unidentified	106	–	106
Total	868	550[z]	316

[z]Excludes unidentified taxa.

species; Table 2). Species of *Penicillium* and *Acremonium* dominated this group (89 and 27 different species, respectively), with *P. frequentans* Westl., *P. purpurogenum* Stoll, *P. spinulosum* Thom, *P. thomii* Maire, and *A. kiliense* Grütz being the dominant species. These two genera and the next six most dominant genera comprise 194 different species, which represents nearly half of the entire anamorphic ascomycete species richness in peatlands (Table 3). Zygomycetes were also very frequently isolated from peat (67 different species, or 10% of all species; Table 2). In this group, species of *Mortierella* (*M. alpina* Peyronel, *M. isabellina* Oudem. & Koning, *M. minutissima* van Tieghem, *M. ramanniana* (Möller) Linnem., *M. vinacea* Dixon-Stewart) and *Mucor* (*M. hiemalis* Wehmer) comprise 80% of all zygomycetes (Table 3). Several specific surveys for chytridiomycetes yielded 28 species (4% of all species; Table 2), with *Rhizophydium*, *Phlyctochytrium*, and *Septosperma* being the dominant genera (61% of all chytridiomycete species; Table 3). Teleomorphic ascomycetes (22 species, or 3% of all species) and basidiomycetes (25 species, or 4% of all species) were rarely isolated from peat. Among the former group, species of *Chaetomium*, *Gelasinospora*, *Sordaria*, and *Thielavia* predominated (68% of all ascomycete species), while basidiomycete yeasts predominated the latter group (*Cryptococcus* and *Rhodotorula* spp., 36% of all basidiomycete species; Table 3). Lastly, 106 records of fungi from peatlands remained unidentified (*mycelia sterilia* and otherwise unidentified: 77 taxa; yeasts: 12 taxa; pycnidial: 7 taxa) or belonged to taxa with unknown taxonomic affinities (10 taxa; Tables 2 and 3).

It is interesting to note that the majority of microfungi isolated from peat and peatland plants are prolific sporulators with fast growth rates, particularly species of *Penicillium*, *Trichoderma*, *Aspergillus*, *Verticillium*, *Cladosporium*, and the zygomycetes *Mortierella* and *Mucor*. These taxa are easily cultured on most standard media and under most growing conditions. This explains their preponderance in almost all studies, irrespective of location and substrate, and undoubtedly skews the species list towards that group of fungi at the expense of slower-growing and less prolific sporulators. Several groups of fungi are underrepresented in almost all studies, including yeasts, chytridiomycetes, basidiomycetes, and teleomorphic ascomycetes. These groups are characterized by slower growth rates and in some cases require special growth media and conditions. While yeasts were frequently isolated, few studies identified them to either genus or species. Only three surveys for chytridiomycetes have been conducted to my knowledge (Sparrow and Lange 1977; Zattau 1981; Czeczuga 1993), and virtually all records of chytridiomycetes from peatlands are unique. There may be a large diversity of these mostly parasitic and saprobic fungal taxa that have received little attention so far. Surprising also is the under representation of basidiomycetes. Most basidiomycetes on record are yeasts and originated from a single study in Russia (13 of 25 taxa; Polyakova et al. 2001), with 11 of the remaining 12 records originating from a second study in Canada, most of which were not identified to genus or species (9 of 11; Thormann et al. 2001b, 2004a).

Table 3. Dominant fungal taxa from peatlands

Fungal group	Fungal genera/taxa	No. of species
Ascomycetes - anamorphic	*Penicillium* spp.	89
	Acremonium spp.	27
	Verticillium spp.	16
	Aspergillus spp.	15
	Trichoderma spp.	15
	Fusarium spp.	14
	Cladosporium spp.	11
	Oidiodendron spp.	7
Ascomycetes - teleomorphic	*Chaetomium* spp.	6
	Gelasinospora spp.	3
	Sordaria spp.	3
	Thielavia spp.	3
Basidiomycetes	*Cryptococcus* spp.	5
	Rhodotorula spp.	4
Chytridiomycetes	*Rhizophydium* spp.	9
	Phlyctochytrium spp.	5
	Septosperma spp.	3
Zygomycetes	*Mortierella* spp.	34
	Mucor spp.	19
Unidentified	*Mycelia sterilia*	46
	Yeast spp.	12
	Unknown affinities	10

ROLE OF FUNGI IN PEATLAND CARBON CYCLING DYNAMICS

Saprobes

Fungi play fundamental roles in the decomposition processes of organic matter in all ecosystems and may be more important than bacteria in wetlands from a functional perspective, because of their extensive hyphal growth habit, faster growth rates, and ability to translocate nutrients through their hyphal network. Five major "behavioural groupings" of decomposer fungi have been recognized (Table 4). Group 1 fungi, pathogens and weak parasites, can tolerate host defence mechanisms but are generally poor competitors in dead organic matter. These fungi access simple sugars and other storage compounds. Following the senescence and death of plants, all organic matter is sequentially colonized by pioneer saprobes (Group 2), followed by

Table 4. Characteristics of "behavioural" groupings of decomposer fungi (modified from Deacon 1997)

Group	
1. Pathogens and weak parasites	– able to tolerate host defence responses – generally access simple sugars and other storage compounds – generally poor competitors on dead organic matter – include species of *Cladosporium*, *Aureobasidium*, *Botrytis*, and *Alternaria*
2. Pioneer saprobes	– generally use simple sugars and other storage compounds – fast growth rates, good competitors, short life cycles – include mostly zygomycetes, e.g., species of *Mucor* and *Mortierella*
3. Polymer-degraders	– use structural polymers, including cellulose, pectin, and hemicellulose – slower growth rates, able to "defend" substrates via antibiosis – substrate-specialized – may be tolerant to extreme conditions, e.g., high temperature, pH, or salinity – include species of *Fusarium*, *Chaetomium*, *Trichoderma*, and *Penicillium*
4. Recalcitrant polymer degraders	– specialized to use complex polymers, including lignin, tannins, and other polyphenolics – slow growth rates, able to "defend" resources via antagonism or mutual exclusion – access other nutrients previously unexplored – includes species of basidiomycetes
5. Secondary saprobes	– opportunistic and commensal species – tolerate metabolic by-products of other fungi – may be antagonistic – include species of *Pythium*, *Mortierella*, and others

simple polymer-degrading fungi (Group 3), and finally degraders of recalcitrant polymers (Group 4). Secondary, or opportunistic, saprobes (Group 5) are common throughout the entire process of decomposition (Table 4; Deacon 1997). Hence, from the point of senescence to complete decomposition, all organic matter is colonized by a suite of saprobes with specific enzymatic profiles and preferences for specific (non)structural C compounds. This succession has been previously shown in a variety of litters, including leaves, roots, cones, seeds, dung, and wood, in a variety of ecosystems, including forests, wetlands, and grasslands (Wicklow and Yokum 1981; Heilman-Clausen 2001; Lumley et al. 2001).

Fungi from all five behavioural groups of saprobes have been previously isolated from peatlands; however, Group 4 fungi are rarely reported. This is significant, since it is this group of fungi that is able to use the most complex structural polymers, including lignin, tannins, unhydrolyzable residues (also known as "Klason lignin"), and other polyphenolics, which comprise up to 50% of the chemical constituents of peat (Turetsky et al. 2000). There are two reasons why this group is underrepresented in previous studies. First, it is possible that these fungi are naturally rare in peatlands, which is contradicted by the preponderance of conspicuous epigeous basidiomycete fruiting bodies in these ecosystems; however, the majority of these basidiomycetes may be ectomycorrhizal species of *Picea*, *Larix*, and *Salix*. While these fungi can grow in vitro, they have limited abilities to use complex polymers as C sources (e.g., Hutchison 1990; see below). The rarity of this group of fungi may partially explain why organic matter accumulates in peatlands and is not fully decomposed. Second, Group 4 fungi may be abundant in peatlands, but previous isolation protocols may have been inadequate. The dilution plating technique, predominantly used in the infancy of surveys of soil fungi, selects towards those organisms that produce large quantities of propagules. In contrast, the particle plating technique, which has been used more extensively in recent studies, largely avoids that bias; however, other methodological biases are introduced, such as the selectivity of primary isolation media and subsequent culture conditions.

Decomposition of Organic Matter

Decomposition is a complex process, which includes nearly all changes in organic matter that has undergone senescence or death (Brinson et al. 1981). Leaching of soluble organic matter precedes losses due to assimilation by microorganisms or removal by animals. Decomposition is completed with the loss of the physical structure and changes in the chemical constituents of the remaining organic matter. The rate of litter decomposition is affected by moisture, oxygen availability, temperature, acidity, and the nutrient status of ecosystems (primarily N- and P-related surface water chemistry variables; Brinson et al. 1981; Bartsch and Moore 1985; Farrish and Grigal 1988; Gorham 1991; Szumigalski and Bayley 1996; Thormann and Bayley 1997a; Thormann et al. 2001a). In addition, litter quality [total nitrogen (TN), total phosphorus (TP), and total carbon (TC) tissue concentrations, TC:TN quotients] also affects the rate of decomposition (Brinson et al. 1981; Bridgham and Richardson 1992; Szumigalski and Bayley 1996; Thormann et al. 2001a), with litters richer in TN and TP generally decomposing at faster rates. From a mycological perspective, changes in litter quality, the water potential of the litter, temperature, and pH have been shown to affect fungal communities of various substrates (Pugh 1958; Christensen and Whittingham 1965; Pugh and Mulder 1971; Dix 1985; Nilsson et al. 1992; Lumley et al. 2001; Thormann et al. 2003, 2004a).

The Importance of Litter Quality

Macromolecules of plant origins comprise the primary substrate available for fungal decomposers in terrestrial ecosystems (Kjøller and Struwe 1992). Lignin, holocellulose, and cellulose are the dominant structural polymers in plant tissues (>80% of all C polymers; Swift et al. 1979). The decomposition of these macromolecules by fungi is accomplished via the synthesis of a diverse suite of extracellular enzymes, including cellulases, polyphenol oxidases (PPO), pectinases, and amylases among others (Deacon 1997). Many fungi have the ability to degrade simple molecules, including starch; however, their ability to degrade complex structural polymers (e.g., cutin, suberin, "Klason lignin", true lignin, and tannins) is limited (Domsch et al. 1980) and has most often been ascribed to basidiomycetes and select groups of ascomcyetes, such as taxa belonging to the Xylariaceae. As organic matter decomposes, desirable nutrients, such as N, P, amino acids, and simple sugars, become scarce, while more complex structural polymers, such as lignin and lignocellulose, increase proportionally in the litter (Deacon 1997). This generally results in a succession of fungi, both taxonomically and functionally, as plant litters decompose.

Taxonomic succession of fungi during the process of decomposition has been observed in a variety of plant species in terrestrial (Frankland 1966; Saitô 1966; Kasai et al. 1995; Lumley et al. 2001) and wetland (Pugh 1958; Pugh and Mulder 1971; Apinis et al. 1972; Fell and Hunter 1979; Tanaka 1991; Tokumasu 1994; Thormann et al. 2003, 2004a) ecosystems. This succession of saprobic fungi results in the decomposition of the substrate and may be due to the process of facilitation, where species of a particular behavioural group alter the substrate sufficiently to allow other species to become established and form a subsequent community (Lumley et al. 2001). In wetlands, the majority of fungal community succession studies were conducted on plants from marshes and swamps, which generally accumulate little or no peat. Species examined include the emergent macrophytes *Juncus roemaerianus* Scheele, *Carex paniculata* L., *Typha latifolia* L., and *Phragmites communis* Trin. (Pugh 1958; Pugh and Mulder 1971; Apinis et al. 1972; Fell and Hunter 1979; Tanaka 1991; Tokumasu 1994). Newly emerged, senesced, and decomposed leaves were examined in these studies; however, neither precise stages of decomposition nor specific litter quality variables were correlated with the fungal communities. In most cases, temperature and moisture content of the litter were cited as environmental variables most significantly affecting the mycota. This is not surprising, since these macrophytes often begin to decompose in the standing position, where they desiccate, prior to falling into the water column, where they then continue to decompose; however, most peatlands plants do not decompose in this manner. Instead, their leaves abscise and moisture is rarely a limited factor while they decompose.

In one of the very few studies that directly linked litter quality changes of specific litters to their mycotas throughout the process of decomposition in peatlands, Thormann et al. (2003) found that distinct patterns of microfungal succession occurred in two of their five litters [*Sphagnum fuscum* (Schimp.) Klinggr. plants and *Carex aquatilis* Wahlenb. leaves], with litter quality variables correlating most frequently with the respective fungal communities (TP, TN, and TC tissue concentrations as well as litter TC:TN quotients). Particularly elevated TP tissue concentrations figured prominently during the latter stages of their decomposition period (365–730 days). In contrast, surface water chemistry variables were of less consequence to the mycota and only the pH and TP in the surface water correlated positively with the mycota in *S. fuscum*. Contrary to expectations, a clear succession pattern of functional groups of fungi, previously demonstrated in other substrates (e.g., Wicklow and Yokum 1981; Heilman-Clausen 2001; Lumley et al. 2001), was not observed by Thormann et al. (2003), i.e., cellulose degraders did not precede lignin and polyphenolic polymer degraders. Instead, microfungi with broad enzymatic profiles co-existed and simultaneously degraded their litters. They determined that species of *Mortierella* (*M. verticillata* Linnem., *M. horticola* Linnem.), *Aspergillus* [*A. niger* van Tieghem, *A. versicolor* (Vuill.) Tiraboschi] and *Trichoderma* [*T. harzianum* Rifai, *T. polysporum* (Link ex Pers.) Rifai] were among those isolated exclusively from early-stage decomposing *S. fuscum*, while *Oidiodendron scytaloides* Gams & Söderström, the *Sporothrix* state of *Ophiostoma stenoceras* (Robak) Melin & Nannf., *Sporothrix* sp. 1, *M. isabellina*, and species of *Acremonium* [*A. chrysogenum* (Thisum. & Sukop.) W. Gams, *A. strictum* W. Gams] appeared only in well-decomposed *S. fuscum* (Thormann et al. 2003). These taxa do not reflect a taxonomic or functional pattern of succession.

It is difficult to ascertain the relationship between in vitro and in situ enzymatic abilities of fungi, because in vitro analyses present individual fungi with optimal, but highly artificial, growth conditions, e.g., ample nutrients for growth and no competition with other organisms. Nonetheless, a positive test result indicates the potential of that fungus to synthesize the specific enzyme(s) under investigation. Enzymatic profiles have been developed for a wide variety of fungi (see Domsch et al. 1980). Those from decomposing *S. fuscum* are summarized in Thormann et al. (2001b) and show that of 55 identified/isolated taxa, only 13 (24%) had the ability to degrade polyphenolic polymers. These included species of *Oidiodendron*, four of ten *mycelia sterilia*, three basidiomycetes, and seven anamorphic taxa with putative ascomycetes affinities. The degradation of polyphenolic polymers requires the synthesis of a suite of different enzymes due to the complex arrangement of the basic building blocks of these polymers, including PPOs, laccase, peroxidases, and others. In contrast, 29 taxa (53%) had the ability to degrade cellulose and 31 had the ability to degrade starch (56%). Cellulose and starch degraders included species of *Acremonium*, *Penicillium*, *Trichoderma*, *Verticillium*, *Mortierella*, and several *mycelia sterilia* (Thormann et al. 2001b). Cellulase and amylase are required for the degradation of these polymers. Pectin, gelatin, chitin, fats, and various other carbohydrates were degraded to variable degrees (7–33%).

More recent approaches used sterilized, natural substrates to assess the role of specific fungal taxa in the decomposi-

tion of organic matter. Thormann et al. (2002) examined the ability of nine frequently isolated fungi from *S. fuscum* to cause mass loss of sterilized spruce wood chips and *S. fuscum* plant tissues. They showed that mass losses of the wood chips generally exceeded those of the bryophyte tissues. After 8 wk, a basidiomycete and an ascomycete caused the greatest mass losses of the wood chips (10.2%) and *S. fuscum* plant tissues (5.1%), respectively. Expectedly, the decay of organic matter is controlled by different mycotas, likely using different approaches to access C and nutrients from the organic matter (Tsuneda et al. 2001). Incidentally, there was no relationship between their natural substrate mass losses and in vitro enzymatic profiles of tannic acid, cellulose, and starch degradation (Thormann et al. 2002). This suggests that physiological profiles obtained from calorimetric tests may have a limited use as an indicator of the ability of specific fungi to decompose organic matter. In fact, such relationships have never been shown previously (Harper 1985; Bowen and Harper 1990).

Many fungi previously isolated from peatlands possess broad enzymatic profiles (e.g., species of *Trichoderma*, *Verticillium*, and *Penicillium*) and consequently are able to degrade a wide variety of structural and storage polymers of peat and peatland plants. Hence, they play crucial roles in the mineralization of plant tissues and peat; however, overall, it appears that the most commonly isolated fungi have a limited ability to degrade the most complex polymers (Thormann et al. 2001b, 2002), which subsequently accumulate in peatlands and increase in proportion with increasing depth in the peat profile (Turetsky et al. 2000). Whether these polymers are not degraded due to environmental constraints, such as low temperature or low oxygen concentrations, or physiological constraints of the prevalent mycota remains unclear.

Mycorrhizas and Other Root Endophytes

Mycorrhizas are mostly mutualistic associations between fungi and the roots of higher plants, in which the fungi form consistently recognizable and physically distinct associations without causing any perceivable negative effect (Fernando 1995). It is thought that in excess of 90% of all land plants are mycorrhizal, irrespective of environmental conditions, climate, ecosystem, soil type, and vegetation communities (Read 1991). There are five common types of mycorrhizas: ectomycorrhizas, vesicular-arbuscular mycorrhizas (VAM), ericoid mycorrhizas, arbutoid mycorrhizas (ectendomycorrhizas), and orchid mycorrhizas – the former three being by far the most dominant ones in most ecosystems, including peatlands. Detailed information on these different types of mycorrhizas and their roles as nutrient scavengers is provided elsewhere (Read 1991; Smith and Read 1997; Read et al. 2004). Dalpé (2003) reviewed the current state of mycorrhizal research in Canada. The widespread occurrence of mycorrhizas suggests that they play ecologically significant roles (Wetzel and van der Valk 1996; Näsholm et al. 1998; van der Heijden et al. 1998), including the acquisition, storage, and translocation of nutrients. Host plants frequently have elevated tissue concentrations of N and P, show reduced wilting due to water stress (Smith and Read 1997) or high salinity (Rozema et al. 1986), and have higher water-uptake rates than non-infected plants (Smith and Read 1997). The significance of mycorrhizas has been shown in many studies, particularly in stressed ecosystems, such as those at high altitude (Haselwandter and Read 1982) and latitude (Kohn and Stasovski 1990) and under nutrient-limited (Haselwandter 1987) or heavy metal pollution stress (Turnau et al. 2001).

The most comprehensive surveys of the mycorrhizal status of wetland plants were conducted in marshes in Connecticut, USA (Cooke and Lefor 1998) and along a bog-fen-marsh gradient in central Alberta, Canada (Thormann et al. 1999). The results among different studies are remarkably consistent. Briefly, all ericaceous plant species along the wetland gradient were ericoid mycorrhizal (species of *Andromeda*, *Rhododendron*, *Vaccinium*, and *Oxycoccus*). This is not surprising, since the mycorrhizal status of members of this family has been demonstrated numerous times in the past (Malloch and Malloch 1982; Bledsoe et al. 1990; Stoyke and Currah 1991; Treu et al. 1996; Hambleton and Currah 1997), irrespective of the habitat (alpine, arctic, boreal, parkland, and peatlands). All woody, non-ericaceous plant species in all fens and bogs were ectomycorrhizal (species of *Picea*, *Larix*, *Salix*, and *Betula*) (Thormann et al. 1999). The ectomycorrhizal status of these plants has been previously demonstrated in boreal forest (Malloch and Malloch 1981, 1982; Currah and van Dyk 1986), arctic (Kohn and Stasovski 1990; Bledsoe et al. 1990; Treu et al. 1996), and alpine ecosystems (Haselwandter and Read 1982; Dhillion 1994). Hence, trees and shrubs appear to be consistently ectomycorrhizal in many different ecosystems, including peatlands. None of the dominant herbaceous plant species along the bog-fen-marsh wetland gradient was VA-mycorrhizal (Thormann et al. 1999). This was surprising, since previous studies showed that some species of *Carex* (Wetzel and van der Valk 1996; Cooke and Lefor 1998; Miller et al. 1999; Turner et al. 2000; Bauer et al. 2003), *Typha* (Stenlund and Charvat 1994; Cooke and Lefor 1998), and various other, less dominant herbaceous plants were VA-mycorrhizal (Currah and van Dyk 1986; Cooke and Lefor 1998). These discrepancies can arise because of different sampling protocols, species examined, and sample sizes.

Ericoid Mycorrhizal Fungi

Fungal strains belonging to the *Hymenoscyphus ericae* (Read) Korf & Kernan – *Scytalidium vaccinii* Dalpé, Litten & Sigler complex, species of *Oidiodendron* (most notably *O. maius* Barron and *O. griseum* Robak) and an unnamed variable white taxon (VWT), have been implicated most often as being mycorrhizal fungi of members of the Ericaceae (Read 1991; Hambleton and Currah 1997; Hambleton et al. 1999; Monreal et al. 1999). Various additional taxa, including *Phialocephala fortinii* Wang & Wilcox, have been isolated from roots of ericaceous plants (Hambleton and Currah 1997); however, their function remains speculative.

While ericoid mycorrhizal fungi are abundant in peatlands, their ability to use peat as a C source has received

limited attention (Jefferys et al. 1953; Domsch 1960; Bending and Read 1997; Rice and Currah 2001; Piercey et al. 2002). Rice and Currah (2001) developed physiological profiles of 22 strains of *O. maius*, isolated primarily from ericaceous plants. They found that most of their strains had the ability to use lignin, cellulose, chitin, starch, pectin, and gelatin as C sources. Lipids were not used by any of their strains. Jefferys et al. (1953) and Domsch (1960) showed that *O. griseum* is able to use cellulose and starch as C sources and Bending and Read (1997) showed the production of peroxidases and PPOs, a suite of enzymes required for tannic acid and lignin degradation. A more limited enzymatic profile was shown by *H. ericae* (Leake and Read 1989, 1990). Currah and Tsuneda (1993) showed that *P. fortinii* is lignolytic and laccase positive, indicating the ability to use complex polyphenolic polymers as C sources. Hence, ericoid mycorrhizal fungi appear to have the potential to degrade a wide variety of structural polymers common in peat (Read et al. 2004).

While these studies used specific media, recent studies have used mass loss of standard organic matter to assess the saprobic abilities of selected fungi in vitro. Piercey et al. (2002) showed that *O. maius* caused the greatest mass loss of *S. fuscum* compared with *H. ericae* and VWT (11.2% vs. 8.6 and 6.7%, respectively) after 70 d. Based on these data, there appears to be a positive relationship between enzymatic diversity and the ability to cause mass loss of organic matter, i.e., ericoid mycorrhizal fungi with broad enzymatic profiles (e.g., *O. maius*) may be better adapted to use organic matter as C sources than those with more limited enzymatic profiles (e.g., *H. ericae*). The presence of ericoid mycorrhizal fungi in peatlands not only enables ericoid plants to thrive in harsh, nutrient poor, acidic ecosystems (Hambleton and Currah 2000), these fungi may also cause the formation of high molecular weight organic acid polymers via a series of complex biogeochemical pathways. Hence, ericoid mycorrhizal fungi may also contribute to the accumulation of organic acids, and hence C, in peatlands (Bending and Read 1997), playing significant roles as mycorrhizas and as saprobes (Kox 1954).

Ectomycorrhizal Fungi

Previous surveys of conspicuous epigeous fruiting bodies revealed a great diversity of ectomycorrhizal fungi in peatlands (Salo 1993; Dhillion 1994; Thormann et al. 1999). Species of *Lactarius*, *Hebeloma*, *Laccaria*, *Russula*, *Tomentella*, and *Cortinarius* are most frequently collected and are associated with the roots of species of *Picea*, *Larix*, *Salix*, and *Betula*.

Several studies have investigated the abilities of ectomycorrhizal taxa to degrade organic matter (reviewed in Read et al. 2004), producing variable results. Durall et al. (1994) showed that four ectomycorrhizal fungi of *Pseudotsuga menziesii* (Mirb.) Franco readily degraded hemicellulose and cellulose, while more complex polymers, including humic substances and needles, were more decay resistant. In support, Hutchison (1990) and Bending and Read (1997) showed that ectomycorrhizal fungi (mostly species of *Lactarius*, *Hebeloma*, *Laccaria*, *Russula*, *Tomentella*, *Cortinarius*, *Suillus*, *Amanita*, *Boletus*, *Rhizopogon*, and *Tricholoma*) had limited abilities to use a variety of complex organic compounds, including polyphenolic polymers (e.g., tannic acid and lignin), cellulose, and pectin. Simpler structural carbohydrates, including starch, gelatin, and urea, were more frequently used, but utilization patterns were genus-specific, e.g., species of *Laccaria* were able to use urea but not starch as a C source (Hutchison 1990). Conversely, other studies showed that ectomycorrhizal fungi could synthesize complex polymer-degrading enzymes (Giltrap 1982; reviewed in Read et al. 2004).

Based on these variable results, the role of ectomycorrhizal fungi in peatland C dynamics is uncertain. It has been suggested that many ectomycorrhizal fungi may be able to survive as saprobes; however, this notion appears to be based on circumstantial evidence and resulted from either misidentified specimens or incorrect interpretation of the colonized substrate, according to Hutchison (1990). The generally reported low enzymatic activities of ectomycorrhizal fungi may be an adaptation to a symbiotic life, where the fungus must avoid eliciting host defence responses, which may be caused by extracellular enzymes (Ramstedt and Söderhäll 1983). As it stands, most ectomycorrhizal fungi appear to have limited saprobic capabilities, sufficient to colonize the roots of their hosts, and tend to require their plant hosts for the acquisition of C. Nonetheless, due to the preponderance of ectomycorrhizal fungi in peatlands (Salo 1993; Dhillion 1994; Thormann et al. 1999), their combined effect on soil C dynamics at the ecosystem level may be significant (Bending and Read 1997; Read et al. 2004).

Vesicular-arbuscular Mycorrhizal Fungi

VA-mycorrhizal fungi belong to a small, yet widely distributed group of fungi. They are all members of the Glomales (Zygomycota), with about 160 different species known to colonize roots of almost all herbaceous plants. Previous surveys of VA-mycorrhizal fungi in wetlands revealed species of *Glomus* [*G. caledonium* (Nicol. & Gerd.) Trappe & Gerd., *G. fasciculatum* (Thax. *sensu* Gerd.) Gerd. & Trappe emend. Walker & Koske, *G. intraradicis* Schenck & Smith, *G. aggregatum* Schenck & Smith, *G. claroideum* Schenck & Smith, *G. manihotis* Schenck & Smith] and *Gigaspora* [*G. gigantea* (Nicol. & Gerd.) Gerd. & Trappe, *G. albida* Schenck & Smith] (Anderson et al. 1984; Rickerl et al. 1994; Wetzel and van der Valk 1996; Cooke and Lefor 1998), with the former genus appearing to be the dominant one.

VA-mycorrhizal fungi have variable quantities of extraradical mycelium (mycelium penetrating the soil surrounding host plant roots). Their superior ability to acquire P from the soil is unquestioned; however, it is thought that VA-mycorrhizal fungi are obligate biotrophs, i.e., wholly dependent on their plant partners for C. There is limited evidence to suggest that these fungi are able to live as saprobes in the soil as well, i.e., using complex C substrates to acquire C (Nicolson 1959; Hodge et al. 2001). These reports remain speculative though, and to what extent VA-mycorrhizal fungi are involved in the decomposition of organic matter in situ remains unknown. Based on the distribution of their

hosts in peatlands, VA-mycorrhizal fungi may not be of great significance in bogs, where herbaceous plants are less dominant compared with trees and ericaceous shrubs (Thormann and Bayley 1997b); however, their role may be larger in sedge-dominated fens and marshes, where their host plants are more predominant. Ultimately, VA-mycorrhizal fungi likely do not play a significant role in C cycling in wetlands.

Mycelium radicis atrovirens

In addition to the aforementioned typical structures formed by ericoid, ectomycorrhizal, and VA-mycorrhizal fungi, a diverse assemblage of hyphae frequently occurs in and on the roots of most plant species, including peatland plants. Recent studies designated some species of *Leptodontidium* (*L. orchidicola* Sigler & Currah), *Phialocephala* (*P. fortinii*, *P. dimorphospora* Kendrick), and *Phialophora* (*P. finlandia* Wang & Wilcox) as *Mycelium radicis atrovirens* (MRA), in addition to some isolates of pezizalean and entirely unknown affinities (Currah et al. 1988; Currah and Tsuneda 1993; Fernando and Currah 1995; Caldwell et al. 2000). The hyphae of these unidentified taxa can be dematiaceous (darkly pigmented), hyaline, septate, aseptate, with and without clamp connections, some of them forming microsclerotia and others sclerotial plaques attached to the surfaces of plant roots (Jumpponen and Trappe 1998; Thormann et al. 1999). Extracellular hyphae terminate in appressoria (swollen hyphal structures used for attachment in the early stages of infection) on root surfaces, while others grow intracellularly. These fungi are rarely identified and may belong to the MRA complex (Melin 1922), which partially or entirely overlaps with the dark septate endophyte (DSE) complex of fungi (Jumpponen and Trappe 1998; Caldwell et al. 2000). MRA and DSE taxa occur frequently in roots of herbaceous (Currah et al. 1987; Stoyke and Currah 1991) and woody (Summerbell 1987; Danielson and Visser 1990; Hennon et al. 1990) plants in temperate, alpine, and arctic habitats.

The ecological significance of MRA taxa remains uncertain (Jumpponen and Trappe 1998). Previous work showed that *P. fortinii* and *P. finlandia* are able to use cellulose, laminarin, starch, and xylan as C sources; however, lignolytic enzymes were not detected (Caldwell et al. 2000). In contrast, PPOs and laccases were reported by Currah and Tsuneda (1993) and Fernando and Currah (1995). Based on these enzymatic profiles, Caldwell et al. (1996) suggested that MRA (and DSE) fungi are able to access common detrital C and P polymers. While it is still uncertain if these fungi actually decompose organic matter in situ (Jumpponen and Trappe 1998), they have the potential to play significant roles in C cycling dynamics in peatlands, where they are common (Thormann et al. 1999).

CURRENT KNOWLEDGE GAPS, RESEARCH NEEDS, AND CONCLUSIONS

Our understanding of peatland microbial communities composition and dynamics and their roles is growing, with nearly 650 different species of microfungi having been isolated and identified from peatland globally. Most of these fungi are sabrobic or mycorrhizal in nature and are intricately involved in C cycling dynamics. How these communities respond to natural and anthropogenic disturbances remains uncertain. This uncertainty is troublesome in light of a changing climate and associated disturbance regimes, including permafrost degradation and wild fire frequency, which may have potentially significant impacts on the global C cycle due to altered mineralization rates of organic matter, especially in peatlands with their significant C stocks. There are a number of significant gaps that need to be addressed in the near future:

- Impacts of climate change and associated disturbances
  - Elevated atmospheric CO_2 concentrations have the potential to alter leaf litter chemistry and hence decomposition dynamics, possibly altering rates of C and N cycling in ecosystems (O'Neill and Norby 1996; Randlett et al. 1996). Although several studies have examined decomposition rates of leaf litters grown at ambient and elevated CO_2 concentrations, results were variable and mainly depended on the experimental design, the litter used, and the length of the experiment (Melillo 1983; Rastetter et al. 1992; Randlett et al. 1996; Hirschel et al. 1997). How fungal communities respond to litter quality changes remains largely unknown.
  - Temperature has been recognized as an important factor influencing rates of decomposition; however, its effects on microbial populations are rarely examined and only recently have received some attention (Kandeler et al. 1998; Bardgett et al. 1999; Thormann et al. 2004b).
  - Permafrost in peatlands recently has begun to degrade and continues to degrade at the southern limit of the discontinuous permafrost zone in Canada with no evidence of regeneration (Halsey et al. 1995; Beilman et al. 2001; Payette and Delwaide 2004). How microbial communities respond to changes in the local hydrology, insolation, plant community composition, landscape topography, and biogeochemical processes (Beilman 2001; Turetsky et al. 2002) is unknown.
  - Fire frequency, although highly variable on an annual basis, has increased in the second half of the 20th century in Canada (Amiro et al. 2001). Many peatlands, particularly bogs, burn regularly, and substantial quantities of peat, and hence C, can be burned off (Turetsky and Wieder 2001). Regardless of the intensity of the fire, fungal communities, which are most prevalent in the fire-prone acrotelm, are affected as well; however, how fungal communities, i.e., colonization dynamics, community structure, and physiological profiles, respond to fire is uncertain.
- Few fungi with the ability to degrade polyphenolic polymers (e.g., tannins, lignin, and Klason lignin), primarily basidiomycetes, have been isolated from peat, which is surprising given the widespread occurrence of this group of fungi in adjacent upland ecosystems.

Rates of immigration of polyphenolic polymer degrading fungi from upland ecosystems into peatlands need to be quantified. Colonization of peatlands by upland basidiomycete taxa is undoubtedly occurring via spores and fruiting body fragments; however, their success in acidic, nutrient-poor peatlands is unknown. Selecting isolation media or media additives, including benomyl, *o*-phenylphenol, or dichloran (Worrall 1991), or employing molecular approaches, including environmental PCR, should lead to an increased isolation of these taxa and a better understanding of their diversity and roles.

- The roles of ectomycorrhizal and VA-mycorrhizal fungi and DSE taxa in C cycling need to be clarified. These fungi are prevalent in peatlands and may play significant roles as saprobes, yet their physiological responses to changing environmental conditions is uncertain.
- The relative contribution of fungi and bacteria to organic matter decomposition needs to be clarified. To date, only Thormann et al. (2004b) compared decomposition dynamics of the most frequently isolated bacteria and fungi from peatland plants. Their data show that these microbial groups respond differently to increasing temperatures in vitro, as determined by altered decomposition dynamics, and hence C dynamics, of peatland plant litters.

ACKNOWLEDGEMENTS

I thank Dr. J. Bhatti for inviting me to contribute to this special edition of the Canadian Journal of Soil Science and Dr. I. Bauer for providing valuable feedback during the development of this paper (both Northern Forestry Centre, Edmonton, AB). I also thank Dr. Ken Mallett (Northern Forestry Centre, Edmonton, AB), Prof. Line Rochefort (Université Laval, Ste-Foy, QC), and one anonymous reviewer for their critiques of an earlier version of this manuscript.

Anderson, R. C., Liberta, A. E. and Dickman, L. A. 1984. Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil-moisture gradient. Oecologia **64**: 111–117.

Amiro, B. D., Stocks, B. J., Alexander, M. E., Flanigan, M. D. and Wotton, B. M. 2001. Fire, climate, carbon and fuel management in the Canadian boreal forest. Int. J. Wildland Fire **10**: 405–413.

Apinis, A. E., Chester, C. G. C. and Taligoola, H. K. 1972. Colonisation of *Phragmites communis* leaves by fungi. Nova Hedwigia **23**: 113–124.

Bardgett, R. D., Kandeler, E., Tscherko, D., Hobbs, P. J., Bezemer, T. M., Jones, T. H. and Thompson, L. J. 1999. Below-ground microbial community development in a high temperature world. Oikos **85**: 193–203.

Bartsch, I. and Moore, T. R. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can. J. Bot. **63**: 1241–1248.

Bauer, C. R., Kellogg, C. H., Bridgham, S. D. and Lamberti, G. A. 2003. Mycorrhizal colonization across hydrologic gradients in restored and reference freshwater wetlands. Wetlands **23**: 961–968.

Beilman, D. W. 2001. Plant community and diversity changes due to localized permafrost dynamics in bogs of western Canada. Can. J. Bot. **79**: 983–993.

Beilman, D. W., Vitt, D. H. and Halsey, L. A. 2001. Localized permafrost peatlands in western Canada: Definition, distributions, and degradation. Arct. Antarct. Alp. Res. **33**: 70–77.

Bending, G. D. and Read, D. J. 1997. Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. Mycol. Res. **101**: 1348–1354.

Beyer, W. 1994. Weniger bekannte inoperculate Discomyceten aus Moorresten in Oberfranken. Zeitschr. Mykol. **60**: 203–209.

Bisby, G. R., Timonin, M. I. and James, N. 1935. Fungi isolated from soil profiles in Manitoba. Can. J. Res. Sec. C, **13**: 47–65.

Bledsoe, C., Klein, P. and Bliss, L. C. 1990. A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. Can. J. Bot. **68**: 1848–1856.

Blodau, C. 2002. Carbon cycling in peatlands – A review of processes and controls. Environ. Rev. **10**: 111–134.

Blodau, C. and Moore, T. R. 2003. Micro-scale CO_2 and CH_4 dynamics in a peat soil during a water fluctuation and sulfate pulse. Soil Biol. Biochem. **35**: 535–547.

Boswell, J. G. 1955. The microbiology of acid soils. IV. Selected sites in northern England and southern Scotland. New Phytol. **54**: 311–319.

Bowen, R. M. and Harper, S. H. T. 1990. Decomposition of wheat straw and related compounds by fungi isolated from straw in arable soils. Soil Biol. Biochem. **22**: 393–399.

Bridgham, S. D. and Richardson, C. J. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biochem. **24**: 1089–1099.

Brinson, M. M., Lugo, A. E. and Brown, S. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. **12**: 123–161.

Bubier, J., Costello, A., Moore, T. R., Roulet, N. T. and Savage, K. 1993. Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. Can. J. Bot. **71**: 1056–1063.

Caldwell, B. A., Jumpponen, A. and Trappe, J. M. 2000. Utilization of major detrital substrates by dark-septate, root endophytes. Mycologia **92**: 230–232.

Caldwell, B. A., Trappe, J. M. and Jumpponen, A. 1996. Physiological characters of dark septate root endophytes. Page 19 *in* First International Conference on Mycorrhizae, 1996 Aug. 4–9, Berkeley, CA.

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**: 882–89.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. **53**: 747–757.

Clymo, R. S. 1984. The limits to peat bog growth. Phil. Trans. R. Soc., Lond. Biol. Sci. **303**: 605–654.

Clymo, R. S., Turunen, J. and Tolonen, K. 1998. Carbon accumulation in peatlands. Oikos **81**: 368–388.

Cooke, J. C. and Lefor, M. W. 1998. The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. Restor. Ecol. **6**: 214–222.

Cormier, Y., Mériaux, A. and Brochu, G. 1988. Effects of processing on peat moss microflora. Can. J. Microbiol. **34**: 131–133.

Croft, M., Rochefort, L. and Beauchamp, C. J. 2001. Vacuum-extraction of peatlands disturbs bacterial population and microbial biomass. Appl. Soil Ecol. **18**: 1–12.

Currah, R. S. and Van Dyk, M. 1986. A survey of some perennial vascular plant species native to Alberta for occurrence of mycorrhizal fungi. Can. Field-Nat. **100**: 330–342.

Currah, R. S. and Tsuneda, A. 1993. Vegetative and reproductive morphology of *Phialocephala fortinii* (Hyphomycetes, *Mycelium radicis atrovirens*) in culture. Trans. Mycol. Soc. Jpn. **34**: 345–356.

Currah, R. S., Sigler, L. and Hambleton, S. 1987. New records and new taxa of fungi from the mycorrhizae of terrestrial orchids of Alberta. Can. J. Bot. **65**: 2473–2482.
Currah, R. S., Hambleton, S. and Smreciu, A. 1988. Mycorrhizae and mycorrhizal fungi of *Calypso bulbosa*. Am. J. Bot. **75**: 739–752.
Czeczuga, B. 1993. Aquatic fungi of the Gorbacz and Ostrówski peatbogs. Acta Mycol. **28**: 69–75.
Dal Vesco, G. 1974–75. Funghi del suolo di un pianoro acquitrinoso in valle di cogne (Aosta) [Soil fungi from a mountain bog in the Cogne Valley (Aosta)]. Allionia **20**: 81–92.
Dalpé, Y. 2003. Mycorrhizal fungi biodiversity in Canadian soils. Can. J. Soil Sci. **83**: 321–330.
Danielson, R. M. and Visser, S. 1990. The mycorrhizal and nodulation status of container-grown trees and shrubs reared in commercial nurseries. Can. J. For. Res. **20**: 609–614.
Deacon, J. W. 1997. Modern mycology. 3rd ed. Blackwell Sci. Publ., Boston, MA.
Dedysh, S. N. 2002. Methanotrophic bacteria of acidic *Sphagnum* peat bogs. Microbiology **71**: 638–650.
Dhillion, S. S. 1994. Ectomycorrhizae, arbuscular mycorrhizae, and *Rhizoctonia* sp. of alpine and boreal *Salix* spp. in Norway. Arct. Alp. Res. **26**: 304–307.
Dickinson, C. H. and Dooley, M. J. 1967. The microbiology of cut-away peat. I. Descriptive ecology. Plant Soil **27**: 172–186.
Dickinson, C. H. and Dooley, M. J. 1969. Fungi associated with Irish peat bogs. Proc. R. Ir. Acad., Sect. B **68**: 109–136.
Dix, N. J. 1985. Changes in relationship between water content and water potential after decay and its significance for fungal successions. Trans. Br. Mycol. Soc. **85**: 649–653.
Domsch, K. H. 1960. Das Pilzspektrum einer Bodenprobe. 3. Nachweis der Einzelpilze. Arch. Mikrobiol. **35**: 310–339.
Domsch, K. H., Gams, W. and Anderson, T.-H. 1980. Compendium of soil fungi. Vols. 1 & 2. Academic Press, London, UK.
Dooley, M. and Dickinson, C. H. 1971. The ecology of fungi in peat. Ir. J. Agric. Res. **10**: 195–206.
Durall, D. M., Todd, A. W. and Trappe, J. M. 1994. Decomposition of ^{14}C-labelled substrates by ectomycorrhizal fungi in association with Douglas-fir. New Phytol. **127**: 725–729.
Farrish, K. W. and Grigal, D. F. 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci. **145**: 353–358.
Fell, J. W. and Hunter, I. L. 1979. Fungi associated with the decomposition of the black rush, *Juncus roemerianus*, in south Florida. Mycologia **71**: 322–342.
Fernando, A. A. 1995. *Leptodontidium orchidicola* (*Mycelium radicis atrovirens* complex, Fungi Imperfecti): conidiogenesis and interaction with some subalpine plants in culture. M.Sc. Thesis, University of Alberta, Edmonton, AB.
Fernando, A. A. and Currah, R. S. 1995. *Leptodontidium orchidicola* (*Mycelium radicis atrovirens* complex): aspects of its conidiogenesis and ecology. Mycotaxon **54**: 287–294.
Frankland, J. C. 1966. Succession of fungi on decaying petioles of *Pteridium aquilium*. J. Ecol. **54**: 41–63.
Gilbert, D., Amblard, C., Bourdier, G. and Francez, A.-J. 1998a. The microbial loop at the surface of a peatland: structure, function, and impact of nutrient input. Microb. Ecol. **35**: 83–93.
Gilbert, D., Amblard, C., Bourdier, G. and Francez, A.-J. 1998b. Short-term effects of nitrogen enrichment on the microbial communities of a peatland. Hydrobiologia **173/374**: 111–119.
Giltrap, N. J. 1982. Production of polyphenol oxidases by ectomycorrhizal fungi with special reference to *Lactarius* spp. Trans. Br. Mycol. Soc. **78**: 75–81.
Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Applic. **1**: 182–195.
Halsey, L. A., Vitt, D. H. and Zoltai, S. C. 1995. Disequilibrium response of permafrost in boreal continental western Canada to climate change. Climatic Change **30**: 57–73.
Hambleton, S. and Currah, R. S. 1997. Fungal endophytes from the roots of alpine and boreal Ericaceae. Can. J. Bot. **75**: 1570–1581.
Hambleton, S. and Currah, R. S. 2000. Molecular characterization of the mycorrhizas of woody plants. Pages 351–373 *in* S. M. Jain and S. C. Minocha, eds. Molecular biology of woody plants. Kluwer Acad. Publ., the Netherlands.
Hambleton, S., Huhtinen, S. and Currah, R. S. 1999. *Hymenoscyphus ericae*: a new record from western Canada. Mycol. Res. **103**: 1391–1397.
Harper, S. H. T. 1985. Colonization and decomposition of straw by fungi. Trans. Br. Mycol. Soc. **85**: 655–661.
Haselwandter, K. 1987. Mycorrhizal infection and its possible ecological significance in climatically and nutritionally stressed alpine plant communities. Angew. Bot. **61**: 107–114.
Haselwandter, K. and Read, D. J. 1982. The significance of a root-fungus association in two *Carex* species of high alpine communities. Oecologia **53**: 352–354.
Heilman-Clausen, J. 2001. A gradient analyses of communities of macrofungi and slime molds on decaying beech logs. Mycol. Res. **195**: 575–596.
Hennon, P. E., Shaw, C. J. and Hansen, E. M. 1990. Symptoms and fungal associations of declining *Chamaecyparis nootkatensis* in southeast Alaska. Plant Dis. **74**: 267–273.
Hirschel, G., Körner, C. and Arnone III, J. A. 1997. Will rising atmospheric CO_2 affect leaf litter quality and *in situ* decomposition rates in native plant communities? Oecologia **110**: 387–392.
Hodge, A., Campbell, C. D. and Fitter, A. H. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature **413**: 297–299.
Hurley, J. E. 1981. Bog fungi and studies of their activity. M.Sc. Thesis, University of New Brunswick, Fredericton, NB.
Hutchison, L. J. 1990. Studies on the systematic of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. Can. J. Bot. **68**: 1522–1530.
Intergovernmental Panel on Climate Change. 2001. Third assessment report. [Online] Available: http://www.ipcc.ch/
Jefferys, E. G., Brian, P. W., Hemming, H. G. and Lowe, D. 1953. Antibiotic production by the micofungi of acid heath soils. J. Gen. Microbiol. **9**: 314–341.
Jumpponen, A. and Trappe, J. M. 1998. Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol. **140**: 295–310.
Kandeler, E., Tscherko, D., Bardgett, R. D., Hobbs, P. J., Kampichler, C. and Jones, T. H. 1998. The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. Plant Soil **202**: 251–262.
Kasai, K., Morinaga, T. and Horikoshi, T. 1995. Fungal succession in the early decomposition process of pine cones on the floor of *Pinus densiflora* forests. Mycoscience **36**: 325–334.
Kjøller, A. and Struwe, S. 1992. Functional groups of microfungi in decomposition. Pages 631–652 *in* G. C. Carrol and D. T. Wicklow, eds. The fungal community: Its organization and role in the ecosystem. 2nd ed. Marcel Dekker, Inc., New York, NY.
Kohn, L. M. and Stasovski, E. 1990. The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high arctic site. Mycologia **82**: 23–35.
Kox, E. 1954. Der durch Pilze und aerobe Bakterien veranlaßte Pectin- und Cellulose-Abbau im Hochmoor unter besonderer Berüchtigung des *Sphagnum*-Abbaus. Arch. Mikrobiol. **20**: 111–140.

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.

Leake, J. R. and Read, D. J. 1989. Biology of mycorrhiza in the Ericaceae. XIII. Some characteristics of the extracellular proteinase activity of the ericoid endophyte *Hymenoscyphus ericea*. New Phytol. **112**: 69–76.

Leake, J. R. and Read, D. J. 1990. Chitin as a nitrogen source for mycorrhizal fungi. Mycol. Res. **94**: 993–995.

Lumley, T. C., Gignac, L. D. and Currah, R. S. 2001. Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. Can. J. Bot. **79**: 76–92.

Maciejowska-Pokacka, Z. 1971. Results of one year studies on the influence of various soils on the mycoflora under cocksfoot. Acta Mycol. **7**: 31–40.

Malloch, D. and Malloch, B. 1981. The mycorrhizal status of boreal plants: species from northeastern Ontario. Can. J. Bot. **59**: 2167–2172.

Malloch, D. and Malloch, B. 1982. The mycorrhizal status of boreal plants: additional species from northeastern Ontario. Can. J. Bot. **60**: 1035–1040.

Malmer, N. 1986. Vegetation gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. **64**: 375–38.

Melillo, J. M. 1983. Will increases in atmospheric CO_2 concentrations affect litter decay rates? Pages 10–11 *in* The ecosystem center annual report. Marine Biological Laboratory, Woods Hole, MA.

Melin, E. 1922. On the mycorrhizas of *Pinus sylvestris* L. and *Picea abies* Karst. A preliminary note. J. Ecol. **9**: 254–257.

Miller, R. M., Smith, C. I., Jastrow, J. D. and Bever, J. D. 1999. Mycorrhizal status of the genus *Carex* (Cyperaceae). Am. J. Bot. **86**: 547–553.

Monreal, M., Berch, S. M. and Berbee, M. 1999. Molecular diversity of ericoid mycorrhizal fungi. Can. J. Bot. **77**: 1580–1594.

Näsholm, T., Ekblad, A., Nordin, A., Glesler, R., Högberg, M. and Högberg, P. 1998. Boreal forest plants take up organic nitrogen. Nature **392**: 914–916.

National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series. No. 24. Sustainable Development Branch, Environment Canada, Ottawa, ON, and Poly Science Publications, Inc., Montréal, QC.

Nilsson, M., Bååth, E. and Söderström, B. 1992. The microfungal communities of a mixed mire in northern Sweden. Can. J. Bot. **70**: 272–276.

O'Neill, E. G. and Norby, R. J. 1996. Litter quality and decomposition rates of foliar litter produced under CO_2 enrichment. Pages 87–103 *in* G. W. Koch and H. A. Mooney, eds. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, CA.

Payette, S. and Delwaide, A. 2004. Dynamics of subarctic wetland forests over the past 1500 years. Ecol. Monogr. **74**: 373–391.

Piercey, M. M., Thormann, M. N. and Currah, R. S. 2002. Mycorrhizal and saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. Mycorrhiza **12**: 175–180.

Polyakova, A. V., Chernov, I. Yu. and Panikov, N. S. 2001. Yeast diversity in hydromorphic soils with reference to a grass-*Sphagnum* wetland in western Siberia and a hummocky tundra region at Cape Barrow (Alaska). Microbiology **70**: 617–622.

Pugh, G. J. F. 1958. Leaf litter fungi found on *Carex paniculata* L. Trans. Br. Mycol. Soc. **41**: 185–195.

Pugh, G. J. F. and Mulder, J. L. 1971. Mycoflora associated with *Typha latifolia*. Trans. Br. Mycol. Soc. **57**: 273–282.

Ramstedt, M. and Söderhäll, K. 1983. Protease, phenoloxidase and pectinase activities in mycorrhizal fungi. Trans. Br. Mycol. Soc. **81**: 157–161.

Randlett, D. L., Zak, D. R., Pregitzer, K. S. and Curtis, P. S. 1996. Elevated atmospheric carbon dioxide and leaf litter chemistry: influences on microbial respiration and net nitrogen mineralization. Soil Sci. Soc. Am. J. **60**: 1571–1577.

Rastetter, E. B., McKane, R. B., Shaver, G. R. and Melillo, J. M. 1992. Changes in C storage by terrestrial ecosystems: how C-N interactions restrict responses to CO_2 and temperature. Water Air Soil Pollut. **64**: 327–344.

Read, D. J. 1991. Mycorrhizas in ecosystems. Experientia **47**: 376–391.

Read, D. J., Leake, J. R. and Perez-Moreno, J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can. J. Bot. **82**: 1243–1263.

Rice, A. V. and Currah, R. S. 2001. Physiological and morphological variation in *Oidiodendron maius*. Mycotaxon **74**: 383–396.

Rickerl, D. H., Sancho, F. O. and Ananth, S. 1994. Vesicular-arbuscular endomycorrhizal colonization of wetland plants. J. Environ. Qual. **23**: 913–916.

Robson, T. M., Pancotto, V. A., Ballaré, C. L., Sala, O. E., Scopel, A. L. and Caldwell, M. M. 2004. Reduction of solar UV-B mediates changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. Oecologia **140**: 480–490.

Roulet, N. T., Ash, R., Quinton, W. and Moore, T. 1993. Methane flux from drained northern peatlands: effect of a persistent water table lowering on flux. Global Biogeochem. Cycles **7**: 749–769.

Rozema, J., Arp, W., van Diggelen, J., van Esbroek, M. and Broekman, R. 1986. Occurrence and ecological significance of vesicular arbuscular mycorrhiza in a salt marsh environment. Acta Bot. Neerl. **35**: 457–467.

Saitô, T. 1966. Sequential pattern of decomposition of beech litter with special reference to microbial succession. Ecol. Rev. **16**: 245–254.

Salo, K. 1993. The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland. Karstenia **33**: 61–99.

Searles, P. S., Kropp, B. R., Flint, S. D. and Caldwell, M. M. 2001. Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. New Phytol. **152**: 213–221.

Sewell, G. W. F. 1959a. Studies of fungi in a *Calluna*-heathland soil. I. Vertical distribution in soil and on root surfaces. Trans. Br. Mycol. Soc. **42**: 343–353.

Sewell, G. W. F. 1959b. Studies of fungi in a *Calluna*-heathland soil. II. By the complementary use of several isolation methods. Trans. Br. Mycol. Soc. **42**: 354–369.

Smith, S. E. and Read, D. J. 1997. Mycorrhizal symbiosis. 2nd ed. Academic Press, New York, NY.

Sparrow, F. K. and Lange, L. 1977. Some bog chytrids. Can. J. Bot. **55**: 1879–1890.

Stenlund, D. L. and Charvat. I. D. 1994. Vesicular arbuscular mycorrhizae in floating wetland mat communities dominated by *Typha*. Mycorrhiza **4**: 131–137.

Stenton, H. 1953. The soil fungi of Wicken fen. Trans. Br. Mycol. Soc. **36**: 304–314.

Stoyke, G. and Currah, R. S. 1991. Endophytic fungi from the mycorrhizae of alpine ericoid plants. Can. J. Bot. **69**: 347–352.

Summerbell, R. 1987. Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. Can. J. Bot. **67**: 1085–1095.

Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems. Blackwell Sci. Publ., Oxford, UK.

Szumigalski, A. R. and Bayley, S. E. 1996. Decomposition along a bog-fen gradient in central Alberta, Canada. Can. J. Bot. **74**: 573–581.

Tanaka, Y. 1991 Microbial decomposition of reed (*Phragmites communis*) leaves in a saline lake. Hydrobiology **220**: 119–129.

Thormann, M. N. and Bayley, S. E. 1997a. Decomposition along a moderate-rich fen – marsh peatland gradient in boreal Alberta, Canada. Wetlands **17**: 123–137.

Thormann, M. N. and Bayley, S. E. 1997b. Aboveground net primary production along a bog - fen - marsh gradient in southern boreal Alberta, Canada. Écoscience **4**: 374–384.

Thormann, M. N., Currah, R. S. and Bayley, S. E. 1999. 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. 2002. The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon sources. Can. J. Microbiol. **48**: 204–211.

Thormann, M. N., Currah, R. S. and Bayley, S. E. 2003. Succession of microfungal assemblages in decomposing peatland plants. Plant Soil **250**: 323–333.

Thormann, M. N., Currah, R. S. and Bayley, S. E. 2004a. Patterns of distribution of microfungi in decomposing bog and fen plants. Can. J. Bot. **82**: 710–720.

Thormann, M. N., Bayley, S. E. and Currah, R. S. 2004b. Microcosm tests of the effects of temperature and microbial species number on the decomposition of sedge and bryophyte litter from southern boreal peatlands. Can. J. Microbiol. **50**: 793–802.

Thornton, R. H. 1956. Fungi occurring in mixed oakwood and heath soil profiles. Trans. Br. Mycol. Soc. **39**: 485–494.

Tokumasu, S. 1994. Trophodynamic structure of a swampy bog at the climax stage of limnological succession III. Filamentous fungi associated with the standing leaves of *Typha latifolia*. Water Air Soil Pollut. **76**: 491–499.

Treu, R., Laursen, G. A., Stephenson, S. L., Landolt, J. C. and Densmore, R. 1996. Mycorrhizae from Denali National Park and Preserve, Alaska. Mycorrhiza **6**: 21–29.

Tsuneda, A., Thormann, M. N. and Currah, R. S. 2001. Modes of cell-wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. Can. J. Bot. **73**: 93–100.

Turetsky, M. R. and Wieder, R. K. 2001. A direct approach to quantifying organic matter lost as a result of peatland wildfire. Can. J. For. Res. **31**: 363–366.

Turetsky, M. R., Wieder, R. K. and Vitt, D. H. 2002. Boreal peatland C fluxes under varying permafrost regimes. Soil Biol. Biochem. **34**: 907–912.

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. Écoscience **7**: 379–392.

Turnau, K., Ryszka, P., Gianinazzi-Pearson, V. and van Tuinen, D. 2001. Identification of arbuscular mycorrhizal fungi in soils and roots of plants colonizing zinc wastes in southern Poland. Mycorrhiza **10**: 169–174.

Turner, S. D., Amon, J. P., Schneble, R. M. and Friese, C. F. 2000. Mycorrhizal fungi associated with plants in ground-water fed wetlands. Wetlands **20**: 200–204.

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. and Sanders, I. R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature **396**: 69–72.

Vitt, D. H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. **104**: 35–59.

Vitt, D. H. 1994. An overview of factors that influence the development of Canadian peatlands. Mem. Entomol. Soc. Canada **169**: 7–20.

Wartiainen, I., Hestness, A. G. and Svenning, M. M. 2003. Methanotrophic diversity in high arctic wetlands on the islands of Svalbard (Norway) – denaturing gradient gel electrophoresis analysis of soil DNA and enrichment cultures. Can. J. Microbiol. **49**: 602–612.

Wetzel, P. R. and van der Valk, A. G. 1996. Vesicular-arbuscular mycorrhizae in prairie pothole vegetation in Iowa and North Dakota. Can. J. Bot. **74**: 883–890.

Wicklow, D. T. and Yokum, D. H. 1981. Fungal species numbers and decomposition of rabbit feces. Trans. Br. Mycol. Soc. **76**: 29–32.

Williams, R. T. and Crawford, R. L. 1983. Microbial diversity of Minnesota peatlands. Microbial Ecol. **9**: 201–214.

Worrall, J. J. 1991. Media for selective isolation of hymenomycetes. Mycologia **83**: 296–302.

Zvyagintsev, D. G., Dobrovol'skaya, T. G., Golovchenko, A. V., Zenova, G. M. and Smagina, M. V. 1991. The structure of a saprotrophic microbial complex in the peat-bogs [in Russian]. Microbiology (Moscow) **60**: 155–164.

Zattau, W. C. 1981. Topographic features of chytrids collected from a *Sphagnum* bog. Mycologia **73**: 1189–1194.