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FUNCTIONAL AND TAXONOMIC DIVERSITY OF SAPROBIC FILAMENTOUS FUNGI FROM *TYPHA LATIFOLIA* FROM CENTRAL ALBERTA, CANADA

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Abstract: The fate of vascular plant detritus and the microbial communities and processes involved during the decomposition of litter are important aspects in elucidating energy flow and nutrient cycling in wetlands. Therefore, we collected and identified conspicuous fungal sporocarps *in situ* and isolated microfungi from living and dead *Typha latifolia* (cattail) leaf tissues. Cattail is a dominant plant species in southern boreal and temperate marshes and abundant in the Low Boreal Mixedwood ecoregion in central Alberta, Canada. Following two successive field collections in early and late summer 2001, 45 different fungal taxa were identified. There were 26 ascomycetes, five basidiomycetes, and 14 anamorphic taxa, most of them with putative ascomycetous affinities. Twenty-four taxa represented new records for *T. latifolia*, 12 were new to Canada, and seven were new to North America. Also, five taxa were new reports outside of the country of the type locality. To elucidate their roles in the decomposition of *T. latifolia* leaves, we examined 33 taxa for their ability to use cellulose, gelatin, starch, tannic acid, and lignin as carbon sources (based on calorimetric tests), as well as to cause mass losses of sterile *T. latifolia* leaves. The number of fungi using cellulose and gelatin as carbon sources was significantly greater than those using starch, tannic acid, or lignin. Mass losses of *T. latifolia* leaf tissues by ascomycetes and basidiomycetes ranged from 1.3 to 54.6% and −0.4 to 52.1%, respectively. There was a positive relationship between mass loss of *T. latifolia* leaves and cellulose degradation but not between mass loss and any of the other carbon sources. Our data showed that a taxonomically diverse suite of fungi effectively degrades this plant material; however, additional studies examining the decomposer communities of other dominant wetland plants are necessary to gain a better understanding of nutrient and energy dynamics in wetlands at the ecosystem level.

Key Words: *Typha latifolia*, fungi, enzymatic abilities, mass losses, decomposition, carbon

INTRODUCTION

Marshes are characterized by shallow water, water levels that fluctuate daily, seasonally, or annually, and emergent macrophytes, including species of cattails (*Typha*), sedges (*Carex*), and rushes (*Juncus*) (National Wetlands Working Group 1997). Although marshes are restricted in the boreal landscape (Vitt et al. 2001), their total plant production on a per m^2 basis often exceeds that of other wetlands, such as bogs and fens (Brinson et al. 1981, Thormann and Bayley 1997a, Campbell et al. 2000). *Typha* often dominates aboveground plant production, with values reaching 1643 g m^{-2} $year^{-1}$ in southern boreal and temperate marshes in North America (summarized in Campbell et al. 2000).

Like many other macrophytes, the dead biomass of *Typha* spp. begins to decompose in the standing position each fall prior to its collapse into the aquatic environment, often one to two years following its abscission. Previous work indicated that fungi are the dominant decomposer microbes of this standing dead biomass (Bärlocher and Biddiscombe 1996, Gessner et al. 1997, Hackney et al. 2000, Komínková et al. 2000); however, information on the fungi involved in this process and the components of the substrate these fungi degrade is sparse (e.g., Tokumasu 1994). Presently, over 150 fungal taxa have been isolated from *Typha*

spp. worldwide, about 90 specifically from *T. latifolia* L. (Pugh and Mulder 1971, Tokumasu 1994, Farr et al. 2004; compiled data from 74 sources). There are generally limited data available on the enzymatic profiles of these taxa, and their roles in the decomposition dynamics of this dominant wetland macrophyte remain unclear.

Understanding the fate of vascular plant detritus is a critical component in elucidating energy flow and nutrient cycling in wetlands (Wetzel 1990). Despite this, establishing a link between these processes and the microbial communities involved in them has rarely been done in previous studies. Therefore, the purpose of this study was to (1) identify fungi from *T. latifolia* in the Low Boreal Mixedwood ecoregion in Alberta, where this plant is a dominant component of wetlands and likely contributes significantly to nutrient mineralization; (2) elucidate the enzymatic capabilities of these fungi by assessing their abilities to degrade selected carbon (C) sources; and (3) quantify the mass losses they incur on sterile *T. latifolia* leaves *in vitro.*

MATERIALS AND METHODS

Study Area and Site Descriptions

Elk Island National Park (EINP, 53.6° N, 112.88° W) is located in the Low Boreal Mixedwood ecoregion in Alberta, Canada (Strong 1992), characterized by mild summers and cold, snowy winters. The mean annual temperature is 1.4 °C, and the mean annual precipitation is 403 mm (Vegreville CDA weather station; Environment Canada 1993). Three sites in EINP were chosen to represent a diverse range of *T. latifolia* habitats in order to maximize the number of fungal taxa collected and isolated from this substrate. They included a small, open pond surrounded by a 4–6 m-wide fringe of *T. latifolia* (53°42′35″ N, 112°52′00″ W, Site 1), a large *T. latifolia*-dominated marsh with no open water (53°39′80″ N, 112°51′80″ W, Site 2), and a small ephemeral lake with *T. latifolia* forming a narrow (<1 m wide), patchy border interspersed with water arum (*Calla palustris* L.) and sedges (*Carex* spp.) (53°41′50″ N, 112°48′60″ W, Site 3).

Isolation and Identification of Fungi

Plant samples were collected on 27 June and 27 September 2001 by randomly walking through each site and by examining individual *T. latifolia* plants for conspicuous fungal fruiting bodies. Fruiting bodies were collected by removing about 0.5–1.0 cm of the leaf above and below the fruiting body. In addition, two standing *Typha* plants, one live (current year's growth) and one dead (previous year's growth), were cut at the base and collected from each site for use in moist chamber incubations. The plant material was carefully rinsed with distilled water to remove attached coarse ''alien'' debris before excising 6-cm leaf sections at intervals of 30 cm starting from the leaf base (yielding sections at distances of 0, 36, 72, and 108 cm from the leaf base). These sections were peeled apart with forceps to separate the sheathing leaves and culm (if present), surface-sterilized (washed in 70% ethanol for about 30 s, rinsed 3x with sterile, distilled water (sd-H_20)), and incubated on dampened filter paper in plastic Petri dishes in the dark at 25 °C. They were monitored daily for fungal growth over a three-month period. Fruiting bodies and vegetative growth on these sections were used to obtain pure cultures.

Sporocarp-forming basidiomycetes were cultured using surface-sterilized stipe explants. Discomycetes were washed with sd-H_20 (if < 2 mm diameter) or surface-sterilized (if > 2 mm) before being used as inoculum. Perithecial ascomycetes, coelomycetes, and macroscopically visible hyphomycetes were sub-cultured directly from spores, spore masses, or fruiting bodies that had been washed in sd-H_20 and/or were surface-sterilized. Induction of sporulation of some sterile colonies was successful following refrigeration, exposure to black light (UV), and/or growing on various media, including oatmeal agar (20.0 g oatmeal (Quaker™, large flakes), 20.0 g agar (Difco), 1.0 L sd-H_2O), mixed Pablum® cereal agar (CA, 100.0 g mixed cereal (Pablum®, H. J. Heinz Company of Canada Ltd.), 15.0 agar (Difco), 1.0 L sd-H_2O), potato dextrose agar (39.0 g potato dextrose agar (Difco), 1.0 L sd-H_2O), corn meal agar (17.0 g corn meal agar (Difco), 1.0 L sd-H_2O), and autoclaved *T. latifolia* leaves on water agar (17.0 g agar (Difco), 1.0 L sd-H_2O). All media were amended with oxytetracycline (0.01%) to suppress bacterial growth.

Fungi were identified using morphological characters either from direct mounts, hand or freezing-microtome sections of fruiting bodies (for some coelomycetes), or slide cultures (Sigler 1993). *Periconia typhicola*, *Hymenopsis typhae*, *Hyphoderma sambuci*, and *Psathyrella typhae* were obtained in November 1999 and/or May 2000 from *T. latifolia* floating mats in a beaver pond just outside the eastern border of EINP during a previous study. New records for fungi were determined by searching current databases (i.e., Farr et al. 2004, Biological Abstracts, and Biological Sciences Internet databases) and the most recent literature on fungi from *Typha* spp.

Degradation of Selected C Sources

Thirty-three taxonomically diverse fungi were selected to measure their abilities to use a variety of C

sources *in vitro* (cellulose, gelatin, lignin, starch, tannic acid, n = 3 per fungus per substrate), as well as to cause mass losses of sterile *T. latifolia* leaves (see below). Each enzymatic test was visually ranked on a four-point scale, with ''0'' indicating no reaction and ''3'' the strongest reaction of those observed relative to uninoculated controls (i.e., an ''index of degradability''). While this approach was not a precise quantitative analysis, it allowed for a comparison of the relative ability of these fungi to degrade the C substrates. We did not determine if the 33 fungal taxa produced ''retained'' vs. ''diffusible'' enzymes (i.e., enzymes that are chemically bound to the cell wall surfaces vs. those that are released into the surrounding substrate, respectively). Plates were inoculated by transferring a 5.5-mm circular plug of mycelium from the growing edge of a colony on CMA. All treatments were stored at 25 °C in the dark. The strongest positive result from each isolate was recorded. These physiological tests are widely used to assess enzymatic abilities of fungi (e.g., Hutchison 1990, Thormann et al. 2002).

Cellulolytic abilities were tested using the cellulose-azure method (Smith 1977), using modified Melin-Norkrans agar (MMN, 1.0 g glucose, 2.0 g malt extract (Difco), 1.0 g yeast extract, 0.5 g KH_2PO_4, 0.25 g $(NH_4)_2HPO_4$, 0.15 g $MgSO_4 \cdot 7H_20$, 0.05 g $CaCl_2$, 0.025 g NaCl, 0.012 g $FeCl_3 \cdot 6H_20$, 15.0 g agar (Difco), 1 L sd-H_2O) substituted as the nutritive medium (Hutchison 1990). About 15 mL of MMN were added to 25 mL scintillation vials, these were autoclaved, and the medium was allowed to solidify. A 2% (w v^{-1}) cellulose-azure preparation in MMN was autoclaved separately and 1.5–2.0 mL of the suspension was aseptically transferred into each scintillation vial. Degradation of cellulose was indicated by the release of the azure dye from the cellulose agar and its diffusion into the lower, clear layer of MMN after 12 weeks of incubation. Tests were ranked according to the optical density of the azure dye in the basal medium as compared to the cellulose-azure in MMN in the top layer: ''0'' was ranked when the lower MMN layer was the same colour as the controls, ''1'' when the base MMN layer was slightly more azure than the controls but substantially less colored as the top MMN layer, ''2'' when the base MMN layer was almost as azure as the top MMN layer, and ''3'' was ranked when both top and base MMN layers showed the same coloration.

Starch degradation was assessed using MMN containing 2.0 g L^{-1} soluble starch (Hutchison 1990). After a maximum of five weeks incubation (faster-growing fungi were tested when the mycelium covered about two-thirds of the plate), plates were flooded with an iodine solution (5.0 g KI in 1.5 g I/100 mL d-H_2O) for 5 min, which chemically binds to the starch remaining in the medium. Negative tests turned the medium dark-brown, while positive reactions gave a clear zone with an otherwise dark-brown background. Tests were ranked according to the degree of clearing: ''0'' had no clear zone, ''1'' a faint clear zone, ''2'' a highly visible clear zone, and with ''3'' the entire plate was clear.

Wood-powder medium (0.01% guaiacol (v v^{-1}), 0.2% spruce (*Picea* sp.) wood powder (w v^{-1}), 1.8% agar (Difco) (w v^{-1}), 1.0 L sd-H_2O) (modified from Miyamoto et al. 2000) was used to test for lignolytic abilities. Positive reactions were indicated by a reddish-brown pigment on a colorless medium caused by the reaction of polyphenol oxidases with guaiacol. Plates were monitored weekly for five weeks. Tests were ranked according to the proportion of the plate with the pigment present and the darkness of the pigment: ''0'' had no pigmentation, ''1'' light pigmentation around the base of the plug, ''2'' dark pigmentation extending up to halfway to the edge of the plate, and ''3'' dark pigmentation extending more than halfway to the edge of the plate.

The ability to degrade tannic acid was tested using tannic acid medium (5.0 g tannic acid (Baker analyzed), 15.0 g malt extract (Difco), 20.0 g agar (Difco), 1.0 L sd-H_20) (Davidson et al. 1938). A dark-brown pigment released into an otherwise cream-colored medium indicated the presence of polyphenol oxidases. Tests were ranked according to the proportion of the plate with the pigment present and the darkness of the pigment: ''0'' had no pigmentation, ''1'' light pigmentation around the base of the plug, ''2'' dark pigmentation extending up to halfway to the edge of the plate, and ''3'' dark pigmentation extending more than halfway to the edge of the plate.

Gelatin degradation was tested using MMN containing 120 g L^{-1} gelatin instead of agar (Hutchison 1990). The degradation of the gelatin manifests itself as the gelification and ultimate liquification of the medium. Tests were ranked according to the degree of gelification and liquification: ''0'' had no gelification, ''1'' gelification extending up to halfway from the inoculum plug to the edge of the plate (no liquification), ''2'' gelification extending over halfway to the edge of the plate with limited liquification, and ''3'' extensive liquification.

Based on the results from the five enzymatic tests, we developed an ''index of degradability'' for each of the ten fungal orders, which were represented by the 33 fungal taxa in this study (seven ascomycete orders: Aa = fungi with putative ascomycete affinities (n = 9), Doth—Dothideales (n = 6), Euro—Eurotiales (n = 2), Hypo—Hypocreales (n = 1), Leot—Leotiales (n = 6), Pezi—Pezizales (n = 1), Sord—Sordariales (n = 3); three basidiomcyete orders: Ba—taxa with putative

basidiomycete affinities (n = 2), Agar—Agaricales (n = 2), and Ster—Stereales (n = 1)). The indices were obtained by averaging the abilities of fungal taxa belonging to the same order to degrade each of the five C sources (if $n > 1$) and allowed us to compare qualitatively and quantitatively the abilities of different fungal orders to degrade the major C polymers of *T. latifolia* leaves.

Decomposition of *T. latifolia* Leaves *in vitro*

Thirty-two fungi were used to test for their abilities to cause mass losses of *T. latifolia* leaves *in vitro.* Green leaves were collected, air-dried to constant mass, and cut into about 8.5-cm-long segments. Weighed 1.00 ± 0.10 g portions containing multiple leaf sections were autoclaved for 21 min at 121 °C (liquid cycle), placed on peptone broth agar (20.0 g agar (Difco), 1.0 g peptone-broth (Difco), 1.0 L sd-H_2O) in plastic Petri dishes, inoculated with one mycelial plug in the center and three additional mycelial plugs near the perimeter of the plate, and incubated at 25 °C in the dark (n = 3 per isolate). After 12 weeks, leaf segments were dried at 80 °C to a constant mass, weighed, and the percent mass loss determined for each fungal taxon. Mass loss due to leaching was obtained from uninoculated leaf segments (controls; subtracted from measured mass loss). Box and whisker plots show relationships between the indices of degradability of each of the five C sources and mass losses by the fungi isolated from *T. latifolia*. These plots show the lower and upper quartiles, median (vertical line in box), range (upper and lower whiskers, 1.5 × the interquartile range), and outliers (circles, >1.5 × the interquartile range).

RESULTS AND DISCUSSION

Fungi from *T. latifolia* Leaves

Isolates belonged to 45 taxa: five basidiomycetes, 26 ascomycetes, and 15 anamorphic taxa (13 with putative ascomycetous affinities and two with putative basidiomycetous affinities). Most taxa originated from fructifications on leaves *in situ* (37). Four species originated from the sporocarps of other fungi growing on *T. latifolia* leaves (Table 1). This study yielded no zygomycetes or chytridiomycetes. Yeasts were not examined in this study. Of the 37 fungi identified to species, 24 are new reports from *Typha* spp., 12 are new to Canada, seven are new to North America, and the records for *Albotricha acutipila*, *Hyaloscypha glyceriae*, *Phaeosphaeria typhae*, *P. typhicola*, and *Rivilata ius* are the first outside of the country of their type locality (Great Britain, Czech Republic, Germany, Great Britain, and U.S.A., respectively). *Phialophora melinii*, *Talaromyces ohiensis*, *Coprinopsis radiata*, and *H. sambuci* had not been recorded previously from *Typha* leaves. In contrast, species such as *P. typhae*, *Verticillium lecanii*, *Alternaria alternata*, and *Aureobasidium pullulans* were previously reported from *T. latifolia* and other wetland monocots (Tokumasu 1994, Redhead 1981).

Although the limited collection period did not allow us to estimate abundances of individual taxa, *Cladosporium herbarum*, *Phoma typhicola*, *H. glyceriae*, *Mollisia* sp., and *Stagonospora vitensis* were frequently observed in field and/or laboratory material (data not shown), suggesting that they were common colonizers of *T. latifolia*. *Verticillium lecanii*, *Podospora* cf. *glutinans*, cf. *Bjerkandora adusta*, and *Thielavia terrestris* were isolated from sporocarps of other fungi growing on *T. latifolia*. *Podospora* spp., *B. adusta*, and *T. terrestris* are common saprobes on dung, wood, and soil/plant materials, respectively, as were several other fungi isolated directly from leaf material (e.g., *Sordaria fimicola* and *P. melinii*).

We used 70% ethanol to surface-sterilize our plant materials before isolating fungi from them. This approach likely eliminated most surficial contaminants; however, it may have also eliminated some active saprobic fungi, as ethanol penetrated into the *Typha* plant tissues. Hence, our list of fungi from *T. latifolia* may be conservative.

Enzymatic Abilities of Fungi from *T. latifolia*

Cellulose degradation was observed in 32 of the 33 isolates (97%), while 27 degraded gelatin (82%), 24 starch (73%), 20 tannic acid (61%), and 19 lignin (58%; Table 1). Taxonomically, cellulose and gelatin generally were used equally well by all fungi of all taxonomic groups. In contrast, the remaining three C sources showed variable patterns of use among the fungal groups (Figure 1). For example, *Fusarium sporotrichioides* (Hypocreales) showed strong abilities to use starch and tannic acid (index of degradability = 3) but was less able to use lignin (index of degradability = 1; Table 1). Many members of the Hypocreales are plant pathogens and saprobes, and their ability to synthesize a broad suite of enzymes enables them to colonize many substrates and overcome host defense mechanisms. Lignin was well-degraded by most of the basidiomycetes and most members of the Pezizales and Leotiales (ascomycetes) but was not well-degraded by the remaining fungal groups (Figure 1). Many basidiomycetes synthesize polyphenol oxidases, which allow them to degrade lignin-rich substrates. Hence, they are often the primary decomposers of wood (Eriksson et al. 1990). Members of the Leotiales

and Pezizales are often associated with roots of conifers and ericaceous shrubs. They are also encountered on stems of herbaceous plants, dung, wood, soil, and fruits and cones. These substrates are typically lignin-rich, and the ability of these taxa to produce polyphenol oxides allows them to access C from complex structural polymers (Eriksson et al. 1990).

The apparent trade-off between the ability to hydrolyze cellulose and tannic acid vs. lignin is not surprising, given the more complex chemical structure of lignin and lignin-like polymers. Lignin and its relatives are formed via the polymerization of phenolic monomers, resulting in complex and often irregularly bonded phenylpropanoid polymers. The degradation of these polymers requires a suite of different polyphenol oxidase enzymes, which few fungi other than basidiomycetes can synthesize (Domsch et al. 1980, Paul and Clark 1996). This predisposition may be the result of their ability to hydrolyse xylan, which is a necessary step in the release of lignin embedded in the cell wall matrix (Eaten and Hale 1993). Conversely, cellulose is a less complex molecule, consisting of long chains of repeating D-glucose residues. It is likely that cellulose is the major structural component of *T. latifolia* leaves, as well as other herbaceous plant tissues. Hence, there is a predisposition by many fungi to degrade this structural polymer.

Although we could not find any data on the structural polymer composition of *T. latifolia* leaves, other members of the Poales, including *Nardus stricta* L. (matgrass) and *Zea mays* L. (corn), have cellulose concentrations of 660–680 mg g^{-1} (Rowland and Roberts 1994, Escher et al. 2000). A relationship between the number of fungi degrading a given polymer and its concentrations in the substrate is also apparent in the relative abilities of the fungi tested to degrade starch (73%) and lignin (58%), which is consistent with the proportional concentrations of these polymers in *Z. mays* (40 and 20 mg g^{-1}, respectively; Escher et al. 2000). The large number of fungi utilizing gelatin, an indicator of the ability to degrade nitrogen-rich compounds, is consistent with the higher nitrogen content of *T. latifolia* leaves compared to other wetland monocots (Thormann and Bayley 1997b); however, this does not preclude these fungi, many of which produce abundant spores, from colonizing other wetland plants with lower nitrogen content.

Our data contrast with findings from aquatic hyphomycetes. Hasija and Singhal (1991) showed that all of 39 aquatic hyphomycetes tested positively for cellulases (similar to our results), but 35 of their taxa produced lignases, a much higher proportion than in our study (90% vs. 58%). Bergbauer et al. (1992) also found strong lignolytic abilities in aero-aquatic hyphomycetes (five species tested). This suggests that fungi common to aquatic environments may have strong lignolytic and cellulolytic capabilities, which appears to be in contrast to fungi in non-aquatic environments. Since *Typha* and other emergent wetland plants, such as *Scirpus*, *Spartina*, and *Carex* species, begin to decompose in the standing position, they are first colonized by fungi whose spores are aerially deposited onto their leaf tissues. Our results indicate that these fungi preferentially use cellulose and other simple compounds as C sources, leaving more complex polymers, including lignin, behind. Once the structural integrity of the standing dead leaves is sufficiently compromised and they fall into the water column, aquatic hyphomycetes, with their stronger lignolytic abilities, decompose the remaining plant materials. This succession from aerially deposited fungal taxa on standing dead plant tissues to aquatic hyphomycetes (and bacteria, which are also important decomposer organisms in this milieu) on submerged plant tissues has been demonstrated previously by Newell et al. (1995; *Carex walteriana* Bailey in Georgia, USA), Kamínková et al. (2000; *Phragmites australis* (Cav.) Trin. *ex* Steud. in Switzerland), and Kuehn et al. (2000; *Juncus effuses* L. in Alabama, USA) among others. A similar succession likely occurs on *T. latifolia* as well; however, further studies on cellulose:lignin ratios in these materials are needed to confirm this hypothesis.

Contrary to our findings, Flanagan and Scarborough (1974) found that of fungi on living *Eriophorium angustifolium* Honckeny (tall cottongrass) and *Carex aquatilis* Wahlenb. (water sedge) leaves, 1.3 and 25.6% were able to use cellulose and starch, respectively, as C sources. This trend was reversed in decomposing leaves of these two plant species (ability to use cellulose: 30.5%; ability to use starch: 10.5%), indicating a succession of fungal taxa from living to decomposing plant tissues. These values are substantially lower than ours, especially for cellulosis, and may be the result of differences in origin of their plant materials (Arctic) but more likely their isolation techniques for fungi (i.e., dilution plating). This is significant because their study has been used as a model for studies on fungal functional diversity (Kjøller and Struwe 1992).

Mass Loss of *T. latifolia* Leaves *in vitro*

Our taxa caused a wide range of mass losses from 54.6 to −0.4% (Table 1). Mass losses due to leaching (18%) were similar to the previously estimated 14–16% for *Typha* × *glauca* Godr. (Nelson et al. 1990). The large mass losses obtained in our study are consistent with those reported for *T. latifolia* leaves *in situ* (e.g., Bärlocher and Biddiscombe 1996: 54.5% mass loss in seven months; Thormann and Bayley 1997b:

Table 1. Fungi isolated from *Typha latifolia* leaf tissues. Isolations are from moist chambers (MC), fructifications from leaves *in situ* (N), and/or fruiting bodies of other fungi (F). UAMH = University of Alberta Microfungus Collection and Herbarium, ALTA = University of Alberta Cryptogamic Herbarium, "n" is the number of replicates, TAM = tannic acid medium, mass loss data originated from sterilized *T. latifolia* leaves inoculated individually with the fungal taxa over a 12-week period *in vitro*, indices of degradability range from 0 (no ability to use the carbon source) to 3 (relative maximum ability to use the carbon source).

Fungal taxa and taxonomic positions	Source	Accession numbers	Carbon source degradation					Mass loss (%)	n
			Cellulose	Gelatin	Starch	TAM	Lignin		
ASCOMYCOTA									
Anamorphic ascomycetes									
Acremonium sp.	MC	UAMH 10078	3	3	2	3	1	54.6 (3.1)	3
Alternaria alternata (Fr.) Keissler	MC	—	—	—	—	—	—	—	—
Arthrobotyris superba Corda	N	UAMH 10288	—	—	—	—	—	—	—
Aureobasidium pullulans (de Bary) Arnaud	MC	ALTA 13095	3	3	0	3	0	29.3 (22.2)	2
Epicoccum purpurascens Ehrenb. *ex.* Schlecht	MC & N	ALTA 13103	3	3	1	2	0	10.2 (12.6)	3
Periconia typhicola Mason & Ellis	MC	UAMH 10289	2	3	2	0	1	39.1 (15.7)	2
Phialophora melinii (Nannf.) Conant	MC & N	UAMH 10077	3	3	0	2	0	21.7 (16.2)	2
Septofusidium herbarum (Brown & Smith) Samson	N	ALTA 13118	—	—	—	—	—	—	—
Verticillium lecanii (Zimm.) Viégas	F	—	2	0	0	0	0	7.0	1
Hymenopsis typhae (Fuckel) Sacc.	MC & N	UAMH 10290	3	3	1	3	1	21.4 (5.5)	3
Pseudoseptoria stomaticola (Bäumler) Sutton	N	UAMH 10292	1	0	1	2	0	3.4	1
Stagonospora vitensis Unamuno	MC	UAMH 10293, 10319	3	3	0	2	1	40.1 (2.5)	3
Stagonospora nodorum (Berkley) Castenalli & Germano	N	ALTA 13121, 13122	—	—	—	—	—	—	—
Dothideales									
Cladosporium cladosporioides (Fres.) de Vries	MC	ALTA 13098	1	3	1	3	0	2.6 (0.3)	3
Cladosporium herbarum (Pers.) Link *ex* Gray	MC & N	ALTA 13099	1	3	2	3	1	3.1 (16.0)	2
Mycosphaerella recutita (Fr.: Fr.) Johanson	N	ALTA 13115	—	—	—	—	—	—	—
Leptospora rubella (Pers.: Fr.) Rabenh.	N	ALTA 13110	—	—	—	—	—	—	—
Massariosphaeria typhicola (Karst.) Leuchtmann	N	ALTA 13111, UAMH 10283	3	0	2	2	0	29.0 (2.2)	3
Phaeosphaeria typhae (Karst.) Shoemaker & Babcock	N	UAMH 10284	3	2	2	1	2	—	—
Rivilata ius Kohlmeyer	N	UAMH 10285	1	2	1	1	1	—	—
Sporormiella minima (Auersw.) Ahmed & Cain	N	ALTA 13120	2	3	1	0	1	38.6 (2.2)	3
Phoma typhicola Oud.	MC & N	ALTA 13116	—	—	—	—	—	—	—
Eurotiales									
Aspergillus fumigatus Fres.	MC	ALTA 13094	3	0	0	0	0	31.0 (12.2)	2
Talaromyces ohiensis Pitt	N	UAMH 10287	3	1	3	0	0	18.7 (12.6)	2
Hypocreales									
Fusarium sporotrichioides Sherb.	MC	ALTA 13104	3	3	3	3	1	34.5 (0.2)	3

Table 1. Continued.

Fungal taxa and taxonomic positions	Source	Accession numbers	Carbon source degradation					Mass loss (%)	n
			Cellulose	Gelatin	Starch	TAM	Lignin		
Leotiales									
Albotricha acutipila (Karst.) Raitviir	N	—	1	3	2	1	3	2.0 (1.7)	3
Cistella sp.	N	ALTA 13097	—	—	—	—	—	—	—
Hyaloscypha glyceriae Velen.	N	ALTA 13105, 13106, 13107	—	—	—	—	—	—	—
cf. *H. glyceriae*	N	—	3	3	1	0	1	47.5 (7.4)	5
Hymenoscyphus repandus (Phillips) Dennis	N	—	0	2	1	0	0	4.8 (1.5)	2
Hymenoscyphus scutula (Pers.: Fr.) Phillips	N	—	1	3	1	0	3	5.0	1
Coryne sp.	N	ALTA 13101	—	—	—	—	—	—	—
Mollisia sp.	N	ALTA 13112, 13113, 13114	—	—	—	—	—	—	—
Tapesia sp.	N	ALTA 13123, 13124	3	3	2	0	2	5.6 (1.7)	2
Tapesia sp.	N	—	2	3	2	3	3	1.3 (2.6)	3
Pezizales									
Iodophanus carneus (Pers.: Fr.) Korf	N	ALTA 13108, 13109	—	—	—	—	—	—	
Scutellinia heterosculpturata Kullman & Raitviir	N	UAMH 10286	3	3	0	3	0	12.5 (6.9)	3
Sordariales									
Podospora cf. *glutinans* (Cain) Cain	F	—	3	0	0	0	0	25.6 (7.4)	5
Sordaria fimicola (Rob.) Ces. & de Not.	N	ALTA 13119	3	3	1	0	1	37.8 (9.8)	3
Thielavia terrestris (Apinis) Malloch & Cain	F	UAMH 10291	3	3	2	1	3	44.8 (4.2)	3
BASIDIOMYCOTA									
Anamorphic basidiomycetes									
Sclerotium hydrophilum Sacc. *apud* Rothert	MC & N	ALTA 13117, UAMH 10282	3	2	2	2	3	25.5	2
cf. *Bjerkandera adusta* (Willd.: Fr.) Karst.	F	ALTA 13096	1	3	0	0	0	−0.4 (3.8)	3
Agaricales									
Coprinopsis radiata (Bolton) Redhead, Vilgalys & Moncalvo	MC	ALTA 13100	3	3	2	0	3	45.8 (6.3)	3
Loreleia marchantiae (Singer & Clemençon) Redhead	N	—	—	—	—	—	—	—	—
Psathyrella typhae 1 (Kalchbrenner) Pearson & Dennis	N	UAMH 10280	3	3	1	2	3	50.3 (4.3)	3
Psathyrella typhae 2	N	UAMH 10281	3	3	1	1	3	52.1 (0.2)	2
Stereales									
Hyphoderma sambuci (Pers.) Jülich	N		3	3	1	1	3	44.6	3

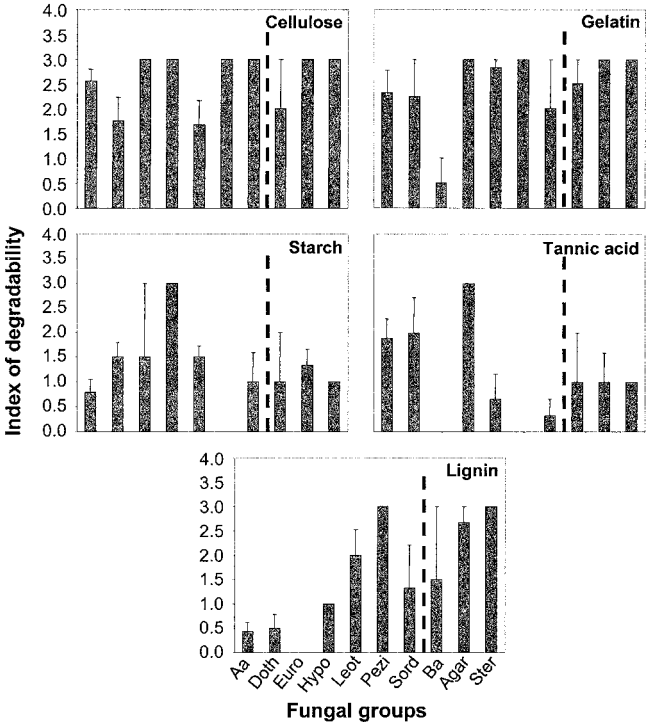

Figure 1. The ability of taxonomically different groups of fungi isolated from senesced *Typha latifolia* leaves from marshes in central Alberta, Canada to use selected carbon sources *in vitro.* Bars represent mean ''indices of degradability'' for ten fungal groups. Dashed lines separate ascomycetes (left) from basidiomycetes (right). Aa = fungi with putative ascomycete affinities (n = 9), Doth—Dothideales (n = 6), Euro—Eurotiales (n = 2), Hypo—Hypocreales (n = 1), Leot—Leotiales (n = 6), Pezi—Pezizales (n = 1), Sord—Sordariales (n = 3), Ba—taxa with putative basidiomycete affinities (n = 2), Agar—Agaricales (n = 2), and Ster—Stereales (n = 1). Error bars represent standard deviations of variation in the indices of degradability in each of the fungal orders.

64% mass loss in one year). However, the continuous distribution of mass losses contrasts with Osono and Takeda (2002), who found that only eight of 79 taxa (10%) from beech litter caused a mass loss > 10%, and most produced mass loss < 5% (after eight weeks at 20 °C). They also found that the most efficient saprobes were basidiomycetes, in particular members of the Agaricales (up to 57.6% mass loss), and some ascomycetes, particularly members of the Xylariales (up to 14.4% mass loss). Members of these two families are widespread, are frequently found growing on wood and herbaceous plant materials, and are actively involved in their decomposition (Pointing et al. 2003). Although our study showed similarly large mass loss caused by the basidiomycetes *P. typhae*, *C. radiata* (Agaricales), and *H. sambuci* (Stereales) (45–50%), similar or greater mass loss was caused by *Acremonium* sp. and various ascomycetes (up to 55%; Table 1). This indicates that *T. latifolia* leaves are effectively decomposed by a great diversity of fungi, possibly as a result of the relatively higher nitrogen and phosphorus content compared to other emergent macrophytes. Similar to our results, Thormann et al. (2002) found that of fungi isolated from *Sphagnum fuscum* (Schimp.) Klinggr., the greatest mass loss was produced by an ascomycete and several anamorphic taxa with putative ascomycete affinities (up to 5.1% after eight weeks at 20 °C), while their basidiomycete caused only 1.7% mass loss. These mass losses on average are substantially lower than ours and those reported previously from other substrates, possibly because of the poorer litter quality of their bryophyte material (Thormann et al. 2001).

Relationships between Enzymatic Profiles and Mass Losses

Relationships between observed litter mass losses and enzymatic profiles of fungi should be intuitive; however, to our knowledge, they have not been shown previously. In our study, the ability of fungi to use cellulose as a C source showed a positive relationship with *T. latifolia* leaf mass loss (i.e., as the index of cellulose degradation increased, so did the observed mass loss of the leaf tissues; Figure 2). This relationship is not surprising because cellulose is likely the major structural polymer in *T. latifolia* leaves (see above); however, it is the first time to our knowledge that such a relationship has been shown. This contrasts with results from Torzilli (1982), Harper (1985), and Bowen and Harper (1990), who found no correlation between enzymatic activities and mass loss caused by fungi *in vitro.* Compared to our study, those studies used different assays for determining enzymatic activities and smaller sets of taxonomically more closely related fungi; hence, direct comparisons remain speculative. It is possible that the relationship between enzyme production and mass loss capabilities can only be seen on a broader scale or that other *in vitro* techniques may mask correlations. Our data showed no relationships between mass loss and starch, gelatin, tannic acid, and lignin degradation (Figure 2).

Enzymatic test results from our *in vitro* studies were limited by the use of crude tests that may or may not represent the enzymatic activity of fungi *in situ*; however, these tests clearly demonstrated that our taxa are capable of producing these enzymes under some conditions. In addition, we used green leaves for mass loss determinations, which are richer in nitrogen and phosphorus than naturally senesced plant material, possibly resulting in an overestimation of mass losses. This may have been exacerbated by autoclaving the leaves prior

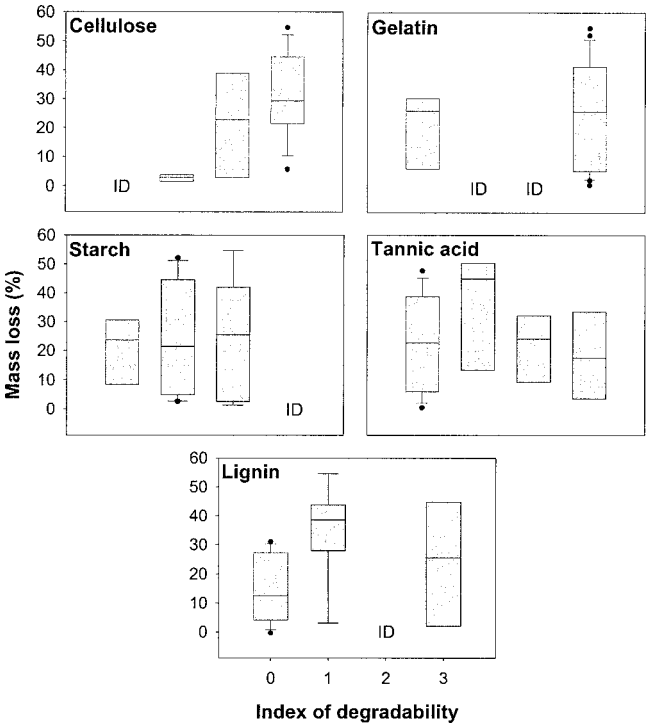

Figure 2. Box-and-whisker plots showing the relationship between mass loss of *Typha latifolia* leaves and indices of degradability of five carbon sources by fungi isolated from senesced *T. latifolia* leaves from three marshes in central Alberta, Canada. ID—insufficient data to generate a box-and-whisker plot (less than five data points for the specific index of degradability).

to inoculation with the fungi, although controls were used, and Tsuneda et al. (2001) found no discernable changes to *Sphagnum* leaf morphology after autoclaving. Potential changes in tissue chemistry were assessed neither in their study nor our study. Despite these limitations, our data are valuable in that they indicate potential enzymatic abilities of and mass losses by these fungi. Additional studies of this nature are necessary to gain a better understanding of decomposition dynamics from a microbial perspective, especially in wetlands, which are often nutrient-poor and characterized by tight nutrient-cycling mechanisms.

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