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Wetland dicots and monocots differ in colonization by arbuscular mycorrhizal fungi and dark septate endophytes

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Abstract As an initial step towards evaluating whether mycorrhizas influence composition and diversity in calcareous fen plant communities, we surveyed root colonization by arbuscular mycorrhizal fungi (AMF) and dark septate endophytic fungi (DSE) in 67 plant species in three different fens in central New York State (USA). We found colonization by AMF and DSE in most plant species at all three sites, with the type and extent of colonization differing between monocots and dicots. On average, AMF colonization was higher in dicots (58±3%, mean±SE) than in monocots (13±4%) but DSE colonization followed the opposite trend (24±3% in monocots and 9±1% in dicots). In sedges and cattails, two monocot families that are often abundant in fens and other wetlands, AMF colonization was usually very low (<10%) in five species and completely absent in seven others. However, DSE colonization in these species was frequently observed. Responses of wetland plants to AMF and DSE are poorly understood, but in the fen communities surveyed, dicots appear to be in a better position to respond to AMF than many of these more abundant monocots (e.g., sedges and cattails). In contrast, these monocots may be more likely to respond to DSE. Future work directed towards understanding the response of these wetland plants to AMF and DSE should provide insight into the roles these fungal symbionts play in influencing diversity in fen plant communities.

Keywords Wetlands · Calcareous fens · Arbuscular mycorrhizal colonization · Dark septate fungi · Plant diversity

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Introduction

Arbuscular mycorrhizal fungi (AMF) can influence plant community composition and diversity when growth and nutrition benefits conferred by AMF differ among plant species (van der Heijden 2002; Urcelay and Diaz 2003). For example, in chalk grasslands, AMF increased plant diversity by more strongly benefiting subordinate forbs than dominant grasses (Grime et al. 1987; van der Heijden et al. 1998), leading to greater community evenness. Conversely, in tallgrass prairies, AMF reduced evenness and diversity by transferring greater benefits to dominant C4 grasses than to subordinate C3 grasses (Hartnett and Wilson 1999).

Another group of fungal root symbionts, dark septate endophytes (DSE; reviewed by Jumpponen and Trappe (1998), have been characterized as mycorrhizas because their effects on host plants can span the range of effects produced by other mycorrhizal types, i.e., DSE impact on plant growth and nutrition can range from positive to negative, depending on plant species and environment (Jumpponen 2001). Because plant species responses to DSE can vary, they may affect plant diversity in a manner similar to AMF, although this has not been tested.

In this paper, we document the extent and type of mycorrhizal colonization among plant species in calcare-

ous fens, peat-accumulating wetlands that are dominated hydrologically by mineral-rich ground water and typically have species-rich plant communities (Godwin et al. 2002). While fen hydrology, geochemistry, and nutrient limitation influence plant diversity in these communities (Bedford et al. 1999), mycorrhizal fungi could also play a role. For a fen in central New York State, USA, Cornwell et al. (2001) found that monocots and dicots differed considerably in their colonization by AMF; colonization was typically found among dicots and seldom found among monocots, e.g., sedges, which can be quite abundant in this type of wetland community. Sedges have been reported as non-mycorrhizal (Powell 1975), although there are exceptions (Miller et al. 1999; Muthukumar et al. 2004), and one report of sedges colonized by AMF in a calcareous fen indicates that colonization could occur seasonally as a function of phenology (Bohrer et al. 2004). Nevertheless, patterns of colonization observed by Cornwell et al. (2001) suggested the possibility that AMF influence fen community structure, as only dicots appeared to be in a position to receive AMF benefits.

Cornwell et al. (2001) did not examine DSE colonization, and only a small number of studies have reported on DSE colonization among plants in wetland communities (Thormann et al. 1999; Addy et al. 2000). DSE colonization appears to be most common in nutrient-limited ecosystems, and therefore might occur regularly in calcareous fens (Peterson et al. 2004). DSE can act as saprotrophs, degrading organic matter, and liberating nutrients (Caldwell et al. 2000), which could benefit host plants in nutrient limited peatlands. Though often poorly colonized by AMF, sedges are often hosts of DSE (Read and Handselwandter 1981; Muthukumar et al. 2004). The possible presence of DSE in fen monocots might indicate a mutualism that in some ways could compensate for low levels of AMF colonization.

Because differences in root symbiont types among fen plant species might affect plant performance and influence community composition and diversity, our primary objectives in this study are to document the extent and type of colonization (AMF or DSE) in fen plant species and to evaluate whether AMF and DSE colonization differs between monocots and dicots.

Materials and methods

Study sites

We sampled plants at three calcareous fens located near Ithaca, New York (42° N 76° W): Belle School Fen (BSF), Fish Fen (FF), and Larry's Fen (LF). Belle School Fen is a 0.25-ha gently sloping peatland (peat depth 0.5 m), situated within a rural agricultural community in the Six Mile Creek watershed in Tompkins County, New York. Larry's Fen, also situated in an agricultural setting, is a 0.2-ha sloping peatland (peat depth 0.5 m) fed by hillside seepage and draining into the Fall Creek watershed in Tompkins County. Fish Fen, in Cortland County, is a 0.25-ha sloping depressional peatland (peat depth ranges from 1–5 m), surrounded by upland forest, and also drains into the Fall Creek watershed. The water table at these sites typically is within 5 cm of the soil surface, although bryophyte hummocks at BSF and FF create patches where the distance from the surface to the water level can be greater. Table 1 summarizes selected groundwater and soil chemistry characteristics of these fens.

Plant communities

Godwin et al. (2002) describe typical plant communities of fens from this region. Plant community composition for the three fens in this study was estimated as part of a separate study started in 1999 at BSF and 2000 at FF and LF (Drs. Barbara Bedford and Carmen Chapin, unpublished). The BSF plant community includes 76 vascular plant species, dominated by *Thelypteris palustris*, *Solidago patula*, *Typha latifolia*, and a group of sedges, *Eleocharis elliptica*, *Carex sterilis*, *C. flava*, and *C. hystericina*. The plant community at FF is dominated by *Typha angustifolia*, an invasive exotic, and shrubs (*Cornus sericea* and multiple *Salix* species), but also contains 55 understory herbs, sedges, and grasses. Larry's fen harbors a plant community composed of 71 vascular plants, dominated by sedges (*C. sterilis* and *E. elliptica*), a shrub (*Dasiphora floribunda*), and skunk cabbage (*Symplocarpus foetidus*). Bryophytes, including *Sphagnum* species and members of the Amblestegiaceae, cover 40–60% of the surface area at all three sites. Nomenclature with authorities and wetland indicator status for all vascular species discussed in this paper is located in Table 2.

Plant collection, root processing, and AMF colonization

In late July and early August of 2000, we collected a total of 67 plant species from the three different fens. In total, 34, 27, and 44 species were sampled at BSF, FF, and LF, respectively. We collected at least five individuals of each species from within each fen. Specific plants were selected for sampling by picking the individual closest to randomly determined locations in the fen. For small herbaceous species, we largely kept plants' rooting systems intact by gently working our hands through the peat and underneath the roots, extracting the entire rooting system. For species with

Table 1 Groundwater and soil characteristics (mean and SE) at Belle School Fen (BSF), Fish Fen (FF), and Larry's Fen (LF)

Site	Groundwater chemistry[a]			Soil characteristics			
	pH	Alkalinity[b] (mg l^{-1})	Total P (mg l^{-1})	Bulk density[c] (g cm^{-3})	Soil moisture[c] (%)	Organic matter[c] (%)	Labile inorganic P[d] (g cm^{-3})
BSF	7.2 (0.1)	183 (8)	0.05 (0.02)	0.28 (0.03)	86 (0.3)	68 (2)	0.005 (0.0003)
FF	7.1 (0.1)	218 (8)	0.07 (0.03)	0.21 (0.02)	91 (0.1)	85 (2)	0.010 (0.001)
LF	7.4 (0.1)	287 (14)	0.004 (0.001)	0.42 (0.03)	85 (0.3)	57 (1)	0.007 (0.001)

[a] Bailey (2005). Based on monthly samples drawn during the summers of 1999 and 2000 from five or more well clusters per site (0.10–0.25 m depth) and from water collected in shallow (0.25 m) pits. Total number of samples is 26, 35, and 34 for BSF, FF, and LF, respectively.
[b] Expressed as $CaCO_3$ equivalence
[c] Based on at least 10 samples per site, all obtained in the same general area of plants sampled for AMF.
[d] Data provided by Carmen T. Chapin based on five samples per site, taken to a depth of 10 cm. Labile inorganic P determined by sequential extraction procedure described by Hedley et al. 1982 and characterized by Cross and Schlesinger (1995).

extensive rooting systems (e.g., large clonal plants, such as *Typha* species or woody shrubs), we sampled partial rooting systems by removing lateral roots found near the base of the stem until sufficient fine root length was accumulated.

Within 24 h of plant collection, we washed roots under running tap water and stored them at 6°C in 50% ethanol. After cutting all terminal fine roots of an individual plant into 1-cm segments, we cleared a subsample of terminal roots in 10% KOH by heating on a hot plate at 90°C or autoclaving at 121°C. Heating times required to clear the roots varied widely with species, depending upon root pigmentation. Pigments that resisted clearing roots were bleached with an alkaline H_2O_2 solution (Johnson et al. 1999). After clearing, we stained roots by heating at 90°C in 0.1% Chlorozol Black E in lactoglycerol (Brundrett et al. 1994) or vinegar and ink (Vierheilig et al. 1998), which we found comparable to the former stain. Roots soaked in a lactoglycerol destaining solution for at least 1 day before we mounted them on microscope slides. We assessed the percent root length colonized by AMF at 400× magnification using a line intersection method (McGonigle et al. 1990), scoring at least 100 intersections on 30 root segments per plant (or all of a plant's terminal root segments, if less than 30 cm were present). We scored intersections with aseptate hyphae, vesicles, arbuscules (including coils), and DSE (microsclerotia and hyphae were scored collectively). We report total mycorrhizal colonization as the percentage of intersections with aseptate hyphae, vesicles, or arbuscules. We analyzed the effects of site and vegetation class (monocot vs dicot) on colonization by AMF and DSE using 2-way ANOVAs. Spore-bearing plant species and those that regularly formed ectomycorrhizas were excluded from this analysis. Additionally, we used Pearson's correlation to evaluate the relationship between AMF and DSE colonization among all plant species except those colonized by EMF. Statistical analyses were conducted in SYSTAT 7.0.

Results

Of the 67 species surveyed, 50 formed fully developed arbuscular mycorrhizas, with arbuscules (and/or coils) and vesicles in at least one individual at one or more sites (Table 2). An additional six species hosted aseptate hyphae and vesicles characteristic of AMF, but contained no arbuscules or coils. Five species hosted ectomycorrhizal fungi (EMF), including four *Salix* species and *Alnus incana*, which we observed to host AMF on root segments where EMF were absent. Seven species (*Carex lasiocarpa*, *C. prairea*, *Eleocharis elliptica*, *Scheonoplectus acutus*, *Scirpus atrovirons*, *Leersia oryzoides*, and *Typha angustifolia*) contained no AMF or EMF structures at any of the sites where the plants were found. Additionally, dark septate endophytic fungi (DSE) colonized the roots of most species. DSE structures observed included microsclerotia and both melanized and hyaline hyphae. In many plant species surveyed, DSE and AMF colonization cooccurred in the roots of individual plants, although typically one type of colonization was obviously superior to the other.

Total AMF colonization was greater in dicots (58±3, mean±SE) than in monocots (13±4; determined by ANOVA: df=93, F=55, P<0.00001; Fig. 1). Colonization ranged from 17 to 98% in dicots and 0 to 77% in monocots. No significant variation in AMF colonization was detected across sites and the interaction of site and plant classification also was not significant (ANOVA: P>0.05). Unlike AMF, DSE colonized dicot roots (9±1) less than they colonized monocot roots (24±3; determined by ANOVA: df=93, F=41, P<0.00001; Fig. 1), Dark septate colonization did not vary significantly with site, and significant

Table 2 Percent root length colonized by AMF and DSE at Belle School Fen (BSF), Fish Fen (FF), and Larry's Fen (LF)

Plant species	WIS	BSF				FF				LF			
		T	V	A	D	T	V	A	D	T	V	A	D
Dicots													
Aceraceae													
Acer rubrum L.	fac		43	12	17[a]	3							
Apiaceae													
Hydrocotyle americana L.	obl		76	44	49	13	81	23	80	2			
Zizia aurea (L.) W.D.J. Koch	fac									92	33	15	1
Asclepiadaceae													
Asclepias incarnata L.	obl					26	18	5[a]	0				
Asteraceae													
Doellingeria umbellata (P. Mill.) Nees	facw									58	24	11	29
Eupatorium maculatum L.	facw	54	27	34	10	71	36	40	5	17	5	6	6
Eupatorium perfoliatum L.	facw	28	22	16	25	51	24	23	8	59	10	39	13
Euthamia graminifolia (L.) Nutt.	fac	39	9	15	31					52	17	17	35
Packera aurea (L.) A.&D. Löve	facw	61	37	42	9	62	27	49	1	78	38	16	3
Solidago patula Muhl. ex Willd.	obl	84	20	31	9					57	17	12	26
Solidago rugosa P. Mill.	fac	56	11	17	24								
Solidago uliginosa Nutt.	obl					73	14	14	17				
Symphyotrichum boreale (Torr. & Gray) A.&D. Löve	obl									40	19	9	35
Symphyotrichum puniceum (L.) A.&D. Löve	obl	46	6	22	25					32	11	10	29
Balsaminaceae													
Impatiens capensis Meerb.	facw	29	28	20	12	67	26	58	7				
Betulaceae													
Alnus incana (L.) Moench	facw	3[b,c]	2	0	0								
Campanulaceae													
Lobelia siphilitica L.	facw	74	44	33	5								
Caprifoliaceae													
Viburnum dentatum L.	fac	65	20	52[a]	1								
Clusiaceae													
Triadenum virginicum (L.) Raf.	obl					64	30	34	2				
Cornaceae													
Cornus sericea L.	facw	80	75	13[a]	0	51	48	5[a]	5	71	27	15[a]	0
Droseraceae													
Drosera rotundifolia L.	obl					27[c]	18	0	11	0	0	0	0
Grossulariaceae													
Ribes hirtellum Michx.	fac					58	31	21	16				
Lamiaceae													
Lycopus americanus Muhl. ex W. Bart.	obl	78	46	60	21	64	18	47	18	85	30	45	6
Lycopus uniflorus Michx.	obl	67	50	52	15	63	45	43	7	73	22	45	7
Mentha ×piperita L. (pro sp.) [aquatica × spicata]	facw									84	48	7	0
Prunella vulgaris L.	facu									83	41	4	0
Onagraceae													
Epilobium coloratum Biehler	facw					16	9	3	3				
Primulaceae													
Lysimachia ciliata L.	facw									65	5	24	0
Ranunculaceae													
Clematis virginiana L.	fac	86	48	36	5					80	25	27	2
Thalictrum pubescens Pursh	facw									98	54	8	0
Rosaceae													
Dasiphora fruiticosa (L.) Rydb.	facw									67	29	5	0
Fragaria virginiana Duchesne	facu									82	37	7	6
Geum rivale L.	obl									61	16	20	2
Rubus pubescens Raf.	facw	70	41	70	6	28	13	6	16	85	43	8	2
Rubiaceae													
Galium labrodoricum (Wieg.) Wieg.	obl					48	13	7	16				
Salicaceae													

Table 2 (continued)

Plant species	WIS	BSF				FF				LF			
		T	V	A	D	T	V	A	D	T	V	A	D
Salix bebbiana Sarg.	facw					0[b]	0	0	0				
Salix discolor Muhl.	facw					0[b]	0	0	0				
Salix lucida Muhl.	facw									0[b]	0	0	0
Salix sericea Marsh.	obl	0[b]	0	0	0								
Scrophulariaceae													
Chelone glabra L.	obl	35	20	24	12					39	6	16	1
Urticaceae													
Pilea pumila (L.) Gray	facw					32	4	23	5				
Violaceae													
Viola cucullata Ait.	facw	58	8	44	1					76	12	29	2
Monocots													
Araceae													
Symplocarpus foetidus (L.) Salisb. ex Nutt.	obl									8	1	2	1
Cyperaceae													
Carex flava L.	obl	2[c]	0	0	34					2[c]	1	0	21
Carex hystericina Muhl. Ex Wild.	obl	0	0	0	35					6[c]	4	1	46
Carex lasiocarpa Ehrh.	obl	0	0	0	0					0	0	0	0
Carex leptalea (Wehlenb.)	obl					0	0	0	31	2[c]	2	0	20
Carex prairea Dewey ex Wood	facw					0	0	0	27				
Carex sterilis Willd.	obl	0	0	0	25					18[c]	6	3	17
Eleocharis elliptica Knuth	obl	0	0	0	33	0	0	0	48	0	0	0	0
Eriophorum viridcarinatum (Engelm.) Fern.	obl									11[c]	6	2	55
Schoenoplectus acutus (Muhl. ex Bigelow) A.&D. Löve	obl	0	0	0	0								
Scirpus atrovirens Willd.	obl									0	0	0	0
Iridaceae													
Iris versicolor L.	obl									41	5	22	10
Juncaceae													
Juncus brachycephaulus (Engelm.) Buch.	obl	0	0	0	62					11	1	0	11
Juncus tenuis Willd.	fac									5	4	2	2
Poaceae													
Agrostis stolonifera L.	facw									45	25	9	47
Bromus ciliatus L.	facw	57	42	6	19					78	42	10	19
Calamagrostis canadensis (Michx.) Beauv.	facw					34	5	7	16	31	9	7	10
Glyceria striata (Lam.) A.S. Hitchc.	obl	37	13	13	14					47	16	3	3
Leersia oryzoides (L.) Sw.	obl	0	0	0	46								
Typhaceae													
Typha angustifolia L.	obl					0	0	0	45				
Typha latifolia L.	obl	0	0	0	47					2[c]	0	2	44
Pteridophytes													
Dryopteridaceae													
Onoclea sensibilis L.	facw					55	10	37	23				
Thelypteriaceae													
Thelypteris palustris Schott.	facw	46	44	5	1	75	5	59	3	53	20	19	0
Equisetophytes													
Equisetaceae													
Equisetum arvensis L.	fac	2[c]	2	0	7					13[c]	1	1	6

Plant nomenclature used is from USDA, NRCS (2005). Wetland Indicator Status is from US Fish and Wildlife Service (1996): *obl* obligate wetland, *facw* facultative wetland (includes facw+), *fac* facultative, *facu* facultative upland, and *upl* obligate upland.

T Total% AMF, *V* % vesicles, *A* % arbuscules, and *D* % DSE

[a] Intracellular coils are included in arbuscule reporting.

[b] Ectomycorrhizal roots were common in these populations.

[c] Most individuals in these populations lacked AMF.

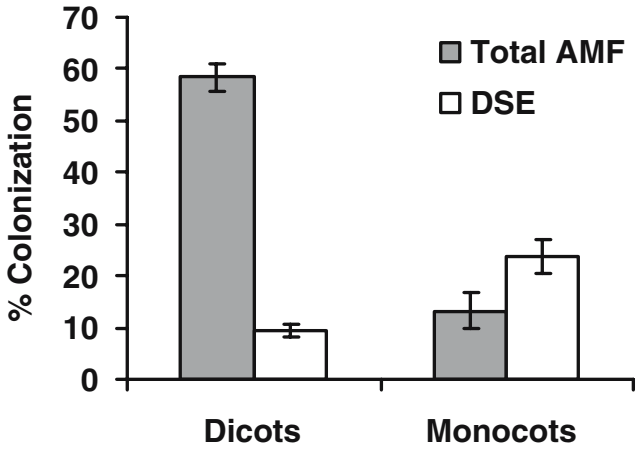

Fig. 1 Mycorrhizal colonization differed significantly between calcareous fen dicots and monocots ($P<0.00001$ for both AMF and DSE)

interactions between site and plant classification factors were not detected (ANOVA: $P>0.05$). Colonization of plant species by dark septate fungi correlated inversely with total AMF colonization across all species and sites; Pearson's $r=-0.53$, -0.57, and -0.29, at BSF, FF, and LF, respectively. The correlation was significant at BSF and FF ($0.01>P>0.001$) but not at LF ($P>0.05$).

Discussion

Our survey of the mycorrhizal status of plant species in three calcareous fens in New York State indicates that colonization is common in these species-rich wetland plant communities, but varies considerably among different fen plant species, with dicots and monocots differing significantly in their colonization by both AMF and DSE. While wetland plant responses to AMF and DSE remain poorly characterized, colonization patterns suggest mechanisms by which these fungi could influence fen plant community structure.

AMF colonization

Although some studies have suggested that AMF are relatively uncommon among wetland plant species (Peat and Fitter 1993), our study adds to a growing body of literature that documents the opposite trend (e.g., Aziz et al. 1995; Wetzel and van der Valk 1996; Turner et al. 2000). We found that fen dicot species were nearly always colonized by AMF. The only exceptions include species that were regularly colonized by ectomycorrhizas (*Alnus* and *Salix* species) and *Drosera rotundifolia*, a carnivorous plant that was irregularly colonized (i.e., in only two individuals examined) by aseptate hyphae and vesicles, but never arbuscules.

AMF colonization in monocots was lower than in dicots (Fig. 1). This trend was driven by little or no colonization in most sedges, cattails, and rushes that were examined. Sparse colonization in these families is consistent with another survey of AMF in a New York State calcareous fen (Cornwell et al. 2001) and several other reports (e.g., Khan 1974; Powell 1975; Thormann et al. 1999; Fontenla et al. 2001). Studies that have reported greater colonization in sedges (Miller et al. 1999; studies reviewed in Muthukumar et al. 2004; Bohrer et al. 2004) have implicated the physical environment (pH, soil moisture or water table, and nutrients) or phenology and sampling time as controlling factors. High pH and low nutrient levels at the three fen sites (Table 1) should favor colonization of *Carex* species, according to Miller et al. (1999) but persistent groundwater saturation levels may inhibit colonization, presumably by decreasing oxygen availability. Because sedges, rushes, and cattails rooted in saturated soils frequently hosted other fungal symbionts (DSE), the explanation that groundwater inhibited AMF colonization in these plants is not entirely satisfying.

Bohrer et al. (2004) reported that AMF colonization in fens in Ohio was seasonally dynamic and found colonization of sedge and cattail species primarily during vegetative growth phases. In the central New York region, *Carex* and *Typha* species typically flower by the time of our survey in late July, but vegetative growth continues through August (F. Robert Wesley, personal communication). We acknowledge that, before fruit development, AMF could have colonized *Carex* and *Typha* species more extensively than we found in our midsummer survey. However, while arbuscules are known to be ephemeral, AMF hyphae in roots are known to live longer and persist even after they become inactive (Smith and Read 1997). In over 70 individual sedges, cattails, and rushes that we sampled, we found no traces of aseptate hyphae characteristic of AMF (Table 2). Therefore, we assert that the contrast in AMF colonization levels between monocots and dicots is accurate for the fens in this study, and not merely a phenology-related sampling artifact.

DSE colonization

While plant-AMF interactions have received considerable attention, there are fewer studies of plant-DSE interactions. Thormann et al. (1999) and Addy et al. (2000) report the occurrence of these fungal symbionts in wetlands, but to our knowledge, this study represents the most comprehensive list of their occurrence across wetland species. The regular occurrence of DSE in our study makes us question whether these fungi have been overlooked or misidentified as AMF in other studies that report mycorrhizal coloniza-

tion in wetland plants. We found that DSE often cooccurred with AMF in the roots of several species, but also occurred regularly among most monocot species that were poor hosts to AMF (e.g., sedges and cattails; Table 2). Sedges often host DSE (Read and Handselwandter 1981; Muthukumar et al. 2004) and it is possible that DSE in sedges share functional similarity to AMF in other species (Jumpponen 2001; Muthukumar et al. 2004). The negative relationship between DSE and AMF across all species was weak, and may merely reflect the differences between dicots and monocots. However, this correlation could also indicate some weak competitive or antagonistic interaction between the two fungal groups, perhaps over root-derived C resources. Other studies have reported positive relationships between AMF and DSE (Ruotsalainen et al. 2002; Korhonen et al. 2004), highlighting the need for studies that explore the interactions between these two fungal groups, in addition to plant-DSE interactions.

Implications for AMF and DSE in fen plant communities

We hypothesize that differences in AMF and DSE colonization in monocots and dicots could affect diversity in fen communities Conceptual models of AMF-plant interactions suggest that when differences in the mycorrhizal responsiveness of dominant and subordinate plant species exist, mycorrhizas can influence plant diversity, primarily by mediating plant competition and influencing community evenness (van der Heijden 2002; Urcelay and Diaz 2003). Following similar logic to the conceptual models that describe the influence of AMF on plant community diversity, Jumpponen (2001) speculated that DSE might also help to structure communities.

In fens, AMF could help structure plant communities by influencing competition between monocot species and dicot species. Dicots constitute a majority of the species richness in the fens surveyed, but only a few of these dicot species account for more than 1% of the total plant coverage in any of the fens we surveyed. In contrast, three sedge and one cattail species account for over 40% of the vascular plant cover at BSF and LF, and at FF, *Typha angustifolia* is the most abundant species, constituting 16% of the plant cover (Dr. Carmen Chapin and Barbara Bedford, unpublished data). Thus, the fens in our study feature a small number of dominant monocot species and a considerably greater number of dicot species that are subordinate to them. If dicots colonized by AMF are affected by this symbiotic relationship, then AMF could affect fen communities by influencing the growth of these species relative to that of dominant monocots. If fen plants benefit from AMF colonization, AMF may help dicots to compete better with nonmycorrhizal sedges and cattails, leading to a more diverse community.

However, wetland plant responses to AMF are not well known. Because positive, negative, and neutral interactions of wetland plants with AMF have been reported in the literature (Miller and Sharitz 2000; Jayachandran and Shetty 2003; Dunham et al. 2003; Weishampel 2005), one should not assume that benefits typically ascribed to AMF (e.g., increased nutrient acquisition and growth) are conferred to mycorrhizal plant species in fens. Therefore, studies that directly measure fen plant and community response to AMF are needed to test hypothesis regarding AMF impacts on diversity in these wetland communities.

Like AMF, DSE might also exert some influence on fen plant community diversity. In fens, we found more DSE colonization among monocots than among dicots. As DSE have been reported to be both mutualists and parasites, their presence in fen communities could potentially increase or decrease competition among plants, with consequent effects on plant community diversity. As with AMF, additional research addressing fen plant response to DSE is needed to evaluate their role in influencing composition and diversity in species-rich fen plant communities.

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