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Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass *Panicum hemitomon* along a wide hydrologic gradient

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Abstract Although wetland plant species usually aggregate into zones that correspond with their water depth/dryness tolerances, it is not known whether associated arbuscular mycorrhizal (AM) fungi show a similar zonation. We assessed the distribution of AM fungi in two similar depressional wetlands dominated by the semi-aquatic grass *Panicum hemitomon* by sampling soil in plots along dry-to-wet gradients that spanned 80 cm in relative elevation, and identifying/counting viable AM fungal spores. We found that eight of nine AM fungal species were common to both of the wetlands. Within each wetland, there were significant differences in species composition related to relative water depth. The zonation patterns were not identical between wetlands but revealed that certain species were relegated to the drier portions of the gradient in both. No species were relegated to only the wet portions of the wetlands; those that dominated there were also present in the drier areas. Our data show that water depth is an important factor determining the distribution of the AM fungi, even when, as in our study wetlands, the host plant remains constant along a dry-to-wet gradient. This suggests that the fungi are not physiologically equivalent in their tolerance to wetland conditions.

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Introduction

Water depth is an important variable for determining both the biomass and the community composition of plants and other species in most wetlands (Hutchinson 1975; Spense 1982). When propagule pools are equal, both flooding and fluctuation in the water table have been found to reduce plant species richness (Weiher and Keddy 1995). In this way, surface water may be thought of as an environmental filter that eliminates those species that are not tolerant to flooding, while allowing the spread of those that are (Keddy 1992). Because wetlands are an ideal system for studying the role of physiological tolerances in determining plant species distribution, there has been considerable research on plant zonation in these systems. However, there has been little research on the zonation of associated organisms, namely the arbuscular mycorrhizal (AM) fungi, in response to flooding.

AM fungi have been found in the roots of many plants in wetlands (e.g., Stevens and Peterson 1996; Wetzel and van der Valk 1996), salt marshes (e.g., Brown and Bledsoe 1996; Hoefnagels et al. 1993), and aquatic systems (e.g., Clayton and Bagyaraj 1984). This is significant because the fungi are believed to require well-aerated soils, and are thought to be ill adapted to flooded conditions (Mosse et al. 1981). There are at least two, non-mutually exclusive, potential mechanisms by which mycorrhizal fungi may survive and function in the low-oxygen conditions of wetland sediment. First, the fungi may avoid oxygen stress by concentrating in well-oxygenated portions of the root system (Brown and Bledsoe 1996). Second, there may be some degree of fungal tolerance to conditions imposed by flooding, which is species specific. If there are differential tolerances to flooding, we would expect a shift in the presence and/or abundance of mycorrhizal fungal species along a

dry-to-wet gradient, with flood-tolerant species being more common in the wetter end of the gradient and flood-intolerant species in the drier end.

It is difficult to determine how flooding affects sporulation of mycorrhizal fungal species because making generalizations about the presence and abundance of AM fungal species along a wet-to-dry gradient requires minimization of variables such as host plant identity and climatic and edaphic variables. The AM fungi are considered to be generalists; however, the identity of the host plant is known to be an important factor affecting AM fungal sporulation rates (Bever et al. 1996; Hetrick and Bloom 1986). In most wetlands, minimizing differences in host plant identity along this gradient is difficult because plant species are aggregated into zones corresponding with their water depth/dryness tolerances (Mitsch and Gosselink 1993). Consequently, although previous studies have shown a shift in species composition along wetland gradients (e.g., Anderson et al. 1984; Khan 1993a, 1993b), they have not been able to eliminate differences in host plant species as a potentially major influence on this pattern.

In this study, we examined the composition of AM fungi in a monospecific stand of the semi-aquatic grass *Panicum hemitomon*. This grass is useful for the study of mycorrhizal patterns in wetlands because it grows along a wide hydrologic gradient (e.g., from dry roadsides to water about 1 m deep); this allowed us to examine the effect of flooding on AM fungal distribution while keeping the host plant constant. Specifically, we measured abundance of spores of different AM fungal species in plots with a range of hydroperiods in two depressional wetlands dominated by this grass.

Materials and methods

Study sites and soil collection

Soils for spore extraction, enumeration, and identification were collected from two freshwater wetlands in the Savannah River drainage basin in Aiken County, South Carolina, USA. These two wetlands are Carolina bays dominated by the semi-aquatic wetland grass, *P. hemitomon*. The bays are shallow, isolated depressional wetlands shown to have dilute nutrient pools and low productivity in comparison to other freshwater wetlands (Schalles and Shure 1989).

The two bays sampled in this study (Castor and Mona Bays) are similar in many important respects. Both are dominated by the same semi-aquatic grass, they have a similar hydroperiodicity, and they are both on the Williman soil series (loamy, siliceous, thermic Ultisols; Soil Survey Staff 1990). Previous chemical analyses have shown that the soils of both bays have a low pH (Mona Bay 4.5, Castor Bay 4.7) and low available phosphorus (Mona Bay 7.8 ppm, Castor Bay 8.8 ppm, measured as Bray P; S. Miller, unpublished data). Because the bays occasionally dry completely (during extended droughts), much of the accumulated organic matter oxidizes and, consequently, these bays have very low organic carbon in their soils (usually under 5%) even in the wettest zones. In a previous study conducted in August 1995 (Miller 1998), *P. hemitomon* was found to be mycorrhizal in these wetlands. In Castor Bay, total AM colonization in *P. hemitomon* roots decreased linearly from the driest (upland) portion of the bay (approximately 40%) to the bay shoreline (close to 0%) but then rose from 0 to low levels (5–12%) between water depths 20–60 cm. This, in part, led us to surmise that the wetter portions of the bay may support different mycorrhizal fungal species than the drier sections.

We established two transects that originated in the center, deepest portion of each bay and radiated outward toward the shoreline. These transects were in the same half of each bay, but each half was split and one transect was randomly located in each of the two bay quadrants. In each bay, three sampling elevations were chosen based on the hydrologic history of the bay over 2 previous years (Fig. 1), as measured by weekly staff gage readings. Although it was not possible to match the sampling elevations precisely between bays, the three elevations generally corresponded to predominantly dry, intermittently wet, and predominantly wet over the previous 2 years. In both bays, there was a difference of 40 cm in elevation between the wet and intermediate plots, and between the intermediate and dry plots. In both bays, the dry sites (i.e., sites where the water table was usually below the soil surface) were dry 95% of the time during the previous 2 years. In Mona Bay, the wettest site dried during a drought in the winter of 1996, and so it was dry 12% of the time as opposed to 0% in Castor Bay; the intermediate site was dry 25% of the time in Mona Bay and 34% in Castor Bay. At each of these three elevations, 1-m^2 plots were established along each transect in dense stands of *P. hemitomon*. In each plot, three replicate soil cores (approx. 5 cm diameter by 15 cm deep) consisting of soil and roots of *P. hemitomon* were collected for a total of six per elevation, 18 per bay, and 32 total, on 16 February 1997. Each plot was established within a dense stand of the grass, and although not quantified, the stem density appeared to be approximately equal at the three elevations sampled. The cores were refrigerated until spore extraction on 12 March.

Spore extraction and enumeration

To collect spores from the samples, we chopped the soil cores with roots into small pieces and mixed each sample manually. Spores were then extracted from the soil by blending a 50-cm^3 soil subsample in water for approximately 5 s in a Waring-type blender, collecting the spores from the mixture on a 38-μm sieve, and separating the spores from soil and other organic matter using a sucrose

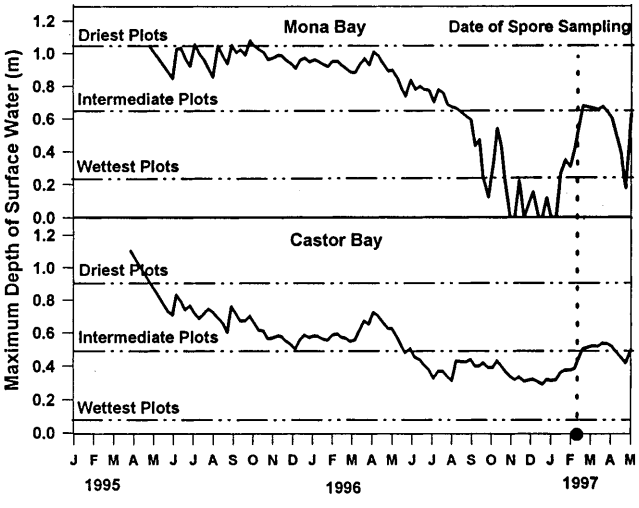

Fig. 1 Hydrographs of Mona and Castor Bays from early summer 1995 to early summer 1997. The *heavy solid line* represents the fluctuation in bay depth as measured from a stationary staff gage in the deepest portion of each bay; therefore, the line tracks change in maximum bay depth. The *horizontal* dotted-*dashed lines* represent the elevations of the sampling plots relative to the points on the staff gage. The *vertical dotted line* indicates the date of soil sampling for arbuscular mycorrhizal (AM) fungal spores

gradient centrifugation (Daniels and Skipper 1982). Spores were examined under a binocular stereoscope and a Nomarski interference microscope. Species identification was based on spore size, color, surface ornamentation, and wall structure using reference cultures from the International Collection of Vesicular and Arbuscular Mycorrhizal Fungi (INVAM) (Morton et al. 1993) and species descriptions (Schenck and Perez 1990). Only spores that appeared to be viable based on color, shape, surface conditions, and spore contents were counted. Spores from each sample were spread as evenly as possible over a petri plate underlain by a grid with 0.25-cm^2 squares. All species were counted at ×25 under a binocular stereomicroscope, except the small-spored *Acaulospora trappei*. For this species, spores were counted at ×50 in 30 randomly chosen grid squares. The diameters of as many spores as possible were measured (up to 30 per species) using an optical micrometer and used to convert average spore numbers per sample to spore volume.

Statistical analysis

The overall dependence of spore abundance, spore volume, and species richness of AM fungi on water depth was analyzed with analysis of variance (ANOVA), and differences between individual means were tested using Tukey's procedure in SAS (1986). Shifts in the AM fungal community composition were tested using multivariate ANOVA of abundance of the most common fungi. Only frequently occurring species could be included in this analysis and rare fungi were omitted. The spore counts were not normally distributed and the variance of counts was not homogeneous across the treatments; this pattern has been found in other studies of AM fungi (Bever et al. 1996; St. John and Koske 1988). Conversion of the spore counts into ranks greatly improved the normality and the homogeneity of variance and so the statistical analysis was performed on the ranks. The ranks were analyzed with a three-way multivariate ANOVA with profile contrasts (Morrison 1976) using the general linear models procedure of SAS (1986). The overall effects and the interaction of effects with the profile were tested using Wilks' lambda criterion because it is derived from a likelihood ratio approach (SAS 1986); however, multivariate tests using Pillai's trace and Hotelling-Lawley trace gave similar results. The interaction of water depth with the profile (i.e., the dependence of the shape of the profile on the treatments) is of particular interest because it specifically tests whether the relative ranks of spore numbers varied with water depth. When the multivariate tests were significant, the ranks of spore numbers of AM fungal species were tested individually. For all analyses, the water depth × transect × bay term was used as the error term, which tests whether the distributions of the fungi were consistent across the four transects. We were also interested in knowing whether the influence of the water on the distribution of species was consistent across the two bays, for which we tested the effect of water over the water depth × bay interaction.

Results

We found nine species of AM fungi in the two wetlands: *A. trappei*, *A. koskei*, *A. laevis*, *Enterophospora columbiana*, *Glomus clarum*, *G. etunicatum*, *G. gerdmannii*, *G. leptotichum*, and *Scutellospora heterogama*. All nine species were found at both bays, except *E. columbiana*, which was recovered from only one sample in the dry elevation at Mona Bay. The spores of *A. koskei* and *A. laevis* were indistinguishable under the dissecting microscope and so were counted together.

Our data show that there were significant differences in total spore abundance by water depth ($F = 11.67$, $df = 5$, $P = 0.0001$). Overall, the highest total spore numbers were in the intermediate and wettest portions of the Carolina bays. However, because spores were unequal in size (with *A. trappei*, for example, being several orders of magnitude smaller than *A. laevis*), spore volume was a more accurate measure than spore abundance of resource allocation to sporulation (Koske 1987; Morton et al. 1995). When the numerical abundance of *A. trappei* was converted to spore volume, their dominance in the wetter portions of the bay was reduced (Table 1). When fungal abundance was expressed in terms of spore volume, there were significant differences by water depth ($F = 5.12$, $df = 5$, $P = 0.002$), but no clear pattern (Table 1).

There were significant differences in AM fungal species richness by water depth ($F = 4.6$, $df = 5$, $P = 0.003$). The overall trend was for fewer species in wetter sites than in drier sites (Fig. 2). In both Castor and Mona Bays, the driest plots had the greatest number

Table 1 Abundance of arbuscular mycorrhizal (AM) fungal species present in two Carolina bay wetlands. Data are presented in terms of total spore volume/100 cm^3 of soil (in units of 10^6 μm^3) to give an indication of overall abundance. Spore volume was calculated by multiplying the average number of spores observed by the average volume of individual spores, as calculated from their average diameter and the formula for a sphere. Significant differences ($P < 0.05$) in total spore volume and counts are indicated by different letters (P indicates species present in sample but not included due to low abundance)

AM fungi	Total spore volume						Spore diameter (μm)	INVAM accession number
	Castor Bay plots			Mona Bay plots				
	Driest	Intermediate	Wettest	Driest	Intermediate	Wettest		
Acaulospora trappei	19.0	196.9	10.0	0.0	46.9	405.1	80	AU219
A. laevis/koskei	37.0	97.2	0.0	881.6	366.7	0.0	192	AU211/PL116
Enterophospora columbiana	0.0	0.0	0.0	13.0	0.0	0.0	104	CL356
Glomus clarum	12.6	82.2	30.3	65.7	P	323.7	213	FL979A
G. etunicatum	30.7	1.9	P	82.4	145.4	3.7	96	NE108A
G. gerdemannii	121.2	138.5	0.0	69.2	0.0	69.2	298	
G. leptotichum	0.0	0.0	452.5	135.2	124.8	93.6	215	NC171
Scutellospora heterogama	198.4	11.3	0.0	31.6	0.0	0.0	205	IL203
Total spore volume	420^b	528^b	493^b	1279^a	688^{ab}	896^{ab}		
Total spore counts	203^b	794^b	132^b	489^b	613^b	1607^a		

of species and the rank-abundance curves had shallow slopes, suggesting a relatively equitable distribution of species. In Mona Bay, this is also true of the intermediate plots, although there were fewer species. In contrast, the wet and intermediate plots in Castor Bay and the wet plots in Mona Bay show steep slopes, suggesting a strong sequential numerical dominance and a relatively less equitable species distribution (Tokeshi 1993).

There were significant differences in overall spore composition both between the bays and at different water depths (Table 2, Fig. 3). The relative abundance of the fungal species differed with water depth, as tested by the interaction of rank profiles with the water depth effect (Table 2). While the patterns between the bays were generally similar, differences between the bays were substantial enough to remove the significance of the water effect when tested over the water × bay interaction.

The distribution of five of the six fungal species depended significantly on water depth (Table 3). Three species were found only on the drier end of the gradient in both bays: *A. laevis* and *A. koskei* (counted together) and *S. heterogama*. Spores of *G. etunicatum* were present in the highest numbers in the drier two elevations of the gradient in both bays, but in small numbers in the wettest plots. Overall, there were species that were relegated to only the driest sites, but none relegated to only the wettest sites (Fig. 3). Spores of *A. trappei* were numerically dominant at the intermittent plots in Castor Bay and the wettest plots in Mona Bay. The spores of *G. clarum* were distributed evenly across all sites, although a large number were found in the wettest plots of Mona Bay. The spores of *G. leptotichum* were evenly distributed across the plots in Mona Bay, but were only found in the wettest plot of Castor Bay. The univariate analyses show that while most spore abundances differed with water depth, this was usually accompanied by a significant interaction term between bay and water depth (Table 3). Therefore, while depth appears to be an important determinant of AM fungal distribution, the exact distributional patterns differ between the bays.

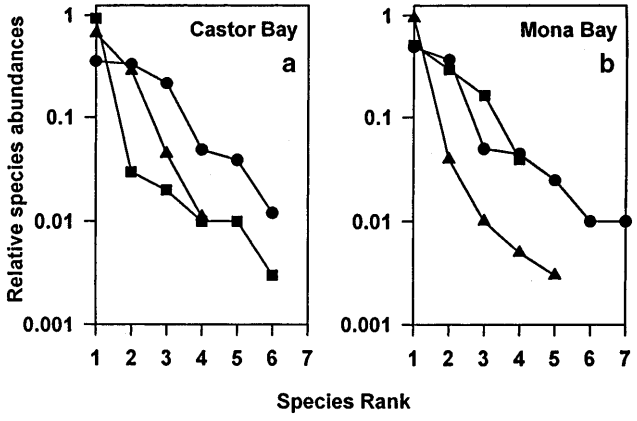

Fig. 2 Rank-abundance diagrams showing relative abundance of each AM fungal species at Castor Bay (**a**) and Mona Bay (**b**) (*circles* driest plots, *squares* intermediate plots, *triangles* wettest plots)

Discussion

Soil moisture has been shown to be an important determinant of the species spectrum of fungi in a given area (Read and Boyd 1986), and other researchers have shown differences in AM fungal composition in wetlands along a hydrologic gradient. Anderson et al. (1984) found that *Gigaspora gigantea* was associated with two wetland plants along a moisture gradient, and that *Glomus caledonium* was only found at the dry end. Similarly, Khan (1993a, 1993b) found *Glomus mosseae* to be abundant in drier areas and *Gigaspora margarita* to be more abundant in swampy areas. In those studies, however, separating the effects of the host plant on sporulation from the effects of the flooding was not possible. This study suggests that there is indeed zonation of AM fungi along a wetland gradient where the host plant is a constant. The shift in AM fungal species along the gradient suggested by the pattern in infection rates (Miller 1998) is borne out in the fact that spores of different AM fungal species were numerically dominant in the dry, intermediate, and wet elevations of Castor Bay (*G. etunicatum*, *A. trappei*, and *G. leptotichum*, respectively) and Mona Bay (*A. laevis*/*koskei*,

Table 2 Multivariate analysis of variance of effects of bay, water depth, and transect on spore counts of AM fungi. Spore counts were made for each water depth ($n = 3$) and these counts were ranked within each fungal species; the analysis was then carried out on the ranks. *Overall differences* presents tests for effects of treatments on total sporulation (considered across all fungal species). *Interaction with profile* presents tests for the specific hypothesis that the relative rank of spore abundance of the different fungal species depends on the designated treatment effects. All effects were tested using bay × transect × water depth as the error term

Effect	Numerator *df*	Denominator *df*	Wilks' lambda	*F* ratio	*P*
Overall differences					
Water depth	12	36	0.015	21.55	0.0001
Bay	6	18	0.117	22.64	0.0001
Water depth × bay	12	2	0.00016	12.93	0.074
Interaction with profile					
Water depth	10	4	0.0011	11.47	0.016
Bay	5	2	0.084	4.33	0.2
Water depth × bay	10	4	0.0008	13.5	0.011

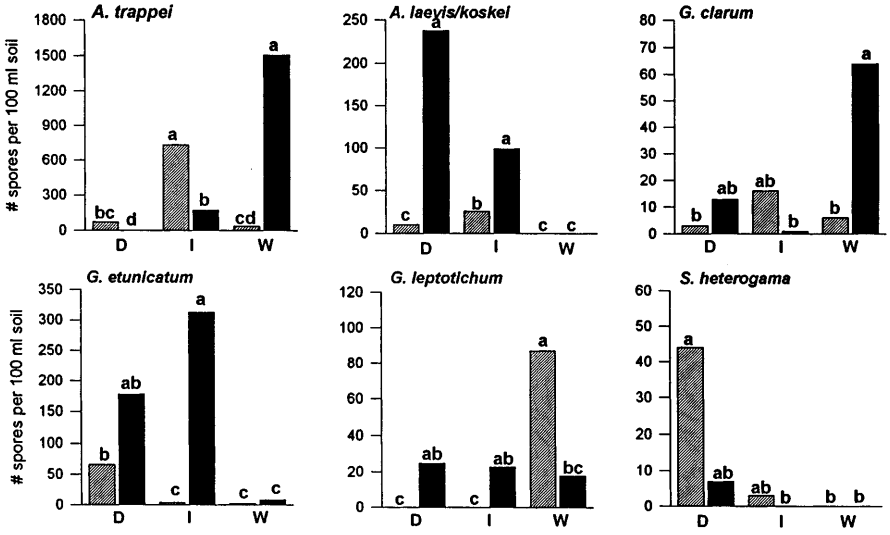

Fig. 3 Distribution of AM fungi at three sampling elevations (*D* driest plots, *I* intermediate plots, *W* wettest plots), by bay (*hatched bars* Castor Bay, *filled bars* Mona Bay). Significant differences ($P < 0.05$) in spore numbers are indicated by different letters. All statistical tests were done on spore ranks; however, mean sporulation is shown for ease of interpretation

Table 3 Results from the univariate analyses of variance of effects of bay and relative water depth on ranks of AM fungal spore counts, considering each fungal species separately. Shown are the sums of squares and significance levels of effects for each species. Spore counts were made for each plot and ranked within each species; the analysis was then carried out on the ranks. Effects were tested using bay × transect × water depth as the error term

	Bay	Water depth	Bay × water depth	Error
df	1	2	2	4
A. trappei	7	1313*	1562**	165
A. laevis/koskei	700**	1615**	481*	61
G. clarum	158	205	971	439
G. etunicatum	1003**	1328**	660*	76
G. leptotichum	190*	483*	1236**	84
S. heterogama	82	518*	58	146

*$P < 0.05$; **$P < 0.01$

G. etunicatum, and *A. trappei*, respectively). However, it remains a possibility that the patterns observed in spore distribution do not reflect the activity of these species within the roots, but rather the propensity of these species to sporulate along a moisture gradient. Current techniques do not allow us to identify whether these species were also dominant within the roots, but previous work on host influences on fungal growth rates suggests that patterns in sporulation do reflect differences in fungal density (Bever et al. 1996). Moreover, the distribution of species measured by spore abundance was supported by sporulation within trap cultures set up from soil from these sites (as in Bever et al. 1996) and grown within a neutral greenhouse environment (S.P. Miller, unpublished data).

The distribution of species that we observed, with several AM fungal species never being found in the wettest plots but none being restricted to the drier areas, suggests that the presence of flooding may eliminate some species. Specifically, since they were not found in the wettest end of the gradient, it is tempting to suggest that *A. laevis*, *A. koskei*, and *S. heterogama* are intolerant of flood conditions and cannot form functional associations with roots under these conditions. Flooding, however, can have both direct effects on the fungi and indirect effects through the host plant. With our limited knowledge of the natural history of AM fungal species, and of the influence of flooding on carbon allocation from the host plant to the fungi, it is not possible to identify the mechanism excluding these fungi from flooded sites. For example, the possibility remains that these species are able to form functional associations under flooded conditions, but are either unable to gain enough carbon from the grass to sporulate or cannot produce spores in flooded environments.

Although the deepest portions of these depressional wetlands will occasionally dry completely (during extended droughts), they are usually wet and represent a constant selective pressure on the fungal community for those species that can form or maintain functional associations with the host plant under these conditions. To our knowledge, there has been no assessment of relative tolerances of AM fungi to low-oxygen conditions. As is true of many other organisms, it is likely that the AM fungal species have a range of stress tolerances. Those species found in higher numbers in the wetter portions of the gradient (e.g., *A. trappei*, *G. leptotichum*, and *G. clarum*) must have previously formed functional associations with *P. hemitomon* under wet conditions in order to have undergone sporulation. However, it is also possible that an accumulation of spores of these species in wet areas is due to sporulation followed by a lack of spore germination. Le Tacon et al. (1983) reported that anaerobic conditions inhibited the germination of *G. mosseae*, but that this effect was reversible upon exposure of the spores to air. It is not clear that the inability of spores to germinate in wet soils is widespread across species, or even that it would be the main barrier to mycorrhizal fungal infection in wetlands. It has been suggested that once mycorrhizal formation has taken

place, mycorrhizas may endure prolonged exposure to flooding (Filer and Broadfoot 1968); thus species that germinated during a drawdown may survive in oxygenated portions of the root and root zone after reflooding.

Soil moisture appears to be a significant factor influencing the total number of spores found in a given area, but there have been conflicting reports in the literature as to the nature of this relationship. It has been suggested that because the AM fungi are obligate aerobes, flooding would reduce sporulation (Aziz et al. 1995), and spore numbers have been found to be negatively correlated to soil wetness and redox potential (Anderson et al. 1984; Khan 1993a, 1993b). In contrast, Rickerl et al. (1994) found an average of 5000 spores kg^{-1} in wet soil compared with 2740 spores kg^{-1} in drier soil and suggested that the high sporulation was a stress response of the fungi to the wet conditions. Abundance data are difficult to interpret without conversion to spore volume, however, and higher numbers of spores in wet areas, as was found in this study, may be an artifact of the prevalence of small-spored species in flooded areas. In the Carolina bays, the lack of a clear pattern in total spore volume along the gradient suggests that the fungi can gain a comparable amount of carbon from the plant for allocation to spores regardless of the extent or duration of flooding.

This study suggests that there are differences in the extent to which different mycorrhizal fungal species are successful symbionts in flooded conditions. This has implications for our basic understanding of the biology of these fungi, which have long been assumed to be intolerant of flooded conditions. An understanding of the distribution of these organisms is also a potentially important aspect of basic wetland ecology and wetland restoration. While the benefits of AM fungal symbiosis to wetland plants have not been well elucidated, it is becoming increasingly apparent that these fungi are commonly present, and in some cases ubiquitous (Cooke and Lefor 1998) in hydrophytes, including those occurring in recently restored wetlands (Turner and Friese 1998). The possibility that a flood gradient may result in a sorting of the AM fungal community should be considered in the context of wetland restoration and the use of "donor soils" from existing wetlands. If certain AM fungal species are more tolerant of wetland conditions than others, they may be more successful symbionts with hydrophytes and therefore the addition of soil from existing wetlands to those being restored or newly created could improve the success of planted or colonizing plants. To our knowledge, there is little available information on this topic and it is an area that warrants further study.

Although we found that spore abundance depends significantly on water depth, these findings are limited by the fact that this study was conducted only once. Monitoring spore numbers throughout the year would provide useful data, but temporal patterns would be confounded by seasonal fluctuations in water levels at sample sites. It would be more informative to examine the effects of flooding on spore abundances in a controlled setting, for example by collecting soil samples along a gradient and exposing them to different flood regimes experimentally. Using these types of approaches, we can better understand how flooding is a factor determining the composition of AM fungal species associated with wetland plants.

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