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The mycorrhizal status of an emergent aquatic, *Lythrum salicaria* L., at different levels of phosphorus availability

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Abstract The relationship between nutrient availability and mycorrhizal status has been well studied for terrestrial plant species, but has been examined rarely in aquatic and emergent aquatic species. The purpose of this study was to determine the effect of phosphorus availability on the arbuscular mycorrhizal (AM) status of an emergent aquatic, *Lythrum salicaria* L. *L. salicaria* was grown in hydroponic sand culture at five phosphorus concentrations (0, 100, 1000, 10 000, and 47 500 μg PO_4/l nutrient solution) for 49 days with or without mycorrhizal inoculum obtained from wetland soil. Inoculated plants at the lowest three phosphorus concentrations were colonized by AM, whereas there was no colonization of plants grown at the highest two phosphorus concentrations. Colonization by AM fungi occurred in conjunction with symptoms of phosphorus deficiency in *L. salicaria* under experimental conditions: plants at the lowest three phosphorus concentrations had lower biomass and higher root: shoot weight ratios than plants at the highest two concentrations. However, total biomass and internal phosphorus concentration did not differ between inoculated and control plants. Further studies are needed under conditions more closely mimicking natural dynamics.

Key words Arbuscular mycorrhizae · *Lythrum salicaria* · Phosphorus · Wetland · Emergent aquatic

Introduction

In terrestrial systems, there is a wealth of data relating arbuscular mycorrhizal (AM) colonization to plant mineral nutrition and nutrient availability (Marschner and Dell 1994; Smith and Read 1997). Phosphorus availability in particular has been shown to play an important role in plant/mycorrhizal relations (Mosse 1973a; Hayman 1983). Low phosphorus availability has been repeatedly shown to encourage AM colonization, which in turn improves plant phosphorus nutrition (Daft and Nicolson 1969; Hayman and Mosse 1971). This is frequently evidenced by increased plant growth, decreased root: shoot ratios, and increased internal phosphorus concentrations (Abbott and Robson 1984; Smith and Gianinazzi-Pearson 1988; Smith and Read 1997). In contrast, AM colonization is often reduced at high phosphorus supply levels, where few direct benefits of mycorrhizal colonization for the plant have been observed (Mosse 1973b; Jasper et al. 1979; Koide 1993).

Such data are almost entirely absent for aquatic and emergent aquatic plants, largely due to the long-standing paradigm that plants in aquatic systems are non-mycorrhizal (Harley 1969; Khan 1974). Studies of water gradients generally conclude that waterlogging discourages AM colonization (Anderson et al. 1984; Dhillion 1993; Rickerl et al. 1994; Stevens and Peterson 1996; Wetzel and van der Valk 1996). Yet arbuscular mycorrhizae are not completely absent from these systems. Mycorrhizal colonization, including arbuscular colonization, has been described for both submerged macrophytes (Søndergaard and Laegaard 1977; Clayton and Bagyaraj 1984) and emergent aquatic species (Khan and Belik 1995; Stevens and Peterson 1996; Cooke and Lefor 1998; Cantelmo and Ehrenfeld 1999). Other authors have found that AM associations in aquatic systems lack arbuscules (Liberta et al. 1983; Stenlund and Charvat 1994), suggesting that mycorrhizal colonization may be non-functional under submerged conditions (Anderson et al. 1984).

One of the first steps toward understanding the role of mycorrhizae in aquatic systems is determining whether plant/fungal/nutrient interactions are fundamentally the same for aquatic as for terrestrial plants. The anaerobic condition of waterlogged soil leads to nutrient dynamics substantially different from those of

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terrestrial systems (Gambrell and Patrick 1978). For example, the reduced state of waterlogged soils increases phosphorus availability (Shapiro 1958; Patrick and Khalid 1974). Given the divergent nutrient environments of aquatic and terrestrial systems, it seems inappropriate to assume that plant/mycorrhizal interactions in aquatic systems are necessarily similar to terrestrial systems.

Consequently, the goal of this study was to look at the AM colonization and plant response of purple loo sestrife, *Lythrum salicaria* L., at different levels of phosphorus availability. *L. salicaria* is an emergent aquatic native to Eurasia, that is a widespread invader of wetlands in North America (Thompson et al. 1987; Mal et al. 1992). Reports on the mycorrhizal status of *L. salicaria* in the field are varied. While some authors have reported *L. salicaria* to be non-mycorrhizal (Mejstrik 1972; Mal et al. 1992), others have found substantial mycorrhizal colonization (Stevens and Peterson 1996; Cooke and Lefor 1998). Laboratory trials indicated that *L. salicaria* is facultatively mycorrhizal (Stevens and Peterson 1996), but mycorrhizal colonization of this plant in the context of phosphorus availability has not been determined.

Materials and methods

To examine the effect of phosphorus availability on the mycorrhizal status of *L. salicaria*, a factorial experiment was undertaken with five phosphorus levels (0, 100, 1000, 10 000, or 47 500 μg PO_4/l nutrient solution) and two mycorrhizal treatments (inoculated or control). The phosphorus levels are equivalent to 0, 1.05, 10.5, 105, and 500 μM, respectively. The highest phosphorus concentration corresponds to half-strength Hoagland's solution. Four *L. salicaria* seedlings were randomly assigned to each combination of treatments, with a total of 40 plants.

Four-week-old *L. salicaria* seedlings were planted individually into 10-cm-diameter pots containing a 2:1 mixture of No. 40:No. 20 autoclaved sand. Inoculated plants received both root and spore inoculum that originated from a *Typha/Lythrum* floating mat at Lake Owasso, Roseville, Minn., USA (45°2'30"N, 93°07'30"W). Previous work at this site (Stenlund and Charvat 1994) identified four AM fungal species: *Glomus caledonium* (Nicol. and Gerde.) Trappe & Gerdemann, *G. albidum* Walker & Rhodes, *G. etunicatum* Becker and Gerdemann, and *G. microcarpum* Tul. & Tul. Each inoculated plant received 0.5 g wet weight field-collected *L. salicaria* roots, as well as approximately 100 spores isolated from the wetland soil using sucrose density centrifugation (Daniels and Skipper 1982). Inoculum was added directly to the seedling root system. The pots were individually placed in plastic saucers and both pot and saucer were covered with aluminum foil to prevent algal growth in the nutrient solution.

Plants were maintained in two environmental chambers under a 12 h:12 h, 30 °C:20 °C photo- and thermoperiod, and were randomized once a week to counter any environmental differences between or within the chambers. Average illumination values in the two chambers were 4500 lux and 4200 lux, respectively. Plants were watered with modified half-strength Hoagland's solution (Hoagland and Arnon 1938) containing the appropriate phosphorus level for each treatment. All solutions were standardized to a pH of 7.1. Plants were given completely fresh nutrient solution every other day. Additional solution was added on intervening days as necessary to insure that plants had continuous access to nutrient solution and that the sand substrate remained saturated. Plants were harvested after 49 days growth due to the large size and imminence of flowering in some individuals.

Each plant was removed from its substrate, the shoot separated from the roots, and the root system divided in half by fresh weight. The shoot and half the root system were dried at 65 °C and weighed to calculate total plant dry mass and root/shoot mass ratios. Shoot material was then ground and sent to the University of Minnesota Research and Analytical Laboratories for inductively coupled plasma atomic emission spectroscopy (ICP) analysis of plant tissue phosphorus concentration. Due to the small size of plants at lower phosphorus levels, material was bulked within each phosphorus/inoculation factor level combination to obtain sufficient material for analysis. Root material was analyzed in a like manner. Mean phosphorus content values for roots and shoots in each treatment were calculated using mean plant mass for each factor level combination.

The remainder of each root system was cleared with 10% KOH, acidified with 10% HCl, and stained with acid fuchsin using a protocol modified from Kormanik and McGraw (1982). Percent AM fungal colonization was determined by the gridline intersect method using a dissecting microscope (Giovannetti and Mosse 1980). Percent colonization was determined using the percentage of intersects with arbuscules, vesicles, or internal spores. Internal hyphae, external hyphae, or external spores were also noted, but not included in percent colonization calculations. Because roots were examined at ×50 magnification with this method, arbuscule presence was difficult to determine, and percent colonization values accurately reflect only vesicle and internal spore colonization. To confirm the presence of arbuscules, roots from each sample were mounted on slides and examined using a Wild M-20 brightfield microscope at ×100–400 magnification. For samples containing arbuscular mycorrhizae, arbuscular colonization was then evaluated using the magnified intersection method (McGonigle et al. 1990). Figures were prepared using a Nikon Eclipse E800 photomicroscope. Digital images were collected using a CoolCam liquid cooled three-chip color CCD camera (Cool Camera Company, Decatur, Ga.) and captured to a Pentium II 300 MHz personal computer using Image Pro Plus v3.0 software (Media Cybernetics, Silver Springs, Md.).

Because control plants did not show mycorrhizal colonization, percent colonization was compared statistically only among the inoculated treatments using one-way ANOVA. Total plant weight and root/shoot weight ratios were each compared among all treatments using two-way ANOVA. Post-hoc paired comparisons were made for each analysis using Tukey's Honestly Significant Difference (HSD) at $\alpha = 0.05$. All values were log transformed before analysis to normalize the data and homogenize variances. Due to lack of replication, statistical analysis was not performed for plant tissue phosphorus values.

Results

Mycorrhizal colonization

Inoculation resulted in mycorrhizal colonization for *L. salicaria* plants grown at the lowest three phosphorus concentrations (Fig. 1). AM fungal colonization was highest for plants grown at 100 or 1000 μg PO_4/l, followed by plants in the 0 μg PO_4/l treatment ($F = 116.69$, $P < 0.001$). Examination of root subsamples under high magnification showed that all inoculated plants in these treatments had arbuscular colonization, implying a functional mycorrhizal relationship (Fig. 2A, B). Using the magnified intersection method (McGonigle et al. 1990), arbuscular colonization averaged 9.2 ± 2.8% (± S.E.) in the 0 μg PO_4/l inoculated treatment,

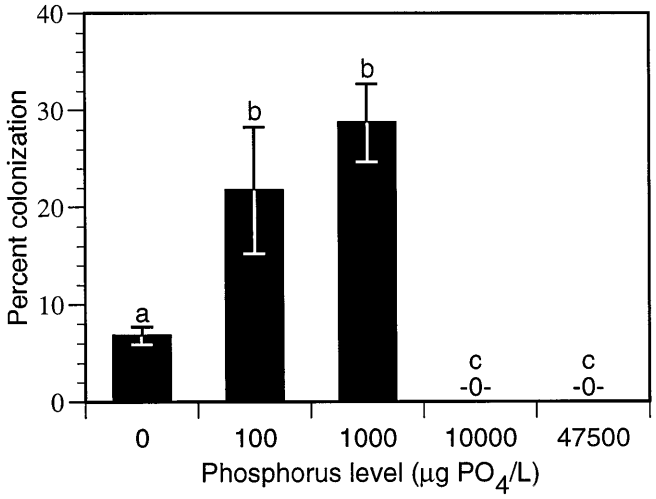

Fig. 1 Mean ±SE percent mycorrhizal colonization of inoculated *Lythrum salicaria* plants after 49 days growth at different phosphorus supply levels. Means with different letters are significantly different at $\alpha = 0.05$. Non-inoculated control plants at each phosphorus level did not exhibit mycorrhizal colonization and are not depicted

12.2±3.5% in the 100 μg PO_4/l inoculated treatment, and 35.0±3.5% in the 1000 μg PO_4/l inoculated treatment. Plants grown under 10 000 or 47 500 μg PO_4/l showed almost no mycorrhizal colonization. The inoculated plants in the 10 000 μg PO_4/l treatment had scattered incidence of external hyphae, but only one intersect for one plant showed internal AM structures (vesicles). Inoculated plants at 47 500 μg PO_4/l showed no AM colonization. The corresponding control plants at all phosphorus levels also showed no AM colonization, indicating that cross contamination of treatments did not occur.

A number of samples possessed thick-walled internal structures resembling spores more than vesicles (Fig. 2C). This suggests the presence of *G. intraradices* Schenck & Smith in many of the colonized samples. However, external spores were almost entirely absent from the samples and, thus, further taxonomic identification of AM fungal species was not attempted.

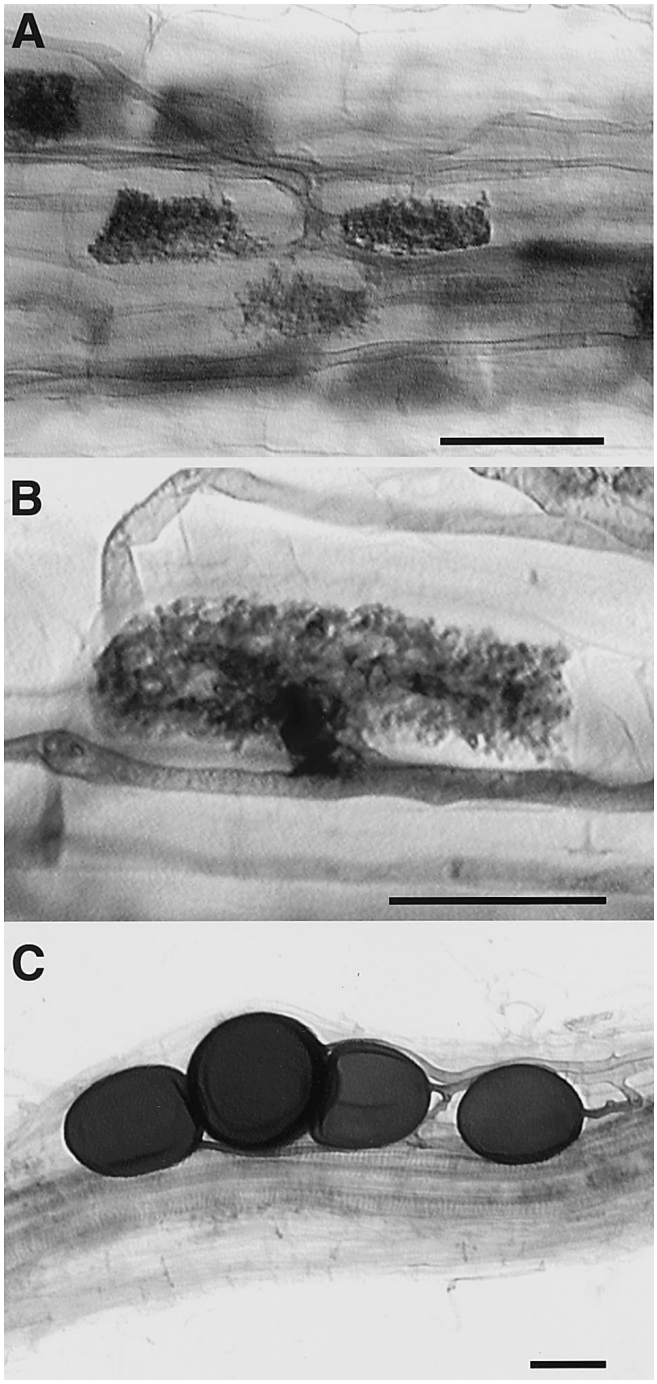

Fig. 2 Arbuscules (**A**, **B**) and internal spores (**C**) observed in roots of inoculated *L. salicaria* plants grown at 1000 μg PO_4/l nutrient solution; *bar* 50 μm for *A*, 25 μm for *B*, and 50 μm for *C*

Plant growth characteristics

Lythrum salicaria plants grown at 0, 100, or 1000 μg PO_4/l showed physical signs of phosphorus deficiency, regardless of inoculation treatment. Shoots and roots of plants in the 0 and 100 μg PO_4/l treatments exhibited anthocyanin accumulation and had severely stunted growth. Plants given 1000 μg PO_4/l had dark green leaves, rather than the reddish leaves found in the lower two treatments, but still lacked the biomass of plants at 10 000 or 47 500 μg PO_4/l, which were not visually distinguishable. The total dry mass values of plants in the lower three phosphorus treatments were significantly lower than those of plants in the two highest phosphorus treatments (P-level main effect $F = 71.19$, $P < 0.001$; Fig. 3A). Mycorrhizal inoculation, however, had no direct effect on total plant mass (inoculation main effect $F = 0.72$, $P = 0.40$), nor was there an interactive effect between mycorrhizal inoculation and phosphorus level (P-level by inoculation interactive effect $F = 0.55$, $P = 0.70$).

L. salicaria root/shoot mass ratios also differed significantly among phosphorus treatments (P-level main effect $F=80.51$, $P<0.001$), with plants grown at 100 μg PO_4/l having the highest root/shoot mass ratios, followed by plants grown at 0 and 1000 μg PO_4/l (Fig. 3B). Plants in the 10 000 and 47 500 μg PO_4/l treatments had significantly lower root/shoot mass ratios than any of the other three treatments. For this parameter, inoculation treatment also had a significant effect, with inoculated plants having significantly greater root/shoot mass ratios than control plants (inoculation main effect $F=7.64$, $P=0.010$). Phosphorus level and inoculation treatments showed no significant interaction ($F=1.30$, $P=0.29$).

Plant tissue phosphorus

Internal phosphorus concentration and content of harvested *L. salicaria* shoots and roots are presented in Table 1. Plants in the lowest two phosphorus treatments showed little difference in phosphorus concentration, whereas each of the higher phosphorus treatments resulted in substantially increased phosphorus concentrations (Table 1). In contrast, the differences in internal phosphorus concentration between inoculated and control plants within phosphorus treatments were small, particularly for the phosphorus treatments where mycorrhizal colonization occurred (0, 100, and 1000 μg PO_4/l). Internal phosphorus content at mean plant mass (Table 1) showed essentially the same pattern as internal phosphorus concentration, with little indication of increased phosphorus uptake in mycorrhizal plants.

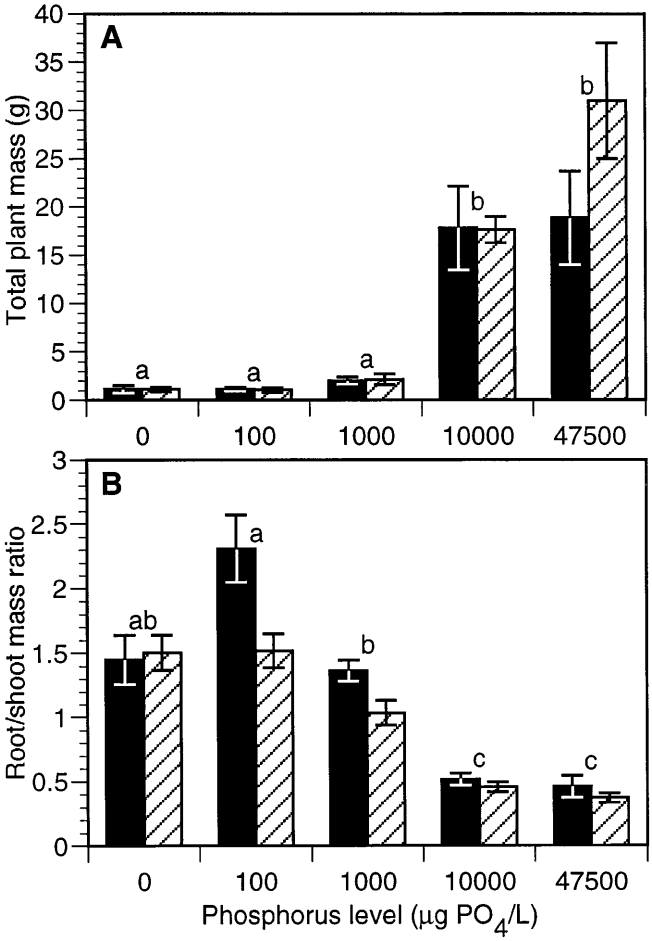

Fig. 3 Mean ±SE total plant masses (**A**) and root/shoot mass ratios (**B**) of inoculated (*solid bars*) and control (*hatched bars*) *L. salicaria* plants after 49 days growth at different phosphorus supply levels. Means with different letters are significantly different at $\alpha=0.05$ with respect to the phosphorus main effect

Discussion

AM colonization of *L. salicaria* increased with increasing phosphorus at the lower three phosphorus concentrations, but was completely absent at the highest two concentrations tested. This pattern is consistent with that predicted by Mosse (1978) for terrestrial plants, which generally has been borne out experimentally. For example, similar response patterns have been described for sorghum [*Sorghum bicolor* (L.) Moench.] by de Miranda et al. (1989), and sunflower (*Helianthus annuus* L.) by Koide and Li (1990). Mendoza and Pagani (1997) suggested that phosphorus is limiting to both fungus and plant growth at low concentrations.

Only limited information has been published on the mycorrhizal status of aquatic plants in relation to phosphorus availability. Tanner and Clayton (1985) found that colonization of a submerged *Ranunculus* species was lower when rock phosphate was added than when rock phosphate was absent. Wetzel and van der Valk (1998) attempted to look at mycorrhizal colonization, nutrient status, and water level of three wetland species, but omitted the mycorrhizal component of the study because of inadequate colonization levels in the inoculated treatments. A number of other studies have correlated the mycorrhizal status of emergent aquatics to nutrient availability in the context of a water gradient (Anderson et al. 1984; Rickerl et al. 1994; Wetzel and van der Valk 1996; Turner and Friese 1998; Miller et al. 1999). In general, these studies found decreased AM presence with increased moisture and nutrient levels. However, the large number of covarying characteristics in these systems make it impossible to attribute the observed mycorrhizal patterns to any characteristic in particular.

Colonization by AM fungi in this study was clearly associated with phosphorus stress in *L. salicaria*. Shamsi and Whitehead (1977) previously described increased root/shoot ratios and decreased growth of *L. salicaria* in response to phosphorus deficiency. The plants grown at the lowest three phosphorus concentrations in the present study exhibited these symptoms, as well as in-

Table 1 Tissue phosphorus concentration and total phosphorus content of *Lythrum salicaria* shoots and roots grown at different phosphorus supply levels

Nutrient solution concentration ($\mu g\ PO_4/l$)	Shoot tissue phosphorus concentration (mg P/g plant weight)		Root tissue phosphorus concentration (mg P/g weight)	
	Inoculated	Not inoculated	Inoculated	Not inoculated
0	0.31	0.30	0.21	0.21
100	0.35	0.30	0.28	0.28
1000	0.56	0.56	0.54	0.44
10000	2.75	2.45	1.29	1.38
47500	5.02	4.50	2.30	3.10
Nutrient solution concentration ($\mu g\ PO_4/l$)	Shoot tissue phosphorus content (mg P/plant)		Root tissue phosphorus content (mg P/plant)	
	Inoculated	Not inoculated	Inoculated	Not inoculated
0	0.145	0.134	0.141	0.140
100	0.114	0.124	0.218	0.171
1000	0.474	0.567	0.614	0.484
10000	31.933	29.523	7.977	7.670
47500	67.057	100.935	12.609	26.458

ternal phosphorus concentrations well below the optimal range for plant growth (3–5 mg PO_4/g dry plant matter; Marschner 1995). Emery and Perry (1995) measured phosphorus concentrations of *L. salicaria* shoots in 12 wetlands around the Minneapolis/St. Paul metro area and found concentrations ranging from 1.39 to 3.96 mg PO_4/g. Templer et al. (1998) reported even higher phosphorus concentrations for *L. salicaria* in a New York wetland ($\sim$5.75 mg PO_4/g). These internal phosphorus concentrations are comparable to those seen in the highest two treatments in the present study, which did not become mycorrhizal when inoculated. This suggests that high levels of AM colonization of this species do not occur under wetland field conditions. Indeed, Stevens and Peterson (1996) found only very low levels of colonization under wet conditions in the field. However, because no study has looked at both the mycorrhizal status and nutrient status of *L. salicaria* under field conditions, no definitive conclusions can be drawn.

The only observed growth response to mycorrhizal inoculation was an increase in root/shoot mass ratio. This pattern contrasts with the decrease in root/shoot ratio usually described in response to AM colonization in terrestrial systems (Smith and Read 1997). It is unclear whether this greater allocation to roots represents some benefit under aquatic conditions, or is indicative of lack of benefit from mycorrhizal colonization. Total plant mass did not differ between inoculated and control treatments, nor was there evidence for increased phosphorus in the plant tissue of colonized plants. Lack of growth benefit in pot-culture studies of terrestrial plants has been attributed to factors such as the carbohydrate cost of supporting the fungus, especially under low light conditions, (Bethlenfalvay et al. 1983; Son and Smith 1988), mycorrhizal benefit only occurring during certain stages of the plant life cycle (Sanders and Fitter 1992), or introduction of non-beneficial soil microorganisms with the non-sterile inoculum (Hetrick et al. 1986; Cerligione et al. 1988). Any of these factors could have had an effect in the present study. It is also possible that the experiment simply did not last long enough for a growth benefit to be observed.

Nevertheless, it is clear that mycorrhizal colonization of *L. salicaria* occurs in conjunction with plant phosphorus deficiency, as would be predicted from terrestrial systems. The extent to which *L. salicaria*, or any other aquatic plant, benefits from such colonization has yet to be determined. Showing plant benefit is notoriously difficult under field conditions even in terrestrial systems (Smith and Read 1997), and is likely to be much more difficult in highly dynamic aquatic systems where AM are relatively rare. Consequently, further controlled studies mimicking natural conditions as closely as possible are needed.

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