Mycorrhiza (2002) 12:277–283
DOI 10.1007/s00572-002-0184-7

ORIGINAL PAPER

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Phosphorus, arbuscular mycorrhizal fungi and performance of the wetland plant *Lythrum salicaria* L. under inundated conditions

Received: 31 January 2002 / Accepted: 21 May 2002 / Published online: 5 July 2002

Abstract The role of arbuscular mycorrhizal (AM) fungi in aquatic and semi-aquatic environments is poorly understood, although they may play a significant role in the establishment and maintenance of wetland plant communities. We tested the hypothesis that AM fungi have little effect on plant response to phosphorus (P) supply in inundated soils as evidenced by an absence of increased plant performance in inoculated (AM+) versus non-inoculated (AM–) *Lythrum salicaria* plants grown under a range of P availabilities (0–40 mg/l P). We also assessed the relationship between P supply and levels of AM colonization under inundated conditions. The presence of AM fungi had no detectable benefit for any measures of plant performance (total shoot height, shoot dry weight, shoot fresh weight, root fresh weight, total root length or total root surface area). AM+ plants displayed reduced shoot height at 10 mg/l P. Overall, shoot fresh to dry weight ratios were higher in AM+ plants although the biological significance of this was not determined. AM colonization levels were significantly reduced at P concentrations of 5 mg/l and higher. The results support the hypothesis that AM fungi have little effect on plant response to P supply in inundated conditions and suggest that the AM association can become uncoupled at relatively high levels of P supply.

Keywords AM fungi · Inundation · Phosphorus · Wetland communities

Introduction

The importance and functioning of arbuscular mycorrhizal (AM) associations in terrestrial systems are well documented, but this is not the case for aquatic or semi-aquatic systems (White and Charvat 1999). While many studies have documented the occurrence of AM fungi in aquatic systems, few have attempted to clarify their importance (see Khan and Belik 1995 for a review). Benefits to maintaining the AM association under inundated conditions have, however, been suggested for *Oryza sativa* (Solaiman and Hirata 1996, 1997, 1998; Purakayastha and Chhonkar 2001), and *Casuarina equisetifolia* (Osundina 1998). These beneficial effects of AM fungi in aquatic and semi-aquatic environments suggest some parallels with terrestrial systems.

In terrestrial systems, improved phosphorus (P) acquisition is the most common benefit attributed to the AM association (Smith and Read 1997). In terrestrial soils, a depletion zone often develops around roots, resulting from a faster rate of nutrient uptake than can be replenished by diffusion, the main process for the movement of P to the root surface (Marschner 1995). AM fungi, by extending their hyphae beyond the zone of depletion, are able to tap into a supply of P otherwise unavailable to the plant and in this way provide a benefit to the host (Smith and Read 1997; Smith et al. 2001). However, rates of diffusion in terrestrial systems are limited by water availability (Nye and Tinker 1977) and, thus, the depletion zone should be minimized in inundated soils. We propose, therefore, in inundated soils that AM fungi provide little benefit in terms of P acquisition and that this is reflected by the absence of enhanced performance by AM-inoculated plants grown under inundated conditions.

AM fungi have been implicated also in the structuring and maintenance of terrestrial plant communities (Van der Heijden et al. 1998). Given this role, significant impacts on plant community composition and ecosystem functioning may result from events that lead to the uncoupling of the AM association. In terrestrial systems, AM uncoupling is effected by increased P availability (Smith and Read 1997). This has not been determined in aquatic systems, although altered patterns of nutrient cycling, through the addition of sewage discharge, fertilizer amendments and accelerated watershed runoff, have

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resulted in large fluxes of P and other nutrients to receiving waters across North America (Daniel et al. 1998; Correll 1998). Wetlands, and more specifically wetlands plants, are increasingly being recognized for their importance in moderating the effects of flooding and drought, in providing habitat, and as filters of commercial and agricultural effluent (Keddy 2000). Therefore, it is critical to understand the factors that can influence plant performance, community structure and, consequently, ecosystem functioning in wetlands.

Given the paucity of information regarding the functioning of AM fungi in aquatic systems, and the potential impacts AM fungi may have on wetland plant community structure, this study was designed to determine the relationship between P supply, AM fungi, and plant performance under inundated conditions. The wetland plant species *Lythrum salicaria* L. was chosen as a test species due to its prevalence in wetland habitats in North America (Thompson et al. 1987) and its capacity to harbor AM fungi under inundated conditions (Stevens and Peterson 1996). Two questions are addressed in this study: 1. Under inundated conditions, do AM fungi make a positive contribution to plant performance when plants are grown with limited available P? 2. Under inundated conditions, is there a negative correlation between P supply and levels of AM colonization?

Materials and methods

Experimental design

To determine the relationship between P supply, AM fungi and plant performance under inundated conditions, *L. salicaria* plants were grown with or without a source of AM inoculum (AM+, AM–), at one of five levels of P supply (0, 1.25, 5, 10, 40 mg/l). The experiment was a completely randomized design with 10 replicates per treatment combination, for a total of 100 plants.

Pretreatment

Seeds of *L. salicaria* were collected from several locations in Guelph, Ontario in the fall of 1997 and refrigerated. In the fall of 2000, seeds were scattered onto the surface of filter paper moistened with distilled water in 15-cm Petri dishes sealed with Parafilm and the dishes kept under greenhouse conditions. Lighting was supplemented to maintain a 16/8-h light/dark cycle (70 µmol m^{-2} s^{-1} minimum light intensity). After 6 days, 192 germinated seedlings were transferred individually to sand-filled (Nepheline syenite, Unimin Canada Ltd., Blue Mountain, Ontario, Canada) seedling trays. Plants were watered when necessary to maintain moist soil conditions and fertilized with a modified (1/2 strength for all nutrients except P which was added at 1/4 strength) Long Ashton solution (Hewitt 1966) 2 weeks after transfer to the seedling trays.

AM inoculation

After 6 weeks of growth, 100 plants were selected randomly from the seedling trays and transplanted to sand-filled, clear, 1-l polypropylene containers (15 cm high, 11 cm diameter, TwinPak, Newport News, Va., USA). Several small holes were made in the bottom for drainage. One half of the seedlings were inoculated with AM fungi by placing approximately 3 g of finely chopped AM-colonized leek (*Allium porrum* cv. Giant Musselburgh) roots in a hole in the sand into which the plants were transferred. To ensure compatibility between the AM fungi and *L. salicaria*, AM cultures were established from soils collected from several wetland sites in Southern Ontario where *L. salicaria* was abundant. AM colonization of the leeks was verified following staining with Chlorazol Black E (Brundrett et al. 1984) and viewing at ×200 magnification using a Leitz photomicroscope. No attempt was made to identify the AM fungal species present in the inoculum. Non-inoculated plants received a root wash prepared by collecting the filtrate from washed AM-colonized roots after passing through a series of sieves (smallest pore size 20 µm). Lids with a 1-cm-diameter hole in the middle were fitted onto the container to allow the seedling to grow through but also to prevent rapid drying. A second 1-cm-diameter hole was located off center to allow watering. A total of 50 inoculated and 50 non-inoculated plants were transferred to the containers and grown under greenhouse conditions for a 6-week period to permit seedling establishment. Container locations were randomized at approximately 12-day intervals.

Treatment application

To facilitate flooding, each container was placed directly into a second 15×11-cm container that lacked drainage holes. Deionized water was added until the soils were inundated (water levels reached the soil surface). Phosphorus was added as $NaH_2PO_4 \cdot 2H_2O$. All other nutrients and micronutrients were maintained at one-fifth the concentration of standard Long Ashton nutrient solution (Hewitt 1966). P levels were checked at 12-day intervals. Water samples were collected in AccuVac ampules (Hach Co., Loveland, Colo., USA) from two containers per treatment combination. Orthophosphate levels were determined using the molybdovanadate method for orthophosphate (Hach Water Analysis Handbook, 3rd edn. Hach Co.) and quantified with a DREL 2010 spectrophotometer (Hach Co.). Mean P levels per treatment combination were determined and P added to maintain the desired treatment level.

Plant performance

Total plant height (main shoot + all branches) was determined prior to treatment application and biweekly until harvesting. Plants were harvested 56 days after treatment application and above and below-ground plant performance quantified. Pots were emptied under water and the root systems gently agitated to remove any remaining sand particles. Roots and shoots were separated, placed in a salad spinner to remove excess moisture, lightly blotted between paper towel, and the fresh weights obtained. Dry weights of the shoots were obtained following drying at 80°C for 24 h. Root systems were stored in 50% ethanol. Entire root systems were digitized using a Hewlett Packard ScanJet 4C/T scanner and the total root length and total root surface area determined using WinRhizo (Regent Instruments Inc. Quebec City, Quebec). A subsample of non-woody fine roots was randomly selected from each plant in each treatment, fixed in 50% ethanol, cleared in 5% KOH and stained with Chlorazol Black E (Brundrett et al. 1984). For each sample, the percentages of AM fungal structures (arbuscules, vesicles, internal hyphae, external hyphae, spores) and non-AM fungal contaminants were determined following the assessment of 100 intersections per slide at ×250 magnification (McGonigle et al. 1990).

Data analysis

All statistical analyses except plant height were conducted using the Generalized Linear Model (Proc GLM) in SAS (SAS Institute). Plant height was analyzed using a Mixed Model (Proc Mixed) with repeated measures and initial plant height included as

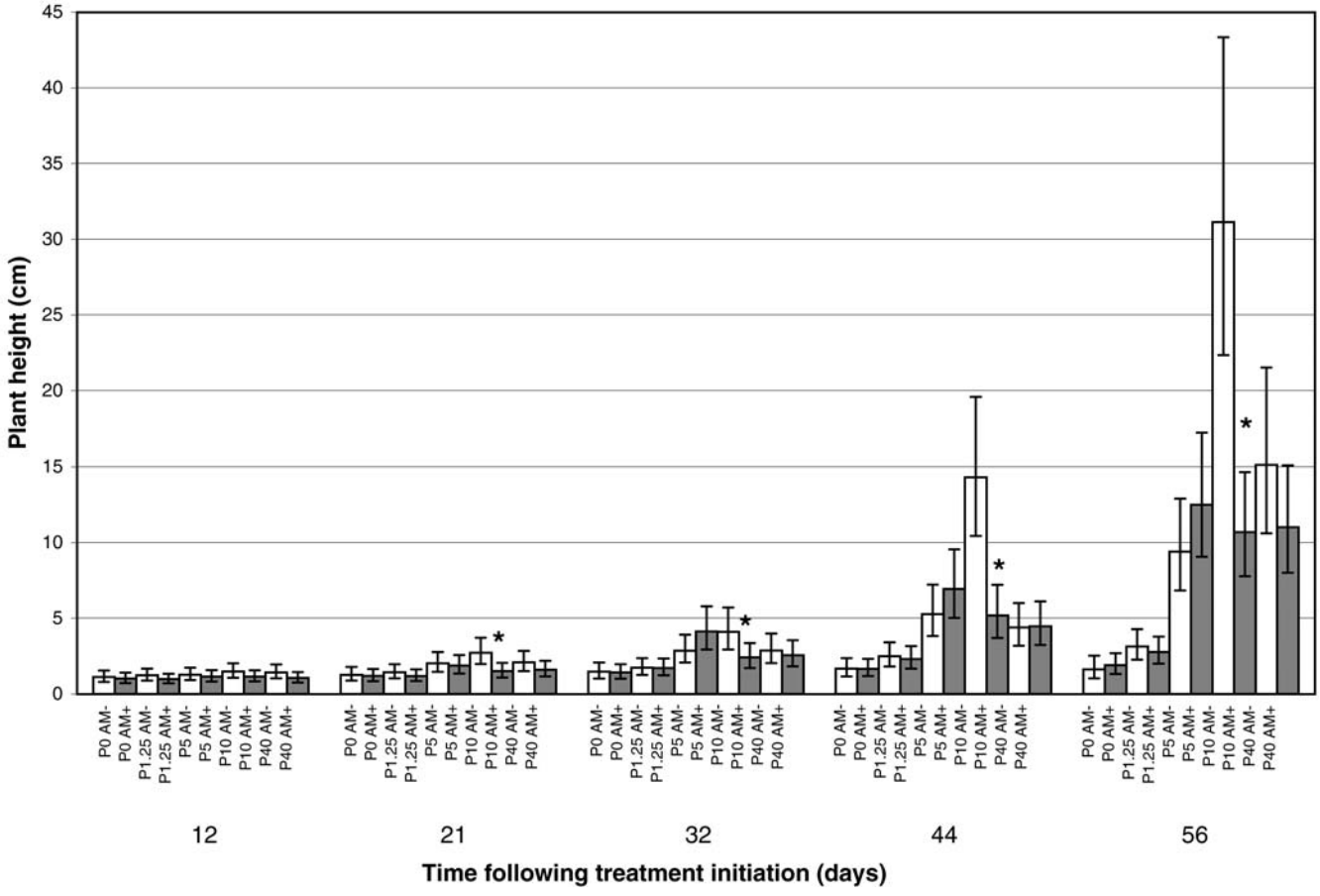

Fig. 1 Repeated measures analysis of the effect of arbuscular mycorrhizal (AM) fungi on plant height at each of five levels of phosphorus (P) supply. Data presented are back transformed, least squares means with 95% confidence intervals. * indicates significant difference between colonized and non-colonized plants within a single level of P supply ($P<0.05$) (*P0* P withheld, *P1250* 1.250 mg/l P, *P5000* 5 mg/l P, *P10000* 10 mg/l P, *P40000* 40 mg/l P, *AM–* non-inoculated with AM fungi, *AM+* inoculated with AM fungi)

a covariate. Since we were only interested in comparing the performance of inoculated versus non-inoculated plants at each level of P supply, comparisons were conducted using contrasts. To satisfy the requirements of normality and equal variance, the following transformations were used: plant height, root and shoot fresh weight, shoot dry weight, shoot fresh/dry weight ratio $y=\log(y)$; shoot/root fresh weight ratio, root length and root surface area = $\mathrm{sqrt}(y)$; arbuscular, internal and external hyphal colonization, other colonization $y=\log(y+1)$; vesicular colonization $y=1/\log(y+10)$.

Results

Total plant height generally increased with time and with increasing P supply (Fig. 1); however, significant differences ($P<0.05$) between AM– and AM+ plants were detected only at P levels of 10 mg/l. Within 3 weeks of treatment application, AM– plants in the 10 mg/l P treatment had a significantly greater total shoot height than the AM+ plants, a trend that persisted for the duration of the experiment (Fig. 1). There were no detectable differences ($P<0.05$) between AM+ and AM– treatments at any level of P supply in shoot fresh weight, shoot dry weight, root fresh weight, total root length or total root surface area, although, in general, all increased with increasing P supply up to 10 mg/l then decreased at 40 mg/l (Figs. 2, 3). Shoot fresh/dry weight ratios increased with increasing P supply and, overall, were significantly lower in the AM– treatment. Within P treatments, the shoot fresh/dry weight ratio was significantly lower in the AM– treatment at 10 mg/l P than in the AM+ treatment. Shoot/root fresh weight ratios increased with increasing levels of P but were not significantly affected by AM inoculation (Fig. 2).

Levels of AM colonization generally decreased with increasing P supply (Fig. 4). Arbuscular colonization levels were highest at 0 and 1.25 mg/l P, intermediate at 5 mg/l and lowest at 10 and 40 mg/l (Fig. 4). Vesicular colonization and internal hyphal colonization were significantly higher in the 0 and 1.25 mg/l P treatments than the 5, 10, or 40 mg/l P treatments (Fig. 4). External hyphal and colonization levels were significantly lower in the 10 and 40 mg/l P treatments than the 0 and 1.25 mg/l P treatments, while intermediate levels were found at 5 mg/l P (Fig. 4). There were no detectable differences in levels of non-AM fungal contaminants.

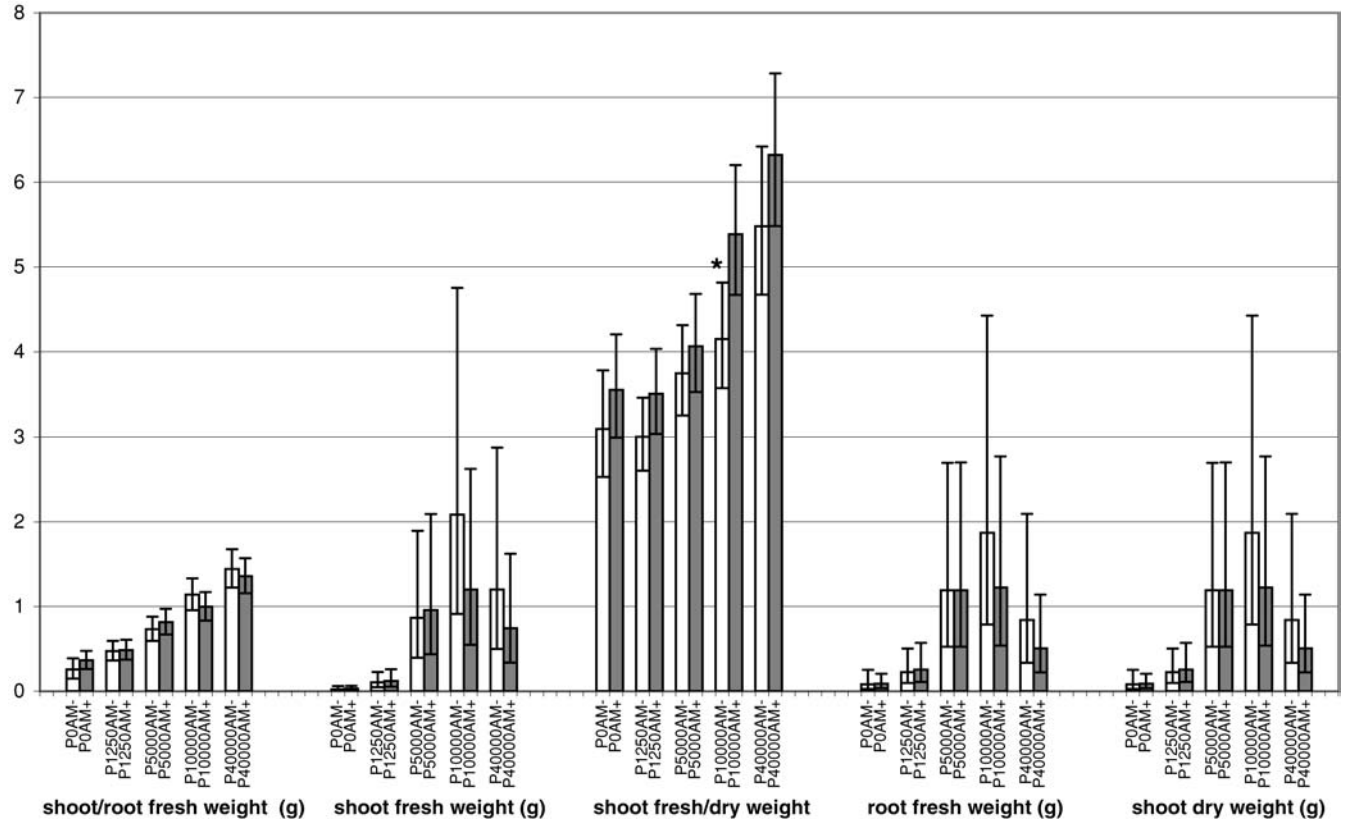

Fig. 2 Effects of AM fungi on shoot/root fresh weight ratio, shoot and root fresh weight, shoot fresh to dry weight ratio and shoot dry weight at each of five levels of P supply. Data presented are back transformed, least squares means with 95% confidence intervals. * indicates significant difference between colonized and non-colonized plants within a single level of phosphorus supply ($P<0.05$). Abbreviations as in Fig. 1

Discussion

P supply and plant response

The phosphorus levels used in this study corresponded to those used by White and Charvat (1999) and represent the range of P concentration detectable by the equipment employed. While these levels far exceed levels required to designate a water body as eutrophic (20 µg/l; Daniel et al. 1998 and references therein), they are considerably less than those used in Long Ashton nutrient solution (approximately 200 mg/l; Hewitt 1966). Since plant performance was reduced at the lowest levels of P supply, 0 and 1.25 mg/l, peaked at 10 mg/l P, then decreased at 40 mg/l P, it is likely that the levels chosen were sufficient to span the range of P response from deficiency to toxicity. Furthermore, this suggests that the optimal P levels for growth of *L. salicaria* in this study occurred between 5 and 40 mg/l.

In a similar study, White and Charvat (1999) examined the effects of P supply, mycorrhizal status and plant performance of *L. salicaria* under drained as opposed to inundated conditions. They did not, however, find a reduction in plant performance at the highest level of P supply, 47.5 mg/l P, even though this was higher than the levels we employed (40 mg/l P). An important distinction between the two studies, however, was that P levels in our study were monitored at 12-day intervals and topped up if needed, while this was not the case in the study of White and Charvat (1999). As a result, P supply over the course of the experiments probably differed in the two studies and may explain the disparity in plant performance.

AM contribution to plant performance

The differences in plant height became evident 3 weeks following inundation and by the end non-inoculated plants were approximately threefold higher than inoculated plants at 10 mg/l P. AM– plants also had a lower shoot/fresh to dry weight ratio, suggesting that these plants were woodier than AM+ plants. The mechanisms behind this are unknown, although AM fungi may have been a carbon drain limiting plant development soon after inundation, and this response was simply augmented with time. Further research is required to ascertain the factors involved in this response. Although the significance of this is unclear, it does indicate that AM fungi have the potential to influence plant morphology in inundated soils.

In terrestrial systems, colonized plants often differ in their patterns of resource allocation to roots and shoots compared with non-colonized plants, which may be reflected by an increase in shoot/root mass ratios in colo-

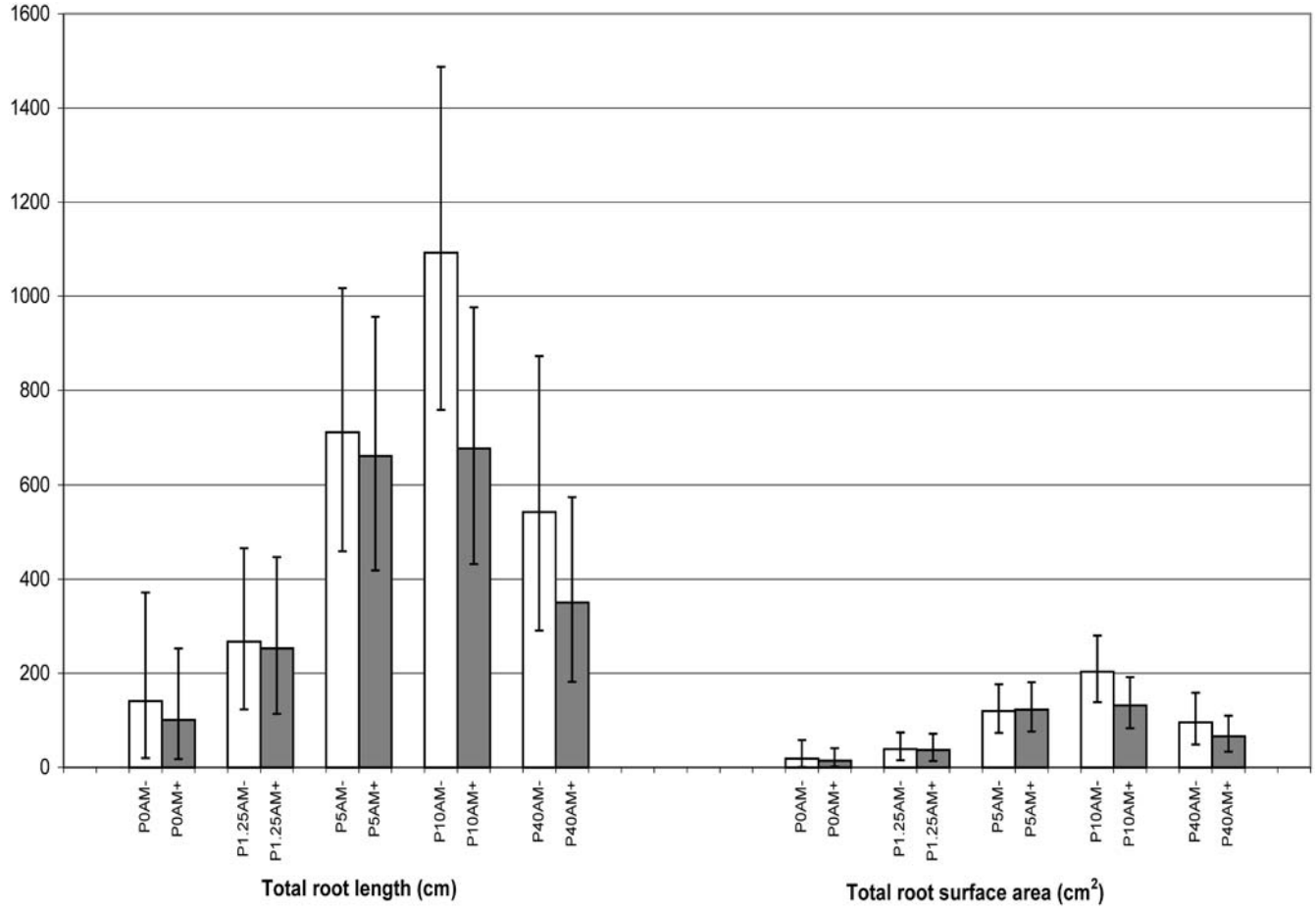

Fig. 3 Effects of AM fungi on total root length and total root surface area at each of five levels of P supply. Data presented are back transformed, least squares means with 95% confidence intervals. Abbreviations as in Fig. 1

nized plants, or a reduction in biomass of the root system (Smith and Read 1997). We did not, however, detect differences in shoot/root ratios between inoculated and non-inoculated plants at any level of P supply. It was not possible to obtain root dry weights, since this material was processed for the assessment of AM colonization levels; thus, the effect on root dry weights and ratios constructed from this value are unknown.

When assessed in terms of shoot dry weight, shoot fresh weight, total shoot height or height of the main stem, the presence of AM fungi did not lead to an increase in plant performance. In fact, the only detectable effect of AM fungi on plant performance was a reduction in plant height and an increase in the shoot fresh to dry weight ratio compared with non-inoculated plants at 10 mg/l P. The mechanisms behind this are unknown as is its significance, yet it does indicate that AM fungi have some potential to influence plant morphology in inundated soils. There was also no effect of AM inoculation on plant performance of *L. salicaria* grown across a range of P levels in drained soils; total dry mass was not significantly affected by AM inoculation (White and Charvat 1999). While a reduction in plant performance associated with AM colonization, or a lack of an effect, is not uncommon (Johnson et al. 1997), it is unlikely that this is attributable to incompatibilities between the host and fungus in both cases. In the study of White and Charvat (1999) and our study, AM inoculum was obtained from wetland habitats in which *L. salicaria* was growing.

While the lack of enhanced performance in inoculated versus non-inoculated plants under inundated conditions contradicts the results of previous studies, this may be attributable to differences in methodologies and limitations of these studies. In several cases, measures of performance were not compared through comprehensive statistical analysis (Iqbal et al. 1978; Tanner and Clayton 1985a; Miller and Sharitz 2000), or data were confounded by differences in inoculated and non-inoculated plants prior to inundation or flooding (Solaiman and Hirata 1996) or the pooling of data (Solaiman and Hirata 1995). In other cases, descriptions and micrographs of the fungi suggest highly atypical mycorrhizal associations (Wigand and Stevenson 1994, 1997) or the plant species investigated were not wetland species (Hartmond et al. 1987; Osundina 1998). The apparent absence of a beneficial growth response in inoculated plants in the current study does not necessarily imply that field-grown plants

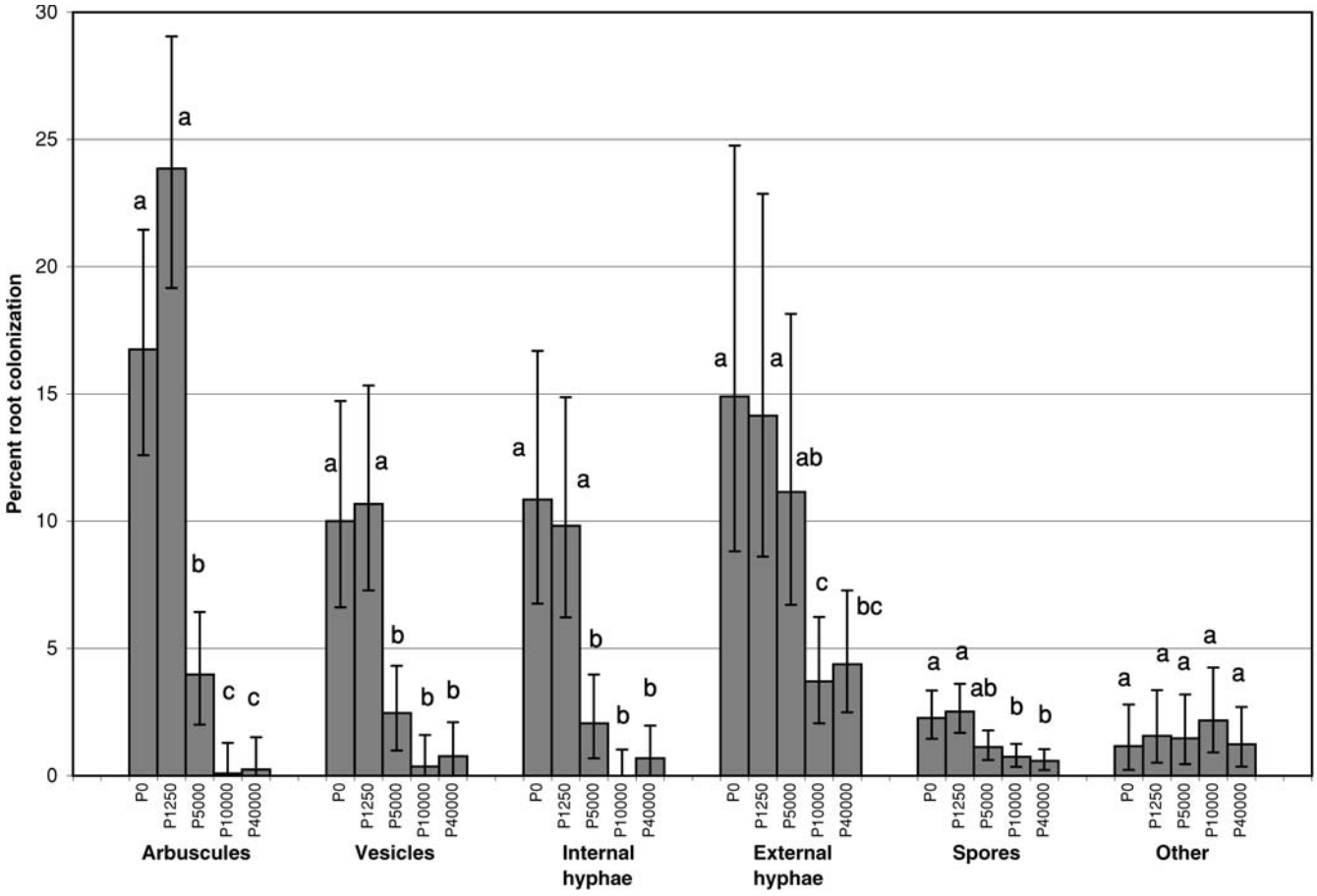

Fig. 4 Effects of P supply on AM (arbuscules, vesicles, internal hyphae, external hyphae and spores) and non-AM (other) fungal colonization levels. Data presented are back transformed, least squares means with 95% confidence intervals. Identical letters within a measure of colonization indicate groups that do not differ significantly ($P<0.05$). Abbreviations as in Fig. 1

would not benefit from the association, but that the benefit may be related to factors not assessed in this study. For example, Stevens and Peterson (1996) suggested that plants benefit if the water levels fall and previously inundated plants are exposed to drier conditions.

P supply and mycorrhizal status

AM structures were found at all levels of P supply, although overall the percentage root length containing AM structures decreased with increasing P. This negative correlation between P availability and AM colonization is well-documented in terrestrial systems (Smith and Read 1997) and may also prevail in aquatic systems. In aquatic environments, reductions in AM colonization levels have been generally associated with soil inundation or flooding (Kahn and Belik 1995; Stevens and Peterson 1996; Miller 2000); however, the underlying mechanisms have not been established. Since nutrient availability, and particularly P availability, is highly dependent on soil water content, the observed reductions in AM colonization in inundated or flooded soils may be attributable to increased P availability rather than a direct result of increased water levels. If the opposite were true, and AM colonization levels are dependent on water availability rather than P, colonization levels should remain constant under inundated conditions. This, however, was not the case in the current study and a similar reduction in colonization levels with increasing P was found for *L. salicaria* grown under saturated conditions (White and Charvat 1999). Additionally, the fact that many submerged aquatics maintain an AM association (Sondergaar and Laegaard 1977; Clayton and Bagyaraj 1984; Tanner and Clayton 1985b) implies that inundation or flooding does not necessarily prevent the association from developing.

The importance and functioning of AM in aquatic and semi-aquatic habitats is just beginning to be understood. While this understanding is hampered by conflicting reports, this may be attributable to differences in methodology and limitations of the studies involved. Additionally, it is not unlikely that plant species respond differently to inundation, placing different demands on the AM association. This may be particularly important when comparisons are made between species adapted to wetland habitats and those that are not. This study suggests that, unlike terrestrial systems, AM fungi contribute little to P acquisition in aquatic or semi-aquatic sys-

tems. However, as in terrestrial systems, high levels of P availability can lead to an uncoupling of the AM association. Additionally, AM fungi have the potential to alter at least some aspects of plant morphology under inundated conditions but further research is needed to understand the mechanisms by which AM fungi alter plant morphology and its adaptive significance. As the demand grows for preserving and re-establishing wetland plant communities for the many beneficial functions they provide, it will be increasingly necessary to understand the role AM fungi play in these areas.

Acknowledgements We thank Erin Barley, Sarah Cassel and Mike Pavone for help with harvesting, Bob Frank for equipment usage, the Ontario Graduate Scholarship Program and the Natural Sciences and Engineering Research Council of Canada for partial funding of this project, and the two anonymous reviewers for their constructive comments.

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