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The effect of a water gradient on the vesicular-arbuscular mycorrhizal status of *Lythrum salicaria* L. (purple loosestrife)

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Abstract The mycorrhizal status of *Lythrum salicaria* (Lythraceae) was assessed under growth room and field conditions. Growth room studies indicated that *L. salicaria* is facultatively mycorrhizal and capable of forming vesicular-arbuscular associations with six *Glomus* species, but not with *Gigaspora margarita.* Overall, hyphal and arbuscular colonization levels were significantly higher in the wet treatments than in the dry treatments ($P<0.0001$). However, taken individually, significant increases in arbuscular colonization ($P<0.05$) were found only in *L. salicaria* colonized with *Glomus clarum, G. aggregatum,* and *G. versiforme* and exposed to the wet treatments compared with the dry treatments, while significant increases in hyphal colonization were found in *L. salicaria* colonized with *G. clarum,* and *G. versiforme* exposed to the wet treatments. There was no overall effect of water availability on levels of vesicular colonization or differences in vesicular colonization levels within species under dry or wet conditions. In contrast, field studies along an existing water gradient revealed that hyphal and arbuscular colonization levels were significantly higher ($P<0.05$) in the dry and intermediate regions of the gradient than in the wet regions. Vesicular colonization was not significantly affected by the gradient. Total stem height was significantly affected by water availability, plot location and an interaction of the two ($P<0.05$), and was generally higher in the intermediate and wet plots.

Keys words *Lythrum salicaria* · *Glomus* spp · *Gigaspora* · Water · Vesicular-arbuscular mycorrhiza

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Introduction

The vesicular-arbuscular mycorrhizal (VAM) association is the most common type of mycorrhiza (Harley and Smith 1983). As well as having an impact on nutrient uptake (Harley and Smith 1983; Barea et al. 1987), the VAM association has been shown to play a role in drought tolerance in *Allium cepa* (Nelsen and Safir 1982), *Triticum aestivum* (Allen and Boosalis 1983) and *Glycine max* (Bethenfalvay et al. 1988), in increased growth of *Aster tripolium* under salinity stress (Rozema et al. 1986), in flooding survival in *Nyssa sylvatica* (Keeley 1980), and in offspring vigour in *Abutilon theophrasti* (Lewis and Koide 1990).

Lythrum salicaria L. (Lythraceae), purple loosestrife, is an erect perennial herb which has gained considerable attention due to its spread into North American wetlands since its introduction from Europe in the 1800s (Thompson et al. 1987). Although considered a plant of wet places (Gleason and Cronquist 1991), *L. salicaria* has been noted in drier upland regions (Grand River Conservation Authority, personal communication). Mal et al. (1992) stated that mycorrhizae had not been reported in *L. salicaria* and that samples obtained from two sites in southern Ontario, Canada, lacked mycorrhizae. Mejstrik (1965), however, found endotrophic mycorrhizae in *L. salicaria* collected at the National Nature Reserve, Hrabanovske Cernavy, Czechoslovakia, but noted that colonization varied seasonally. In April, with water levels 10 cm above the soil surface, Mejstrik (1965) found that *L. salicaria* was not colonized, while in June and September, with water levels at 3 and 6 cm below the soil surface, roots were colonized with an endophytic fungus. In contrast, a subsequent 9-month study in the same area with water levels on average 30 cm below the soil surface, showed *L. salicaria* to be nonmycorrhizal (Mejstrik 1972).

The ability of *L. salicaria* to inhabit both dry and wet regions and the potential for VAM colonization provide an opportunity to study the dynamics of this

relationship across a water gradient and examine the influence of the VAM association on the ability of *L. salicaria* to inhabit soils with various water availabilities. The influence of soil water availability on VAM colonization levels in this species has not been assessed. The specific objectives of this study were:

1. To determine whether *L. salicaria* forms VAM associations with several known VAM fungal species under growth room conditions and whether water availability influences the level of VAM colonization with these species.
2. To determine whether there is a relationship between plant height and VAM colonization of *L. salicaria* and water availability under field conditions.

Methods and materials

Growth room study

Cultures of the VAM fungi *Gigaspora margarita* Becker and Hall, *Glomus aggregatum* Schenck and Smith, *Glomus fasciculatum* (Thaxter) Gerd. and Trappe, *Glomus clarum* Nicol. and Schenck, *Glomus monosporum* Gerd. and Trappe, *Glomus versiforme* Daniels and Trappe) Berch, and *Glomus intraradices* Schenck and Smith were maintained on corn (*Zea mays* L.) growing in Turface (Montmorillonite Clay, International Minerals and Chemical Corporation, Ill.) under growth room conditions (21 °C, 16/8 h light-dark cycle, 125 μmol m^{-2} s^{-1}). Several corn plants were removed from pots containing each fungal species, the substrate washed from the roots, and the fresh mass of the roots determined. Roots were cut into approximately 1-cm pieces, and thoroughly mixed with enough Turface to fill 10 Cone-tainers. The dry mass of a subsample of the fresh roots was used to extrapolate the dry mass of the inoculum as g per Cone-tainer employed for each fungal species: *Glomus aggregatum* 1.12, *G. fasciculatum* 0.746, *G. clarum* 0.655, *G. monosporum* 1.032, *G. versiforme* 0.638, *G. intraradices* 1.154, *Gigaspora margarita* 0.363, control O.

Seeds of *L. salicaria* were collected from an established stand along the eastern bank of the Grand River, 100 m south of the Lorne Bridge, Brantford, Ontario, Canada, on 23 September 1992. Seed capsules were stored in paper bags and allowed to dry at room temperature for 2 weeks, after which the seeds were shaken from the capsules and stored at room temperature for a further 2 weeks. To facilitate germination, seeds were scattered over the surface of moist Turface and allowed to germinate and develop under the previously mentioned growth room conditions. Once the seedlings had developed the third set of leaves, they were transplanted to Cone-tainers containing the desired inoculum. Seedlings inoculated with each of the fungal test species (with the exception of *Gigaspora margarita*) were exposed to two watering regimes with five replications of one seedling per Cone-tainer for each treatment. The limited inoculum of *Gigaspora margarita* only permitted one treatment of dry conditions. Dry treatments were watered daily with 10 ml of deionized H_2O, while the wet treatments were given 60 ml. Watering was supplemented every other day with 10 ml of 50% Long Ashton nutrient medium (Hewitt 1966). On the days when watering was supplemented with nutrient medium, the dry treatments received no additional watering, while the wet treatments received an additional 50 ml of deionized water.

Harvesting occurred 6 weeks after inoculation. Plants were removed from the Cone-tainers and the Turface rinsed from the roots. Roots were then severed from the plants and stored and fixed in formyl acetic alcohol (FAA). After fixing for a minimum of 24 h, the roots were cleared by autoclaving in 5% (w/v) KOH at 121 °C for 12 min, stained with 0.1% (w/v) chlorazol black E for 1 h at 55 °C, and then destained in glycerol (Brundrett et al. 1984). A random subsample of these roots was then obtained and mounted on glass slides in glycerine. Assessment of mycorrhizal colonization followed the modified gridline method of McGonigle et al. (1990), using a Leitz photomicroscope under ×200 magnification. A total of 150 intersections were observed for the assessment of each root system, and the percentages of hyphal, arbuscular, and vesicular colonization were recorded.

Differences in the hyphal, arbuscular, and vesicular colonization levels between the two treatment means were analysed for each fungal species, with the exception of *Gigaspora margarita* and the controls. All data were tested for equal variance using the Levene median test (Kuehl 1994), and for normality using the Kolmogorov-Smirnov test (Steel and Torrie 1980) at the 5% level of significance. A two-tailed, unpaired, Student's *t*-test (Steel and Torrie 1980) was used to detect differences in treatment means within each fungal species. To meet the requirements of normality and equal variance, levels of hyphal colonization were square root transformed for *G. aggregatum* and *G. clarum.* The overall effect of water availability on hyphal, vesicular and arbuscular colonization was assessed using a two-way analysis of variance (Steel and Torrie 1980). All data were analysed using Sigma Stat (Jandell Corporation).

Field study

The study area was located in Mercer's Glenn on the grounds of the Royal Botanical Gardens, Burlington, Ontario. Mercer's Glenn is an isolated shallow pond originally part of a large valley connecting Cootes Paradise to Hamilton Bay which, as result of growth and expansion of the transportation system in the area and draining of the pond to eliminate carp, has undergone considerable changes in both vegetation and topography (Benckhuysen and Simser 1993). The establishment of *L. salicaria* in this study site occurred following drainage, and as a result none of the plants within the site was older than 3 years (J. A. Benckhuysen, personal communication).

Two sites were established along an existing water gradient. Three 3×10-m plots were aligned in each of the sites with the short axis running parallel to the gradient. The plots were placed to allow for one plot in the driest region, one plot in the wettest region, and one plot in the intermediate region of the gradient. The dry plots were completely dry by mid-spring, while the wet plots were characterized by several centimetres of standing water. *L. salicaria* was abundant throughout the entire study area.

Sampling occurred in late July, 1993. Prior to sampling, 10 random locations were generated for each plot. Ten plants were then selected from each of the plots by choosing the plant closest to the random locations within each plot. Entire plants were excavated, wrapped in polyethylene bags and transported to the laboratory, where they were refrigerated at 4 °C until assessment could take place. During assessment, all stems were removed from each plant and their numbers and heights recorded to the nearest 0.5 cm. Total stem height was determined by summing the height of all stems for each plant. All root systems were washed clean of any remaining substrate and a subsample of roots not exhibiting secondary growth was obtained and stored in FAA. Clearing, staining and assessment of roots for hyphal, arbuscular and vesicular colonization followed the same methods used for the growth room experiments.

All data were tested using a Kolmogorov-Smirnov test for normality (Steel and Torrie 1980) and Levene median test for equal variance (Kuehl 1994) at the 5% level of significance. To meet the requirements of normality and equal variance, hyphal and arbuscular colonization levels were transformed using a square-root transformation [$\mathbf{x} = \mathrm{sqrt}(\mathbf{y} + 0.325)$]. Plant height was transformed using a log transform ($\mathbf{x} = \log \mathbf{y}$). If significant site, treatment, or site by treatment effects were detected ($P < 0.05$), a multiple pairwise comparison was performed using the Student-

Newman-Keuls method (SNK) to isolate significantly different groups (Kuehl 1994). In all cases, treatment effects refer to the water availability within each plot and treatment means are presented ± standard errors of the means.

A Kruskal-Wallis one-way analysis of variance of ranks was used to assess vesicular colonization levels, since these could not be transformed to achieve equal variance and normality (Steele and Torrie 1980). Group(s) that were significantly different were then isolated using Dunn's pairwise multiple comparisons (Conover 1980).

A Spearman rank order correlation was used to determine the relationships between untransformed levels of total stem height, hyphal, arbuscular, and vesicular colonization levels, and water availability (Steele and Torrie 1980). All analyses were performed using Sigma Stat (Jandel Corporation).

Results

Growth room study

Mycorrhizal associations were formed between *L. salicaria* and all species of *Glomus* tested under both wet and dry conditions (Table 1). Considerable variation in levels of colonization occurred among species, and there was no indication of mycorrhizal associations formed between *L. salicaria* and *Gigaspora margarita* or in the controls. Overall, hyphal and arbuscular colonization levels were significantly higher in the wet treatments ($P<0.0001$). However, taken individually, significantly higher levels of arbuscular colonization ($P<0.05$) were found only in *L. salicaria* colonized with *G. clarum, G. aggregatum,* and *G. versiforme* exposed to the wet treatments than in the dry treatment, while significantly higher levels of hyphal colonization were found in *L. salicaria* colonized with *G. clarum,* and *G. versiforme* exposed to the wet treatments. There were no overall significant differences or differences between wet and dry treatment means for vesicular colonization levels in any of the fungal species tested.

Field study

Hyphal colonization was significantly affected by water levels ($P<0.0001$), but not location ($P=0.856$) at the field site. The SNK multiple comparison procedure indicated that hyphal colonization was significantly lower ($P<0.05$) in the wet plots (5.53 ± 1.64) than in the dry (57.61 ± 4.50) and intermediate plots (48.78 ± 4.60) (Fig. 1). There were no significant differences in hyphal colonization between or within the dry and intermediate plots, and no differences in colonization between the wet plots.

Arbuscular colonization levels were affected by both location of the field sites ($P<0.0331$) and by water availability ($P<0.0001$). The mean level of arbuscular colonization in site 1 was $12.357\pm2.174\%$, while site 2 had a mean colonization level of $18.092\pm2.966\%$. Arbuscular colonization levels were lower in the wet plots (with a combined mean of $2.20\pm0.959\%$) than in the dry and intermediate plots (combined means of $24.95\pm2.993\%$ and $19.59\pm2.706\%$, respectively). The SNK pairwise comparison method indicated no differences in arbuscular colonization levels between or among the dry and intermediate plots or between the wet plots (Fig. 2).

The Kruskal-Wallis one-way analysis of variance on ranks indicated significant differences in vesicular colonization among treatment groups ($P<0.001$, $H=22.6$ with 5 df). Multiple comparisons using Dunn's method (Fig. 3) indicated that vesicular colonization levels in the intermediate plot of site 2 were significantly higher than both the dry plot in site 2, and the wet plot of site 1, although the mean percentage of vesicular colonization did not exceed 3% for any plot. All other levels or vesicular colonization were not significantly different.

Stem length was significantly affected by site, treatment, and site by treatment interaction ($P<0.0001$). SNK multiple pairwise comparisons indicated lower total stem lengths in site 1 than site 2 ($P<0.05$), with a

Table 1 Mean levels of hyphal, arbuscular, and vesicular colonization of *Lythrum salicaria* (±1 SEM) for each fungal test species exposed to dry and wet treatments. (*n* number of replicates surviving until the end of the experiments, *NA* data not available)

Species	Treatment	n	Hyphae	Arbuscules	Vesicles
Glomus aggregatum	Wet	5	49.5±9.6	30.3±5.9*	2.7±0.7
	Dry	4	22.3±7.8	10.2±2.8	3.2±1.5
Glomus fasciculatum	Wet	5	31.7±7.5	20.1±5.4	3.5±1.5
	Dry	3	25.3±9.5	15.1±5.1	2.9±0.4
Glomus clarum	Wet	5	18.7±6.7*	10.3±3.7*	2.5±1.1
	Dry	5	2.5±1.4	0.8±0.4	0.7±0.4
Glomus monosporum	Wet	4	34.0±4.4	20.5±4.4	1.8±0.5
	Dry	2	13.3±9.3	6.7±6.0	0.7±0.7
Glomus versiforme	Wet	4	19.5±3.6*	10.0±1.7*	3.7±1.5
	Dry	4	7.0±2.9	3.5±1.4	1.3±0.9
Glomus interadices	Wet	5	33.5±6.8	20.0±5.1	2.5±0.8
	Dry	2	8.7±5.3	4.7±2.7	0.7±0.0
Giaspora margarita	Wet	NA	NA	NA	NA
	Dry	3	0	0	0
Control	Wet	5	0	0	0
	Dry	4	0	0	0

* Significantly different at $P<0.05$

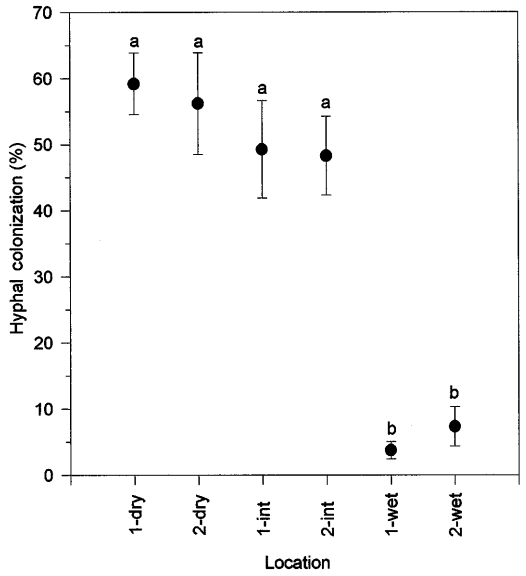

Fig. 1 Percentage root length of *Lythrum salicaria* colonized by VAM fungal hyphae. Plants were sampled from a dry, intermediate (*int*) and wet plot from each of two sites. Means of 10 observations ± SEM are presented. Identical lowercase letters above the SEM bars show groups that do not differ significantly ($P > 0.05$, Student-Newman-Keuls pairwise multiple comparisons)

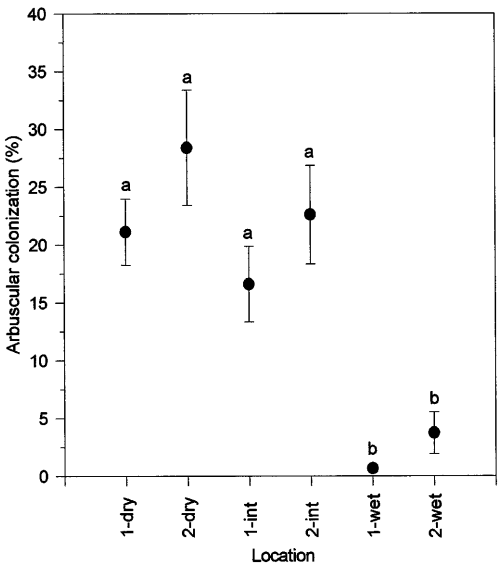

Fig. 2 Percentage root length of *L. salicaria* containing arbuscules. Plants were sampled from a dry, intermediate (*int*) and wet plot from each of two sites. Means of 10 observations ± SEM are presented. Identical lowercase letters above the SEM bars show groups that do not differ significantly ($P > 0.05$, Student-Newman-Keuls pairwise multiple comparisons)

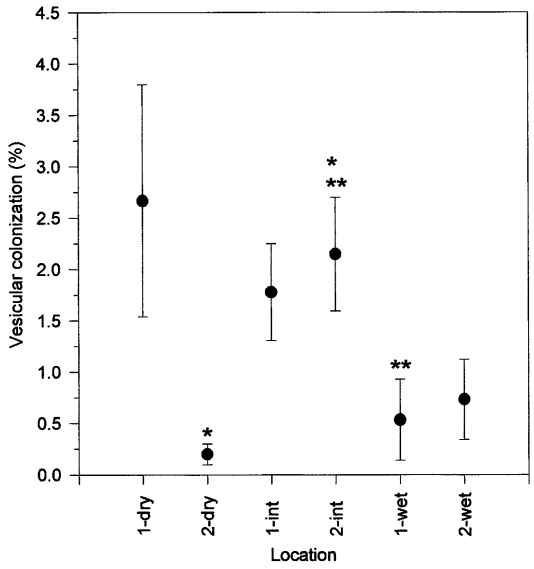

Fig. 3 Percentage root length of *L. salicaria* containing vesicles. Plants were sampled from a dry, intermediate (*int*) and wet plot from each of two sites. Means of 10 observations ± SEM are presented. * and ** indicate significant differences between treatment means ($P > 0.05$, Dunn's pairwise multiple comparisons)

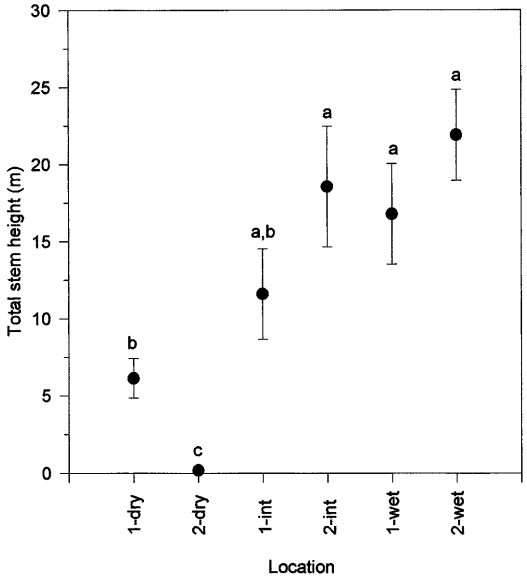

Fig. 4 Total stem height of *L. salicaria.* Plants were sampled from a dry, intermediate (*int*) and wet plot from each of two sites. Means of 10 observations ± SEM are presented. Identical lowercase letters above the SEM bars show groups that do not differ significantly ($P > 0.05$, Student-Newman-Keuls pairwise multiple comparisons)

mean total stem height in site 1 of 11.698 ± 1.701 m and 13.380 ± 2.379 m in site 2. There were no significant differences in total stem height between or among the intermediate or wet plots (Fig. 4). Mean total stem height in the dry plot of site 1 was significantly different than mean stem height of all treatments, with the exception of the intermediate treatment at site 1, while the mean total stem height in the dry plot of site 2 was significantly lower than all other treatments.

Spearman rank order coefficients, which measure the strength of the association between pairs of variables, and their associated probabilities are presented in

Table 2 Spearman's rank order correlations (r) for hyphal, arbuscular and vesicular colonization, water availability (treatment) and total plant height of *L. salicaria.* Data were collected from two field sites each containing three plots along an existing water gradient

Variable	Treatment	Hyphae	Arbuscules	Vesicles
Plant height	0.70*	−0.43*	−0.51*	0.214
Treatment	–	−0.77*	−0.75*	−0.145
Hyphae	–	–	0.90*	0.385*
Arbuscules	–	–	–	0.326*

* Significant relationship between two variables at $P<0.05$

Table 2. Arbuscular and hyphal colonization at the field sites were both negatively associated with water availability. Total stem length was positively associated with water level, and negatively associated with both arbuscular and hyphal colonization.

Discussion

Survival of noninoculated controls in the growth room study and the absence of colonization in some plants in the wet plots of the field site indicate that *L. salicaria* is a facultatively mycorrhizal species. The absence of VAM colonization in plants inoculated with *Gigaspora margarita* may have resulted from either an incompatablity between these two species or from the low levels of inoculum available for *Gigaspora margarita.* The significantly higher levels of hyphal and arbuscular colonization in the wet treatments of the growth room study are in direct contrast to the results of the field study, in which colonization was highest in the dry and intermediate areas. This may have resulted from a different composition of the VAM fungi present at the field site, although this was not determined, or from a difference in water availabilities. Redhead (1975) found that the amount of water optimal for plant growth also resulted in the greatest production of VAM spores. Water levels that allowed for the greatest plant growth would likely provide the greatest source of photosynthate, which would then be available for fungal growth and development. Since there was no comparison of soil moisture levels between the growth room and field study, or of the water-holding capacities of the two soils, it is not known how these characteristics may have influenced the results. However, it is possible that the wet treatment of the growth room study had water availabilities more similar to the dry or intermediate plots of the field study, and that the dry treatment may have been further from the range of optimal growth conditions for *L. salicaria* than the wet treatment.

Decreased colonization levels in response to increased soil moisture observed in the field study are consistent with results reported for *Schizachyrium scoparium* (Cerligione et al. 1988), *Andropogon gerardii* (Hetrick et al. 1986), and *Lupinus* spp. (Trinick 1977). Rickerl et al. (1994) also found arbuscular and hyphal colonization levels to be consistently lower in wet than in dry soils in several wetland species. Anderson et al. (1984) found VAM associations in *Polygonum coccineum, Eleocharis smallii* and *Prosperpinaca palustris* in the drier, lower nutrient portion of a soil-water gradient, but an absence of colonization in the wetter, high nutrient sites. The abundance of VAM spores followed a similar pattern. Khan (1974) found that VAM spores were present but rare in permanently waterlogged soils, and that species of *Phragmites, Typha, Juncus* and *Eichhornia* lacked mycorrhizae in these soils. Soil around the roots of temporarily waterlogged *Ipomoea carnea* plants lacked spores, whereas the soil around adjacent plants of the same species growing on drier soils contained many (Khan 1974). Although there was no quantification, spores were isolated from soil taken from all plots in the field study reported here. VAM colonization has been noted in several aquatic plant species (Sondergaar and Laegaard 1977; Clayton and Bagyaraj 1984; Ragupathy et al. 1990), indicating that water levels are not limiting to the formation of a VAM association in all plants. Keeley (1980) found that *Nyssa sylvatica* seedlings survived flooded conditions to a greater extent when colonized by VAM fungi.

It is unclear whether colonization was limited by water availability in *L. salicaria,* or if colonization was limited by other factor(s). Nutrient availability, oxygen levels, and levels of toxic ion accumulation, which are greatly affected by soil moisture levels, were not assessed. If the wet plots provided optimal nutrient conditions for the growth of *L. salicaria,* the plant itself may have restricted VAM formation in a similar manner to that shown when plants are provided with increased levels of phosphorus. Conversely, if the wet sites provided less than optimal conditions for growth, colonization levels may have been reduced as a result of a limited supply of oxygen to the fungus. The presence of VAM fungi in some of the flooded *L. salicaria,* roots, although at low levels, may indicate that there is some immediate advantage to retaining the VAM association either in the acquisition of nutrients unavailable to the plant, as a mechanism of flood tolerance, or as an assurance of VAM colonization if the immediate conditions changed. This may also indicate that the plant is unable to accomodate a higher level of colonization, although the requirements of the plant would favour higher levels, or unable to restrict VAM colonization when the benefits to the plant are minimal. Until the optimal growth requirements of *L. salicaria* are determined, it is unclear which of these factors prevail in the wet plots.

Although total stem height was significantly lower in the dry plot of site 2, there were no differences exhibited in hyphal or arbuscular colonization between this plot, the dry plot of site 1, or either of the intermediate sites. The factor(s) causing the limited growth of plants in this area are unknown. Mean stem heights were greatest in the wet and intermediate plots sampled, indicating that these conditions were closer to the opti-

mal conditions for growth than the drier plots. Since both hyphal and arbuscular colonization levels were up to 10 times greater in the intermediate sites, with no significant difference in plant heights between these regions, the VAM association may act as a buffer against limited water availabilities in the intermediate sites. Given that both arbuscular and hyphal colonization levels did not differ significantly between the dry and intermediate plots, there may be a limit at which maintaining a higher VA mycorrhizal load does not compensate for the cost of maintaining the VAM fungi at the field site. The dry plots represented the outermost area in which *L. salicaria* was found and, since these plants were smaller than those in the wet and intermediate site, this may represent a limit in which increasing levels of VAM cannot compensate for increasing environmental constraints imposed by lower soil water availabilities.

In summary, although Mal et al. (1992) stated that *L. salicaria* had not been reported as mycorrhizal, and that samples collected from two sites in southern Ontario did not show signs of mycorrhizal colonization, the results of this study indicate that *L. salicaria* is facultatively mycorrhizal and that colonization levels are inversely proportional to water availability or some factor(s) that vary with water availability. Further, plant height has also been shown to be positively affected by water availability. Studies in which the availability of water is strictly controlled will be required to determine whether the VAM association has an effect on the ability of *L. salicaria* to colonize both wet and dry regions.

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