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Effects of drought stress and arbuscular mycorrhiza on the growth of *Gliricidia sepium* (Jacq). Walp, and *Leucaena leucocephala* (Lam.) de Wit. in simulated eroded soil conditions

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Abstract A greenhouse investigation was conducted to determine the effect of arbuscular mycorrhiza and drought on the growth of two tropical hedgerow legume trees (*Gliricidia sepium* and *Leucaena leucocephala*) under simulated eroded soil conditions. It was a factorial design with two levels of watering regime (adequate watering and drought), inoculation with *Glomus deserticola* (with and without), and two soil types (0–30 cm topsoil and 30–60 cm subsoil). Each treatment was replicated 3 times. After ten drought cycles, the growth of *Gliricidia sepium* in the subsoil was enhanced by mycorrhizal inoculation under both watering regimes whereas there was no significant contribution of mycorrhizal inoculation to the growth of *L. leucocephala* in both soil types under the two watering regimes. Drought stress significantly reduced most growth parameters for the two tree species in both soils with or without fungal inoculation. The N-fixing activity of *Gliricidia sepium* benefited from *Glomus deserticola* inoculation while that of *L. leucocephala* was not significantly affected in the topsoil. Mycorrhizal colonization was reduced for both tree species in the subsoil compared to the topsoil while it was significantly increased for both species in the subsoil when compared to the uninoculated subsoil counterpart. In the subsoil, inoculation of *Gliricidia sepium* with the mycorrhizal fungus increased root colonization by 89% and 73% under adequate watering and drought, respectively, whereas *L. leucocephala* had only a 38% and 42% increase in root colonization under comparative conditions in the subsoil. Thus *Glomus deserticola* inoculation may be beneficial to the growth of *Gliricidia sepium* in a badly eroded site where topsoil is missing.

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Introduction

Arbuscular mycorrhizal fungi (AMF) can be found in almost all habitats and climates (Barea et al. 1997) and at different depths of soil (Michelsen and Rosendahl 1989; Dalpe et al. 2000). The significant contributions of mycorrhizae to the nutrition and growth of plants are well established (Smith and Read 1997). They are particularly important for slowly diffusing ions such as PO_4^{3-} (Jacobsen et al. 1992), although the uptake of highly mobile nutrients such as NO_3^- can also be enhanced by mycorrhizal association under drought conditions (Azcon et al. 1996; Subramanian and Charest 1999).

Tropical soils of humid and sub-humid African countries are prone to degradation (Sanchez 1976; Agboola 1987) leading to low agricultural productivity and erosion of degraded soils. Furthermore, most of the soils are low in nutrients, particularly P and N (Kang and Wilson 1987). Many of these regions are subject to erratic rainfall, increasing the risk of water erosion. Poor management strategies and a lack of environmental impact assessments have significantly increased desert encroachment (Akinbola 1999). Hence, badly eroded sites could be reclaimed by afforestation, particularly in areas that are prone to drought. Among the promising multipurpose legume species that are known to be fast growing and drought resistant are *Gliricidia sepium* (Jacq). Walp (Nitrogen Fixing Tree Association 1989) and *Leucaena leucocephala* (Lam.) de Wit. (National Research Council 1984). Past investigations on the use of multipurpose trees have focussed on the improvement of farming systems (Fagbola et al. 1998a, b; Osonubi et al. 1991) with little or no attention to their possible use in reclaiming badly eroded or degraded land. The renewed efforts in afforestation in many tropical countries make it essential to understand how AMF interact with multipurpose legume trees that are commonly being used in the tropics.

The aim of the present investigation was to evaluate whether arbuscular mycorrhizae can improve the growth of hedgerow legume tree species in badly eroded sites, particularly when moisture is limiting. For this, the effects of AMF inoculation and drought stress have been compared in *G. sepium* and *L. leucocephala* growing in non-sterile top- and subsoil, to simulate non-eroded and eroded soil conditions.

Materials and methods

Collection of soil samples

Two different profiles of an alfisol, namely topsoil (0–30 cm) and subsoil (30–60 cm), were collected from Ajibode village (University of Ibadan experimental farm site). Topsoil and subsoil characteristics were, respectively: 72% and 64% sand; 15% and 21% silt; 13% and 15% clay; pH(H_2O) 7.0 and 6.4; 0.72% and 0.26% organic C; 4.0 mg kg^{-1} and 15.0 mg kg^{-1} total N; 1.61 mg kg^{-1} and 1.20 mg kg^{-1} extractable P (Bray-1).

Experimental design

The experiment was a completely randomized design with three replicates and a factorial combination of two watering regimes (adequately watered and drought treatments), inoculation with *Glomus deserticola* Trappe, Bloss and Menge (INVAM, CA113) (inoculated and uninoculated control) and two soils (0–30 cm topsoil and 30–60 cm subsoil).

Planting of materials and application of inocula

Seeds of *L. leucocephala* were scarified in hot water (100°C) for 5 min and were left in cold water overnight. *Gliricidia sepium* seeds were surface sterilized in sodium hypochlorite (1%) for 3 min and washed in several changes of distilled water. Four seeds were planted into each pot containing 4 kg soil and thinned to one seedling per pot, 1 week after emergence. All seedlings were watered daily for 6 weeks to allow proper establishment. Those designated as drought treatments were then subjected to drought stress for ten cycles of 1 week each (no watering), while the adequate-watering treatments were watered daily.

Glomus deserticola (kindly supplied by P. D. Millner of USDA-ARS Beltsville, Md.) was propagated in a sterile potted soil cropped with maize. The inoculum consisted of a root-soil-fungal spore mixture, of which 20 g was blended into the central third of the soil (Carling et al. 1978).

At germination, all seeds were inoculated with rhizobia isolated from nodules of the corresponding legumes growing at IITA, Ibadan. Isolation of rhizobia was carried out following the procedure described by Vincent (1970). Two millilitres of yeast mannitol broth cultures of *Rhizobium* containing approximately 10^9 cells/ml was inoculated close to the root (3 cm below the soil surface) of each 7-day-old seedling.

Growth conditions

Plants were raised from April to August in a greenhouse with the following conditions: photosynthetic active radiation 1,500 μmol m^{-2} s^{-2}, average day/night temperature 35/25±2°C, light intensity 27,900 (morning hour) to 74,600 lux (peak sunshine), and relative humidity between 45% and 75% during the day.

Measurements and harvest

Sixteen weeks after planting (ten drought cycles), the following parameters were measured; plant height, stem diameter at 3 cm from the base, root length, shoot and root dry weights, number of nodules, nodule dry weight, midday xylem pressure potential, relative leaf water content, N and P content of shoot and percentage mycorrhizal colonization.

Stem diameters were determined with the aid of a micrometer screw gauge while root lengths were measured as described by Tennant (1975). Root, shoot and nodule dry weights were taken after oven-drying the samples at 70°C for 48 h. Midday xylem pressure potential was measured using a pressure chamber apparatus (Soil Moisture Instruments, Santa Barbara). Leaf relative water content was determined following the method of Kramer and Kozlowski (1979). Total N and P content of shoot samples were determined using methods described by the International Institute of Tropical Agriculture (IITA 1982). Nutrient concentrations were expressed as shoot uptake by multiplying the respective values with the corresponding shoot dry weight (Osonubi et al. 1991).

Mycorrhizal colonization was quantified after clearing root samples for 15 min at 121°C in 10% KOH and staining in chlorazol black E (Brundrett et al. 1984) by the grid-line intersect method (Giovannetti and Mosse 1980).

Statistical analyses

All data were analysed using Genstat (three-way) ANOVA (Rothamsted Experimental Station) to determine the effect of factors and interactions between factors. The means were compared using Duncan's multiple range test. Correlation analyses were also carried out to determine the relationship between the different parameters monitored.

Results and discussion

Vegetative plant growth and yield

The biomass production of both tree species, *Gliricidia sepium* and *L. leucocephala*, was generally reduced in the subsoil compared to the topsoil under all treatments (Fig. 1). In the topsoil, the drought-stressed plants had a significantly lower biomass compared to their adequately watered counterparts for both tree species. In the subsoil, shoot dry weights of inoculated drought-stressed *G. sepium* and *L. leucocephala* were not significantly different from inoculated plants in adequate-watering treatments, whereas it was non-inoculated *G. sepium* that had similar shoot biomasses in both drought and watered conditions. This suggests that *G. sepium* might be better adapted to degraded soils, particularly subsoils where the topsoil has been washed off.

Inoculation of *G. sepium* with *Glomus deserticola* in the subsoil significantly increased plant height, stem girth, leaf and stem dry weights, and root length under both watering regimes, but not leaf dry weight under drought conditions (Table1). Inoculation with AMF in the topsoil significantly increased stem girth and leaf dry weight under adequate-watering conditions while the most significant contribution of AMF inoculation to the yield of root length was under drought conditions. Plant height, stem girth, root length, and leaf and stem dry weights were significantly greater in the topsoil as com-

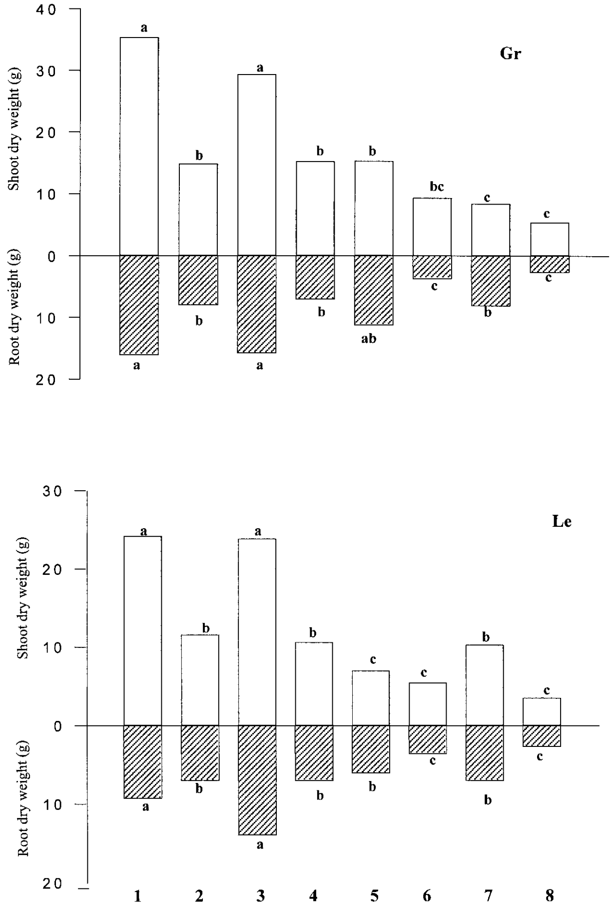

Fig. 1 Biomass yield (g plant^{-1}) of *Glomus deserticola*-inoculated and non-inoculated *Gliricidia sepium* and *Leucaena leucocephala* after 16 weeks' growth in non-disinfected soils. *Bars with different letters* are significantly different at P=0.05 according to Duncan's multiple range test. *Gr Gliricidia sepium*; *Le Leucaena leucocephala*; *1* inoculated, watered topsoil; *2* inoculated, drought-stressed topsoil; *3* non-inoculated, watered topsoil; *4* non-inoculated, drought-stressed topsoil; *5* inoculated, watered subsoil; *6* inoculated, drought-stressed subsoil; *7* non-inoculated, watered subsoil; *8* non-inoculated, drought-stressed subsoil

pared to the subsoil, under both watering regimes with or without inoculation with AMF. Exceptions were stem girth and stem dry weight, which were not significantly different between inoculated drought-stressed topsoil and subsoil. Drought also significantly reduced all parameters with or without AMF inoculation in the topsoil. In the subsoil, however, it was only the stem girth and root length that were significantly reduced by drought with or without AMF inoculation. Height, leaf and stem dry weights were not significantly affected by drought stress in non-inoculated plants, while height and stem dry weight were not significantly affected by drought stress in AMF inoculated plants.

Inoculation of *L. leucocephala* with AMF in the topsoil and subsoil did not significantly affect height, stem girth, leaf and stem dry weights, or root length under either watering regime, except for stem dry weight in the subsoil under adequate watering (Table 2). Growth of *L. leucocephala* in the topsoil was significantly higher than in the subsoil under both watering regimes with or without AMF inoculation. Drought stress significantly reduced these parameters in the topsoil and subsoil, with or without AMF inoculation, except for stem girth and stem dry weight in the subsoil when inoculated with AMF.

Results from AMF studies have shown that variations in plant responses depend on host species (Bethlenfalvay et al. 1982; Krishna et al. 1985; Rajapakse and Miller 1987; Rao et al. 1990). Daft and El-Giahmi (1974) and Mosse et al. (1976) reported increased growth of plants due to AMF inoculation and Atayese et al. (1993) reported an increase in shoot dry weights of leguminous trees due to AMF inoculation. The lack of a significant response of *Gliricidia sepium* and *L. leucocephala* to AMF inoculation in the topsoil in the present investigation may imply high effectiveness, competitiveness or abundance of indigenous AMF in the soil. Since P levels were not very different in the top- and subsoils, the significant responses observed in the subsoil may result from a lower AMF propagule density with soil depth, as reported by Michelsen and Rosendahl (1989). In fact, preliminary studies in our laboratory have shown a reduction of AMF propagule density from 0 to 90 cm soil depth (Unpublished results). However, the decrease in the stem dry weight of *L. leucocephala* under adequate-watering conditions in the subsoil was possibly due to the partitioning of photosynthates under this treatment which might be indirectly due to the photosynthetic ability of the plant (Daft and El-Giahmi 1978).

Development of root symbioses

Inoculation with *Glomus deserticola* in the topsoil did not significantly influence mycorrhizal colonization of either tree species under either watering regime (Tables 3, 4). This implies that the indigenous AMF in the topsoil were abundant and effective. With the exception of drought conditions for *L. leucocephala* in the subsoil, inoculation with AMF increased the percentage mycorrhizal colonization in all the treatments in the subsoil for both tree species. The AM colonization of *Gliricidia sepium* in the subsoil was increased by 89% under adequate-watering conditions and 73% under drought stress as a result of *Glomus deserticola* inoculation (Table 3), whereas only 38% and 42% increases were observed in *L. leucocephala* in the subsoil under drought-stress and adequate-watering regimes, respectively (Table 4). Drought stress reduced the mycorrhizal colonization in all treatments for *Gliricidia sepium*, except in the non-inoculated subsoil, and in all treatments for *L. leucocephala*. Although mycorrhizal colonization levels have sometimes been reported to be unaffected by water stress (Nelsen and Safir 1982; Allen and Boosalis 1983; Simpson and Daft 1990), these results are in agreement with the work of Osonubi et al. (1991) and Busse and Ellis (1985). A reduction in mycorrhizal colonization by drought stress is dependent on root exudates (Graham et al. 1982; Schwab et al.

Table 1 Vegetative growth and biomass yield of *Glomus deserticola*-inoculated and non-inoculated *Gliricidia sepium* after 16 weeks' growth in non-disinfected soils

Soil	Mycorrhizal inoculation	Watering regime	Height (cm)[a]	Stem girth (cm)[a]	Leaf dry weight (g)[b]	Stem dry weight (g)[b]	Root length (m)[b]
Topsoil	Without	Watered	61.17a	1.11b	12.99b	16.46a	113a
		Drought	42.27bc	0.83d	7.10c	8.13b	22d
	With	Watered	65.27a	1.64a	15.48a	19.84a	101a
		Drought	46.00b	0.81de	6.91c	7.92bc	60b
Subsoil	Without	Watered	30.17e	0.70e	4.41d	3.99cd	38c
		Drought	25.50e	0.57f	2.74d	2.63d	8e
	With	Watered	38.83cd	0.97c	6.32c	8.98b	55b
		Drought	36.17d	0.74d	3.77d	5.57bc	25d
ANOVA							
Watering (W)			***	***	***	***	***
Mycorrhizal inoculation (I)			***	***	*	*	***
Soil type (S)			***	***	***	***	***
Interactions							
W×I			NS	**	NS	NS	***
W×S			***	***	***	**	***
I×S			NS	NS	NS	NS	NS
W×I×S			NS	**	NS	NS	***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, *NS* non-significant

[a] For each variate, values followed by the *same letters* are not significantly different at $P \leq 0.05$ according to Duncan's multiple range test

[b] For each variate, values followed by the *same letters* are not significantly different at $P \leq 0.01$ according to Duncan's multiple range test

Table 2 Vegetative growth and biomass yield of *Glomus deserticola*-inoculated and non-inoculated *Leucaena leucocephala* after 16 weeks growth in non disinfected soils. For abbreviations, see Table 1

Soil	Mycorrhizal inoculation	Watering regime	Height (cm)[a]	Stem girth (cm)[a]	Leaf dry weight (g)[b]	Stem dry weight (g)[b]	Root length (m)[b]
Topsoil	Without	Watered	85.0a	0.85a	8.90a	14.93a	60ab
		Drought	59.7b	0..55b	5.02bc	5.62bc	40bc
	With	Watered	86.8a	0.82a	9.83a	14.32a	75a
		Drought	55.3bc	0.56b	6.16b	5.43c	46bc
Subsoil	Without	Watered	46.5c	0.51bc	3.23de	7.09b	34cd
		Drought	32.3d	0.38d	1.73f	1.83d	18d
	With	Watered	50.7bc	0.44 cd	4.31 cd	2.74d	41bc
		Drought	35.0d	0.40d	2.94ef	2.54d	16d
ANOVA							
W			***	***	***	***	***
I			NS	NS	**	*	NS
S			***	***	***	***	***
Interactions							
W×I			NS	NS	NS	*	NS
W×S			**	**	***	***	NS
I×S			NS	NS	NS	NS	NS
W×I×S			NS	NS	NS	*	NS

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

[a, b] See footnote to Table 1

1983) which under drought stress will be limited due to reduced photosynthesis, as stomata most often remain closed to conserve water. In addition, water shortage in the soil can reduce and delay AMF spore germination (Tommerup 1984), root growth and thereby subsequent mycorrhiza development.

Inoculation of *Gliricidia sepium* with *Glomus deserticola* promoted nodule formation except under drought conditions in the subsoil (Table3). Under adequate watering, inoculation resulted in an 80% increase in the number of nodules in the topsoil, a 110% increase in the subsoil and an increase of 56% in the drought-stressed topsoil. Drought stress reduced the number of nodules formed by *Gliricidia sepium* in both topsoil and subsoil, with or without inoculation with *Glomus deserticola*. The effect of *G. deserticola* inoculation on the nodule formation of *L. leucocephala* was not significant in topsoil or subsoil under the two watering regimes (Table 4). A significant reduction in the number of nodules only occurred in the topsoil under drought stress, with or without inoculation with *Glomus deserticola*. Similar results have been reported by Michelsen and Rosendahl (1990). Nodule dry matter was higher in the topsoil than in the subsoil for both tree species (Tables 3, 4). This may have been due to variations in the texture and fertility of the soil as reported by Sanchez (1976) and Agboola (1987). Mycorrhizal inoculation did not significantly increase nodule dry weight for both *Gliricidia se-*

Table 3 Number and dry weight of nodules, mycorrhizal colonization, concentration of N and P of *Glomus deserticola*-inoculated and non-inoculated *Gliricidia sepium* after 16 weeks of growth in non-disinfected soils. For abbreviations, see Table 1

Soil	Mycorrhizal inoculation	Watering regime	Nodule (no. plant^{-1})[a]	Nodule dry weight (mg plant^{-1})[a]	Mycorrhizal colonization (%)[a]	N concentration (%)[b]	P concentration[a] (%) (10^{-2})
Topsoil	Without	Watered	187.7b	723b	33.2bc	1.52b	6.97cd
		Drought	132.3c	737b	15.4e	1.88a	12.37a
	With	Watered	339.3a	1810a	40.2ab	1.44bc	9.07bc
		Drought	206.7b	717b	18.6de	2.10a	10.03ab
Subsoil	Without	Watered	72.0d	193c	25.6 cd	1.63b	5.57d
		Drought	37.0e	167c	18.0de	1.59b	6.10d
	With	Watered	151.3c	317c	48.3a	1.46b	5.27d
		Drought	60.0de	250c	31.2c	1.21c	11.13ab
ANOVA							
W			***	***	***	**	**
I			***	***	***	NS	NS
S			***	***	NS	***	*
Interactions							
W×I			**	***	NS	NS	NS
W×S			NS	***	NS	***	NS
I×S			*	***	*	*	NS
W×I×S			NS	***	NS	*	***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$
[a, b] See footnote to Table 1

Table 4 Number and dry weight of nodules, mycorrhizal colonization, concentration of N and P of *Glomus deserticola*-inoculated and non-inoculated *L. leucocephala* after 16 weeks of growth in non-disinfected soils. For abbreviations, see Table 1

Soil	Mycorrhizal inoculation	Watering regime	Nodule (no. plant^{-1})[a]	Nodule dry weight (mg plant^{-1})[a]	Mycorrhizal colonization (%)[a]	N concentration (%)[a]	P concentration (%) (10^{-2})[b]
Topsoil	Without	Watered	130a	463b	30.0ab	1.82ab	6.77bc
		Drought	79b	337bc	20.6c	2.03a	11.17a
	With	Watered	145a	860a	35.5a	1.84ab	8.47ab
		Drought	51b	433b	20.2c	1.80ab	8.50ab
Subsoil	Without	Watered	65b	327bcd	18.1c	1.37c	2.10d
		Drought	38b	147e	7.7d	1.57bc	4.07cd
	With	Watered	38b	253cde	25.7b	0.25d	5.37c
		Drought	31b	193de	10.6d	0.19d	10.80a
ANOVA							
W			***	***	***	NS	***
I			**	*	*	NS	**
S			NS	***	**	***	***
Interactions							
W×I			***	NS	NS	NS	NS
W×S			NS	NS	NS	NS	NS
I×S			NS	*	NS	NS	***
W×I×S			NS	*	NS	NS	**

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$
[a, b] See footnote to Table 1

pium and *L. leucocephala* in the subsoil (Tables 3, 4). There was a strong correlation ($P<0.05$) between nodule number and N uptake ($r=0.85$ and $r=0.82$ for *G. sepium* and *L. leucocephala*, respectively) as well as nodule number and P uptake ($r=0.82$ and $r=0.65$ for *G. sepium* and *L. leucocephala*, respectively). Similar findings were reported by Islam and Ayanaba (1981) for cowpea.

N and P accumulation

N concentrations were lower for both tree species in the subsoil when compared to the topsoil, and the P concentration for *L. leucocephala* was reduced in all treatments in the subsoil compared to the topsoil, except when it was inoculated or under drought conditions (Tables 3, 4). There was a strong correlation between the total plant dry weight and N uptake and P uptake ($r=0.90$ and $r=0.73$ for N and P, respectively, in *L. leucocephala*, and 0.91 and 0.79 for *Gliricidia sepium*).

In the topsoil, inoculation with *Glomus deserticola* did not significantly affect the shoot N concentration and uptake of either tree species under the two watering regimes (Tables 3, 4; Fig. 2), whereas inoculation of drought-stressed *Gliricidia sepium* in the subsoil led to a significant reduction in N concentrations (Table 3). The concentration of shoot N was also significantly reduced in *L. leucocephala* in the subsoil when inoculated

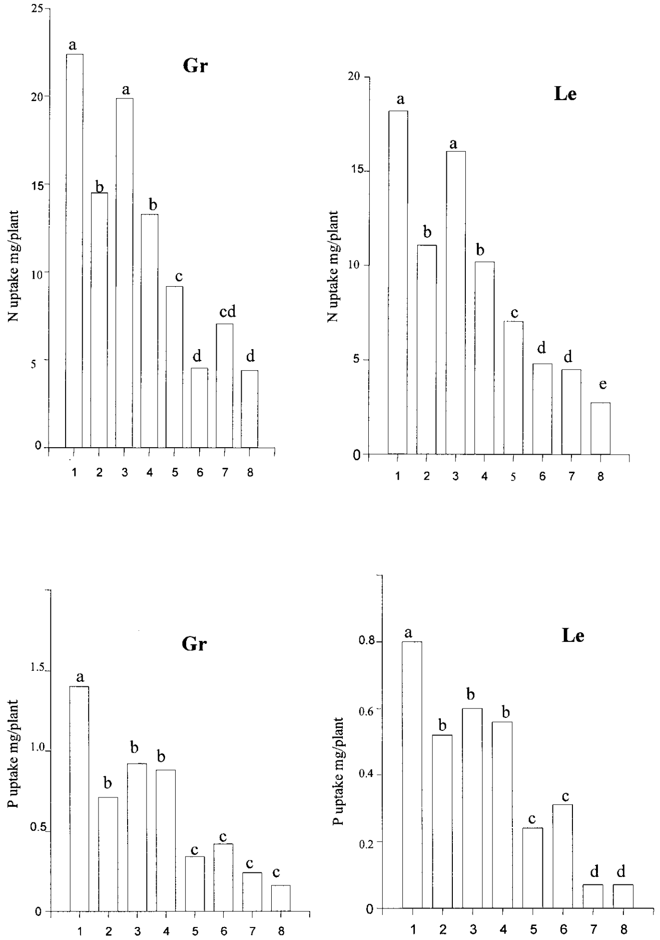

Fig. 2 Shoot N and P accumulation (mg plant^{-1}) of *Glomus deserticola*-inoculated and non-inoculated *Gliricidia sepium* and *L. leucocephala* after 16 weeks growth in non-disinfected soils. *Bars with different letters* are significantly different at P=0.05 according to Duncan's multiple range test. For abbreviations, see Fig. 1

with *Glomus deserticola* under both watering regimes (Table 4). However, total N uptake into shoots of *L. leucocephala* was significantly enhanced by fungal inoculation in the subsoil under both watering regimes (Fig. 2). Inoculation with *G. deserticola* did not increase the shoot P concentration of either tree species in the topsoil. In the subsoil and under drought-stress conditions, there was an 82.5% increase in the P concentration in *Gliricidia sepium* when inoculated plants were compared to non-inoculated plants. However, under adequate watering, plant P uptake was only affected in the topsoil, and this was related to a higher plant biomass. Inoculation of *L. leucocephala* with *Glomus deserticola* led to a 2.6-fold increase in shoot P concentrations in the subsoil with adequate watering, and a 2.7-fold increase under drought conditions. Similarly, mycorrhizal inoculation enhanced the P uptake into shoots under both watering regimes (Tables 3, 4; Fig. 2). Increased P concentrations in both tree species following AMF inoculation in the subsoil could result from a low mycorrhizal propagule density or efficiency and lower P status of the subsoil (Michelsen and Rosendahl 1989). Increased P uptake in mycorrhizal plants is more evident when available P, root growth or both are limiting (Bagyaraj and Manjunath 1980; Kwapata and Hall 1983).

Drought stress increased the shoot N concentration in *Gliricidia sepium* in the topsoil (Table 3), while in *L. leucocephala* there was no significant effect (Table 4), which reflects different responses of N fixation by these tree species under similar conditions. Both tree species behaved similarly to drought stress with respect to P concentration. There were greater shoot P concentrations in the drought-stressed topsoil when *Glomus deserticola* was not added, compared to inoculated plants, but greater P concentrations in the drought-stressed subsoil when the plants were inoculated with AMF compared to their non-inoculated counterparts. This implies a lower density, or reduced efficiency, of indigenous or introduced AMF propagules in both soils (Michelsen and Rosendahl 1989). The effect of water stress on crop plants (Begg and Turner 1976; Tazaki et al. 1980) has been attributed to the reduced ability of plants to tap immobile minerals under drought-stress conditions (Greenway et al. 1969; Dunham and Nye 1976; Manjunath and Habte 1988). Viets (1972) reported that the diffusion rate of P decreases as the soil moisture content decreases. A mycorrhizal P supply is therefore likely to be more advantageous under water stress than under a normal watering regime (Fitter 1985).

Physiological parameters

Inoculation with *Glomus deserticola* only resulted in a higher xylem pressure potential in *L. leucocephala* in topsoil under drought conditions, but not in the other treatments (Table 5). In *Gliricidia sepium*, there was no effect of inoculation with the AMF. Levy et al. (1983), Nelsen and Safir (1982), Graham et al. (1982) and Allen et al. (1981) all reported that inoculation with AMF did not affect the xylem pressure potential. The higher xylem pressure potential observed for *L. leucocephala* in the topsoil under drought conditions suggests that mycorrhizal plants are more efficient in extracting the available soil moisture in drought-affected environments. Huang et al. (1985) also reported higher xylem pressure potentials for mycorrhizal plants, while Allen and Allen (1986) and Allen et al. (1981) reported lower values for mycorrhizal plants. For *G. sepium*, drought stress resulted in a lower xylem pressure potential which was not altered by mycorrhizal inoculation, suggesting a reduced ability of this plant species to cope effectively with drought or to exploit soil moisture when subjected to stress, which explains why it dies back under severe drought stress (Nitrogen Fixing Tree Association 1989). The ability of *L. leucocephala* to cope effectively with drought conditions is indicated by the observation that drought stress only affected the non-inoculated plants in the topsoil and inoculated ones in the subsoil. According to the ANOVA, soil type had no effect on the xylem pressure potential for either tree species (Table 5).

Table 5 Xylem pressure potential and relative water content of *Glomus deserticola*-inoculated and non-inoculated *Gliricidia sepium* and *L. leucocephala* after 16 weeks of growth in non-disinfected soils. For abbreviations, see Table 1

Soil	Mycorrhizal inoculation	Watering regime	G. sepium		L. leucocephala	
			Xylem pressure potential (MPa)[a]	Relative water content (%)[a]	Xylem pressure potential (MPa)[a]	Relative water content (%)[a]
Topsoil	Without	Watered	–1.93a	69.8b	–2.17a	57.7a
		Drought	–3.50b	50.5c	–4.00d	41.2bc
	With	Watered	–1.93a	81.6a	–2.70ab	47.9ab
		Drought	–2.97b	41.2d	–3.20bc	45.9b
Subsoil	Without	Watered	–1.70a	47.9cd	–3.13cd	45.1bc
		Drought	–3.33b	30.0e	–3.67cd	34.1cd
	With	Watered	–2.07a	75.1ab	–2.63ab	40.4bc
		Drought	–3.40b	49.1c	–3.70cd	25.0d
ANOVA						
W			***	***	***	***
I			NS	***	NS	NS
S			NS	***	NS	***
Interactions						
W×I			NS	**	NS	NS
W×S			NS	NS	NS	NS
I×S			NS	***	NS	NS
W×I×S			NS	NS	*	NS

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$
[a] See footnote to Table 1

Inoculation with *Glomus deserticola* increased the relative leaf water content for *Gliricidia sepium* by 57% in the subsoil under an adequate watering regime and by 64% under drought conditions (Table 5). For *L. leucocephala*, there was no effect of fungal inoculation on relative leaf water content (Table 5). The effect of soil type was highly significant ($P \leq 0.001$). The effect of the watering regime was significant only for mycorrhizal *G. sepium*, suggesting that symbiosis with *Glomus deserticola* effectively assisted this plant in water uptake and retention in leaves, thereby increasing physiological activities and giving an enhanced yield. Drought tolerance was not improved in *L. leucocephala* by inoculation with the AMF, neither was it affected by drought stress, suggesting that this plant can cope effectively with drought conditions, which is consistent with reports from the National Research Council (1984) and the National Academy of Science (1977). In contrast, Huang et al. (1985) reported that water relations of *L. leucocephala* were improved by AMF. This contradiction may be due to a lower physiological compatibility of *G. deserticola* with *L. leucocephala*, since variability in compatibility has been reported for various arbuscular mycorrhizal symbioses (Krishna et al. 1985; Rajapakse and Miller 1987; Rao et al. 1990; Mercy et al. 1990).

Conclusion

The contribution of *Gliricidia deserticola* to the growth of *L. leucocephala* in non-sterile topsoil is minimal in terms of dry matter yield, and less than that in subsoil with respect to shoot dry weight. Although the effect of *Glomus deserticola* on the shoot dry weight of *Gliricidia sepium* was minimal in topsoil, there was a significant increase in the growth of mycorrhizal plants in the subsoil. However, inoculation with the AMF did not relieve the effect of drought stress on dry matter yield of either tree species in the topsoil or the subsoil. Since the yield of *G. sepium* was improved when it was inoculated with *Glomus deserticola* in the subsoil, this AMF could be used to improve the adaptation of this hedgerow legume species in afforestation programmes of badly eroded soils where water availability is not a problem. Further screening of these promising hedgerow trees with different AMF should lead to selection of the most appropriate combination for the revegetation of eroded sites.

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