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Growth responses and dependence of *Acacia nilotica* var. cupriciformis on the indigenous arbuscular mycorrhizal consortium of a marginal wasteland soil

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Abstract The responses of *Acacia nilotica* L. var. cupriciformis to phosphorus application and inoculation with the indigenous consortium of arbuscular mycorrhizal (AM) fungi were evaluated in a nursery experiment using soil from a marginal wasteland. A positive growth response to mycorrhizal inoculation was observed at an Olsen-P level of 20 ppm in the presence of the natural population of AM fungi. There was growth stimulation by either inoculation or additional P at the highest soil P of 40 ppm. Colonization was negatively correlated to soil P but P content of both shoot and root were positively correlated. Inoculation with the indigenous AM consortium significantly increased the uptake of P at all levels of applied P. *Acacia* is moderately dependent upon the AM symbiosis and exhibited a maximal mycorrhizal dependence (MD) of 18.25% at 20 ppm Olsen-P level under the conditions studied. A sharp and considerable reduction in MD and dry matter yield observed at 40 ppm P suggests that the external P requirement for maximal production of biomass was met at approximately 20 ppm Olsen-P.

Key words *Acacia nilotica* · Indigenous AM consortium · Infectivity potential · Mycorrhizal dependence · Phosphorus utilization efficiency

Introduction

The advance of wasteland is reaching alarming proportions in the northeastern states of India. Approximately 20% of the total geographical area of India is now wasteland. Growing demand for fuel, fodder, wood, and food has extensively depleted or eliminated protective plant cover and exposed surface soils to processes of degradation, resulting in partial to complete loss of soil productivity (National Wasteland Development Board 1987). Impoverished soils, extreme temperatures and erratic rainfall have also contributed to the perpetuation of the wastelands (Lopez-Sanchez and Honrubia 1992). As a consequence, the production of vegetation for food and other uses has extended to areas under great ecological stress and with less favourable environments. Mycorrhizal fungi are likely to be most beneficial in diverse (wasteland) ecosystems where the proportion of plants able to form mycorrhizas is high and nutrient deficiencies are an important limitation to plant growth. These fungi can make an important contribution to the rehabilitation of wasteland through the following mechanisms:

1. Enhancing establishment and growth of plants by increasing nutrient uptake
2. Maintaining diversity by boosting the ability of host plants to compete for resources
3. Contributing to efficient recycling of nutrients and thus to long-term stability
4. Stabilizing the soil (Allen 1989, Jasper 1994).

The genus *Acacia* is an important component of woody vegetation in the semi-arid and arid zones of the world. It is a relatively fast-growing, drought-resistant, multipurpose legume tree (Michelsen and Rosendahl 1990). However, *Acacia* spp. depend on an adequate supply of P to achieve their potential for rapid growth (Jasper et al. 1988). It is likely that the formation of arbuscular mycorrhizas (AM) will be an important factor in the successful establishment of *Acacia nilotica* and other mycorrhiza-dependent plants (Jasper et. al. 1989) in the phosphorus-deficient soil of a wasteland.

Efforts were made in the present study to evaluate the P requirements of *A. nilotica* L. var. cupriciformis as well as its dependence on AM fungi to attain maximal growth under varying levels of soil P. The current investigation was also concerned with the identification of the critical level of phosphorus in soil that supports optimal AM association and results in a benefit comparable to high input levels of P. This could lead to a significant saving of inorganic P fertilizer.

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Materials and methods

Soil preparation

Sandy loam soil (Hyperthermic Typic Haplustalf) from a wasteland was used as a substrate. The wasteland site is located at Gwal Pahari in Haryana state, India, at longitude 77°12′E and latitude 28°35′N and at 255 m above mean sea level and receives a mean annual rainfall of 500 mm. The land had been repeatedly subjected to active sheet (water) erosion and had not been cultivated for a long period. The nutritional and physical characteristics are unsuitable for all flora except a few seasonal/perennial weeds and grasses. The soil was collected from 0–30 cm depth, air-dried and passed through a 2-mm sieve. Some chemical properties of the soil are listed in Table 1.

Table 1 Chemical properties of the wasteland soil (*EC* electrical conductivity)

Depth	pH (1:2.5 H_2O)	EC (dS/m)	Organic C (%)	Total N (%)	Olsen-P (ppm)
15 cm	8.39	0.22	0.24	0.018	2.00
45 cm	8.42	0.19	0.19	0.012	1.24

AM inoculum production and infectivity test

The wasteland site was dominated by seasonal weeds such as *Argimone maxicana* and *Saccharum munja*, which generally harbour AM in their roots. Random soil samples were processed to isolate indigenous AM (dominated by *Glomus* spp.) by the wet sieving and decanting method (Gerdemann and Nicholson 1963). The isolated consortium (spores/sporocarps, hyphae and root bits) was multiplied and maintained on Sudan grass (*Sorghum bicolor* var. Sudanense) for 1 year in 1-m^2 beds (raised 15 cm above ground) in nursery using similar soil. The beds were solarized (56 ± 3 °C) for 8 days by covering with white translucent polyethylene sheet. After 1 year, the Sudan grass was cut at ground level and the roots chopped into small bits and mixed with the soil mass of the raised beds. This soil-based inoculum was collected in plastic containers and stored at 4 °C.

Prior to use of the inoculum, a serial dilution technique was applied to ascertain the amount of infectious propagules (Plenchette et al. 1989). Six dilutions, 00, 20, 40, 60, 80 and 100% of inoculum, were made with autoclaved soil (121 °C for 1 h at 15 psi). Aliquots (100 g) of substrate containing various levels of inoculum were placed in plastic pots (7 cm in height, 5 cm in diameter). Seeds of *S. bicolor* were germinated in a petri dish for 2 days and eight seeds were sown in each pot. The pots were placed in a growth room (28/22 °C, 78% RH). The plants were watered with deionized water to a moisture content of 60% water holding capacity and harvested after 10 days. The entire root system from each seedling was collected, washed carefully under tap water, and stained using the technique of Phillips and Hayman (1970). Each root system was mounted on a microscopic slide and observed at ×200 under a compound microscope (Gallen III, Leica, Cambridge, UK) attached to a CCD camera and image analyser system (Leica, Switzerland) controlled by Quantimet 500+ software (Leica, Cambridge) with a colour option. The total number of primary entry points (PEP) for all the plants was determined for each dilution. A linear relationship between inoculum concentration and number of infectious propagules was established. A total of 12 infectious propagules per g of soil-based inoculum was determined, compared to 0.96 per g of unsterilized wasteland soil.

Soil P enrichment and AM inoculation

Varying amounts of fertilizer-grade single superphosphate (SSP, 16% P_2O_5) were added to subsamples of soil. After three cycles of wetting (with deionised water to 60% water holding capacity) and drying (shade) during 1 week, the samples were analysed for available soil P (Olsen-P). Based on the results obtained, SSP was added to two sets of soil aliquots to obtain available P levels of 10, 20, and 40 mg kg^{-1} soil.

One set of soil samples was inoculated with AM using 55.8 g (approximately 670 infectious propagules) per polybag (15 cm length, 6 cm diameter, black) (Ross and Harper 1970) to give a final quantify of 400 g substrate (1000 infectious propagules) per polybag. The second set received no AM inoculation. Holes (6–8) were made at in bottom of each polybag to facilitate drainage. Both the AM-inoculated and uninoculated treatments, at all the P levels, were replicated four times.

Seed treatment and planting

Seeds of *A. nilotica* obtained from a selected elite (phenotypically superior) tree from Uttar Pradesh State Forest Department, India were graded by weight (0.186–0.206 g) and given a hot water treatment (100 °C for 15 min) prior to germination under sterile conditions. One seedling was placed in each polybag and the bags were maintained gravimetrically at a moisture content of approximately 60% water holding capacity. The experiment was laid out in a completely randomized design under nursery conditions with 4 replicates per treatment combination (SSP level × inoculation).

Measurements

The plants were harvested after 12 weeks growth and dry weights of root and shoot and percentage of root colonization by AM fungi were recorded. Roots and shoots were dried for 48 h in a hot-air oven at 70 °C. Fresh roots were cleared with KOH and stained with acid fuschin (0.01% in lactoglycerol) (Phillips and Hayman 1970), and the mycorrhizal colonization percentage (MCP) was determined by the grid-line intersection method of Giovannetti and Mosse (1980). Spores were isolated according to the method of Gerdemann and Nicolson (1963) and counted (Gaur and Adholeya 1994). The P contents of soil and plant samples were determined by the methods of Olsen et al. (1954) and Kitson and Mellon (1944), respectively. Mycorrhizal dependence (MD) was calculated according to Plenchette et al. (1983). Phosphorus utilization efficiency (PUE) was expressed as g dry matter produced per mg P taken up by the plant (Manjunath and Habte 1989). The data were statistically analysed by ANOVA and the means separated by Duncan's multiple range test ($P < 0.05$) using Costate software (Cohort, Berkeley, Calif.).

Results

Mycorrhizal colonization

The results show that the AM fungal inoculum in the marginal wasteland soil was adequate for sufficient mycorrhization of *A. nilotica* roots (36.6%) but less beneficial than other treatment combinations (Table 2). Augmentation of soil P marginally depressed the MCP, whereas inoculation of soil with the consortium of AM fungi isolated from the same soil as used in polybags resulted in 69, 102, 108 and 55% increases in MCP over their respective control plants at 0.53, 10, 20, and 40 ppm Olsen-P levels, respectively.

Though colonization by the indigenous consortium of AM fungi tended to decrease with increasing levels

Table 2 Influence of inoculation with an indigenous arbuscular mycorrhizal (AM) consortium at different levels of P on *Acacia nilotica*. Means in each column followed by the same letter are not significantly different ($P<0.05$)

Treatment	Root/shoot ratio	Total dry matter (g per plant)	Mycorrhizal dependence (%)	Mycorrhizal colonization (%)
0.53 ppm P − AM	0.35	0.744e	10.26b	36.67b
0.53 ppm P + AM	0.33	0.829d		62.00a
10 ppm P − AM	0.34	0.760e	14.08ab	28.67bc
10 ppm P + AM	0.32	0.885d		58.00a
20 ppm P − AM	0.38	0.945c	18.25a	26.33bc
20 ppm P + AM	0.36	1.156a		54.67a
40 ppm P − AM	0.39	0.990bc	4.54c	20.67c
40 ppm P + AM	0.38	1.038b		32.00bc
LSD ($P=0.05$)	–	0.0598	4.97	12.09

of soil P, the values for the native P level and the first two P increments did not differ significantly (Table 2). All inoculated treatments had higher MCP values than their equivalent uninoculated counterparts. The maximal MCP values for both inoculated (62%) and uninoculated (36%) treatments were recorded at the lowest level of P tested (0.53 ppm), and none of the growth parameters recorded in the present study showed significantly higher values at this soil P level.

Plant growth

The increase in plant dry weight (Table 2) in AM-inoculated plants compared with uninoculated controls was maximal at 20 ppm Olsen-P level (22.32%), followed by plants at 10 ppm P (16.40%), 0.53 ppm P (11.44%), and 40 ppm P (4.75%). Thus the soil P level achieved by addition of 20 ppm Olsen-P is most suitable for accumulation of plant dry matter and mycorrhization of *A. nilotica* roots. The increase in dry matter was found to be positively correlated to shoot P and root P uptake both for inoculated and uninoculated *A. nilotica* (Tables 1, 2).

Uninoculated plants had higher PUE values at all soil P levels than their inoculated counterparts (Fig. 1), with maxima for uninoculated and inoculated *A. nilotica* of 0.91 and 0.82 respectively, at 0.53 ppm Olsen-P.

P contents of plant tissues

Significant improvements in P uptake with increasing soil P levels were observed for roots and shoots of both inoculated and uninoculated plants (Table 3). The increase in P uptake was, however, significantly greater in inoculated than in uninoculated plants at 0.53–20 ppm Olsen-P levels. Above 20 ppm there was no increase in P uptake by either inoculated or uninoculated plants.

Similar to PUE, the data on shoot P: root P (Fig. 2) indicate that uninoculated plants performed better than their inoculated counterparts, the maximal values for the ratio being at 0.53 ppm P for both uninoculated and inoculated plants, followed by 20 ppm.

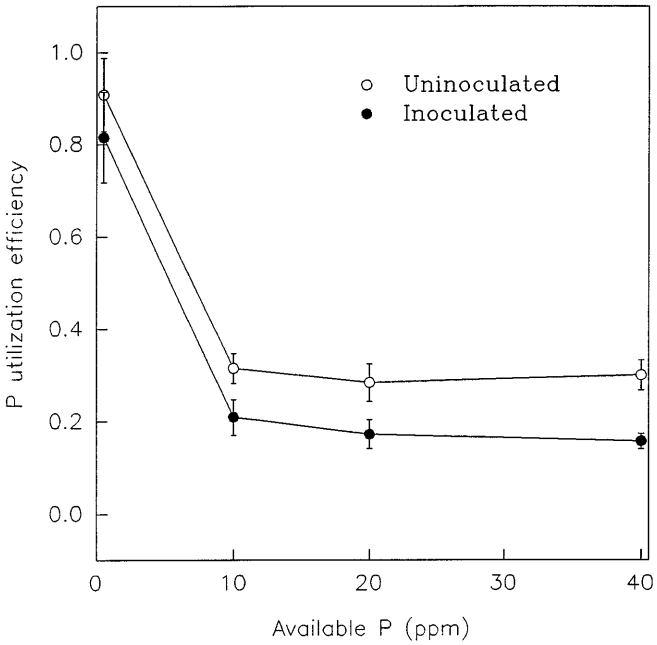

Fig. 1 Influence of the inoculation with indigenous arbuscular mycorrhizal fungi on the phosphorus utilization efficiency of *Acacia nilotica*. Error bars indicate standard error of the mean

Mycorrhizal dependence

The dependence of *A. nilotica* on the indigenous AM consortium increased with the soil P concentration up to 20 ppm and *A. nilotica* exhibited the lowest dependence at the highest concentration of Olsen-P (Table 2). The maximal dependence on the fungus for growth was less than 20% at a soil P concentration of 20 ppm. An almost fourfold reduction in MD was observed at 40 ppm P.

Discussion

The growth of *A. nilotica* var. cupriciformis was substantially increased by addition of phosphorus and by inoculation with AM fungi. It appears likely that this species relies moderately on AM fungi for uptake of

Table 3 P uptake per plant by inoculated *A. nilotica* seedlings compared with uninoculated controls. Means in each column followed by the same letter are not significantly different ($P<0.05$) (R^2 regression coefficient dry matter:P uptake; $P<0.01$)

Plant part	Soil P levels (ppm)	Uninoculated plants		Inoculated plants	
		P uptake (mg)	% Increase	P uptake (mg)	% Increase
Shoot	0.53	0.42g	–	0.50f	–
	10	1.21e	188.09	2.05c	306.93
	20	1.69d	39.66	3.29a	57.23
	40	1.67d	−1.19	3.24b	−1.70
LSD ($P=0.05$)		0.047			
R^2 ($n=32$)		0.68		0.73	
Root	0.53	0.40g	–	0.51f	–
	10	1.20e	200.00	2.17c	323.80
	20	1.63d	35.83	3.41a	57.20
	40	1.62d	−0.62	3.35b	−1.70
LSD ($P=0.05$)		0.038			
R^2 ($n=32$)*		0.67		0.71	

*** $P<0.01$

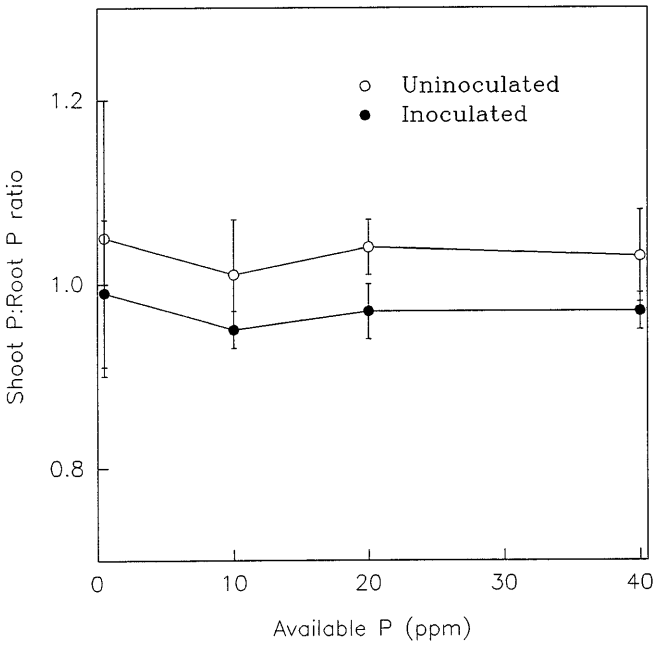

Fig. 2 Influence of the inoculation with indigenous arbuscular mycorrhizal fungi on the shoot P: root P ratio of *A. nilotica*. Error bars indicate standard error of the mean

phosphorus when grown in a coarse-textured (sandy loam in our study) soil, as suggested by Jasper et al. (1989). This may be attributed to a relatively low P adsorption capacity of such soils. An increase in the total dry matter yield with increasing concentration of applied P up to 20 ppm (+mycorrhizal inoculation) (Table 2) indicates the considerable demands for P by *A. nilotica.* A significant reduction in total dry matter yield above this level suggests that the external P requirement for maximal production of dry matter was met, supporting the observation of Manjunath and Habte (1992).

A. nilotica has a relatively coarse root system with few root hairs. Our observation of its significant MD supports the hypothesis of Baylis (1970) that plants with poorly developed root hairs may be obligate mycotrophs in P-deficient soils. The negative effect of P on AM colonization is a function of P in the plant tissue (Daniels 1984; Ratnayake et al. 1978). High levels of soil and tissue P reduced the level of infection of *A. nilotica.* This suggests a low level of tolerance or high degree of sensitivity of the indigenous AM fungus consortium/*A. nilotica* symbiosis to high P concentrations (Habte and Manjunath 1987). The increase in MCP with inoculation may be due to the uniform distribution of AM inoculum in the soil as well as an increase in inoculum potential of AM fungi. The MCP maximum at 20 ppm soil P and minimum at 40 ppm Olsen P clearly brings out the mediating role of soil P in MCP. Soil P levels of 0.53 ppm and those obtained after application of 10 and 20 ppm P appeared optimal for mycorrhization of seedling roots.

Mycorrhizal inoculation increases P uptake from the substrate due to greater exploration of the soil by AM fungus hyphae (Abbott and Robson 1982). This is shown in the present experiment by the almost twofold increase in P recovery by inoculated plants compared with their uninoculated counterparts at each level of P. Mycorrhiza-dependent species typically do not respond appreciably to P unless high levels of nutrient are present in the soil solution (Habte and Manjunath 1987; Linderman and Hendrix 1982).

The data presented in Table 3 indicate that the level of AM inoculum existing in natural soils was not efficient to transfer the fullest benefit of phosphorus added to the soil. On the other hand, inoculated seedlings were able to obtain greater quantities of soil phosphorus and produce more plant dry matter. The efficiency of utilization of P was maximal at 10 ppm Olsen-P but declined at 20 ppm, and none of the additional P in the

40-ppm treatment was utilized. The reduction in PUE can be attributed to utilization of photosynthate by AM fungi where plant species fail to curtail the level of AM colonization (Harris and Paul 1987; Manjunath and Habte 1992). The suppression of AM activity by high soil P could have also led to reduced uptake of Cu and Zn, resulting in the growth depression observed (Lambert and Weidensaul 1991).

The AM-inoculated plants were not as efficient as uninoculated plants in utilizing P for dry matter production. Moreover, the increase in dry matter in uninoculated plants when their internal P content was as high as 3.29 mg (mean root P and shoot P values at 40 ppm soil P level) indicates that the threshold internal P concentration for growth response was not reached. Nevertheless, in nutrient-poor enviromnents and in ecosystems where tight nutrient cycles seem to operate (for example, tropical rain forests), biomass production is likely to be limited by inaccessibility of diffusion-limited nutrients like P, Cu, and Zn and, therefore, AM-infected plants will have a selective advantage under these conditions (Manjunath and Habte 1988, 1989).

The low shoot P: root P ratios of inoculated *Acacia* relative to the uninoculated plants indicates more translocation of P from the root to the shoot in uninoculated plants and is interesting in the light of the lower root: shoot dry matter ratios of inoculated plants. This supports the findings of Clarkson (1985) and Manjunath et al. (1989) that plants probably allocate a greater proportion of assimilates to roots when nutrients such as N and P are limiting and/or when factors other than the rates of P acquisition limit the rate of growth of the plants with consequent luxury accumulation of P (Stribley et al. 1980).

AM-uninoculated plants had lower root : shoot ratios than uninoculated plants. The lower relative root mass of the inoculated plants was probably functionally substituted by the external mycelium of the AM fungi (Michelsen and Rosendahl 1990).

The results of the present study indicate that there is an optimal level of P in the soil at which the benefits of AM fungus inoculation are greatest in respect to biomass increment, mycorrhizal dependence, and P uptake. The 20 ppm soil Olsen-P level was shown to be critical given the host, the endophyte consortium and the prevailing soil conditions in the wasteland selected for the present study. Further increase in applied P brought no increase in growth of inoculated plants and resulted in erasure of the response to inoculation. Thus, future experiments will be continued for longer periods and with more detailed P doses to determine the critical level of P for maximal mycorrhization and growth of *A. nilotica* seedlings, and to achieve maximal savings on P application.

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