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Distribution of roots, arbuscular mycorrhizal colonisation and spores around fast-growing tree species in Senegal

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Abstract

Roots and soil were sampled from around four leguminous tree species in 10-year-old plots at Bandia, Senegal. Assessments of root concentration (cm per 100 cm^3 soil) and mycorrhizal colonisation (% of root length) were made and related to the abundance of spores in the soil and the above ground growth (stem diameter at 30 cm height) of the trees. Root concentrations in *Acacia nilotica* and *Acacia tortilis* plots were greater than those found in *Prosopis juliflora* and *Acacia aneura* plots at all three depths examined (0–10, 10–25, 25–50 cm). Root concentration decreased with soil depth in all plots and was greatest nearest the tree in the *Acacia nilotica* and *Acacia tortilis* plots. Mycorrhizal colonisation was highest on *Prosopis juliflora* roots and lowest on *Acacia tortilis* roots. Colonisation was not affected by distance from the tree and decreased with depth only in the *Acacia aneura* plot. Numbers of spores recovered from soils were generally low (27 per 100 g dry wt. soil) and were concentrated in the upper 10 cm of soil. Spores were most numerous in the *Acacia aneura* plot and least numerous in the *Prosopis juliflora* plot. Positive relationships were found between spore numbers and root concentration in the *Prosopis juliflora* plot and between spore numbers and mycorrhizal colonisation in the *Acacia aneura* plot. Of the four tree species examined, root and mycorrhizal distributions of *Prosopis juliflora* and *Acacia nilotica* showed most promise for use in agroforestry systems.

Keywords: Root distribution; Arbuscular mycorrhizas; Spore numbers; Tree species

1. Introduction

Dry land degradation is a problem affecting many semi-arid areas of Africa. In the Sahel, expanding agricultural activities are leading to over exploitation of soil nutrients, increasing soil erosion and a decline in overall land productivity (Van Keulen and Breman, 1990). There is an urgent need to identify and introduce agricultural practices which will ameliorate or sustain soil fertility and conserve water resources.

Fast-growing, multipurpose tree species are widely used in agroforestry systems in conjunction with agricultural crops. The trees stabilise and ameliorate the soils while providing products of direct benefit to rural populations (Kang and Wilson, 1987). Al-

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though it has been assumed that crop yields benefit indirectly from ameliorated soil conditions and that tree and crop root systems are distributed in different horizons of the soil, there is increasing concern that tree and crop roots are in competition for soil water and nutrients (Jonsson et al., 1988; Singh et al., 1989; Ong et al., 1991). As a result Schroth (1995) has proposed that tree root characteristics, such as low root competitiveness and a root distribution complementary to that of the crop, should be preferred when selecting trees for agroforestry.

Most of these plant species depend, to some extent, on arbuscular mycorrhizal (AM) fungi for the acquisition of nutrients and water from the soil and the maintenance of growth. These ubiquitous soil fungi associate with a wide range of host species (both trees and crops) and predominate in dry tropical soils. In agroforestry systems, tree root mycorrhizas may therefore play an additional role by maintaining levels of active fungal propagules in the soil which can rapidly colonise developing crop root systems (Wilson et al., 1991).

Although several studies have examined growth responses following inoculation of these tree species with AM fungi, little is known of the distribution of mycorrhizal populations occurring in agroforestry systems. In this study, root and mycorrhizal distributions of fast-growing, multipurpose tree species were examined in order to determine differences between species and highlight those tree root systems which might facilitate optimal growth and minimal competition with crop roots. AM spore populations were also assessed as an indicator of mycorrhizal propagule distribution around the trees. The work formed part of a wider study of the above and below ground growth and nutrient/water use efficiencies of such species, in order to identify which were most appropriate for use in the Sahel.

2. Materials and methods

2.1. Site

The study site was at the Institut Sénégalaise de Recherches Agricoles (ISRA) experimental research station at Bandia, Senegal (14°30′N, 17°0′W). Individual plots of nine tree species (40 provenances in total) had been planted in 1984, with each plot replicated within four blocks. Each plot consisted of 49 trees arranged in a 7×7 layout with 5 m spacing between trees.

The climate at Bandia is typical of semi-arid regions of West Africa with mean monthly temperatures ranging between 26 and 30°C and an annual precipitation of 600–700 mm, which occurs mostly during a single rainy season (June–October).

The soil in the plots is described (O. Diagne, personal communication, 1995) as a hydromorphic, clay vertisol with ferruginous concretions to a depth of 1.5–2.0 m, overlying a solid sand/clay base material. Soil pH was determined (KCl) as 5.6 with C, N and P (available P_2O_5) contents of 1.02%, 0.11% and 0.002%, respectively. The soil had been uncultivated prior to planting in 1984.

2.2. Tree species

Tree species/provenances examined were *Acacia aneura* F. Muell. ex Benth., ISRA seedlot 84/965 ex. Australia, *Acacia nilotica* (L.) Willd. ex Del., ISRA 81/443 ex. Senegal, *Acacia tortilis* (Forsk.) Hayne, ISRA 84/977 ex. India and *Prosopis juliflora* (Swartz) D.C., ISRA 82/746 ex. Senegal. As this work formed part of intensive studies of above and below ground growth and nutrient acquisition, it was possible to study only one plot of each species/provenance. Plots were selected from the third replicate block on the basis of uniformity of site topography, above ground growth and optimal survival.

2.3. Sampling

Samples were taken in March 1994, during the dry season and 10 years after establishment of the plots. Three transects were established in each plot with each transect located between two diagonally opposite trees (approximately 7 m apart). Where possible, transects were selected on the basis of uniformity of the paired transect trees and absence of ground vegetation along the transect. A shortage of suitable trees in the *P. juliflora* plot meant that two of the transects were located on opposite sides of the same tree. Sampling points were located near to the trees (50 cm), at the quartile positions and at the

midpoint, giving five sample points on each transect. Due to the exceedingly hard nature of the soil in the dry season, sampling was restricted to the upper 50 cm. Soil was removed from each sample point using a 7 cm diameter auger with sharpened cutting edges and separated into 0–10 cm, 10–25 cm and 25–50 cm depth sub-samples.

2.4. Assessments

Mean bulk density of the soil was determined so that soil volumes could be calculated from the weight of each soil sample. Stem diameter of the transect trees at 30 cm height was measured so that the effect of tree size on root biomass could be accounted for in the data analysis. Amounts of ground vegetation in each plot were noted, as this vegetation comprised other AM plants which may have been responsible for additional inputs of AM spores.

All root material was extracted from the soil over a 500-μm sieve and total root length in each sample determined by the grid-line intersect method (Tennant, 1975). Fine roots (< 2 mm) were removed and stained using the method of Phillips and Hayman (1970) as modified by Koske and Gemma (1989). Mycorrhizal colonisation was assessed on a sub-sample of 20 × 1 cm root fragments mounted on glass slides. Slides were observed under a compound microscope, recording the presence or absence of hyphae, arbuscules and vesicles at 1 mm intersect points along the root axis, adopting methods similar to those used by Allen and Allen (1980) and McGonigle et al. (1990).

AM spores were extracted from 100 g sub-samples of soil following the method of Walker et al. (1982). Spores were counted and categorised as 'live' or 'dead'; 'dead' spores typically lacking cytoplasm and/or showing signs of parasitism. Where possible, spores were identified to species. A sample of each soil was dried at 80°C so that results could be expressed on a dry weight basis.

2.5. Statistical analysis

Data were examined by analysis of variance (ANOVA) using tree species, transect point and depth as treatment factors. The layout of the experiment determined that tree species and transect were also block factors. ANOVA of root concentration was adjusted using the relevant stem diameter as a covariate. Before analysis, arcsine and log $(n + 1)$ transformations were performed on mycorrhizal colonisation percentages and spore numbers, respectively, and Bartlett's test (Sokal and Rohlf, 1995) was used to ensure that sample variances were homogenous. Means were compared using Fisher's LSD test when the F-test from ANOVA was significant at $P < 0.05$. Correlation coefficients were determined to examine relationships between parameters.

Although the study did not have replication to detect differences between tree species, as these differences were potentially important, the transect variance was used to provide an indicator of significant species differences.

3. Results

3.1. Above ground growth

Stem diameter measurements of transect trees are given in Table 1 and compared with the plot mean.

Table 1
Stem diameter (cm) at 30 cm height of trees in study plots at Bandia, Senegal

	P. juliflora		*A. nilotica*		*A. tortilis*		*A. aneura*	
	Tree 1	Tree 2	Tree 1	Tree 2	Tree 1	Tree 2	Tree 1	Tree 2
Transect 1	18.9 [a]	21.5	13.1	13.6	13.2	16.2	15.5	16.5
Transect 2	19.1	22.1	13.5	17.5	14.3	23.0	16.6	15.2
Transect 3	18.9 [a]	15.9	11.0	17.3	17.5	24.7	15.5	17.2
Transect mean (± SE)	19.4 ± 0.9		14.3 ± 1.0		18.1 ± 1.9		16.1 ± 1.3	
Plot mean (± SE)	16.8 ± 0.9		12.0 ± 0.5		15.6 ± 0.9		14.4 ± 1.3	

[a] Transects 1 and 3 were located on opposite sides of the same tree in the *P. juliflora* plot.

Table 2
Root concentration (cm per 100 cm^3), mycorrhizal colonisation (%) and AM spore number (per 100 g dry wt. soil) associated with four different tree species growing at Bandia, Senegal

	P. juliflora	*A. nilotica*	*A. tortilis*	*A. aneura*	*P* value
Root concentration	32 bc [a]	58 a	47 ab	26 c	0.003
Mycorrhizal colonisation	64 a [b]	55 b	31 c	47 b	0.013
Total spore number	8.4 d [c]	32 b	19 c	51 a	< 0.001
'Live' spore number	0.5 c [c]	2.8 b	2.1 b	9.5 a	< 0.001

[a] Letters indicate significant differences within each row at $P < 0.05$ as determined by ANOVA and Fisher's LSD test.
[b] Arcsine transformations were performed on mycorrhizal percentages for statistical analysis; significance is given against untransformed data.
[c] Log $(n + 1)$ transformations were performed on spore numbers for statistical analysis; significance is given against untransformed data.

Transect means were larger than plot means, however, the relative differences in size between tree species were similar with *P. juliflora* trees being the largest and *A. nilotica* trees the smallest. Data collected on the above ground growth of all tree species/provenances in all four blocks at this site showed that tree height, stem diameter and survival of *P. juliflora* was considerably better than that of *A. tortilis*, *A. nilotica* and *A. aneura*. This data will be reported separately (J.D. Deans, personal communication, 1996).

Amounts of ground vegetation also differed between the plots according to the above ground growth of the four tree species and the degree of canopy closure, with *A. aneura* having most ground vegetation and *P. juliflora* least.

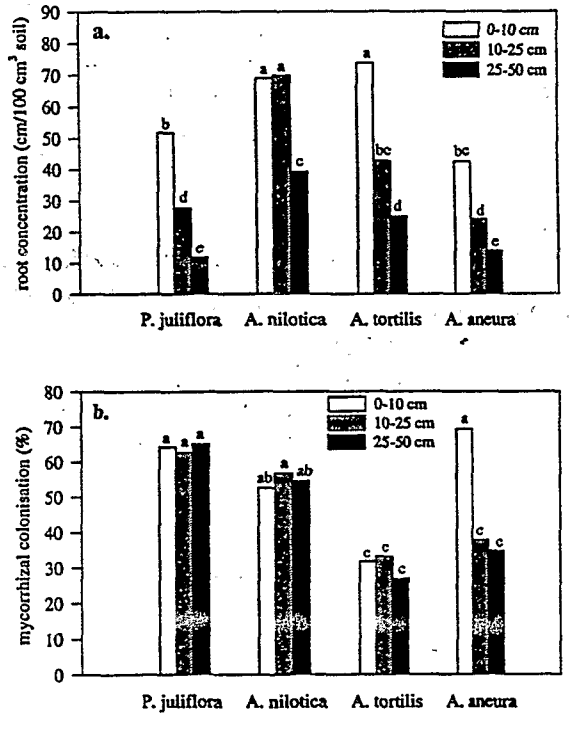

Fig. 1. Root concentration (a) and mycorrhizal colonisation (b) of four tree species at three depths in plots at Bandia, Senegal. Columns with different letters are significantly different at $P < 0.05$ as determined by ANOVA and Fisher's LSD test.

Table 3
Root concentrations (cm per 100 cm^3), mycorrhizal colonisation (%) and AM spore numbers (per 100 g dry wt. soil) found at different soil depths at Bandia, Senegal

	0–10 cm	10–25 cm	25–50 cm	*P* value
Root concentration	59 a [a]	41 b	23 c	< 0.001
Mycorrhizal colonisation	55 a [b]	48 b	45 b	0.003
Total spore number	63 a [c]	14 b	5.2 c	< 0.001
'Live' spore number	8.8 a [c]	2.1 b	0.4 c	< 0.001

[a] Letters indicate significant differences within each row at $P < 0.05$ as determined by ANOVA and Fisher's LSD test.
[b] Arcsine transformations were performed on mycorrhizal percentages for statistical analysis; significance is given against untransformed data.
[c] Log $(n+1)$ transformations were performed on spore numbers for statistical analysis; significance is given against untransformed data.

Table 4
Effect of distance along transect on root concentration (cm per 100 cm^3) in plots of four different tree species at Bandia, Senegal

	Tree 1		Transect point		Tree 2	P value
	50 cm	1st quartile	Midpoint	2nd quartile	50 cm	
P. juliflora	32	26	33	30	33	0.329
A. nilotica	63 b[1]	50 c	55 bc	46 c	83 a	< 0.001
A. tortilis	39 b	29 b	39 b	57 b	73 a	0.008
A. aneura	34	32	24	21	24	0.072
Mean	44 b	36 c	38 c	37 c	51 a	< 0.001

[1] Letters indicate significant differences within each row at $P < 0.05$ as determined by ANOVA and Fisher's LSD test.

3.2. Root concentration

Root concentration differed between tree species, with *A. nilotica* having most roots and *A. aneura* fewest (Table 2).

Both *A. nilotica* and *A. tortilis* had more roots ($P < 0.001$) at all three depths than *P. juliflora* and *A. aneura* (Fig. 1a). Although most roots were concentrated in the upper soil horizon (0–10 cm) and decreased with depth (Table 3), *A. nilotica* had considerably more roots at depths greater than 10 cm than the other tree species (Fig. 1a).

Some differences in root distribution along the transect were detected between tree species with the *A. nilotica* and *A. tortilis* plots having largest root concentrations nearest the tree, i.e. at the 50 cm points (Table 4). No differences were found in the *P. juliflora* and *A. aneura* plots with roots fairly evenly distributed along the transect.

3.3. Mycorrhizal colonisation

Levels of mycorrhizal colonisation differed between tree species with colonisation of *P. juliflora* roots greater than that of *A. nilotica* and *A. aneura*, which in turn, was greater than that found in *A. tortilis* roots (Table 2).

Although mycorrhizal colonisation appeared to decrease with soil depth (Table 3), a significant tree species × soil depth interaction ($P < 0.001$) indicated that this was due entirely to high levels of colonisation on the *A. aneura* roots found in the upper soil horizon (Fig. 1b). Levels of colonisation on the other tree species were not affected by soil depth.

3.4. AM spore numbers

Although very few 'live' spores were recovered from the soils, numbers of spores (total and 'live') differed between tree species. Most spores were found in the *A. aneura* plot with decreasing numbers found in the *A. nilotica*, *A. tortilis* and *P. juliflora* plots, respectively (Table 2). Spores were also concentrated in the upper soil horizon (0–10 cm) and decreased markedly with depth (Table 3).

Although *Glomus mosseae* (Nicol. and Gerd.) Gerdemann and Trappe and *Glomus etunicatum* Becker and Gerdemann were present in the soils, the number of 'live' spores was not sufficient to enable comparisons of fungal species composition to be made between samples.

Table 5
Correlations (r) between root concentration (cm per 100 cm^3), mycorrhizal colonisation (%) and AM spore number (per 100 g dry wt. soil) associated with four different tree species growing at Bandia, Senegal

	Individual tree spp. ($n = 45$)				All tree spp. ($n = 180$)
	P. juliflora	*A. nilotica*	*A. tortilis*	*A. aneura*	
Root conc. vs. spore no.[a]	0.749 ***	0.613 ***	0.239	0.644 ***	0.426 ***
Root conc. vs. myc. col.[b]	0.177	0.111	0.269	0.463 **	0.092
Spore no. vs. myc. col.	0.003	0.107	0.244	0.520 ***	0.215 *

*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.
[a] Log ($n + 1$) transformations were performed on spore numbers for statistical analysis.
[b] Arcsine transformations were performed on mycorrhizal percentages for statistical analysis.

3.5. Relationships between parameters

An overall positive correlation ($P < 0.001$) was found between root concentration and total spore number. When the four tree species were considered separately, this relationship was strongest in the *P. juliflora* plot, also present in the *A. nilotica* and *A. aneura* plots but absent in the *A. tortilis* plot (Table 5).

Positive correlations were also found in the *A. aneura* plot between mycorrhizal colonisation and total spore number ($P < 0.001$), and between root concentration and total spore number ($P < 0.01$).

4. Discussion

4.1. Root concentration

A. nilotica and *A. tortilis* had greater concentrations of roots than *A. aneura* and *P. juliflora*, which supports the work of Cazet (1989), who examined root distributions of 30-month-old trees at Thienaba, Senegal and found more roots associated with *A. nilotica* and *A. tortilis* than with *P. juliflora*. As only one provenance of each tree species was examined in our study, variation between provenances cannot be ascertained. However, it should be noted that the provenances of *A. nilotica*, *A. tortilis* and *P. juliflora* examined in this study were different from those examined by Cazet.

Roots of all four tree species were most numerous in the top 10 cm of soil and decreased with depth, while lateral distributions showed that although root concentrations tended to be greater nearest the tree, roots of all four tree species had extended to the midpoint, i.e. at least 3.5 m from the tree. Similar vertical and lateral distributions of roots are reported for other agroforestry tree species by Rao and Roger (1990), Ruhigwa et al. (1992), Hauser (1993) and Puri et al. (1994). Other studies of agroforestry tree species by Jonsson et al. (1988), Cazet (1989), Dhyani et al. (1990) and Singh (1994) found proportionally more roots at depths exceeding 25 cm, but these were studies of younger trees growing in plots established less than 5 years before sampling.

Differences in root distribution between tree species indicates that the root systems of *P. juliflora* and *A. nilotica* may possess attributes of potential benefit in agroforestry systems. The low concentration of *P. juliflora* roots found at all three depths suggests that competition with crop roots would be minimal, while the abundance of *A. nilotica* roots at depths greater than 10 cm suggests that this species would be more effective in recycling nutrients from below the crop rooting zone.

4.2. Mycorrhizal colonisation

Levels of mycorrhizal colonisation were generally high in all samples (25–70%) reflecting the mycotrophic nature of the tree species being studied, the age of the plots and the ability of the AM fungi present in the soils to infect a wide range of host species.

Very few spatial differences were detected in levels of mycorrhizal colonisation. Similar levels of colonisation along the transects could be attributed to the fact that roots had extended to at least the midpoint between trees in all plots, resulting in an even distribution and high concentration of mycorrhizal propagules in the soil.

Differences in mycorrhizal colonisation with depth were not found in the *P. juliflora*, *A. nilotica* and *A. tortilis* plots. As levels of mycorrhizal colonisation are thought to decrease with depth (Abbott and Robson, 1991), differences may have been detected had depths greater than 50 cm been examined. However, the ability of *P. juliflora* and *A. nilotica* to maintain high levels of colonisation with increasing depth could be of significant value in agroforestry situations where tree and crop roots compete for water and nutrients in the upper soil horizons. *A. nilotica* had the added advantage of possessing more roots located at depth than the other species and therefore showed the greatest potential for the acquisition of nutrients and water resources from below the crop rooting zone. However, further studies are required to examine root distribution and mycorrhizal activity with increasing depth before firm conclusions can be drawn.

Unlike the other tree species, levels of mycorrhizal colonisation in the *A. aneura* plot decreased with depth and were positively related to numbers of

AM spores. This suggests that this was the only plot where spores contributed significantly to the number of infective mycorrhizal propagules present in the soil.

Levels of mycorrhizal colonisation also differed between tree species. Although *P. juliflora*, *A. nilotica* and *A. tortilis* are all mycotrophic and respond to mycorrhizal inoculation (Reena and Bagyaraj, 1990; Wilson et al., 1991; Osonubi et al., 1992; Dixon et al., 1993), contrasting patterns of root and mycorrhizal development were observed, most notably between *P. juliflora* and *A. tortilis*; *P. juliflora* having high levels of colonisation and few roots while *A. tortilis* had lower levels of colonisation and more roots. Above ground studies conducted in these plots show that tree height, stem diameter and survival of *P. juliflora* at Bandia were better than those of *A. tortilis*, *A. nilotica* and *A. aneura* (J.D. Deans, personal communication, 1996). Therefore, the growth of *P. juliflora* at Bandia demonstrates features often associated with plants exhibiting a high mycorrhizal response, i.e. above ground growth benefits associated with smaller, more efficient nutrient-scavenging root systems, resulting in decreased root/shoot ratios (Azcon and Ocampo, 1981).

4.3. AM spore distribution

Most spores were found in the surface soil layer (0–10 cm depth), which supports the widely held view that spore production is concentrated near the soil surface (Abbott and Robson, 1991). High proportions of dead spores have also been found in semi-arid areas of Kenya (J. Wilson, personal communication, 1990; International Centre for Research in Agroforestry, 1993) and are probably attributable to slow decomposition rates and the accumulation of spore 'husks' over several seasons.

Numbers of 'live' spores recovered from the soil samples were low compared to other studies of spore populations in semi-arid soils (Sieverding, 1991; Shepherd et al., 1996). With the exception of the *A. aneura* plot, spore numbers were not related to levels of mycorrhizal colonisation and are probably of secondary importance as mycorrhizal propagules in these plots. In dry season ecosystems, where soil disturbance is minimal, colonisation of new roots is likely to be achieved primarily via hyphal networks and senescing mycorrhizal roots (Jasper et al., 1989). Further studies are in progress, using 'bait' plants grown in intact soil cores (Brundrett, 1991), to assess the activity of all mycorrhizal propagules present in these soils and consequently, the potential of different soils to effect rapid colonisation of crop roots.

Although spores may be relatively unimportant as mycorrhizal propagules, spore occurrence was related to fine root distribution. The clearest relationship was found with *P. juliflora* which had a closed canopy with limited understorey vegetation; therefore, inputs of AM spores from other mycorrhizal plants were probably lower than with other tree species. In contrast to the *P. juliflora* plot, poor survival of *A. aneura* resulted in open canopy areas and more ground vegetation with concomitant inputs of AM spores. In addition, the open canopy probably resulted in hotter, drier conditions at the soil surface which may have stimulated spore production as a result of plant stress.

This study has indicated differences in root distribution and mycorrhizal colonisation of four tree species growing at Bandia, Senegal. Although the root and mycorrhizal characteristics of *P. juliflora* are desirable attributes, it's rapid growth and canopy closure are less so, as shading may reduce crop yield. Because of the high survival and aggressive above ground growth of *P. juliflora*, this species may be most appropriate for low fertility, degraded soils where soil amelioration is more important than increased crop yield. In contrast, the potential of *A. nilotica* to recycle nutrients from greater depth offers promise, but intense rooting in the upper soil horizon suggests greater competition with crop roots. However, undesirable rooting characteristics can be partially overcome by root pruning/restriction and wider spacing of rows (Hauser, 1993; Schroth, 1995), so that the potential of *A. nilotica* may be realised by applying such practices at sites where topsoil enrichment and crop yield are of primary importance. By careful selection and management an optimal balance between root competition and soil improvement can be achieved thereby utilising the root and mycorrhizal attributes of different tree species most effectively. Below ground processes are an important, yet frequently undervalued, factor in the success of agroforestry systems and should be considered together

with above ground growth, site characteristics and the needs of local farmers when selecting trees to plant.

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