

## Seasonal soil water variation and root patterns between two semi-arid shrubs co-existing with Pearl millet in Senegal, West Africa

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### Abstract

Soil water is an important resource that imposes limitations on optimal plant performance in semi-arid regions. In some of these regions, shrubs form a characteristic component of farmers' fields and potentially impact crop productivity. Consequently, a 2-year study on soil water dynamics and shrub rooting patterns was conducted during the dry season and transition into the wet season with fields having Pearl millet intercropped with shrubs. Millet roots predominantly exploited the 0.2–0.5 m depth range with 95% of shrub roots in the upper 0.5 m. Soil volumetric water content (soil water content) decreased with greater radial distance from shrubs up to 2 m but progressively increased with soil depth. During the dry season, soil surrounding shrub roots was consistently moister than adjacent bare soil albeit at depth, soil moisture content declined steadily in the 0.9–1.2 m depth range due to depletion by shrub roots. On the contrary, the 0.2 and 0.4 m zones depicted slight increments in soil moisture which could be attributed to soil water redistribution by shrub roots. During the rainy season, shrub presence had a considerable impact on the fate of the field soil moisture regime with shrub roots serving as pathways for deep profile recharge. Shrubs exploited the deeper profile (0.9–1.2 m) as opposed to the Pearl millet (0.2–0.5 m) suggesting that intercropping of annual crops with shrub stands could serve as an innovative and viable agronomic option in these vulnerable Sahel agro-ecosystems.

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## 1. Introduction

Soil water is an important resource that imposes limitations on plant growth in semi-arid regions (Gregory, 1989). In these ecosystems, deep tree roots have been shown to tap ground-water reserves to meet plant water demands (Horton and Hart, 1998; James et al., 2002; Meinzer et al., 2003), hence helping to sustain transpiration which is a key physiological process during drought (Dawson, 1993). This study is a contribution to the global scientific debate (Jackson et al., 2000; Shumway, 2000) on the role of perennial woody components in semi-arid areas and how they influence soil water dynamics in these fragile agro-ecosystems.

In Senegal and much of Sub-Saharan Africa, two native perennial woody shrubs, *Guiera senegalensis* and *Piliostigma reticulatum*, both of which are studied herein, are dominant in the landscape and farmers' fields where they co-exist with staple food crops, Pearl millet (*Pennisetum glaucum* (L.) R. Br.) and groundnut (*Arachis hypogaea* L.). Field excursions show that these annuals have >90% of their roots within the 0.2–0.5 m depth range. The shrubs are subjected to traditional management by continuous shoot pruning or coppicing cycles (Wezel, 2000) during the cropping season and sometimes to complete removal in the dry season for fuel, fencing or to increase agricultural acreage (Diack et al., 2000).

A preliminary study in Senegal on shrub root patterns indicates that 5% of the roots of *P. reticulatum* extended beyond the 3 m depth (Kizito et al., 2003, Unpublished). In Mali, root studies on *G. senegalensis* have reported 2% of the roots extending beyond 4 m (Berish and Ewel, 1988). These shrub species remain distinctly green even during periods when soil water levels are barely sufficient for any crop survival (Gaze et al., 1998). We hypothesized that these woody components, similar to their tree counterparts, use their deep roots to tap ground-water reserves and further hypothesize that this behavior could have a positive impact on neighboring annuals. This phenomenon assures shrub resilience to unfavorable environmental conditions and frequent anthropogenic disturbances. Shrubs could be imparting both nutrient- and moisture-related (Gaze et al., 1998; Wezel, 2000) benefits to annual food crops.

Anderson et al. (2001), as well as Callaway and Walker (1997), discuss interactions that exist in intercropped plant communities. Other workers (Ong et al., 1991; Lauenorth and Coffin, 1992; Lauenorth and Burke, 1995) report high competition between annual crops and shrubs for both water and nutrient uptake. The aforementioned interactions could range from competition to facilitation (Fowler, 1986) and their strength and direction can change with prevailing seasonal environmental conditions (Freeman and Emlen, 1995; Callaway, 1997).

Consequently, research on spatial root distribution and seasonal patterns of soil water extraction comprises a critical facet in dryland farming systems. This study sought to: (i) assess shrub impact on profile soil water by comparing bare soil areas and shrub sites in the dry season; (ii) investigate the interactions between millet as an annual crop and two woody perennial shrubs over the wet season; (iii) assess shrub root patterns and determine their role on observed seasonal variation of soil water and millet performance.

## 2. Materials and methods

### 2.1. Study sites description

The study was conducted in the Peanut Basin of Senegal, West Africa. The region is characterized by temporally and spatially variable unimodal rainfall with episodic

droughts and frequent crop failures (Centre de Suivi Ecologique, 2000). The rainy season lasts from July to October, generally as scattered, high intensity, short-duration showers. Air temperature exhibits high diurnal and annual variability. The main food crops are millet (*P. glaucum* (L.) R. Br.), groundnuts (*A. hypogaea* L.), sorghum (*Sorghum bicolor* (L.) Moench), cowpeas (*Vigna unguiculata* (L.) Walp.) and corn (*Zea mays*) in the southern part of the Peanut Basin.

The research was conducted at two sites. Plot size at both sites was 6 m wide (nine rows 90 cm apart) and 10 m long. One study site, Keur Matar Arame, is located in the northern region (N14°45' W 16°51'; 43 m above sea level, slope range 0–1%) of the Peanut Basin with a total mean annual precipitation of 450 mm. The water table at this site lies at 15 m. *G. senegalensis* is the dominant shrub, characteristically 1 m tall with a shrub canopy crown of about 2 m and a highly spreading shallow rooting system in the top 0.45 m and a narrow leading unbranched root to a depth >2.5 m (Kizito et al., 2003, Unpublished). The site has a shrub stand density of 240 shrubs ha<sup>-1</sup>. The mean annual minimum ambient temperature is 20 °C and a mean annual maximum ambient temperature of 33 °C. The area lies on a leached and disturbed ferruginous sand soil. The top horizon (0–0.7 m), is sandy with a friable continuous structure and no distinct horizonation with low clay contents of ≤5% and scanty organic matter content of 0.5%. It is characterized by a base saturation of ~55% and mean pH of 5.5.

The second study site is located at Nioro, in the southern region (N13°45' W 15°47'; 18 m a.s.l, slope range of 0–2%) of the Peanut Basin, with a total mean annual precipitation of 750 mm. *P. reticulatum* is the predominant shrub occurring at a density of 185 shrubs ha<sup>-1</sup> with a well developed and fairly deep rooting system (Diack et al., 2000). The water table lies at 12 m below the soil surface. This site has randomly scattered *Cordyla pinnata* and *Prosopis africana* trees in the landscape. The mean annual minimum ambient temperature is 20 °C and the mean annual maximum ambient temperature is 36 °C. It lies on a fine-sandy, mixed Haplic Ferric Lixisol, a leached ferrugeneous tropical Ultisol (Diack et al., 2000). It is characterized by a leached light brown ferrugeneous top horizon (0–0.6 m). This gradually blends into a red brown lateritic color (0.8–1.5 m) with ferric spots interspersed in the profile.

## 2.2. Field and laboratory methods

### 2.2.1. Soil water variation

Volumetric soil water-content within the soil profile was continuously monitored over a 2-year period (2003–04) below three shrubs and at three adjacent bare soil control plots. The bare adjacent sampling plots were located at least 10 m from the shrubs.

Three shrubs per site were instrumented with ECH<sub>2</sub>O Probe Dielectric Aqua Meter soil water-content sensors (Decagon Devices, Inc.) to determine vertical and radial soil moisture distribution. The probes have an accuracy of 0.01 mm<sup>-1</sup> with soil specific calibration and a maximum temperature sensitivity of ~0.003 m<sup>3</sup> m<sup>-3</sup> per °C (Decagon Devices, Inc). The probes were calibrated gravimetrically under field conditions. For the vertical profile study, probes were installed at 0.2 m depth increments to a depth of 1.20 m. For each radial study, 6 probes were used, located laterally between 0.2 and 2.2 m from the shrub canopy periphery, in equal increments of 0.40 m. Profile stored water was calculated on a depth basis as the product of volumetric water-content and the depth interval (0.2 m) and expressed as millimeters of water.

To account for minute soil water changes in the profile, measurements of soil water potential were conducted for each treatment using screen-cage soil psychrometers (Wescor, Logan, UT, PST-55; Briscoe 1984), calibrated using standard salt solutions (Brown and Bartos, 1982). Psychrometers were installed at depths of 0.2, 0.4, 0.6, 0.8, 1.0 and 1.2 m, below the shrub and below bare soil plots. The psychrometers executed measurements on an hourly basis with a 30-s cooling time for the Peltier effect. Psychrometer data was logged and downloaded from a PSYPRO (Model PST-55, Wescor, Logan, UT) water potential system.

Soil temperature was also monitored using copper–constantan thermocouples starting at 0.1 m below the soil surface and successively at 0.2 m depth increments to a depth of 1.0 m both beneath the shrub canopy and at bare adjacent soil plots.

### 2.2.2. *Shrub–millet interactions*

During the rainy season, Pearl millet was planted as an intercrop with shrubs at a seed rate of 6–10 kg ha<sup>-1</sup> with seeds drilled in rows 90 cm apart. Plants were then thinned to 3 plants per planting hole with a plant population of about 6000 plants ha<sup>-1</sup>. At 15, 30, 45 and 60 days after sowing (DAS) of Pearl millet, the leaf area index (LAI) of millet was measured using a LAI 2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE). In each plot, 10 millet plants were randomly sampled and a mean LAI was scored from these observations. Weed management involved the use of herbicides and hand-hoeing.

Other parameters monitored included Pearl millet plant height changes every 2 weeks, destructive monitoring of mean root spread at 1.5 m away from stalk and root depth to 1 m of millet in plots with shrubs where soil water-content was being monitored (3 plots) and in plots with no shrub (3 plots). Millet roots from both treatments were then oven-dried in a convection oven at 65 °C to a constant dry mass.

Infiltration measurements were performed in plots with millet as a sole crop as well as in shrub–millet plots. These trials were conducted with a disc permeameter following the procedures reported by Perroux and White (1988). Bulk density measurements were performed with a standard core sampler having a volume of 100 cm<sup>3</sup>.

Three central rows, 3 m long, were hand-harvested from each plot to determine grain yield. Before harvest, the number of panicles per square meter was counted in the selected harvest area, then grain from five panicle sub-samples were weighed and corrected for water-content to determine kernel weight following the procedures suggested by Maman et al. (2004). Grains were dried at 65 °C for 72 h to ensure to a constant dry weight. During the dry season (November 2003–July 2004) following the Pearl millet harvest, the fields were left bare except for the perennial shrubs, hence plots had no Pearl millet in association with shrubs.

### 2.2.3. *Shrub root sampling procedures*

In May 2003, three shrubs were selected that were located more than 10 m from the instrumented shrubs in order to investigate their rooting patterns. Root profiles at both study sites were sampled to a depth of 1.2 m and radial extent of 2.2 m from each shrub trunk by soil excavation with spades. We focused our study on the upper 1.2 m based on preliminary results which depicted that 95% of the shrub roots were found within this depth (Kizito et al., 2003 Unpublished). Consequently, we defined “maximum sampled rooting depth” (MSRD) to be the 1.2 m depth for shrub species.

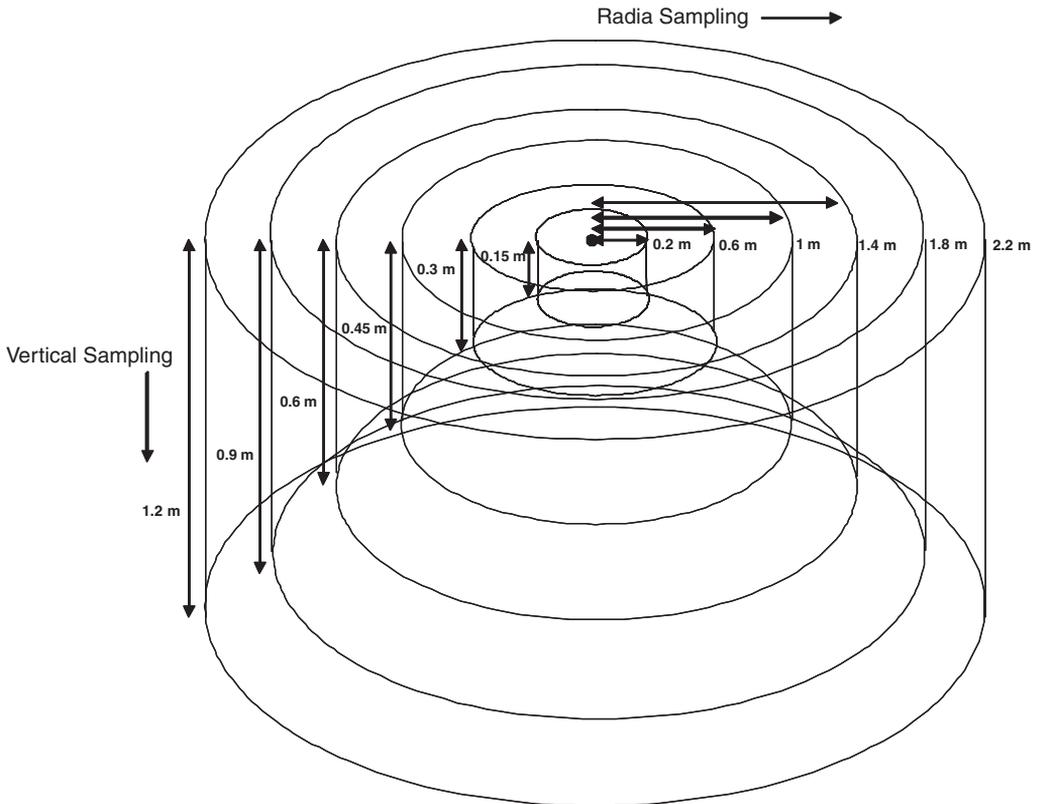


Fig. 1. Root system measurement using six radius sections of 0.2, 0.6, 1, 1.4, 1.8 and 2.2 m beginning at the shrub trunk and vertical sections of 0.15, 0.3, 0.45, 0.6, 0.9 and 1.2 m from the soil surface. Soil water measurements followed a similar sampling methodology with 0.20 m depth increments.

In order to calculate root:shoot ratios, shrub shoot biomass was weighed and dried in a convection oven at 65 °C. Root systems for each shrub were described after spatially dividing them into six concentric sections at depth increments of 0–0.15, 0.15–0.30, 0.30–0.45, 0.45–0.60, 0.60–0.90 and 0.90–1.20 m and at radial increments from the shrub center of 0–0.20, 0.20–0.60, 0.60–1, 1–1.40, 1.40–1.80, and 1.80–2.20 m (Fig. 1).

During shrub excavation, stem bases were staked in order to hold the root systems in their original position and subsequently photographs were taken with a Nikon CoolPix 995 digital camera (Nikon Photo Film Co., Ltd., Tokyo). The original digital images were 640 × 480 pixels, 24 color bit. In the laboratory, these images were carefully processed and manually re-traced with Bezier tools to a gray scale using the Corel TRACE Version 9 software (Corel Corporation and Corel Corporation Limited). The “shape tool” feature for node and line segment manipulation was used followed by trace customization (Fig. 2) to achieve the final output.

#### 2.2.4. Root system analysis

Extreme care was taken to minimize the loss of fine roots ( $\leq 2$  mm). Soil was removed from roots with gentle shaking owing to its sandy nature and the roots were then

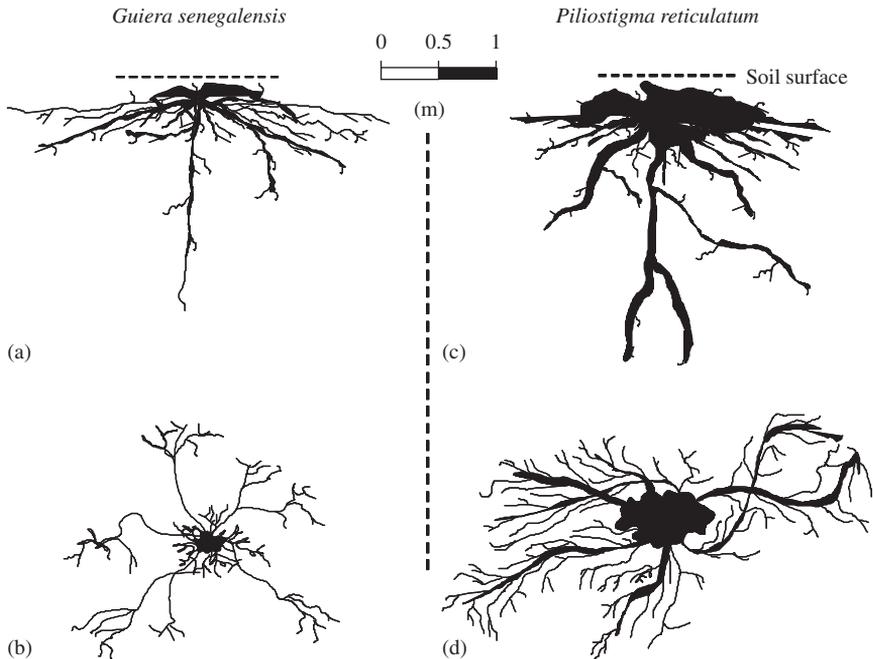


Fig. 2. (a) Lateral and (b) overhead view of *G. senegalensis* and (c) Lateral and (d) overhead view of *P. reticulatum* coarse and few fine roots after re-tracing. The vertical portion of the caption does not represent the MSRD.

cleaned with water using a sprayer nozzle. All root branches, greater than 2 mm in diameter (Lyford, 1980) were recorded at the radii and depths of the cores mentioned (Section 2.2.3).

After excavation, the roots were sorted by type (live and dead). The live roots were placed in plastic sampling bags for root diameter measurement. We then manually separated coarse root diameters ( $>2$  mm) from fine roots ( $<2$  mm) using a vernier caliper with a precision of  $1 \times 10^{-2}$  mm. The corresponding root lengths were measured with a flexible tape measure placed along the root surface. The results were expressed as root length densities per unit volume of soil ( $\text{cm cm}^{-3}$  soil).

Roots were oven-dried in a convection oven at  $65^\circ\text{C}$  until a constant dry mass was ascertained. Total biomass was calculated after determining the mean moisture content and dry weight of 10 root discs taken from different parts of root systems of the sampled shrubs from each site. This was scaled to the total root mass and results were expressed as dry weight of roots per unit volume of soil ( $\text{kg m}^{-3}$ ).

Shrub rooting patterns were studied using a similar method to that proposed by Silva et al. (2003). For each depth layer excavated, root length and root biomass were standardized by assigning values between 0 and 1, as a fraction of total root length and total root biomass, respectively. The standardized values, both cumulative root biomass and cumulative root lengths were computed from the soil surface layer to the MSRD.

The Gale and Grigal (1987) model was used for representing the cumulative vertical distribution of roots as a function of depth. This was based on the following

asymptotic equation:

$$Y = 1 - \beta^d, \quad (1)$$

where  $Y$  is the cumulative root fraction from the soil surface to the sampled depth  $d$  (m). Root fraction is a fraction between 0 and 1 calculated as mass of roots within each sample sub-volume divided by mass of roots in entire sampled volume. The parameter  $\beta$  is an “adjustable parameter” estimated in the model which provides a simple numerical index of rooting distribution (Jackson et al., 1996). This parameter assumes lower values for higher concentrations of roots at surface layers and values closer to 1 for more homogeneous root distributions. The  $\beta$  values were fitted to the data obtained from each of the two sites as elucidated (Section 3.3).

### 2.3. Data analysis

Data were analysed using SPLUS6.1 (S-PLUS: Copyright 1988, 2002 Insightful Corp.) Three replicates were used to test for difference in the response variables in the soil water study using a three factorial completely randomized design using ANOVA ( $\alpha = 0.05$ ). Shrub presence or absence (microhabitat) and soil depth were treated as fixed effects and sampling date (within the year) as a random effect. Analysis was conducted on data from all sample dates of the same shrub species performed at different depths.

For the shrub–millet interactions study, shrub presence and absence in millet plots was also assessed by performing ANOVA ( $\alpha = 0.05$ ) similar to the aforementioned approach. Data were also subjected to standard error computations around the mean.

For the shrub root study, data were analysed using a two-way ANOVA. Soil depth was treated as a fixed effect with seven levels, and number of shrubs as blocks with three levels. The response variables assessed were root length, root diameter, number of laterals, root biomass and root density. Duncan’s new multiple range test ( $\alpha = 0.05$ ) was used to rank the means. Standard errors and Least Significant Differences were also computed for the above variables.

## 3. Results

### 3.1. Seasonal soil water relations

At the beginning of the dry season, mean soil moisture content in the upper 0.40 m was slightly below  $0.02 \text{ m}^3 \text{ m}^{-3}$  at both sites (Fig. 3). During the dry seasons of 2003 and 2004, there were slight increases in soil moisture content with profile depth from 0.02 to  $0.03 \text{ m}^3 \text{ m}^{-3}$  (Fig. 3). For both shrub species, the upper 0.80 m of the soil profile were moister below shrubs than below bare soil. However, during the dry season, this trend was reversed for deeper soil layers; in the 0.9–1.20 m depth range. Soil moisture content was lower below shrubs than bare soil depicting a gradual soil drying with depth from  $0.04 \text{ m}^3 \text{ m}^{-3}$  to about  $0.02 \text{ m}^3 \text{ m}^{-3}$  (Fig. 3).

During the rainy season, soil moisture was consistently higher below both shrub species compared to bare soil (Fig. 3). Whereas the bare soil plots at the *G. senegalensis* site exhibited a slight but continuous increase in soil moisture with depth (Figs. 3a and b), the *P. reticulatum* site revealed soil moisture decrease below the 0.6 m depth in both study

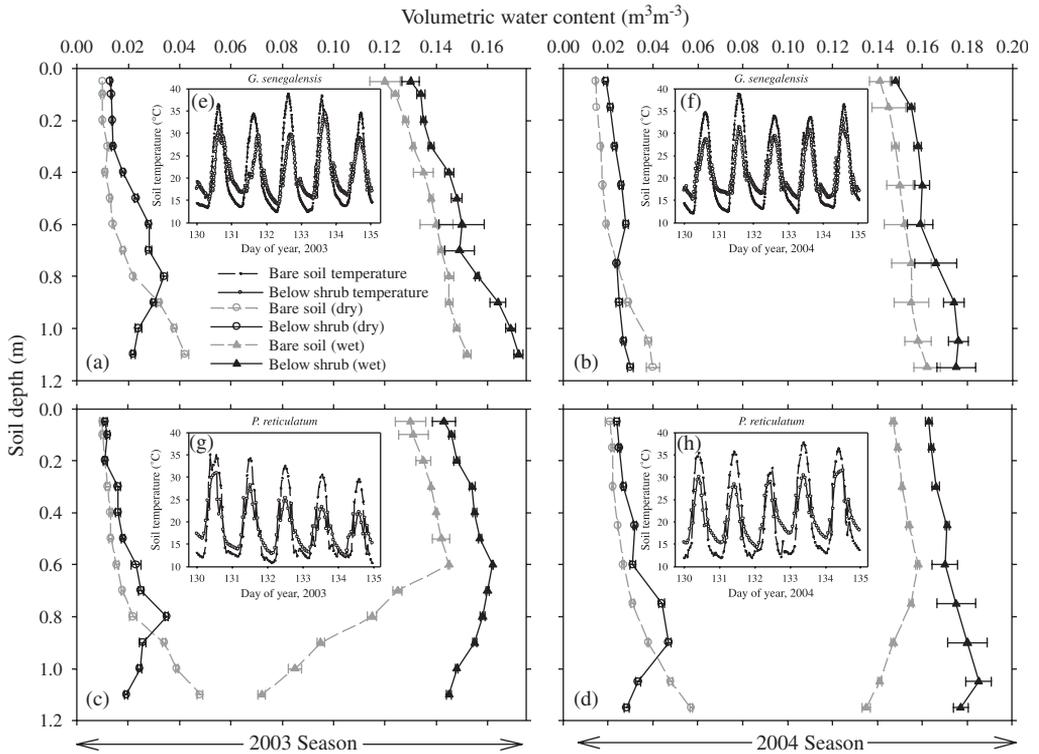


Fig. 3. Variation of mean volumetric moisture content (a) vertically, below *G. senegalensis* root zone and an adjacent bare soil matrix in the 2003 season; (b) vertically, below *G. senegalensis* root zone and an adjacent bare soil matrix in the 2004 season; (c) vertically, below *P. reticulatum* root zone and an adjacent bare soil matrix in the 2003 season; (d) vertically, below *P. reticulatum* root zone and an adjacent bare soil matrix in the 2004 season. Inset graphs are variations of soil temperature 10 cm below shrubs and bare soil at both sites and are labeled as (e) *G. senegalensis* for the 2003 season; (f) *G. senegalensis* for the 2004 season (g) *P. reticulatum* for the 2003 season; (h) *P. reticulatum* for the 2004 season.

years (Figs. 3c and d). In contrast to the bare plots, soil moisture content beneath shrubs remained relatively stable (Figs. 3c and d).

Shrub canopies for both species were associated with lower soil temperatures compared to adjacent bare soil during both study years (Figs. 3e–h). Peak soil temperatures revealed that soil beneath shrubs was approximately 5 °C lower than that at bare adjacent plots. Conversely, at night, soil below shrub canopies was relatively warmer than bare soil areas at both study sites by approximately 2 °C with shrubs appearing to buffer the soil against temperature extremities during both day and night.

In the dry season, profile-stored water increased with sampling depth (Figs. 4a and c). Over the dry season, the 0.20 and 0.40 m depths showed slight increases in profile stored water beneath shrubs with changes ranging between 0.06 and 1.8 mm over a 60 day period (Figs. 4a and c; Table 1). Conversely, the profile stored water in the 0.9–1.2 m depth range declined over a 120 day period (Figs. 4a and c). Steep declines were observed in the dry season of 2003 for the *G. senegalensis* site (Fig. 4a) while the *P. reticulatum* site registered this drop in the dry season of 2004 (Fig. 4c), with both declines corresponding to

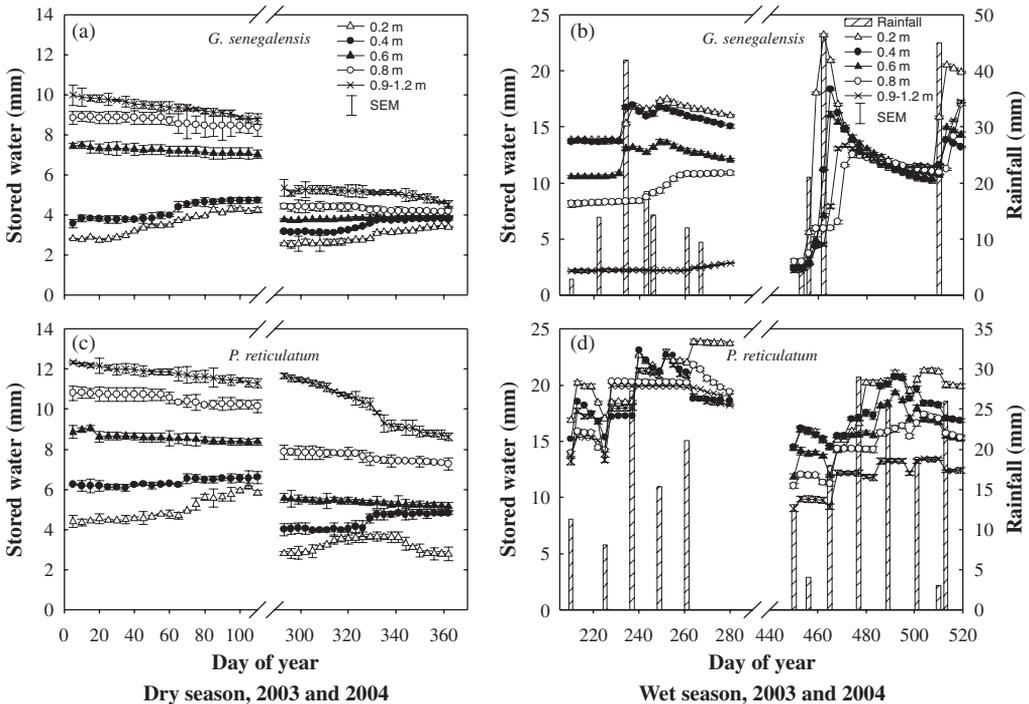


Fig. 4. Seasonal variation in profile stored soil water at both sites in 2003 and 2004. Left sides on each graph are data for 2003 and right sides are data for 2004 (a) dry spell with *G. senegalensis* and (b) dry spell with *P. reticulatum*; (c) transition to rain season for *G. senegalensis* associated with millet (d) transition to rain season for *P. reticulatum* associated with millet. Measurements were performed below the shrub canopy and seasons are expressed as experimental days (from the commencement of the experiment).

approximately 1.5–3.0 mm of profile stored water. These observed depletions correspond to a maximum daily net water use from the 0.9–1.2 m depth in 2003 over the 120 days of about  $0.7 \text{ mm day}^{-1}$  for the *G. senegalensis* site (Fig. 4a) and about  $0.5 \text{ mm day}^{-1}$  (Fig. 4c) for the *P. reticulatum* site.

Spatial changes in soil water potential at both sites supported the observed changes in soil water stored at the respective depths (Table 1). Generally, similar to soil water results, dry season soil water potential beneath shrubs revealed slight gradual wetting in the 0.2 and 0.4 m depths, while the 0.9–1.2 m depth range exhibited consistent soil water depletion (Figs. 4a and c; Table 1).

Higher total rainfall was received at the *P. reticulatum* (Fig. 4d) for both study years while it was lower and sporadic at the *G. senegalensis* site in 2004 (Fig. 4b). During the rainy season, the upper soil horizon responded rapidly to precipitation which gradually infiltrated downward resulting in profile recharge (Figs. 4b and d).

Results from the radial soil water sampling study showed a gradual decrease in soil moisture with distance from the shrub, the change was seen over the entire depth of the profile at the 0–0.2 and 0.2–0.6 m radial distances from shrub trunk (Figs. 5a and b), with pronounced changes in the 0.6 m depth range (Fig. 5b). The magnitude of decrease in soil moisture content away from the canopy was comparable for both shrub species.

Table 1

Changes in mean stored water and soil water potential<sup>a</sup> at varying depths for *Guiera senegalensis* and *Piliostigma reticulatum*

Season	Depth (m)	<i>Guiera senegalensis</i>		<i>Piliostigma reticulatum</i>	
		Δ stored water (mm)	Δ water potential (MPa)	Δ stored water (mm)	Δ water potential (MPa)
2003	0.2	+ 1.56 ± 0.09	−0.95 ± 0.02	+ 1.8 ± 0.16	−0.9 ± 0.03
	0.4	+ 1.19 ± 0.17	−1.10 ± 0.35	+ 0.56 ± 0.18	−0.3 ± 0.01
	0.9–1.2	−1.30 ± 0.13	+ 0.9 ± 0.05	−1.20 ± 0.22	+ 0.8 ± 0.02
2004	0.2	+ 0.89 ± 0.09	−0.68 ± 0.04	+ 0.88 ± 0.20	−0.7 ± 0.10
	0.4	+ 0.06 ± 0.03	−0.22 ± 0.12	+ 0.87 ± 0.16	−0.7 ± 0.12
	0.9–1.2	−0.83 ± 0.19	+ 0.58 ± 0.21	−3.06 ± 0.25	+ 1.2 ± 0.09

<sup>a</sup>Negative values of soil water potential indicate a decrease in tension (wetting) while positive values depict an increase in soil water tension (drying).

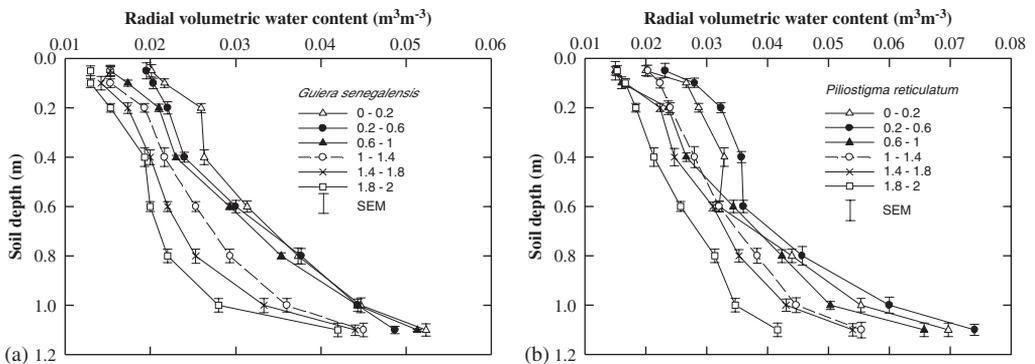


Fig. 5. Mean seasonal radial moisture variation at both sites (a) KMA; (b) Nioro.

For *G. senegalensis*, repeated measures analysis for the soil moisture data on shrub–bare soil interactions had a coefficient of variation of 23.3% with a significant effect on soil moisture from shrub presence and soil depth. The interaction between shrub effect and soil depth was also significantly different (Table 2). However, sampling date as a sole factor did not seem to have significant differences on the observed soil moisture levels during the dry season but the interaction between shrub, soil depth and sampling date yielded significant differences in the observed soil moisture trends (Table 2). The ANOVA results for *P. reticulatum* yielded a coefficient of variation of 26% and also revealed a significant effect on soil moisture of shrub, soil depth as well as shrub–soil depth interaction (Table 2). Similar to the results observed at the *G. senegalensis* site, sampling date did not show significant differences both as a sole factor and after interaction with shrubs and soil depth for the *P. reticulatum* site (Table 2).

### 3.2. Shrub–millet interactions

Notably, profile soil moisture was significantly higher ( $p = 0.05$ ) in millet plots associated with shrubs than sole millet plots. Repeated measures analysis on soil moisture

Table 2

Repeated measures analysis of variance for comparison of soil water variation at shrub bare soil treatments (dry season). Within-subject effects are shrub effect, soil depth, sampling depth and interactions. Presented for each effect are the degrees of freedom, an  $F$  statistic and significance ( $*p > 0.05$ ,  $**p < 0.05$ ,  $***p < 0.01$ ,  $****p < 0.001$ )

Source	Degrees of freedom	$F$	$P$
<i>Guiera senegalensis</i>			
Replication	2	1189.4	****
Shrub effect	1	15.89	****
Soil depth	11	11.71	****
Shrub effect $\times$ soil depth	11	8.58	***
Date	1	1.63	*
Shrub effect $\times$ Date	1	1.25	*
Soil depth $\times$ Date	11	1.42	*
Shrub $\times$ Depth $\times$ Date	11	4.45	***
Error	94	—	—
Coefficient of variation (%)	23.3	—	—
<i>Piliostigma reticulatum</i>			
Replication	2	19.6	****
Shrub effect	1	13.58	****
Soil depth	11	34.01	****
Shrub effect $\times$ soil depth	11	8.53	****
Date	1	3.9	*
Shrub effect $\times$ Date	1	1.68	*
Soil depth $\times$ Date	11	2.14	*
Shrub $\times$ Depth $\times$ Date	11	2.62	*
Error	94	—	—
Coefficient of variation (%)	26	—	—

data for shrub–millet interactions at the *G. senegalensis* site depicted a coefficient of variation of 16.4% with significant shrub effect, soil depth and shrub effect  $\times$  depth interaction (Table 3). Sampling date did not reveal strong significant differences. Further still, the interactions between sampling date with shrub effect or soil depth did not yield any significant differences neither did the interaction of all the 3 factors reveal any significant differences. Soil moisture ANOVA results for *P. reticulatum* had a coefficient of variation of 16.5% and revealed a significant shrub effect, soil depth and shrub effect  $\times$  soil depth interaction (Table 3). Similar to previous results, the sampling date did not reveal any significant differences and the interactions between sampling date with shrub effect as well as with soil depth, did not reveal any significant differences.

From the plant level measurements, both LAI and plant height differences were noted between treatments. Millet in plots with shrubs had higher LAI and shoot height (Table 4). Soil bulk density was slightly lower in shrub plots than the sole millet plots. Pearl millet roots were deeper in plots with no shrubs (Table 4). Mean exploitation depth of Pearl millet roots in association with shrubs was  $\sim 0.5$  m (Table 4). Infiltration rates were higher in millet plots with shrubs than in those with no shrubs. Yield results (Table 4) revealed no significant differences ( $p = 0.05$ ) between no shrub and intercropped shrub–millet plots.

Table 3

Repeated measures analysis of variance for comparison of soil water variation at shrub millet treatments (Wet season). Within-subject effects are repeated shrub effect, soil depth, sampling depth and interaction between shrubs and soil depth. Presented for each effect are the degrees of freedom, an  $F$  statistic and significance ( $*p > 0.05$ ,  $**p < 0.05$ ,  $***p < 0.01$ ,  $****p < 0.001$ )

Source	Degrees of freedom	$F$	$P$
<i>Guiera senegalensis</i>			
Replication	2	24.64	****
Shrub effect	1	11.25	****
Soil depth	2	13.1	****
Shrub effect $\times$ soil depth	2	1.26	*
Date	5	6.7	**
Shrub effect $\times$ Date	5	1.05	*
Soil depth $\times$ Date	10	0.13	*
Shrub $\times$ Depth $\times$ Date	10	3.23	*
Error	70	—	—
Coefficient of variation (%)	16.4	—	—
<i>Piliostigma reticulatum</i>			
Replication	2	17.53	***
Shrub effect	1	8.8	****
Soil depth	2	22.1	****
Shrub effect $\times$ soil depth	2	7.35	****
Date	5	1.2	*
Shrub effect $\times$ Date	5	1.10	*
Soil depth $\times$ Date	10	0.13	*
Shrub $\times$ Depth $\times$ Date	10	0.23	*
Error	70	—	—
Coefficient of variation (%)	16.5	—	—

### 3.3. Shrub root patterns

Root lengths, root diameter, number of laterals, root biomass and root density all decreased with increasing soil depth (Table 5). Based on results of both root biomass (kg) and root density ( $\text{kg m}^{-3}$ ) variation with depth, approximately 60–70% of the roots were located within the upper 0.50 m (Table 5).

Cumulative root biomass (Fig. 6a) followed a smooth exponential pattern with depth for both shrub species. Average root biomass varied between the two sites with *G. senegalensis* registering a mean cumulative biomass of  $1.58 \text{ kg m}^{-2}$  for the MSRD, while *P. reticulatum* demonstrated a mean cumulative biomass of  $3.82 \text{ kg m}^{-2}$  for the MSRD. Root: Shoot ratios were 1.25 and 1.38 for the *G. senegalensis* and *P. reticulatum* sites respectively (Table 6).

Average root densities (Fig. 6b) followed fairly similar patterns to the observed root biomass trends. *G. senegalensis* registered a value of  $0.74 \text{ kg m}^{-3}$  while *P. reticulatum* had higher values in the upper 0.15 m of the profile with a root density of  $1.3 \text{ kg m}^{-3}$ .

For the cumulative root fraction (Fig. 6c), the extinction coefficient ( $\beta$ ) for *G. senegalensis* was 0.96 with a corresponding  $r^2$  of 0.98 while *P. reticulatum* had an extinction coefficient ( $\beta$ ) of 0.97 with a corresponding  $r^2$  of 0.96. Combining data from both our study

Table 4

Pearl millet measurements in association with shrubs at both sites. Values are means  $\pm$  SE within brackets ( $n = 10$  millet plants)

Parameter	<i>Guiera senegalensis</i> site		<i>Piliostigma reticulatum</i> site		
	Millet + shrub	Millet alone	Millet + shrub	Millet alone	
LAI (15 DAS)	0.60 (0.05)	0.45 (0.03)	0.82 (0.02)	0.63 (0.01)	
LAI (30 DAS)	1.94 (0.06)	1.85 (0.03)	1.90 (0.04)	1.88 (0.02)	
LAI (45 DAS)	1.20 (0.04)	0.85 (0.02)	1.34 (0.03)	0.92 (0.02)	
Mean plant height (cm) <sup>a</sup>	96.17 (14.10)	94.67 (13.04)	112.67 (14.81)	105.67 (14.28)	
Mean root depth (cm)	57.33 (0.82)	69.18 (0.78)	49.71 (0.68)	61.33 (0.24)	
Mean root spread (cm)	78.83 (0.46)	84.37 (1.72)	77.67 (1.25)	75.42 (1.94)	
Bulk density (g cm <sup>-3</sup> )	1.48 (0.01)	1.51 (0.04)	1.52 (0.01)	1.54 (0.06)	
Yield*	Grain yield (g m <sup>-2</sup> )	186a	174a	230a	226a
	Panicle number	23a	18b	24b	22b
Infiltration rate (mm/hr) <sup>b</sup>		120.5 (1.52)	94.83 (3.16)	100 (0.73)	89 (0.73)
Soil water content (m <sup>3</sup> m <sup>-3</sup> ) <sup>c</sup>	Case 1	0.11 (0.01)	0.09 (0.01)	0.12 (0.05)	0.10 (0.04)
	Case 2	0.14 (0.03)	0.12 (0.01)	0.17 (0.05)	0.14 (0.03)
	Case 3	0.12 (0.01)	0.08 (0.05)	0.13 (0.05)	0.11 (0.01)

\* Letters followed by similar alphabets indicate there is no significant difference at  $p = 0.05$ .

<sup>a</sup> Mean of 10 millet plants measured at 30 and 45 DAS.

<sup>b</sup> Infiltration was conducted at an applied suction of 5 cm.

<sup>c</sup> Three scenarios at both sites after varying rainfall events at field capacity for the 0.2 m depth.

sites, the average rooting distribution for these ecosystems had an extinction coefficient ( $\beta$ ) of 0.97 with a corresponding  $r^2$  of 0.97.

## 4. Discussion

### 4.1. Seasonal soil water relations

The Peanut Basin of Senegal lies in a region highly prone to short-term water deficits with erratic rainfall patterns (Dancette, 1966; Boffa, 1999), falling within two distinct seasons (dry and wet), hence the observed seasonal soil water-content trends could have important implications for farming systems in this region. The higher soil water-content values observed at all depths (Fig. 3) during the rainy season below shrub plots as compared to bare open plots could be due to higher infiltration that enhanced profile recharge or due to decreased soil evaporation rate associated with shrub areas.

Conversely, in the dry season, the slight increases in soil moisture observed in the 0.2 and 0.4 m depths (Figs. 4a and c) and the decrease in water tension (Table 1) could be a result of the roots at depth tapping residual soil moisture and ground-water reserves and later lifting it to the upper drier portions of the soil profile (Dawson, 1993; Schulze et al., 1996; Shumway, 2000; Burgess et al., 2001). In the absence of precipitation, these moisture increases serve as evidence of hydraulic lift occurrence because lateral flow within the soil profile is likely null in this ecosystem during the dry season. This phenomenon has been

Table 5  
Shrub root patterns

Depth (m)	Length (cm)	Diameter (cm)	Number laterals	Biomass (kg)	Root density (kg m <sup>-3</sup> )
<i>Guiera senegalensis</i>					
0–0.15	0.30 <sup>e</sup>	0.25 <sup>e</sup>	33.43 <sup>e</sup>	1.44 <sup>e</sup>	0.92 <sup>c</sup>
0.15–0.30	0.26 <sup>d</sup>	0.21 <sup>cd</sup>	17.54 <sup>c</sup>	0.81 <sup>d</sup>	0.57 <sup>bc</sup>
0.30–0.45	0.18 <sup>c</sup>	0.19 <sup>bc</sup>	17.58 <sup>cd</sup>	0.38 <sup>c</sup>	0.48 <sup>ab</sup>
0.45–0.60	0.12 <sup>b</sup>	0.17 <sup>b</sup>	14.28 <sup>bc</sup>	0.30 <sup>bc</sup>	0.28 <sup>ab</sup>
0.60–0.75	0.10 <sup>b</sup>	0.14 <sup>a</sup>	12.30 <sup>b</sup>	0.11 <sup>ab</sup>	0.09 <sup>a</sup>
0.75–0.90	0.06 <sup>a</sup>	0.13 <sup>a</sup>	11.74 <sup>ab</sup>	0.08 <sup>ab</sup>	0.06 <sup>a</sup>
0.90–1.2	0.60 <sup>a</sup>	0.12 <sup>a</sup>	7.42 <sup>a</sup>	0.05 <sup>a</sup>	0.05 <sup>a</sup>
CV (%)	10.12	9.30	16.09	30.39	43.43
Treatment mean	0.90	9 × 10 <sup>-4</sup>	1.52	0.079	8.82 × 10 <sup>-2</sup>
SE					
LSD (0.05)	0.04	9 × 10 <sup>-3</sup>	4.68	0.244	0.27
<i>Piliostigma reticulatum</i>					
0–0.15	0.28 <sup>c</sup>	0.03 <sup>d</sup>	26.86 <sup>f</sup>	2.45 <sup>c</sup>	0.01 <sup>f</sup>
0.15–0.30	0.26 <sup>c</sup>	0.21 <sup>cd</sup>	20.93 <sup>de</sup>	1.98 <sup>bc</sup>	0.01 <sup>ef</sup>
0.30–0.45	0.18 <sup>b</sup>	0.19 <sup>bc</sup>	18.52 <sup>cd</sup>	1.32 <sup>abc</sup>	9 × 10 <sup>-3</sup> de
0.45–0.60	0.14 <sup>ab</sup>	0.16 <sup>abc</sup>	14.65 <sup>bc</sup>	0.78 <sup>ab</sup>	8 × 10 <sup>-3</sup> cd
0.60–0.75	0.10 <sup>a</sup>	0.15 <sup>ab</sup>	11.8 <sup>b</sup>	0.31 <sup>a</sup>	6 × 10 <sup>-3</sup> bc
0.75–0.90	0.09 <sup>a</sup>	0.13 <sup>a</sup>	6.13 <sup>a</sup>	0.25 <sup>a</sup>	3 × 10 <sup>-3</sup> ab
0.90–1.2	0.08 <sup>a</sup>	0.11 <sup>a</sup>	5.58 <sup>a</sup>	0.12 <sup>a</sup>	3.3 × 10 <sup>-3</sup> ab
CV (%)	13.9	11.74	11.02	43.05	12.14
Treatment mean	0.01	1 × 10 <sup>-3</sup>	0.95	0.26	5.53 × 10 <sup>-4</sup>
SE					
LSD (0.05)	0.04	3 × 10 <sup>-3</sup>	2.92	1.27	1.7 × 10 <sup>-3</sup>

All tests were performed at  $p = 0.05$ .

Letters followed by similar superscript indicate there is no significant difference at  $p = 0.05$ .

reported elsewhere in similar environments (Richards and Caldwell, 1987; Jackson et al., 2000). Shrubs could supplement soil moisture demands for annual crops in these fragile Sahelian sandy soils with erratic rainfall. This interpretation is further supported by the gradual decline in stored water in the 0.9–1.2 m depth under shrubs. By contrast, over both dry seasons, open bare soil areas registered higher soil moisture than both shrub species at that depth. The gradual decline in soil moisture at the aforementioned depth range could have been due to consumptive water use by shrub roots. Other workers conducting research on desert perennials have also reported incidences of shrubs reducing the amount of soil water or nutrients present in a profile (Fonteyn and Mahall, 1978; Caldwell et al., 1985).

Furthermore, the observed decline in bare plot soil moisture beyond the 0.6 m depth at the *P. reticulatum* site (Figs. 3c and d) was interpreted as resulting from soil textural differences with higher clay contents and compacted soil layers beyond this depth. Since these plots did not have shrub roots to perforate the profile to lower horizons, water could not infiltrate beyond 0.6 m for about 30 days. During the rainy season, the higher soil water values observed under shrub canopies (Fig. 3) could have been due to water reaching deeper horizons under shrubs than in bare plots with higher infiltration rates enhanced by the presence of shrub roots (Kizito et al., 2003 Unpublished).

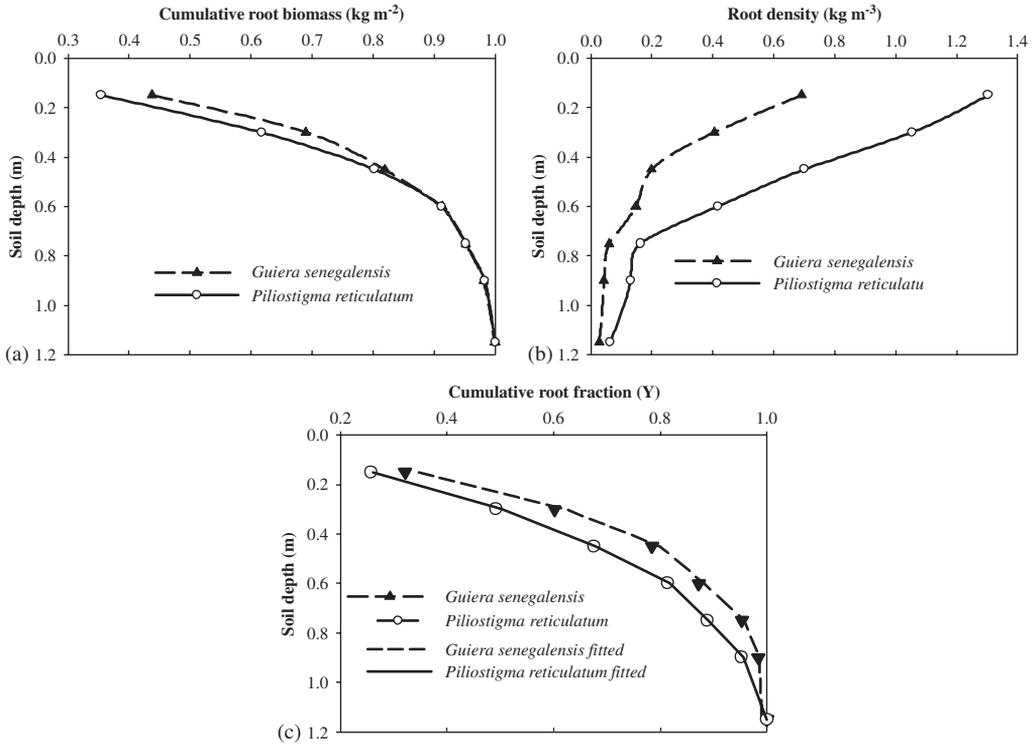


Fig. 6. Cumulative root biomass, root density and cumulative root fraction as a function of soil depth for both shrub species.

Table 6

Values of  $\beta$  and corresponding  $r^2$  for our data using the Gale and Grigal (1987) model; root percentage in the upper 0.5 m and the root:shoot ratios for each species

Species	$\beta$	$r^2$	% roots in upper 0.5 m	Root:shoot ratio <sup>a</sup>
<i>Guiera senegalensis</i>	0.96	0.98	71	1.25
<i>Piliostigma reticulatum</i>	0.97	0.96	62	1.38
Both species	0.97	0.97	66.5	1.32

<sup>a</sup>Root: shoot ratio could vary with the time of sampling especially due to shrub age variation and management practices.

Interactions between shrub presence and soil depth yielded significant differences ( $p < 0.01$ ) for both sites over the dry and wet season (Tables 2 and 3). This further lends itself to observations (Fig. 3) which revealed that shrub presence positively impacted the moisture regime. Similar findings elsewhere beneath shrub canopies allude to these results (Shumway, 2000).

Consistent with other studies (Gutierrez et al., 1993), soil below shrubs was associated with lower soil temperature extremes than adjacent bare soil (Figs. 5a and b), which could be attributed to shade provision by shrub canopies. Additionally, shrubs may enhance soil

water redistribution (Jackson and Caldwell, 1993) and could reduce air and soil temperatures (Shumway, 2000). This shrub-imparted alteration in microclimate (Akpo, 1993; Payne et al., 1996; Kizito, 2001) suggests lower soil evaporation below shrub canopies than in bare soil.

The decrease in soil water-content with increasing radial distance from shrubs (Figs. 5a and b) could be attributed to absence of shrub-imparted microclimate benefits. The higher radiation load on bare soil could result in quicker evaporative losses of surface moisture. In contrast, water is lost at a slower rate beneath shrub canopies due to reduced radiation loads. Consistent with these findings, in Burkina Faso, soil moisture content was reported to decrease significantly with increasing distance from *Vitellaria paradoxa* trees in the 0–20 cm soil depth (Boffa et al., 2000).

#### 4.2. Shrub–millet interactions

Noteworthy was the consistently lower LAI values in sole millet plots as opposed to the shrub–millet plots which potentially benefited from complementary shrub-related influences on soil water (Table 4). Similarly, Maman et al. (2004) have reported a close linkage between shoot growths and environmental stresses which could lead to poor canopy development, suggesting that the presence of the shrubs may be ameliorating environmental stresses to which crops are being exposed to when not intercropped with shrubs.

Conversely, sole millet plots revealed greater root depth and spread than did shrub–millet plots to possibly take advantage of the scanty available moisture and nutrients. Increased rooting depth and root length density have been associated with reduced percolation of soil water beyond the root zone (Payne et al., 1990) and greater soil water extraction from upper and lower soil layers during dry spells (Payne et al., 1996; Maman et al., 2004). It is likely that millet roots in association with shrubs thrived better due to the shrub-imparted soil moisture benefits which when combined with reduced soil evaporation, led to reduced soil exploration by millet roots.

The decrease in soil bulk density in the shrub–millet plots could be indicative of an increase in total porosity resulting in higher rates of water infiltration at the surface (Hillel, 1998), particularly during intense rainfall events, and consequently more rapid recharge at depth. The recharge of the shrub–millet soil below 0.2 m compared to sole millet plots soil indicates that shrub roots enhanced infiltration (Table 4).

Results of this study do not depict a clear millet yield response owing to shrub presence. This was probably because the shrub–millet plots had been established for only a year, too little time to have a significant impact on grain yield. However, shrubs enhanced millet performance through greater LAI values and also contributed to soil microhabitat attributes such as higher soil water-content and better soil physical and hydrological properties (Table 4).

#### 4.3. Shrub root patterns

Similar to the soil water scenario, the observed root distribution patterns in the study could be due to differences in soil textural properties. The *P. reticulatum* site has fairly compacted soils at depth with patches of shallow bedrock interspersed within the profile. These barriers offer mechanical resistance to root penetration. It is not surprising that

comparison of the average rooting distribution results from both sites portrayed *G. senegalensis* with higher  $\beta$  values than *P. reticulatum*, implying that it is more deeply rooted than the latter (Jackson et al., 1996). Consistent with these findings, Richards (1986) highlighted the prevalence of iron pans in tropical savannahs which eventually impact rooting patterns and their distribution.

The percentage of roots found in the upper 0.30 m for both sites was consistent with other studies (Jackson et al., 1996). In particular, for both species, root crowns greatly contributed to the observed biomass and root distribution patterns especially in the upper 0.15 m. For both sites, the fitted  $\beta$  values tended to overestimate the cumulative root fraction at the surface by 16%. This bias could have resulted from the woody shrub basal area or “root crowns” since this is often buried 0.10 m below the soil surface and was considered as a root structure in this study.

The *G. senegalensis* shrubs exhibited a dimorphic rooting pattern with a superficial rooting system in the upper 0.15–0.30 m (Fig. 1) with about 95% of roots in the upper 1 m and sending a narrow leading taproot to depth of >1.2 m (Kizito et al., 2003 Unpublished). The implication of this rooting pattern is a higher relative concentration of roots close to the surface to tap more effectively both moisture and nutrients resulting from the scanty rain showers (FAO, 1989), and a decreasing root density with depth leaving the tap roots to extract deep ground-water reserves (Dawson, 1993; Caldwell et al., 1998). The *P. reticulatum* shrubs revealed a high proportion of oblique roots, with a very pronounced vertical tap root and a high wood strength (Fig. 2) which plays a major role in anchorage as well as tapping ground-water reserves.

#### 4.4. Ecosystem implications

All shrub roots at both study sites extended beyond the maximum sampled root depth of 1.2 m. These roots could therefore play an important strategic role of water uptake during drought (Gaze et al., 1998; Kizito et al., 2003, Unpublished) to maintain transpiration hence permitting plant survival. Additionally, no evidence of competition between shrubs and millet plants was observed in this study suggesting that shrubs could serve as a viable inter-crop option.

Future research efforts geared towards understanding the degree and extent of shrub facilitative effects will provide a clearer understanding of ecosystem functionality. The conventional farming practice of complete shrub removal compromises the afore-mentioned shrub-imparted benefits in this study. If this is not halted, it could potentially reduce profile recharge while increasing runoff, surface soil temperature and soil evaporation, resulting in a long-term detrimental impact on agricultural productivity.

Our results suggest but do not quantify the extent and magnitude of shrub facilitation to annual crops in terms of redistributed water during the dry season. As previously argued, there is circumstantial evidence of soil water redistribution from other semi-arid species elsewhere (Richards and Caldwell, 1987; Dawson, 1995; Caldwell et al., 1998; Jackson et al., 2000). The results reported here on seasonal soil water variation and rooting patterns suggest that shrubs could be performing soil water redistribution. A further study on variation of soil water potential with depth as well as timing and rate of shrub coppicing regimes would therefore be beneficial in teasing out processes in these ecosystems.

## 5. Conclusions

The presence of these two shrub communities in the Sahel impacts seasonal soil water trends. Shrubs confer improved microclimatic regimes (reduced wind speeds and lower soil evaporation) with higher soil water-content within the vicinity of their micro-sites.

Shrub roots depleted deeper layers of the profile during the dry season. In this period, soil surrounding near-surface shrub roots was consistently moister than adjacent bare soil, suggesting a possibility of shrub roots participating in the redistribution of soil water to the drier upper profile from moister deep layers. Shrub root distribution patterns in this study appeared to be an artifact of meager water resources existent for a greater portion of the year in these ecosystems. Conversely, in the rainy season shrub roots had a positive impact on the field soil moisture regime by enhancing higher water entry into the profile. Shrub roots also predominantly exploited different soil horizons compared to Pearl millet roots, an aspect which qualifies both shrub species as potential candidates for intercropping in these fragile dryland agro-ecosystems.

There is need for further research on the occurrence of hydraulic redistribution and its potential effects on neighboring plants with pertinent emphasis on measurements that directly provide evidence of plant function and processes such as plant physiological studies.

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## References

- Anderson, L.J., Brumbaugh, S., Jackson, R.B., 2001. Water and tree-understory interactions: A natural experiment in a savanna with oak wilt. *Ecology* 82, 33–49.
- Akpo, E., 1993. Influence du couvert ligneux sur la structure et le fonctionnement de la strate herbacée en milieu sahélien. Les déterminants écologiques. Paris, ORSTOM, TDM, pp. 174.
- Berish, C.W., Ewel, J.J., 1988. Root development in simple and complex tropical successional ecosystems. *Plant and Soil* 106, 73–84.
- Boffa, J.M., 1999. Agroforestry Parkland Systems in sub-Saharan Africa: FAO Conservation Guide 34. Food and Agriculture Organization of the United Nations, Rome.
- Boffa, J.M., Taonda, S., Dickey, J., Knudson, D., 2000. Field-scale influence of karate (*Vitellaria paradoxa*) on sorghum production in the Sudan zone of Burkina Faso. *Agroforestry Systems* 49, 153–175.
- Brown, R.W., Bartos, D.L., 1982. A calibration model for screen-caged Peltier thermocouple psychrometers. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, pp. 155.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., White, D.A., Ong, C.K., 2001. Tree roots: conduits for deep recharge of soil water. *Oecologia* 126, 158–165.
- Caldwell, M.M., Eissenstat, D.M., Richards, J.H., Allen, M.F., 1985. Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. *Science* 229, 384–386.
- Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113, 151–161.
- Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112, 143–149.

- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Centre de Suivi Ecologique, 2000. Annuaire sur l'environnement et les ressources naturelles du Senegal. Centre de Suivi Ecologique, Dakar, Senegal.
- Dancette, C., 1966. Etude de six microclimats à Bambey. Influence des brise-vent. No. 6. Bambey, Senegal, IRAT-CNRA.
- Dawson, T.E., 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95, 565–574.
- Dawson, T.E., 1995. Determining water use by trees and forests from isotopic, energy balance and transpiration analysis: the roles of tree size and hydraulic lift. *Tree Physiology* 16, 263–272.
- Diack, M., Sène, M., Badiane, A.N., Diatta, M., Dick, R.P., 2000. Decomposition of a native shrub, *Piliostigma reticulatum*, litter in soils in semiarid Senegal. *Arid Soil Research and Rehabilitation* 14, 205–218.
- FAO, 1989. Arid zone forestry: a guide for field technicians. FAO Conservation Guide, 20. Food and Agriculture Organization of the United Nations, Rome.
- Fonteyn, P.J., Mahall, B.E., 1978. Competition among desert perennials. *Nature* 275, 544–545.
- Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17, 89–110.
- Freeman, D.C., Emlen, J.M., 1995. Assessment of interspecific interactions in plant communities: an illustration from the cold desert saltbush grasslands of North America. *Journal of Arid Environments* 31, 179–198.
- Gale, M.R., Grigal, D.F., 1987. Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research* 17, 829–834.
- Gaze, S.R., Brouwer, J., Simmonds, L.P., Bromley, J., 1998. Dry season water use patterns under *Guiera senegalensis* L. shrubs in a tropical savanna. *Journal of Arid Environments* 40, 53–67.
- Gregory, P.J., 1989. Water-use efficiency of crops in the semi-arid tropics. In: Soil, Crop and Water Management Systems for Rainfed Agriculture in the Sudano-Sahelian Zone, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, A.P. 502 324, India. p. 85–98.
- Gutierrez, J.R., Meserve, P.L., Contreras, L.C., Vasques, H., Jaksic, F.M., 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside *Porlieria chilensis* (Zygophyllaceae) in arid coastal Chile. *Oecologia* 95, 347–352.
- Hillel, D., 1998. Environmental Soil Physics. Academic Press Publishers, San Diego, CA, USA.
- Horton, J.L., Hart, S.C., 1998. Hydraulic lift: a potentially important ecosystem process. *Tree* 13 (6), 232–235.
- Jackson, R.B., Caldwell, M.M., 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* 81, 683–692.
- Jackson, R.B., Canadell, J., Elheringer, J., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108, 389–411.
- Jackson, R.B., Schenk, H.J., Jobbágy, E.G., Canadell, J., Colello, G.D., Dickinson, R.E., Field, C.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A., Neilson, R.P., Parton, W.J., Sala, O.E., Sykes, M.T., 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* 10, 470–483.
- James, A.S., Meinzer, F.C., Goldstein, G., Woodruff, D., Jones, T., Restom, T., Mejia, M., Clearwater, M., Campanello, P., 2002. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134, 37–45.
- Kizito, F., 2001. Influence of varying levels of incidence solar irradiance and microclimatic variations on Banana (*Musa spp*) growth and productivity. MSc. Thesis, University of Natal, Pietermaritzburg, South Africa.
- Kizito, F., Dragila, M., Sène, M., Dick, R.P., 2003. Rooting dynamics and soil water variation of native shrubs in Sahel soils. American Geophysical Union Conference, San Francisco December, 2003.
- Lauenroth, W.K., Burke, I.C., 1995. The great plains: climate variability. In: Nierenberg, W.A. (Ed.), *Encyclopedia of Environmental Biology*, vol. 2. Academic Press, San Diego, CA, pp. 237–249.
- Lauenroth, W.K., Coffin, D.P., 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. In: Wali, M.K. (Ed.), *Ecosystems Rehabilitation: Ecosystem Analysis and synthesis*, vol. 2. SPB Academic Publishing, The Hague, pp. 131–150.
- Lyford, W.H., 1980. Development of the root system of northern red oak (*Quercus rubra* L.). Harvard Forestry Paper No. 21, pp. 1–29.
- Maman, N., Mason, S.C., Lyon, D.J., Dhungana, P., 2004. Yield components of pearl millet and grain sorghum across environments in the Central Great Plains. *Crop Science* 44, 2138–2145.

- Meinzer, F.C., James, A.S., Goldstein, G., Woodruff, D., 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell and Environment* 26, 1147–1155.
- Ong, C.K., Corlett, J.E., Singh, R.P., Black, C.R., 1991. Above and below ground interactions in agroforestry systems. *Forest Ecology Manual* 45, 45–57.
- Payne, W.A., Wendt, C.W., Lascano, R.J., 1990. Bare fallowing on sandy fields of Niger. *Soil Science Society America Journal* 54, 1079–1084.
- Payne, W.A., Drew, M.C., Hossner, L.R., Lascano, R.J., 1996. Measurement and modeling of photosynthetic response of Pearl millet to soil phosphorus addition. *Plant and Soil* 184, 67–73.
- Perroux, K.M., White, I., 1988. Designs for disc permeameters. *Soil Science Society of America Journal* 52, 1205–1215.
- Richards, J.H., 1986. Root form and depth distribution in several biomes. In: Carlisle, D., Berry, W.L., Kaplan, I.R., Watterson, J.R. (Eds.), *Mineral Exploration: Biological Systems and Organic Matter*. Prentice-Hall, Engelwood Cliffs, NJ, pp. 82–97.
- Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73, 486–489.
- Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J.R., 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108, 503–511.
- Silva, J.S., Rego, F.C., Martins-Loução, M.A., 2003. Root distribution of Mediterranean woody plants. Introducing a new empirical model. *Plant Biosystems* 137 (1), 63–72.
- Shumway, S.W., 2000. Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia* 124, 138–148.
- Wezel, A., 2000. Scattered shrubs in Pearl millet fields in semiarid Niger. Effect on millet production. *Agroforestry Systems* 48, 219–228.