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The distribution of tree and grass roots in savannas in relation to soil nitrogen and water

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Abstract

Here we describe the fine root distribution of trees and grasses relative to soil nitrogen and water profiles. The primary objective is to improve our understanding of edaphic processes influencing the relative abundance of trees and grasses in savanna systems. We do this at both a mesic (737 mm MAP) site on sandy-loam soils and at an arid (547 mm MAP) site on clay rich soils in the Kruger National Park in South Africa. The proportion of tree and grass fine roots at each soil depth were estimated using the $\delta^{13}\text{C}$ values of fine roots and the $\delta^{13}\text{C}$ end members of the fine roots of the dominant trees and grasses at our study sites. Changes in soil nitrogen concentrations with depth were indexed using total soil nitrogen concentrations and soil $\delta^{15}\text{N}$ values. Soil water content was measured at different depths using capacitance probes. We show that most tree and grass roots are located in the upper layers of the soil and that both tree and grass roots are present at the bottom of the profile. We demonstrate that root density is positively related to the distribution of soil nitrogen and negatively related to soil moisture. We attribute the negative correlation with soil moisture to evaporation from the soil surface and uptake by roots. Our data is a snapshot of a dynamic process, here the picture it provides is potentially misleading. To understand whether roots in this system are primarily foraging for water or for nitrogen future studies need to include a dynamic component.

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1. Introduction

Savanna is a tropical summer rainfall ecosystem characterised by the coexistence of a continuous herbaceous component and a discontinuous woody component (Frost et al., 1986; Scholes and Archer, 1997). Covering 12% of the global land surface, savanna shows considerable structural variation from arid shrublands through lightly wooded grasslands to deciduous woodlands and dry forest (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971). Explanations for the coexistence of grasses and trees under such fundamentally different environmental conditions and the factors that determine the relative proportions of each are an intriguing and unresolved puzzle (Hempson et al., 2007; Higgins et al., 2000; Jeltsch et al.,

2000; Sankaran et al., 2004; Scheiter and Higgins, 2007; Scholes and Walker, 1993; Walter, 1971; Walker and Noy-Meir, 1982).

Hypotheses of grass–tree coexistence can be grouped into either resource-based or disturbance-based hypotheses. The resource-based models explain grass–tree coexistence by invoking a partitioning of the rooting niches of grasses and trees (McLaren et al., 2004; Van Langevelde et al., 2003; Walker and Noy-Meir, 1982; Walter, 1970, 1971). Objections to the rooting niche hypothesis (reviewed by Scholes and Archer, 1997) stimulated the development of disturbance-based models. These models demonstrate that drought, fire and grazing can limit the establishment and recruitment of trees into disturbance resistant size-classes allowing for grass–tree coexistence even in the absence of rooting niche separation (Gardner, 2006; Higgins et al., 2000; Menaut et al., 1990).

The limitations of both disturbance and resource-based models of savanna dynamics have led to a plea for the formal

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integration of resource and disturbance-based theories of grass–tree coexistence (Sankaran et al., 2005). One model of this type illustrates how resource competition and disturbances can both alone and in combination allow grasses and trees to coexist (Scheiter and Higgins, 2007). This model illustrates that even though rooting niche separation is not an essential precondition for grass–tree coexistence, competition in the rooting zone can shape patterns of tree dominance in savannas. To develop models such as these a better understanding of edaphic processes in savanna systems is essential.

Research inspired by Walter's (1970, 1971) hypothesis has assumed that water is the primary niche axis (Caylor et al., 2006; Van Langevelde et al., 2003; Walker and Noy-Meir, 1982). Several empirical studies have, however, shown that soil resources other than water can shape competitive interactions between grasses and trees in savanna (Cramer et al., 2007; Dickie et al., 2007; Okin et al., 2008; Pärtel and Wilson, 2002). A number of studies have also demonstrated considerable overlap between the rooting zones of trees and grasses (Le Roux et al., 1995; Ludwig et al., 2003; Mordelet et al., 1997; Seghieri et al., 1995). There are, however, few studies in Africa that illustrate the distribution of soil water and nitrogen relative to tree and grass roots (see for example Coetsee et al., 2008; Le Roux et al., 1995; Mordelet et al., 1997; Okin et al., 2008). Here we not only describe the fine root distribution of trees and grasses we also describe soil nitrogen and water profiles in both a mesic and a semi arid savanna. The primary objective is to improve our understanding of edaphic processes that may influence competition in the rooting zone in savannas.

2. Methods

2.1. Study site

The two study sites we consider, Satara (31.77' E, 24.40' S) and Pretoriuskop (31.14' E, 25.08' S), are respectively located in the central and southern section of the Kruger National Park in South Africa. The climate of the region is typified by hot wet summers and dry mild winters. Mean annual precipitation is 737 mm at Pretoriuskop and 547 mm at Satara. Mean monthly maximum and minimum temperatures are 26.3 °C and 17.5 °C at Pretoriuskop and 29.8 °C and 16 °C at Satara. Rainfall falls in the summer months and is typically caused by convection storms or tropical cyclones. The distinct seasonality of the rainfall results in a growing season that starts with the first rains in late October and continues to the end of the rains in April (Venter et al., 2003).

The study site at Pretoriuskop can be described as a broad leaved woody savanna. *Terminalia sericea* and *Sclerocarya birrea* are the dominant tree species while *Hyperthelia dissoluta* and *Setaria sphacelata* are common grass species (nomenclature follows Coates Palgrave and Coates Palgrave, 2002 for trees and Gibbs-Russell et al., 1990 for grasses). The soils are derived from the underlying Nelspruit granite suite comprised of migmatite, gneiss and granite and can be described as nutrient poor coarse sands (Barton et al., 1986). Total soil nitrogen values are 3310 kg N/ha (Scholes et al., 2003). Soil

depth although variable in the region was seldom deeper than 1.5 m in our study area. Our study site at Satara can be described as a fine-leaved open savanna. *Acacia nigrescens* and *S. birrea* are the dominant tree species while *Bothriochloa radicans* and *Themeda triandra* are common grasses. The Letaba formation basalts of the Karoo supergroup form nutrient rich clay soils that seldom reach a depth of 1 m in our study area. Total soil nitrogen values are 4635 kg N/ha (Scholes et al., 2003).

2.2. Field sampling and laboratory analyses

We sampled fine roots (defined as root material with diameters less than 2 mm) as these characterise the effective absorbing root surface and are also primarily responsible for ion uptake (De Kroon and Visser, 2003). At both study sites we sampled material at five replicate pits, 30 m apart, both between and under canopies. At each pit, soil was extracted from a 5 cm deep 20 × 20 cm section every 5 cm for the first 20 cm and then every 20 cm to bedrock (150 cm at Pretoriuskop and 60 cm at Satara). The samples were collected at the onset of the dry season at the beginning of June 2006 at Pretoriuskop and June 2007 at Satara. Roots were separated from the soil by dry sieving through an 850 µm sieve after which the sieved soil was further scrutinised for any root material. Prior to mass spectrometry the roots were washed and dried at 70 °C to constant weight before being ground to a fine powder using a Retsch MM200 ball bearing mill (Retsch, Haan, Germany).

For the soil and root samples we determined percentages of total nitrogen and isotopic ratios of both $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ using a Thermo Finnigan Delta plus XP Mass Spectrometer coupled with a conflo III device to a Thermo Finnigan Flash EA1112 Elemental Analyser with automatic sampler (Thermo Electron Corporation, Milan, Italy). Our own independently analysed internal standards were run to calibrate our results relative to atmospheric N_2 for N and Pee Dee Belemnite for C as well as to correct for drift in our reference gas. The deviation from the standard is denoted by the term δ and the results expressed as parts per thousand (‰), using the convention,

$$\delta^n E = (R_i / R_s) * 1000,$$

where n is the heavy isotope of element E and R_i and R_s are ratios of the heavy to light isotope (e.g. $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$) for the sample and standard respectively.

We used the $\delta^{13}\text{C}$ values of fine roots and the mean (end member) $\delta^{13}\text{C}$ values for the roots of dominant tree (C_3) and grass (C_4) species present at our sites to determine the relative proportion of C_3 and C_4 derived carbon in a root sample. The level of discrimination against the heavier ^{13}C isotope differs strongly for C_3 and C_4 plants. C_4 plants have $\delta^{13}\text{C}$ values of approximately –12.5‰ while C_3 plants have $\delta^{13}\text{C}$ values of around –26.5‰ (Cerling et al., 1997; Vogel et al., 1978). This distinction is particularly useful in tropical savanna systems such as the Kruger National Park where the grasses use the C_4 photosynthetic pathway while trees and shrubs use the C_3 pathway (Scholes and Walker, 1993; Vogel et al., 1978). To estimate the $\delta^{13}\text{C}$ value of the end members for grasses and trees fine root samples were obtained for

those species that contribute >80% of tree and grass cover at each site. Note that the greater evenness of species abundance patterns at Pretoriuskop meant that more species were sampled at Pretoriuskop than at Satara (Table 1).

To obtain an estimate of how the proportion of grass and tree root material changes with depth we assume that the isotopic signal of a root sample (S) is a simple mixture of the isotopic signatures of the grass (G) and tree (W) material in the sample. A mixing equation to represent this assumption is

$$S = pW + (1-p)G,$$

where p is the proportion of the sample that is tree root and $1-p$ is the proportion of the sample that is grass root. The end members provide estimates of W and G while the measured isotopic signature of the sample is S , hence the only unknown is p which is $p = (G - S) / (G - W)$.

We used two methods to describe volumetric soil moisture content. We first used capacitance probes (Netafim Irrigation

Inc., U.S.A.) to continuously measure soil moisture at three depths at each site. We do this at one central location at each site from May 2003 to May 2007. We also used a portable capacitance probe (Sentek Sensor Technologies, Stepney Australia) to estimate soil moisture at every 10 cm of the soil profile. The portable capacitance probe measurements were made twice monthly for three months in the summer (January–March) of 2006 at six sites under the canopy of trees and six sites between canopies at both Satara and Pretoriuskop.

2.3. Data analyses

To quantify the level of overlap between grass and tree roots we calculated the Morisita index of niche overlap as described by Mueller and Altenberg (1985). The Morisita index is an index of niche overlap where 1 is equivalent to equal densities of tree and grass roots through the profile and 0 means that there is no overlap at all. We use linear mixed models as implemented in the R statistical language's (R Development Core Team, 2008) nlme package (Pinheiro et al., 2008) to test whether measured variables differed with soil depth, canopy association or site. The linear mixed model structure allows us to control for the fact that samples from a single soil profile are not independent by treating each replicate profile as a random effect. In the results we report mean values of measured variables ± 1 standard error. In the analysis we test for interactions between the main effects, the results of these tests are only reported if a significant interaction was detected.

3. Results

At Pretoriuskop the total root biomass in the soil profile was higher between tree canopies ($8181.1 \pm 1718.4 \text{ g/m}^{-3}$) than under tree canopies ($5347.8 \pm 494.1 \text{ g/m}^{-3}$) while at Satara the root biomass between canopies ($4183.4 \pm 719.91 \text{ g/m}^{-3}$) was similar to that under tree canopies ($3925.8 \pm 405.35 \text{ g/m}^{-3}$). An analysis of variance of the log of these data reveals that the site effect was significant ($F_{1,16} = 9.89, p = 0.006$) while the effect of tree canopy ($F_{1,16} = 1.63, p = 0.22$) and the interaction between site and tree canopy ($F_{1,16} = 1.12, p = 0.31$) on total root biomass in the soil profile were not significant.

The mean of the fine root end member $\delta^{13}\text{C}$ values were $-27.61 \pm 0.60\%$ for trees and $-13.26 \pm 0.26\%$ for grasses at Pretoriuskop and $-26.40 \pm 0.24\%$ for trees and $-12.85 \pm 0.29\%$ for grasses at Satara (Table 1). These values are in agreement with the values found in the literature (Cerling et al., 1997; Vogel et al., 1978). These end members were used to calculate the proportion of tree root material in each root sample and from this the tree and grass root biomass in each sample (Fig. 1). When analysing these data from the soil profiles we take cognisance of the fact that samples taken from a single profile are not independent and that profiles are grouped (blocked) in sites. In the statistical analysis we therefore treat the factors profile and site as random effects (with profile nested within site). The fixed effects are then the factors soil depth and tree canopy association. The resulting linear mixed effects model illustrates that the percentage of root material that is tree

Table 1

Species sampled for the end member determination of the $\delta^{13}\text{C}$ values of grass and tree roots at the two study sites. Nomenclature follows Coates Palgrave and Coates Palgrave (2002) for trees and Gibbs-Russell et al. (1990) for grasses.

Site	Life form	$\delta^{13}\text{C}$	Species name
Satara	Tree	-26.81	<i>Acacia nigrescens</i>
Satara	Tree	-26.16	<i>Cissus cornifolia</i>
Satara	Tree	-25.19	<i>Combretum imberbe</i>
Satara	Tree	-25.68	<i>Dichrostachys cinerea</i>
Satara	Tree	-27.33	<i>Gymnosporia senegalensis</i>
Satara	Tree	-27.08	<i>Ormocarpum trichocarpum</i>
Satara	Tree	-26.39	<i>Ehretia amoena</i>
Satara	Tree	-26.01	<i>Sclerocarya birrea</i>
Satara	Tree	-26.94	<i>Securinega virosa</i>
Satara	Grass	-13.15	<i>Bothriochloa radicans</i>
Satara	Grass	-12.91	<i>Panicum maximum</i>
Satara	Grass	-12.02	<i>Setaria sphacelata</i>
Satara	Grass	-13.33	<i>Themeda triandra</i>
Pkop	Tree	-27.42	<i>Albizia versicolor</i>
Pkop	Tree	-28.97	<i>Turraea nilotica</i>
Pkop	Tree	-28.74	<i>Catunaregam spinosa</i>
Pkop	Tree	-21.38	<i>Dalbergia melanoxylon</i>
Pkop	Tree	-26.75	<i>Dichrostachys cinerea</i>
Pkop	Tree	-29.35	<i>Diospyros lycioides</i>
Pkop	Tree	-25.62	<i>Diospyros mespiliformis</i>
Pkop	Tree	-29.06	<i>Euclea natalensis</i>
Pkop	Tree	-28.54	<i>Gymnosporia senegalensis</i>
Pkop	Tree	-29.13	<i>Ormocarpum trichocarpum</i>
Pkop	Tree	-27.95	<i>Sclerocarya birrea</i>
Pkop	Tree	-28.70	<i>Strychnos madagascariensis</i>
Pkop	Tree	-27.34	<i>Terminalia sericea</i>
Pkop	Grass	-12.36	<i>Andropogon gayanus</i>
Pkop	Grass	-15.29	<i>Elionurus muticus</i>
Pkop	Grass	-12.70	<i>Heteropogon contortus</i>
Pkop	Grass	-12.49	<i>Hyperthelia dissoluta</i>
Pkop	Grass	-13.50	<i>Hyparrhenia filipendula</i>
Pkop	Grass	-13.13	<i>Loudetia flavidia</i>
Pkop	Grass	-13.26	<i>Panicum maximum</i>
Pkop	Grass	-13.53	<i>Pogonarthria squarrosa</i>
Pkop	Grass	-13.71	<i>Setaria sphacelata</i>
Pkop	Grass	-12.62	<i>Themeda triandra</i>
Pkop	Grass	-12.35	<i>Digitaria eriantha</i>

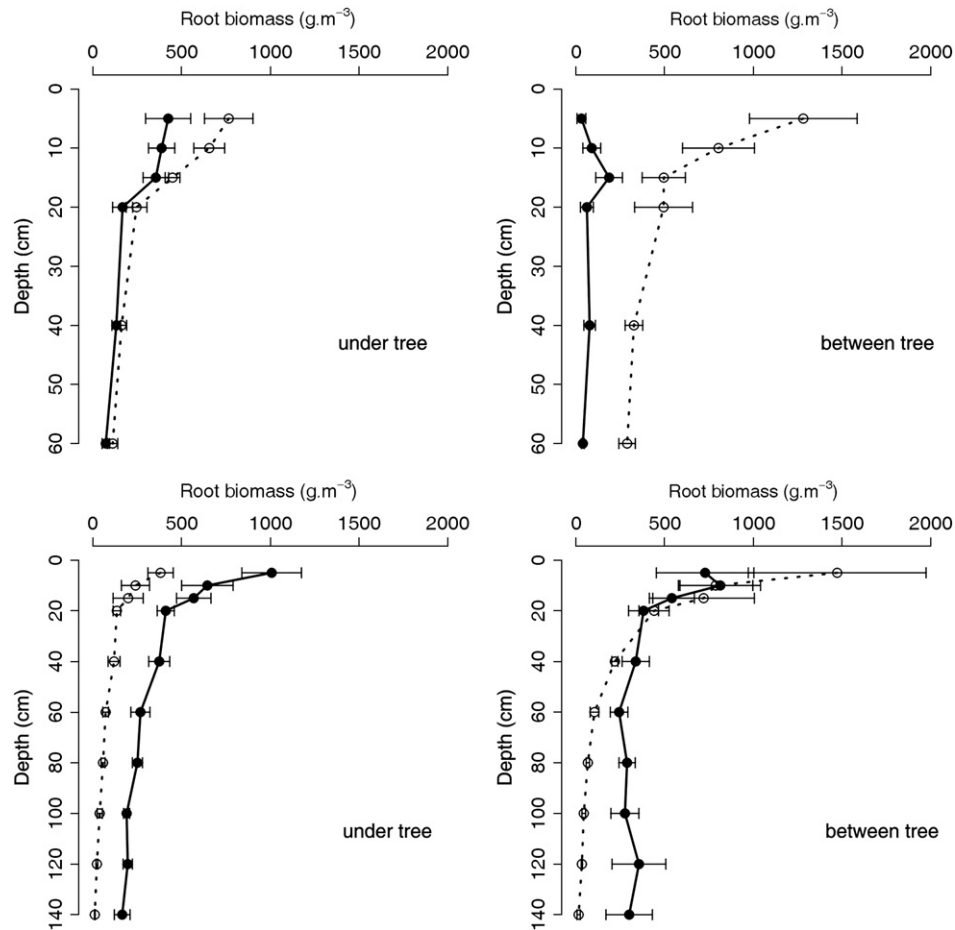


Fig. 1. Vertical distribution of tree (●) and grass (○) root biomass under the canopy of trees (“under tree”) and in the between tree canopy spaces (“between tree”) at Satara (top) and Pretoriuskop (bottom).

root material differs significantly with depth and with tree canopy association (Fig. 1). The proportion of root material that belongs to trees is significantly higher at depth ($F_{149,1}=72.738$; $p<0.0001$) and significantly higher under tree canopies ($F_{149,1}=58.570$; $p<0.0001$). The interaction between canopy association and depth was significant ($F_{149,1}=17.37$; $p=0.0001$). The sign of this interaction is negative, suggesting that the proportion of root biomass that is tree found in the surface soil layers is lower between canopies than one would expect based on the main effects of canopy and depth alone.

We test for rooting niche separation more formally by using the data on the relative density of tree and grass roots to estimate the Morisita index of niche overlap within the rooting zone. The Morisita index of niche overlap was lower between tree canopies ($F_{1,17}=19.76$, $p=0.0004$), but did not differ with site ($F_{1,17}=1.69$, $p=0.21$). The effect of tree canopies reflects the fact that the distributions of the relative density of tree and grass roots are similar under canopies but different between canopies (Fig. 1). More ecologically relevant is the question of whether the indices of niche overlap indicate niche segregation or niche overlap. The mean level of niche overlap was 0.76 and the 95% confidence intervals of the estimated mean niche overlap were 0.67 and 0.85. These confidence intervals show that niche overlap is significantly different from both zero and unity. That

is, the data support neither the hypothesis that there is an absolute partitioning of the rooting niches (Morisita=0), nor does it support the hypothesis that there is an absolute overlap in the rooting niches (Morisita=1). However, at 0.76 the Morisita index tends toward niche overlap rather than separation. The trends in Morisita index are not changed if we calculate the Morisita index with the absolute root densities.

We used the linear mixed model structure described above (profile nested in site as random effects and fixed effects of soil depth and canopy position) to analyse the soil nitrogen parameters (Fig. 2). The log of $\delta^{15}\text{N}$ increases significantly with depth ($F_{1,148}=11.80$, $p=0.0008$), but was not influenced by tree canopy association ($F_{1,148}=0.821$, $p=0.36$). The $\delta^{15}\text{N}$ values were low at the surface and highest at 20–40 cm. This increase is approximately 3‰ at Pretoriuskop and 2–3‰ at Satara (Fig. 2). Total soil nitrogen content (Fig. 2) decreased with depth ($F_{1,148}=82.00$, $p<0.0001$) and was higher under tree canopies ($F_{1,148}=24.71$, $p<0.0001$).

Soil moisture content during the growing season (summer) of 2006 was highest in the intermediate (40–50 cm) soil horizons at both sites (Fig. 3). Using a linear mixed model with profile as a random effect nested in site and fixed effects of soil depth and tree canopy association, we find that soil depth has a significant positive effect ($F_{1,167}=31.19$, $p<0.0001$) on the

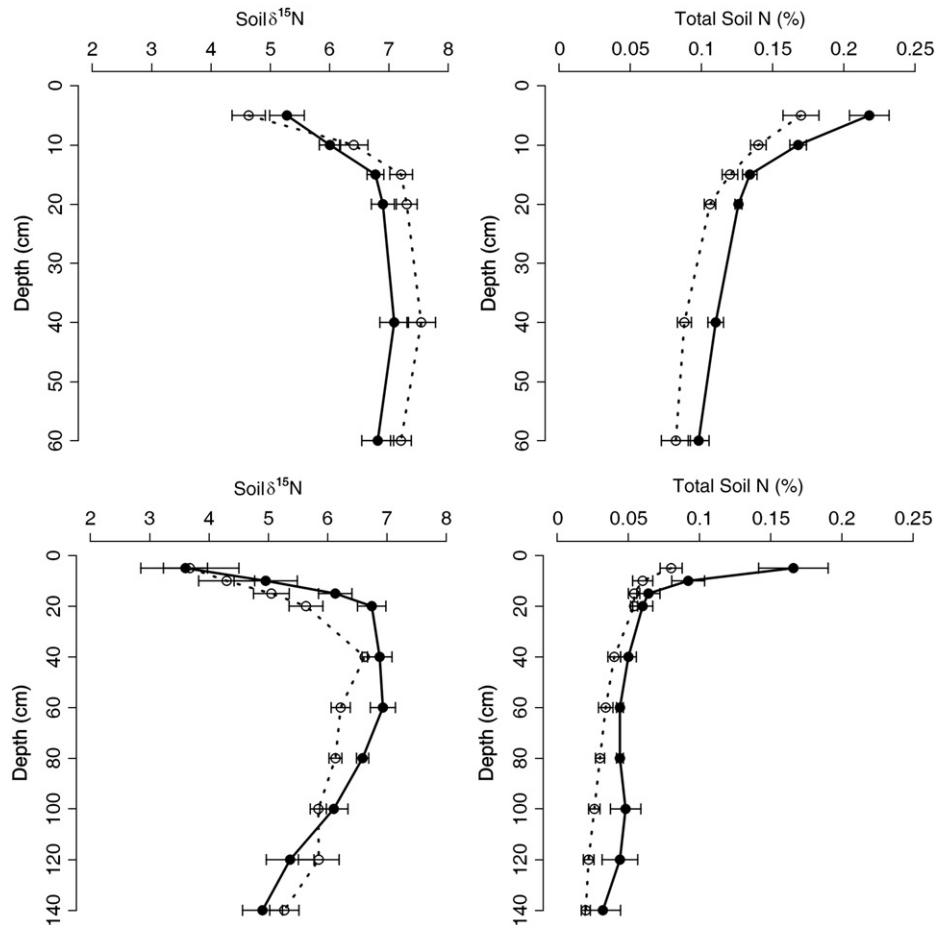


Fig. 2. Vertical distribution of soil $\delta^{15}\text{N}$ values and total soil nitrogen under the canopy of trees (●) and in the between tree canopy spaces (○) at Satara (top) and Pretoriuskop (bottom).

average soil moisture content over the growing season and that canopy association did not influence the average soil moisture content over the growing season ($F_{1,167}=0.022$, $p=0.88$). The continuous monitoring of soil moisture at three depths at the two sites between May 2003 and May 2007 supports and complements the view that the surface horizons are drier than the middle horizons. At Pretoriuskop the middle layer (50 cm) was the wettest, while at Satara the deepest layer (75 cm) was the wettest (Fig. 3).

We tested whether root biomass was related to nitrogen or moisture levels by using a linear mixed model (Fig. 4). Random effects are soil profile nested within site and fixed effects are canopy position and either percentage soil nitrogen or soil moisture content. For the soil moisture content we analyse the average of the bi-weekly samples that were taken during the growing season of 2006. Soil moisture was sampled at 10 cm intervals to a maximum depth of 90 cm but not sampled in the same profiles that were sampled for root biomass. Both soil moisture and roots were, however, randomly sampled from the same statistical population. The moisture–root biomass analyses are therefore based on the mean soil moisture and mean root biomass at different depths at the study sites. We found a significant negative relationship between soil moisture content and root biomass ($F_{1,14}=5.51$, $p=0.034$), but that tree canopy

association had, in this dataset, a negative but insignificant effect on this relationship ($F_{1,14}=1.12$, $p=0.31$; Fig. 4). The analyses of soil nitrogen and root biomass (Fig. 4) show that there is a significant and positive relationship between root biomass and percentage soil nitrogen ($F_{1,148}=42.20$, $p<0.0001$) and that this relationship is significantly influenced by tree canopy association ($F_{1,148}=22.31$, $p<0.0001$).

4. Discussion

Our data show that there is substantial overlap between the rooting zones of grasses and trees. Most tree and grass root biomass are located in the upper layers (top 20 cm) of the soil profile while both grass and tree roots are present at the bottom of the profile (Le Roux et al., 1995; Ludwig et al., 2003; Mordelet et al., 1997; Seghier et al., 1995). We therefore suggest that in both the mesic and semi arid savanna investigated here the spatial patterns of root distributions are consistent with competition between grasses and trees for resource uptake.

Our analysis shows that fine root biomass is in fact negatively correlated with the growing season distribution of soil moisture, but positively correlated with the distribution of soil nitrogen (Fig. 4). The negative correlation between root biomass and soil moisture contradicts theoretical (Collins and

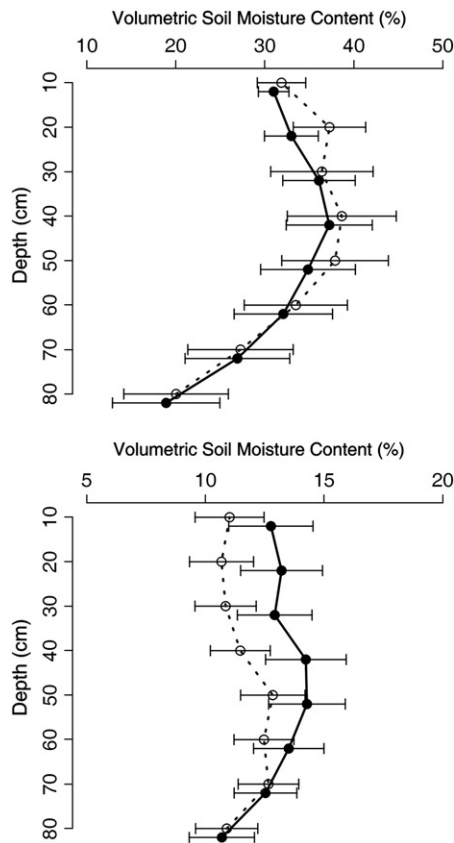


Fig. 3. Vertical distribution of volumetric soil moisture content under the canopy of trees (●) and in the between tree canopy spaces (○) at Satara (top) and Pretoriuskop (bottom).

Bras, 2007; Laio et al., 2006; Schenk, 2008) and empirical studies (e.g. West et al., 2004; Zhou and Shangguan, 2007) that support positive correlations between water availability and root biomass. Our continuous monitoring of soil moisture levels at the study site unambiguously shows that the surface layers are on average drier than the deeper layers and are above wilting point for fewer days per year than deeper soil layers. This negative correlation with soil moisture is not surprising as such a correlation is a representation of a dynamic process where evaporation removes soil moisture from the upper soil layers and that soil moisture might be lower where root biomass and hence uptake capacity are highest.

Our data on soil nitrogen show that total soil nitrogen decreases while $\delta^{15}\text{N}$ increases with soil depth for the first 40 cm of the soil profile (Fig. 2). This is due to decomposition processes which result in the gradual ^{15}N enrichment of residual decomposing material. Since plant available nitrogen is generally linearly and positively related to total soil nitrogen and linearly, but negatively related to the log of $\delta^{15}\text{N}$ (Evans and Ehleringer, 1994) our results indicate that plant available nitrogen decreases with soil depth. Our data on root density are positively related to these changes in nitrogen availability (Fig. 4). These correlations suggest that root distributions may be primarily responding to nitrogen availability and not water availability as proposed by Walter (1970, 1971).

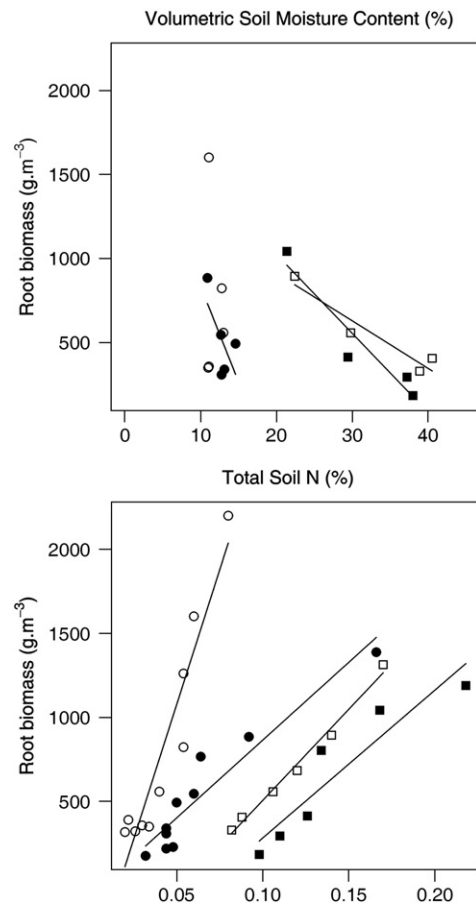


Fig. 4. The relationship between total (tree and grass) root biomass, volumetric soil moisture content and total soil nitrogen under the canopy of trees (“under tree” closed symbols) and between tree canopy spaces (“between tree” open symbols) at Satara (■ □) and Pretoriuskop (● ○). Note that the points plotted are the mean values sampled at each depth in the soil profile even though the statistics reported in the text for the analyses involving nitrogen are based on the individual replicate data points.

We did not, however, collect data throughout the year nor did we examine nitrogen uptake by the roots. Our data therefore represent only a snapshot of a dynamic process. Moreover, nutrients other than nitrogen may contribute to root distributions in savanna (Craine et al., 2008). To better understand whether tree grass competition in the rooting zone is for water or for nutrients we believe that research should focus on the temporal distribution of nutrients and water as well as plant uptake of these resources. The increasing use of isotopic labelling methods in plant ecological research provides an exciting means for generating the required data (Dawson et al., 2002; Sternberg et al., 2004).

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