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# Tree and grass rooting patterns in an African humid savanna

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**Abstract.** Spatial and temporal soil partitioning between roots of the two savanna plant components, i.e. trees and grasses,were investigated in a West African humid savanna. Vertical root phytomass distribution was described for grass roots, large (> 2 mm) and fine (< 2 mm) tree roots, in open sites and beneath tree canopies. These profiles were established monthly over one year of vegetation growth. Natural $^{13}C$ abundance measurement was used to determine the woody/herbaceous phytomass ratio in root samples. Tree and grass root distributions widely overlapped and both were mostly located in the top 20 cm of the soil. Grass root phytomass decreased with depth whereas woody root phytomass peaked at about 10 cm depth. No time partitioning was detected. These structural results do not support the hypothesis of soil resource partitioning between trees and grasses and are thus consistent with functional results previously reported.

**Keywords:** C3 plant; C4 plant; Carbon-13; Côte d'Ivoire; Isotope; Lamto; Root; Tree/grass relationship; West Africa.

## Introduction

In savanna, trees and grasses typically coexist (Menaut 1983). Interactions between both components have been clearly shown at the above-ground level of a humid savanna: tree canopies reduce grass photosynthesis (Mordelet 1993a) and consequently above-ground grass primary production (Mordelet & Menaut 1995). The primary determinants of tree/grass dynamics are considered to be soil water and nutrient availability (Frost et al. 1986). Root interactions between trees and grasses are still poorly understood, and have led to hypotheses which require further testing.

Walter (1971) proposed, for arid savannas, a hypothesis based on partitioning of soil exploitation to explain the coexistence of the two layers: grass roots would be mainly located in the topsoil and first use the incoming water, whereas tree roots would be situated in the subsoil, so that trees could grow only where enough water reached deeper soil horizons. The existing models of tree/grass equilibria are based on this hypothesis (Walker & Noy-Meir 1982; Eagleson & Segarra 1985) and have been widely extended to all savanna types, including neotropical savannas (Sarmiento 1984). In a more general model, Berendse (1979) also concluded that different rooting patterns could mainly account for a stable equilibrium between populations of different species. Walter's hypothesis was partly supported by the grass and shrub root distribution and water use in arid steppes (Sala et al. 1989; Lee & Lauenroth 1994). In Southern African savannas Knoop & Walker (1985) concluded that the woody and herbaceous components used water differently between topsoil and subsoil. However, they observed widely overlapping tree and grass root distributions, as did Belsky (1994) in East Africa. Furthermore, shallow tree root systems were observed in savanna by many authors in West Africa (Lawson et al. 1968; Menaut 1971; Okali et al. 1973).

In these studies, tree roots starting from the base of trunks were dug out, or tree and grass roots were removed together and sorted according to their morphological differences. The first method does not include all fine roots, and the second can lead to incorrect estimates of the tree/grass root ratio due to mistakes on the actual woody or herbaceous origin of the roots (Mordelet 1993b). The use of the stable isotope $^{13}C$ is an alternative approach for estimating below-ground biomass due to differences between C3 and C4 plants (Ludlow et al. 1976; Svejcar & Boutton 1985; Wong & Osmond 1991; Polley et al. 1992). It is particularly relevant in savanna, where natural $^{13}C$ abundance measurements of roots allow discrimination between tree (C3) and grass (C4) contributions to total root phytomass (Scholes & Walker 1993).

In addition to spatial partitioning, time partitioning can reduce competitive interaction between two vegetation components (Parrish & Bazzaz 1976) and may contribute to tree/grass coexistence in savanna (Menaut et al. 1990).

The aim of this study was to improve our understanding of tree/grass relationships at the root level. We describe the root profiles for trees and grasses, both in the open situation and under trees, using $^{13}C$ natural abundance measurements of root samples. Root dynamics were investigated during one year.

## Material and Methods

The study was carried out in a humid savanna, situated at the Lamto Research Station, Côte d'Ivoire (6° 13' N, 5° 02' W). Mean annual temperature averages 27 °C and is constant throughout the year. Rainfall averages 1200 mm/yr (data from Lamto Geophysical Station since 1962). The long wet season extends from February to November and the dry season from December to February. The savanna is burnt annually in mid-January.

Tree density increases along a catena from a herbaceous savanna underneath a plateau to a closed plateau forest at the top (Menaut & César 1979). The study was performed in the most widespread intermediate savanna, where the trees are clumped. A complete description of the plots was given in Mordelet & Menaut (1995). 18 clumps were selected, made up of three species: *Bridelia ferruginea*, *Crossopteryx febrifuga* and *Cussonia barteri*. The grass layer is continuous and dominated by perennial tuft-grasses, especially *Hyparrhenia* spp. and *Andropogon* spp. in the shrubby savanna. Soils are the tropical ferrugineous type with a sandy texture, gravel and stones frequently occurring below 30 cm.

The study was performed during the 1989 growing season (from February 1989 to February 1990). Soil samples were excavated within a 20 cm × 20 cm metallic frame down to 60 cm (120 cm for several profiles), at 10 cm intervals (in the first 10 cm, 0 - 5 and 5 - 10 cm were distinguished). This method ensured that large roots occurring under the trees were included in the samples.

The roots were extracted by washing the soil samples on a 1 mm mesh sieve and then by floating to separate the roots from the remaining mineral particles. Root samples were finally dried at 70 °C until constant weight was achieved. In order to avoid a 'large tree root bias effect', large tree roots (> 2 mm diameter) were separated by hand. For fine roots (< 2 mm diameter) it was shown that it was not possible to separate tree and grass roots according to their colour and morphology (Mordelet 1993b).

To determine the tree/grass ratio within a fine root sample, the $^{13}$C isotopic approach was used. The isotopic ratio $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ is higher for plants with a C4 photosynthetic pathway than for C3 plants (Smith & Epstein 1971), due to a lower carbon isotope fractionation during assimilation. The $^{13}$C natural abundance is expressed as $\delta^{13}$C ‰ units (cf. the PDB International Standard; Craig 1957):

$$\delta^{13}\mathrm{C} = \{(R_{\mathrm{sample}} - R_{\mathrm{standard}})/R_{\mathrm{standard}}\}\times 1000, \qquad (1)$$

Trees have a C3 photosynthetic pattern whereas in Lamto savanna grasses are $C_4$ plants, and exhibit typical mean $\delta^{13}$C values of – 28.1 ‰ and – 12.6 ‰ respectively (Lepage et al. 1993). Consequently, the tree and grass contribution (*t* and *g* respectively) to the root phytomass could be calculated for any mixed root sample (where natural $^{13}$C abundance is $\delta_s$) from the following mass and isotope equations:

$$t + g = 1 \quad \text{and} \quad -28.1\,t - 12.6\,g = \delta_s. \qquad (2)$$

For $^{13}$C abundance measurements, roots were ground to pass through a 80 µm sieve (P14, Fritsch) to obtain an homogeneous powder from which a ca. 1 mg aliquot, corresponding to approximately 0.4 mg of carbon, was analyzed on a system composed of an elemental analyser (CHN NA 1500, Carlo Erba) coupled to an isotope ratio mass spectrometer (Sira 10, Fisons) (Girardin & Mariotti 1991). Contamination of fine roots by soil organic matter fixed by clay remaining on the roots was not estimated. This bias was likely to be very small for the following reasons: (1) the roots were carefully washed under tapwater; (2) the clay content of the soil was low; (3) the soil organic matter was not abundant. Therefore no dispersant was used. Contamination by exogenous carbonates was not possible because they were not present.

During each of the 13 months, 168 samples were collected for phytomass measurements: for six tree clumps, two samples were excavated under tree clumps ('canopy' situation), and two samples outside the tree clumps ('open' situation) for seven depths. Root samples from 2 tree clumps were used for $\delta^{13}$C analysis each month. In order to limit the number of analyses and to ensure enough roots were present, the two replicates of

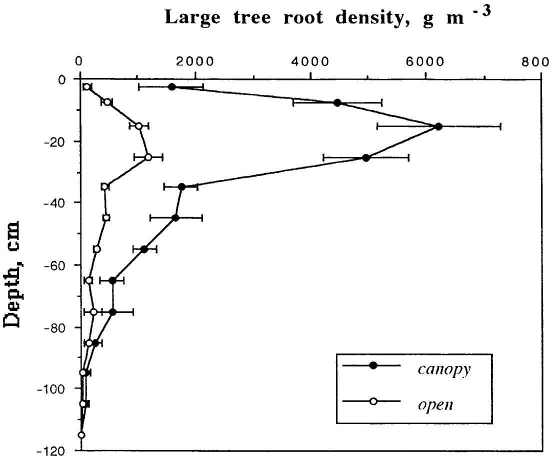

**Fig. 1.** Vertical distribution of large tree root phytomass (> 2 mm) in the open and beneath tree clumps, with associated standard errors (*n* = 156 between 0 and 60 cm; *n* = 6 between 60 and 120 cm).

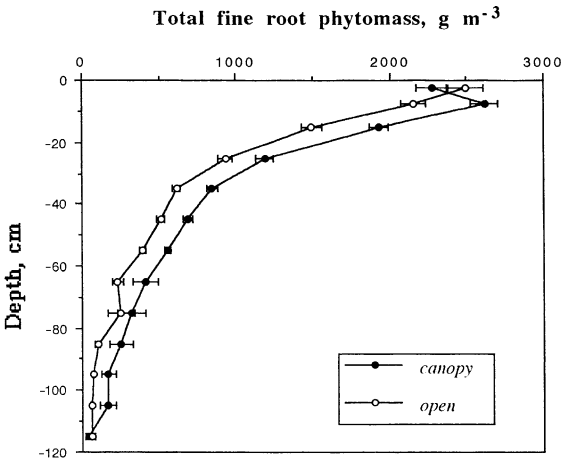

**Fig. 2.** Vertical distribution of total fine root phytomass (< 2 mm) in open savanna and beneath tree clumps, with associated standard errors (*n* = 156 between 0 and 60 cm; *n* = 6 between 60 and 120 cm).

each tree clump were mixed. The mean $\delta^{13}C$ values then referred to two areas of 2 × 20 cm × 20 cm = 800 cm$^2$ per clump.

Data were subjected to analysis of variance with the SAS package (Anon. 1990).

## Results

### *Spatial distribution*

Monthly root profiles were used to compare canopy and open situations. Large tree root density and variability were higher beneath the trees than in the open. In both situations maximum root density was reached at ca. 20 cm depth. Large tree root density decreased markedly below 30 cm and below 60 cm the roots were very scarce (Fig. 1).

Combined tree plus grass fine root densities rapidly decreased with depth (Fig. 2). Fine root density was lower in the open savanna, except in the 0 - 5 cm layer. In the open (Fig. 3a), grass roots were dominant in the shallow horizons (0 - 20 cm) but in the deeper horizons (20 - 60 cm) grass root and tree fine root densities were similar. On the contrary, beneath the canopy (Fig. 3b), tree fine root density was higher than grass root density throughout the profile. The percentage of tree fine roots varied between 62 and 86 % (Fig. 4). Grasses exhibited exactly the same rooting pattern in both situations. On the contrary, tree fine root densities peaked between 5 and 10 cm beneath tree clumps and were more evenly distributed throughout the profile in the open.

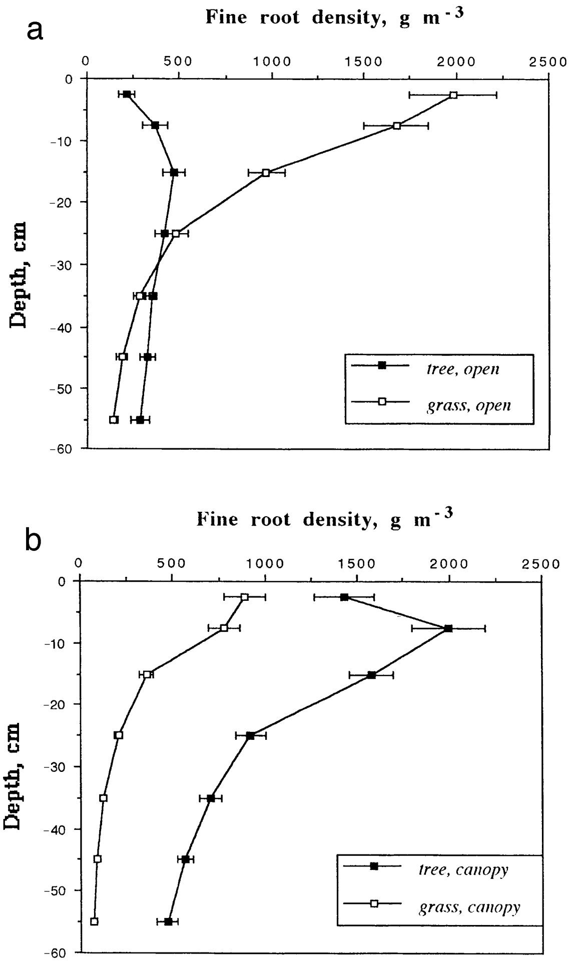

**Fig. 3.** Vertical distribution of fine tree and grass root phytomass in open savanna (a), and beneath tree clumps (b), with associated standard error (*n* = 20), determined from $^{13}C$ natural abundance measurements.

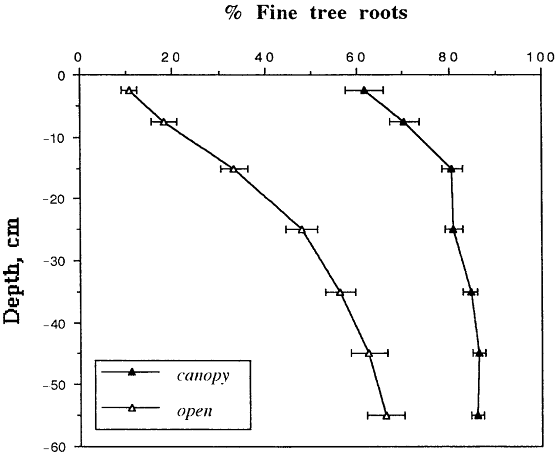

**Fig. 4.** Percentage of fine tree-root phytomass beneath tree canopy and in open savanna from 0 to 60 cm deep (*n* = 20).

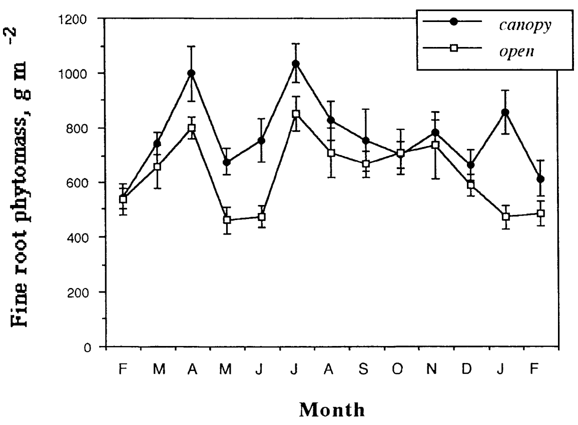

**Fig. 5.** Fine-root phytomass dynamics beneath tree clumps and in open savanna, from 0 to 60 cm deep, with associated standard errors ($n$ = 12).

### *Fine root dynamics*

It is not possible to describe large tree root dynamics due to the high variability associated with their phytomass and their long life span (the root phytomass was not significantly different from one month to the other). Thus, only fine root dynamics are presented. The fine root dynamics were not significantly different from one soil layer to the next. Root phytomass was higher beneath tree clumps than in the open (Fig. 5), but seasonal variations were similar in both situations. Fine root phytomass variations were mainly due to the woody component under tree clumps, whereas they mainly resulted from the grass component in the open. Fine root dynamics did not follow a clear pattern and were broadly similar for trees and grasses (Fig. 6).

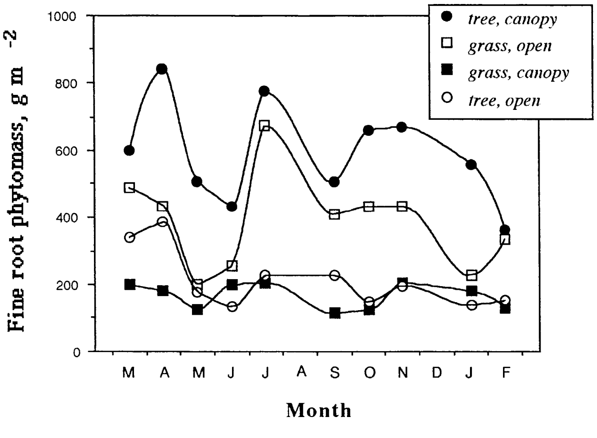

**Fig. 6.** Fine tree and grass root phytomass dynamics, from 0 to 60 cm deep, in open savanna, and beneath tree clumps, determined from $^{13}$C natural abundance measurements.

## Discussion

Spatial root distribution is controlled by both architectural determinants and environmental constraints. The former should act mainly on large roots whereas the latter should influence fine root growth. In the Lamto savanna, tree large roots were shallow, as previously reported by Menaut (1971). In other humid savannas trees also exhibit shallow root systems (Lawson et al. 1968; Okali et al. 1973). Total (tree + grass) fine-root phytomass also showed a shallow rooting pattern, which is in agreement with previous studies in Lamto savanna (see for example Menaut & César 1979). This structure should result from a high soil water availability in the shallow horizons during most of the year. However, in more arid savannas of Senegal, Akpo (1993) found only 55 % of the roots in the top 50 cm of soil.

The tree/grass root ratio within fine root samples was determined by $^{13}$C natural abundance measurements since savanna trees and grasses have C3 and C4 photosynthetic pathways respectively. Grasses make up about 90 % of the above-ground herbaceous phytomass (Menaut & César 1979) and consequently more than this proportion is expected for the below-ground compartment since most species are perennial tuft grasses. Thus, a bias due to possible contribution of herbaceous $C_3$ plants is unlikely. Under forest canopies, isotopic fractionation due to the assimilation of $^{13}$C depleted carbon dioxide coming from mineralisation was observed by Medina et al. (1991). However, in Lamto savanna no significant difference between open and canopy grass $\delta^{13}$C was observed (data from Lepage et al. 1993) probably due to the open structure of the canopies. In addition, the grass species sampled to determined the typical grass $\delta^{13}$C, made up the major part of the above-ground biomass and similarly contributed to the total biomass, both under the trees and in the open (Mordelet & Menaut 1995). Consequently, the typical grass $\delta^{13}$C value should not be biased by a strong species effect.

Trees and grasses seem to have slightly different root profiles, the maximum density being in the 0 - 5 cm layer for grass roots and in the 5 - 10 cm layer for tree fine roots; actually, it is probably a bias due to the sampling which randomly included some tuft bases in the 0 - 5 cm layer samples. Thus, a systematic between-tuft sampling would most likely have led to a maximum density in the 5 - 10 cm layer for grasses as well as tree fine roots. For this study, the relevant question was to compare, at the 1-m$^2$ scale in the bulk soil, tree fine root and grass root densities in canopy-covered and open areas. The shallow rooting pattern of tree fine roots is consistent with the vertical distribution of fine roots of four Tanzanian trees (Jonsson et al. 1988) and in the Nylsvley savanna (Scholes & Walker 1993).

It is noteworthy that total root phytomass was higher under tree clumps than in the open situation. This contributes to improved soil conditions beneath tree clumps as reported by Mordelet et al. (1993): lower bulk density, higher soil organic matter content and thereafter higher soil nutrient availability. Conversely, this should not favour very extensive tree root systems since tree roots would not benefit from foraging in the poorer soil outside the area beneath their crown. On the contrary, roots coming from palm trees outside tree clumps proliferate beneath tree clump canopies (Mordelet et al. 1996), because of the higher soil nutrient availability (Lamont 1973). Consequently, this process emphasizes the nutrient patchiness generated by trees in the savanna and leads to different soil conditions for grass roots beneath the tree canopies than in the open. However, grass roots showed the same density profiles under the canopy and in the open. This indicates that rooting patterns were not altered by the different soil nutrient conditions or by competitive interactions. The lower grass-root densities under tree clumps than in the open should only result from limited above-ground photosynthesis due to tree shading (Mordelet 1993a) resulting in lower phytomass production in grasses. Beneath the tree canopy, tree and grass roots were both mainly located in the top 20 cm of the soil. This similar rooting structure means that both vegetation components potentially use the same soil resources. Moreover, beneath the canopy, tree fine root percentages ranged between 62 and 86 %. This means that at each depth tree root density exceeded grass root density, so that tree roots should have a favoured access to soil water both in deep and shallow horizons.

Thus, the Walter (1971) hypothesis of a vertical spatial partitioning between topsoil herbaceous roots and subsoil tree roots is not validated in this humid savanna, as also suggested by Menaut (1983), and Scholes & Walker (1993) in the Nylsvley savanna. Moreover, from a functional point of view, isotopic studies – with $^{18}O$ and $^{2}H$ in soil water and sap – provided evidence that, in the Lamto savanna, both trees and grassses take up shallow soil water (Le Roux et al. 1995). This was shown to happen during both rainy and dry periods.

Fine root phytomass dynamics similarly fluctuated in each soil layer. This indicates that at the monthly time step, the root system behaves as a single compartment. The fine root phytomass variations were similar in the open and canopied situations. This result requires two conditions: (1) all roots were submitted to the same environmental constraints, and (2) tree and grass roots have the same dynamics. It was previously shown that on the same site, during the study year, soil water content dynamics were very close in both open and canopied situations (Mordelet et al. 1993). The $^{13}C$ natural abundance measurements provided evidence that trees and grasses follow approximately the same fluctuations. It does not support the hypothesis of time-partitioning for soil resources between both vegetation components.

Finally, this study about root distribution of trees and grasses, as well as the previous study about water use pattern of trees and grasses (Le Roux et al. 1995) provides no evidence for below-ground partitioning neither spatially, nor temporally. Consequently, different vegetation components can co-occur even without below-ground niche separation, as noticed by Lamont & Bergl (1991) for three co-dominant shrub species. In semi-arid savannas, the limited water availability is the major environmental feature inducing soil resource partitioning (Walter 1971). On the other hand, in humid savannas, the soil water availability is high during most of the year, and during the short dry season plants have evolved particular phenological strategies to face the water stress: above-ground parts of grassses wither and trees are deciduous. This means that the need for water is reduced both for trees and grasses; therefore neither vegetation component has an important tap root system. In humid savannas the major environmental feature driving rooting patterns could be soil nutrient availability (Le Roux et al. 1995). Soil nutrients are indeed mostly distributed in the shallow horizons and since they are a major limiting growth factor, roots of both trees and grasses are concentrated in the upper part of the soil.

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