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Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna

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Abstract Most savanna water balance models assume water partitioning between grasses and shrubs in a two-layer hypothesis, but this hypothesis has not been tested for humid savanna environments. Spatial partitioning of soil water between grasses and shrubs was investigated in a West African humid savanna by comparing the isotopic composition (oxygen-18 and deuterium) of soil water and plant stem water during rainy and dry conditions. Both grass and shrub species acquire most of their water from the top soil layer during both rainy and dry periods. A shift of water uptake pattern towards deeper horizons was observed only at the end of the dry season after shrub defoliation. The mean depth of water uptake, as determined by the isotopic signature of stem water, was consistent with grass and shrub root profiles and with changes in soil water content profiles as surveyed by a neutron probe. This provides evidence for potentially strong competition between shrubs and grasses for soil water in these humid savannas. Limited nutrient availability may explain these competitive interactions. These results enhance our understanding of shrub-grass interactions, and will contribute to models of ecosystem functioning in humid savannas.

Key words Humid savanna · Stable isotopes · Soil water · Root · Competition

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Introduction

Tropical savannas are defined as seasonal ecosystems with a continuous herbaceous component, and a discontinuous woody component (Frost et al. 1986). Fire, grazing, soil water and nutrient availabilities strongly determine the functional characteristics of these ecosystems, and the balance between grass and woody components. Patterns of soil water use by grasses and trees/shrubs are recognized to be a major determinant of their interactions. Walter (1954, 1971) first suggested the two-layer hypothesis of water resource partitioning between these two life-forms in savanna ecosystems. This hypothesis has been used to model functioning of tropical savannas (Walker et al. 1981; Noy-Meir 1982; Walker and Noy-Meir 1982; Eagleson and Segarra 1985; Skarpe 1990). These models take into account two vegetation components (grass and woody layers) and two soil layers having independent water budgets, except for water recharge of the deeper layer through the upper one. Grasses acquire water only from the upper soil layer, where they are the dominant of the two competitors. The woody vegetation has exclusive access to the deeper soil layer, but is competitively inferior to grasses in the upper layer. This implies that grasses may outcompete the woody species for water, but that the woody layer cannot outcompete grass species in this context.

Some field evidence supports this hypothesis. Knoop and Walker (1985) monitored soil moisture in control plots, and in plots where one of the vegetation components was removed, in two southern African savannas. They suggested that the grass component obtained most of its water from the 0–10 cm soil layer in a *Burkea* savanna, and from the 0–30 cm layer in an *Acacia* savanna, while the woody plants used mainly underlying subsoil water down to 130 cm. A similar water resource partitioning between grasses and shrubs was also observed in a Patagonian steppe (Soriano and Sala 1983; Sala et al. 1989), in a savanna in Kenya (Hesla et al. 1985), and in a North American subtropical savanna (Brown and Archer 1990). However, these water-based savanna models con-

sider only dry savannas and were tested only in these environments. Thus, space partitioning or competition for soil water in mesic or humid savannas remains to be tested. Recently, interesting results were obtained by trenching experiments performed in dry and mesic savanna sites in Kenya (Belsky 1994). Variation in herbaceous productivity in plots where tree roots were excluded suggested that savanna trees competed with herbaceous species and reduced their productivity, especially at wetter sites.

The objective of this study was to determine if spatial partitioning of soil water occurs between grass and shrub components in a West African humid savanna. This was achieved by measuring (1) grass and shrub root profiles, (2) variation in soil water content profiles, and (3) natural stable oxygen and hydrogen isotopic abundances of soil water and plant stem water. Since no isotopic fractionation against isotopic forms of hydrogen or oxygen occurs during soil water uptake by roots (Wershaw et al. 1966; Zimmermann et al. 1967; Allison et al. 1983a; White et al. 1985; Dawson and Ehleringer 1991), the relative dependence of plants upon different water sources (pre-existing water of upper or lower soil layers, rain water, and stream or ocean water) can be assessed by comparing the isotope composition of stem water with that of potential water sources (White et al. 1985; Bariac et al. 1987; Flanagan and Ehleringer 1991; Walker and Richarson 1991; Ehleringer and Dawson 1992). This method has been used to assess the major water source for coastal species (Sternberg and Swart 1987), for plants in semi-arid areas (Ehleringer et al. 1991; Flanagan et al. 1992; Donovan and Ehleringer 1994), for temperate or mediterranean trees and shrubs (Dawson and Ehleringer 1991; Valentini et al. 1992) and for woody plants of a North American thorn woodland (Midwood et al. 1993). This methodology offers a useful means to assess from which soil layers water is withdrawn by the two major vegetation groups in savanna environments.

Deuterium and oxygen-18 isotope ratios of stem water and of soil water down to a depth of 2 m were measured in a West African humid savanna during one wet period and two dry periods. Measurements were performed on one perennial grass species and two deciduous shrub species. Two other herbaceous species were occasionally investigated. The major water source for these species was identified during each period. Consistency of these results with the survey of soil water content profiles performed by a neutron probe and with the vertical distribution of grass and shrub roots was investigated. Implications for competition between grass and shrub components in humid savannas are discussed.

Materials and methods

Study site

The Guinea savanna consists of a tall, dense grass layer with scattered trees where annual precipitation exceeds 1000 mm and where the dry season is less than 2 months (Menaut 1983). In central West Africa, Guinea savannas extend north of equatorial forests to 9°N and cover roughly 0.5×10^6 km^2 (White 1986). The study was conducted at the Lamto Reserve (6°13'N and 5°02'W), in a typical Guinea savanna of the Côte d'Ivoire (i.e. an open shrubby savanna with two well-defined vegetation layers). The herbaceous layer consisted mainly of grass species dominated by *Hyparrhenia* sp. and *Andropogon* sp. (Andropogoneae). The shrub layer (2–6 m height) was dominated by *Cussonia barteri* (Araliaceae), *Crossopteryx febrifuga* (Rubiaceae) and *Bridelia ferruginea* (Euphorbiaceae). Shrubs cover 14.7% of the study area. Granites and derived sands have produced tropical ferrugineous soils. The clay content is low, with kaolinite as the major form. Detailed ecological site description may be found in Menaut and César (1979). Temperatures are relatively constant all year long (annual mean 27°C). Annual precipitation is 1210 mm (statistics for 1962 to 1990 from the Lamto Geophysical Station). Well-defined precipitation periods occur: a long rainy season from February to November, usually interrupted by a short dry season in August, and a long dry season generally in December and January. Savanna fires occur each year during the dry season, generally in January and consume much of the grass layer. This study was conducted during a rainy period (May 1992) and two dry periods, one before fire (November 1991) and one after fire (January 1992).

Stem and soil water isotopic compositions

During each study period, soil was sampled with an auger, and grass crown (i.e. junction between roots and shoots) or shrub stem samples were cut from the plants in the field. Only sapwood was sampled in shrub trunks to avoid any influence of isotopic ratio of heartwood which could be significantly different (White et al. 1985). Grass crowns sampled in this study were not photosynthetic organs and were protected from transpiration loss by several layers of dry sheaths. All the samples were placed immediately in glass vials which were sealed with rubber stoppers. Samples were frozen until water was extracted by cryogenic vacuum distillation (–196°C). The method of Epstein and Mayeda (1953) was used to determine the oxygen isotope composition of water. This was carried out by equilibration of water with CO_2 and measurement of the isotopic ratio of CO_2 by isotope ratio mass spectrometry. The equilibrated CO_2 has a $^{18}O/^{16}O$ ratio which is related to that of the water through a fractionation factor (α = 1.0412 at 25°C; Brenninkmeijer 1983). Hydrogen isotope analyses of water were carried out on hydrogen gas obtained by quantitative reduction of water in a quartz oven filled with metallic uranium turnings at 800°C (UO_2; Bigeleisen et al. 1952). All hydrogen produced by this reaction was collected on metallic uranium UH_3 (Friedman and Hardcastle 1970) at 70°C. The uranium was heated to 650°C to release hydrogen for mass spectrometric analyses. Results were expressed in "δ" units (Eq. 1), by reference to the international standard "V-SMOW" for the oxygen isotope, and to the V-SMOW -SLAP scale for the hydrogen isotope (Gonfiantini 1978):

$$\delta = (R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}} \quad (1)$$

where $R = {}^{18}O/{}^{16}O$ or $R = {}^{2}H/{}^{1}H$. The unit "δ" is expressed in parts per 1000.

The withdrawal of soil water by grass and shrub species during the early dry season was assessed on 9 November 1991. Crown samples were collected between 0600 hours and 1900 hours at 30 min intervals for the grass *Hyparrhenia diplandra* and 1 h intervals for the shrubs *Cussonia barteri* and *Crossopteryx febrifuga*. All shrub samples were collected from the same clump (a group of several individuals dominated by *Cussonia barteri* and *Crossopteryx febrifuga* individuals), and herbaceous species were sampled 3 m beyond the shrub clump canopy. Soil was sampled with three replicates just outside the clump at 10 cm intervals down to 200 cm. No strong differences between the isotopic composition of soil water under or just outside the shrub clump due to soil evaporation were expected because the grass canopy was 1.7 m high and closed at this time.

The major soil water source for regrowing *H. diplandra* during the long dry season was investigated on 22 January 1992, 2 weeks after a fire (7 January 1992). Crown samples of this grass were collected at 1 h intervals between 0640 hours and 1640 hours. Shrubs were leafless at this time. Soil was sampled at 5 cm intervals down to 20 cm, and 10 cm intervals down to 200 cm.

An intensive sampling campaign was conducted during the rainy season on 04 May 1992. Crown samples were collected between 0600 hours and 1900 hours at 30 min intervals for the grass *H. diplandra* and 1 h intervals for the shrubs *Cussonia barteri* and *Crossopteryx febrifuga*. Two other grass species (*Andropogon schirensis* and *Imperata cylindrica*) were occasionally investigated. All shrub samples were collected from the clump investigated in November, and all herbaceous species were sampled 3 m beyond the shrub clump canopy. The soil under the clump and the soil 3 m apart were sampled at 10 cm intervals up to 140 cm and 200 cm, respectively. In order to investigate the heterogeneity induced by the open grass canopy outside the clump, soil was sampled at 1 cm intervals down to 5 cm and 2.5 cm intervals down to 10 cm under a grass tussock and in a bare-soil area.

Soil water content profiles

Along a 1-year-period, and particularly a few days before and after the date when sampling for isotope analysis was performed, soil moisture was measured down to 170 cm by a neutron probe (model Solo 25S, Nardeux Humisol) on 7 access tubes in open areas, and on 3 access tubes located under three different shrub clumps. In open areas, neutron probe measurements were supplemented with gravimetric determinations for the 0–5 and 5–10 cm layers because soil moisture cannot easily be measured near the soil surface by the neutron probe, even using a PVC reflector. The neutron probe was calibrated gravimetrically during the installation of each tube during the rainy season in June 1991, and later during a dry period. Dry bulk density of each soil layer was measured on samples collected by steel cylinders to derive volumetric soil moisture contents. All measurement series were normalized by the neutron counts obtained in a 200-l water barrel before and after each series.

Root profiles

In open areas, roots were collected at 10 cm intervals down to 180 cm soil depth with a 4.4 cm diameter auger. Sixteen cores (four randomly selected in four different open areas) provided a mean profile. Root profiles were also determined under the shrub clump investigated for deuterium and oxygen-18 analysis. Twelve cores randomly selected in this clump provided a mean profile. All the root profiles were determined during the rainy season in July. However, Mordelet (1993) showed that seasonal root dynamics is similar in the different soil layers. Thus, the rooting pattern in Lamto savanna can be assessed by the profile obtained in July. Roots were separated from the soil by means of wet sieving (500 µm) and flotation. The samples were sorted into two size classes (large roots >2 mm diameter, and fine roots <2 mm diameter). Roots were dried to constant weight at 70°C and weighed. The relative proportion of shrub and grass roots in each fine-root sample was assessed by $\delta^{13}C$ measurements. Each sample contained a mixture of C_3 and C_4 plants having a distinct isotopic signature. The isotopic ratio $^{13}C/^{12}C$ is higher for C_4 plants than for C_3 plants (Smith and Epstein 1971). In the Lamto savanna, grasses have the C_4 photosynthetic pathway whereas shrubs have the C_3 photosynthetic pathway. Lepage et al. (1993) showed that in Lamto, fine roots exhibit $\delta^{13}C$ values of –12.6‰ and –28.3‰ for grasses and shrubs, respectively, with negligible interspecific variation. Consequently, the $\delta^{13}C$ measurement of any mixed root sample can indicate accurately its shrub/grass root ratio. The fine root samples were crumbled to 80 µm, carefully homogenized and combusted in an elemental analyser (CHN Carlo Erba NA 1500). Evolved gases were purified cryogenically, separated in a trapping system, and finally introduced in an isotopic mass spectrometer equipped with dual inlet and triple ionic collection systems fitted for rapid switching between reference and samples (Fisons, SIRA 10). ^{13}C abundance was expressed versus Pee Dee Behmnitella. This method was proposed to assess below-ground competition between C_3 and C_4 plants in temperate regions (e.g. Ludlow et al. 1976; Svejcar and Boutton 1985) and was used in a previous study in Lamto (Mordelet 1993).

Results

Shrub and grass rooting patterns

In this humid savanna, both grasses and shrubs were shallow rooted (Fig. 1). Maximum grass root density occurred in the 0–10 cm soil layer in open areas and under the shrub clump. Shrub root density was very low in open areas (more than 20 m beyond any shrub canopy) and was at a maximum in the 0–20 cm soil layer under the shrub clump. Both under the shrub clump and in open areas, plants essentially explored the upper soil layer down to 60 cm, and had limited access to the deeper soil layers.

Isotope analysis

Figures 2 and 3 show the depth profiles of soil moisture and $\delta^{18}O$ of soil water on 4 May 1992. The top soil layers were relatively dry and the profile of $\delta^{18}O$ of soil water exhibited a typical shape for a soil under drying conditions (Zimmermann et al. 1967; Allison et al. 1983b). Soil moisture was lower under the shrub clump than under the grass canopy 3 m away (Fig. 2). $\delta^{18}O$ values were slightly higher under the open grass canopy up to 30 cm (Fig. 3), perhaps due to higher soil evaporation than under the shrub clump. However, isotopic composition of soil water was approximately constant and not significantly different between sites below 30 cm (Fig. 3). In-

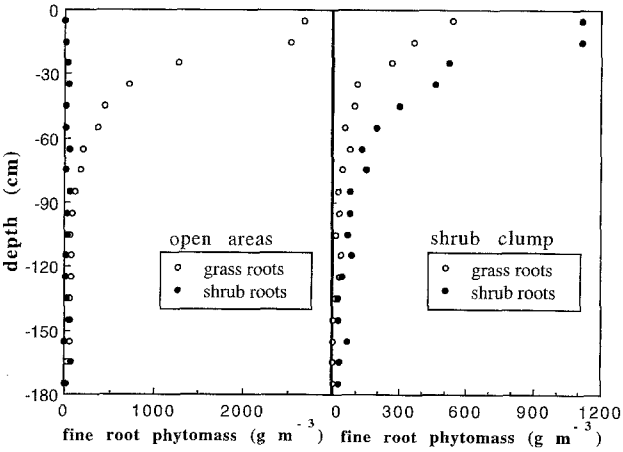

Fig. 1 Grass and shrub fine-root density profiles in open areas (more than 20 m beyond any shrub canopy) and under the shrub clump investigated for isotope analysis, calculated from $\delta^{13}C$ measurements

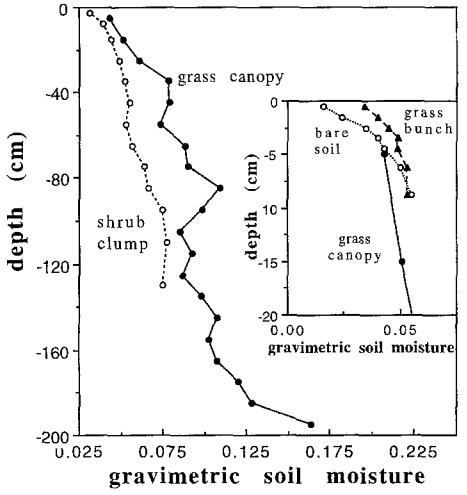

Fig. 2 Gravimetric water content in the soil profiles under the shrub clump and under the grass canopy (3 m apart) on 4 May 1992. The inset shows more detailed profiles performed close to the grass canopy profile under a grass tussock and in a bare soil area

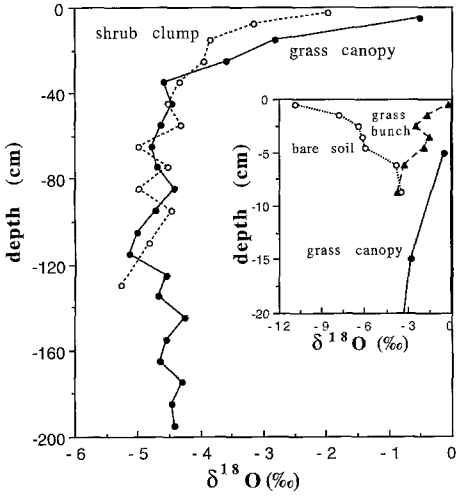

Fig. 3 Oxygen-18 composition (‰) of soil water in the profiles under the shrub clump and under the grass canopy (3 m apart) on 4 May 1992. The inset shows more detailed profiles performed close to the grass canopy profile under a grass tussock and in a bare soil area

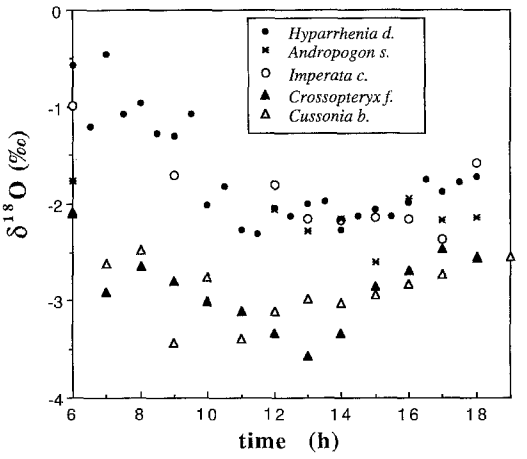

Fig. 4 Oxygen-18 composition (‰) of sap water for the grasses *Hyparrhenia diplandra*, *Andropogon schirensis*, and *Imperata cylindrica*, and the shrubs *Cussonia barteri* and *Crossopteryx febrifuga* during the diurnal cycle on 4 May 1992

sets in Figs. 2 and 3 show that the open grass canopy induced important small-scale spatial variability. Soil moisture and $\delta^{18}O$ values were higher under the grass tussock than under bare soil. In the last case, a dry surface layer was apparent up to more than 5 cm. It probably corresponded to a vapour transport layer (Allison et al. 1983b; Barnes and Allison 1983).

$\delta^{18}O$ of stem water (Fig. 4) was slightly higher for the three grass species than for the two shrub species. Neither the three grass species nor the two shrub species could be discriminated. For all species, the isotopic composition of stem water exhibited a clear diurnal trend with a decrease during the morning, a minimum at midday, and a progressive increase in the afternoon. This could be explained by either (1) a slight shift of mean depth of water uptake by roots in relation to the transpiration rate evolution during the diurnal cycle (Bariac et al. 1994), (2) equilibration of leaf water (which becomes enriched in ^{18}O and ^{2}H during the day) with stem water during the night, or (3) hydraulic lift of water by roots (Caldwell and Richards 1989). However, comparison of stem water and soil water $\delta^{18}O$ values clearly showed that water uptake from the deep soil layers by both grass and shrub species was quantitatively negligible.

The spatial variability of the isotopic composition of the surface soil water must be taken into account to infer the mean depth (integrated signal) of water uptake by each vegetation group. The grasses withdrew water from the uppermost soil layer (mean depth probably between 0 and 5 cm for *H. diplandra*) in the early morning when transpiration flow was very low. The mean depth of water uptake was between 5 and 10 cm near midday. The systematic difference in $\delta^{18}O$ of stem water between the grass and shrub species (Fig. 4) could be explained by the difference of the isotopic composition of surface soil water under and just outside the shrub clump canopy (Fig. 3). The mean depth of water uptake by shrubs was thus not significantly different from that observed for the grass species.

During the November dry period, the isotopic composition of stem water for grasses or shrubs exhibited a diurnal trend similar to that observed during the rainy season (not shown). As observed in May, the ranges of isotopic composition of stem water exhibited by grasses and shrubs overlapped slightly. Water uptake by grass species was confined to the upper soil layer, with a mean depth of ca. 20 cm (Fig. 5). However, the isotopic composition of soil water was not constant with depth in the subsoil and $\delta^{18}O$ values of shrub stem water could be explained either by water withdrawal from a 30 cm mean depth or from the deeper soil layer (below 150 cm). Shrub rooting

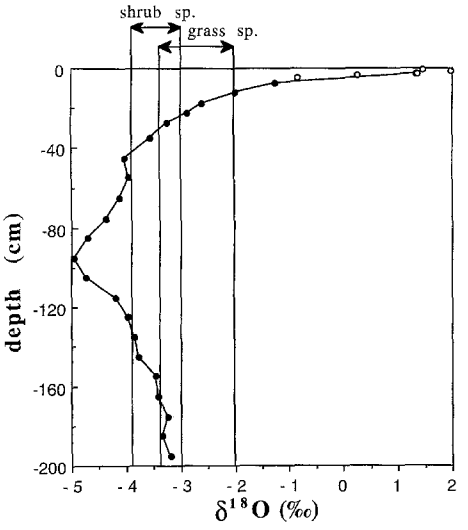

Fig. 5 Oxygen-18 composition (‰) of water in the soil profile on 9 November 1991. The diurnal range of the isotopic composition of the sap water observed for the grass *Hyparrhenia diplandra* and the shrubs *Cussonia barteri* and *Crossopteryx febrifuga* are indicated

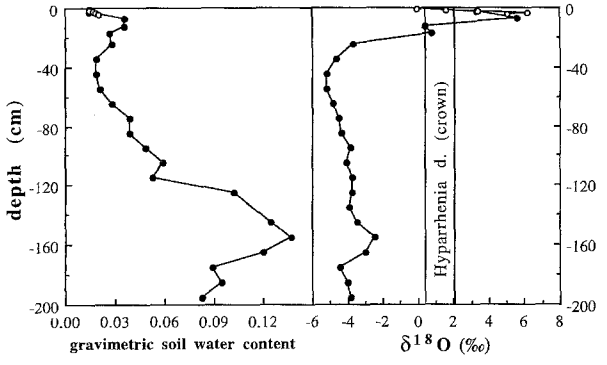

Fig. 6 Gravimetric water content and oxygen-18 composition (‰) of water in the soil profile on 22 January 1992. The diurnal range of the isotopic composition of the sap water observed for the grass *Hyparrhenia diplandra* is indicated

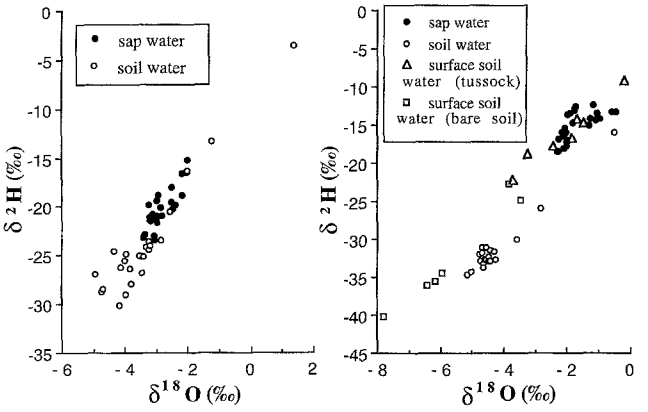

Fig. 7 Soil and *Hyparrhenia diplandra* sap water isotopic compositions during the November 1991 (*left*) and May 1992 (*right*) experiments presented on δ^2H-$\delta^{18}O$ plots

patterns and variations of soil water content profiles observed during the year under shrub clumps suggested that the second hypothesis is highly unrealistic.

During the regrowth period in dry conditions on January 22, the top soil layer was very dry and the profile of $\delta^{18}O$ of soil water exhibited a typical shape, with a vapour transport layer (Allison et al. 1983b; Barnes and Allison 1983) in the first 4–5 cm and a relatively constant isotopic composition below 30 cm (Fig. 6). Because it can be assumed that no water uptake could occur in the dry surface layer, the major water uptake by the regrowing grasses was located at a mean depth of 10–20 cm which corresponded to a relatively wet soil layer (Fig. 6).

Figure 7 presents the isotopic compositions of soil water and grass crown water in a δ^2H-$\delta^{18}O$ plot in May and November. The similarity of the estimation of the mean depth of water uptake from the two isotopes in November (and January, not shown) provides some confidence in the results. In May, discrepancies between the isotopic signals of soil water and surface soil water in bare soil areas or under grass tussocks were observed. These discrepancies are due to the spatial and temporal variability of water components such as rainfall, infiltration, and evapotranspiration. In many cases, data from the literature provide examples of large variations in the intrastorm rainfall isotopic composition (90‰ in δ^2H, McDonnell et al. 1990; 15‰ in $\delta^{18}O$, Kendall 1993). Isotopic enrichment of rain water may also occur because of interception by the canopy and re-evaporation of precipitation on the foliage (Saxena 1986). Site-specific differences in canopy density (from bare soil to soil under grass tussocks), soil hydrodynamic properties and micro-climatic conditions may also occur and can substantially affect the isotopic composition of the residual surface soil water (Melayah 1994). This variability may complicate the interpretation of the isotopic signal measured at the crown level in May. However, the comparison of deuterium composition of soil and crown water in May (Fig. 7) supported the results deduced from analysis of oxygen-18 composition, that is, a water withdrawal by grasses from the uppermost soil layer.

Changes in soil water content

Soil water content in the 0–60 cm soil layer decreased from 69.5 to 55.8 mm and from 62 to 46.6 mm between 28 April and 5 May 1992 in open areas and under shrub clumps, respectively. During this period, variations in the soil moisture profiles observed in open areas or under shrub clumps essentially occurred in the upper 60 cm soil layer (Fig. 8). Maximum soil moisture variations occurred in the 20–40 cm soil layer under shrub clumps, and in the 10–40 cm layer in open areas. However, occurrence of small rainfall events (1.5 and 3 mm) probably reduced the depletion of the top soil moisture. Thus, variations observed during this period were qualitatively consistent with water uptake essentially occurring in the

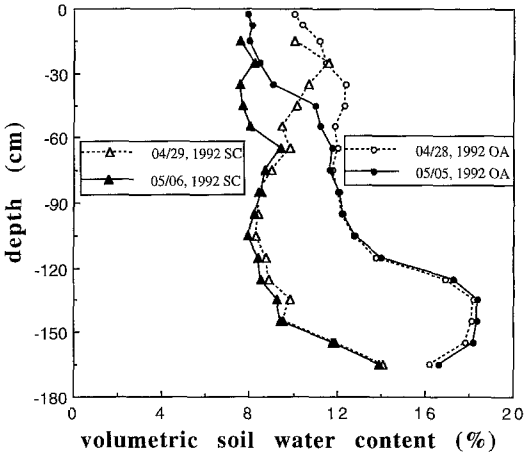

Fig. 8 Variation in the volumetric soil water content in open areas (*OA*) and under shrub clumps (*SC*) during a 7-day-period in May 1992. Rainfall events of 1.5 and 3 mm occurred during this period

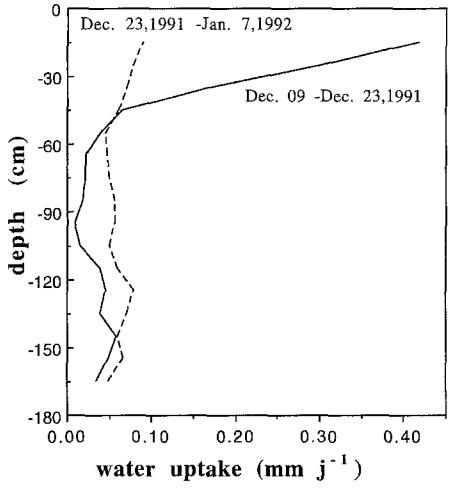

Fig. 9 Profile of soil water uptake by roots in open areas during two drying stages at the end of the dry season in December 1991. Corresponding soil water content was 61 mm, 41.6 mm and 33.9 mm in the 0–60 cm soil layer on 9 December, 23 December and 7 January, respectively

top soil layer as determined from isotope analysis, in the absence of data about water flow from one soil layer to another. The 4–21 November 1991 period corresponded to the begining of the long dry season. Soil water content in the 0–60 cm soil layer decreased from 60 to 44.3 mm in open areas. Grass leaf water potential measurements reached –2.0 MPa on 9 November, which was below potential at incipient plasmolysis (Le Roux 1995). The variations of soil moisture with depth observed at this time in open areas (not shown) were close to those observed in May 1992 and occurred essentially in the upper 60 cm soil layer. No measurements were made under shrub clumps at this time. In January 1992, the regrowth of grasses was weak because of dry conditions. Between 20 and 29 January 1992, the variations in the soil moisture along the entire soil profile were not significant in open areas (from 156.9 to 155.7 mm in the 0–170 cm layer) and very low under shrub clumps (from 125.3 to 121.4 mm). This is explained by the very low grass leaf area index in open areas (ca. 0.1) and because shrubs were leafless at this time.

Variations in the soil moisture profiles could only give qualitative information about water uptake by plants in November 1991 and May 1992 because redistribution of water from one layer to another, and percolation below 170 cm, were probably significant due to the relatively high water content. In January, variation in soil moisture was of the order of the measurement accuracy and thus did not allow any calculation of water withdrawal by plants. However, direct water uptake was assessed from neutron probe measurements during the end of the dry season between 9 December 1991 and 7 January 1992. At this time, shrubs were almost leafless and it is assumed that no appreciable water uptake from this lifeform occurred. Furthermore, soil moisture was low during this period (61, 42 and 34 mm in the upper 60 cm soil layer on 9 December, 23 December and 7 January, respectively) and no precipitation occurred. Hence, the redistribution of water from one layer to another and percolation were assumed to be negligible. Estimated water uptake was maximum in the upper soil layer during the first stage of the drying cycle (Fig. 9) and occurred relatively equally at low rates along the whole profile during the second stage. At this time, grasses exhibited very strong water stress, and leaf water potential reached their annual minimum values (–3.0 MPa) on 6 January (Le Roux 1995).

Discussion

Comparison of stem water and soil water $\delta^{18}O$ and $\delta^{2}H$ values in conjunction with measurements of soil water content showed that water uptake by both grass and shrub species was consistently from the top soil layer in this humid savanna. Similar patterns of soil water uptake by these two functional groups were consistent with their rooting patterns (Fig. 1). Both grass and shrub components were shallow rooted and exhibited maximum root densities in the 0–10 cm and 0–20 cm soil layers, respectively. Similar profiles were observed in a shrubby savanna at Lamto by Mordelet (1993). Because roots of the different shrub species cannot be distinguished, only a composite shrub root profile was available. However, excavation studies in this savanna indicated that *Cussonia barteri* and *Crossopteryx febrifuga* have the major proportion of their roots in the upper 60 cm soil layer, with maximum root density at ca. 20 cm (Monnier 1968). The mean depths of water withdrawal by grasses (ca. 10 to 20 cm) and shrubs (ca. 10 to 30 cm) were thus consistent with their respective rooting patterns.

Good correlation between water uptake rate and rooting density is generally observed at high soil water content (e.g. Taylor and Klepper 1975; Nnyamah and Black 1977; Rambal 1984). However, the amount of water

withdrawn from different soil layers depends on both the root density and the water availability in each layer. This probably explains the variation in soil water uptake pattern with depth observed at the end of the dry season in December (Fig. 9). Several authors have reported a similar gradual downward shift of the location of water uptake by roots as the soil dries for tree species (Levin et al. 1972; Nnyamah and Black 1977; Rambal 1984; Garnier et al. 1986), annual crops (Arya et al. 1975; Taylor and Klepper 1975), and plants in semi-arid environments (Sala et al. 1981). However, our results did not reveal any spatial partitioning between shrub and grass species at this time because shrubs were leafless in December and could not compete efficiently with grasses for the soil water resource.

Shrub root density was higher than grass root density under shrub clumps, while the reverse was true in open areas. Using $\delta^{13}C$ measurements to discriminate C_3 and C_4 plants, Mordelet (1993) found that grass and shrub root densities were comparable just beyond shrub clump canopies. In our study, there was no overlap of the grass and shrub canopies, but the root systems of these two components were intermingled thoroughly. The similarity of the mean depth of soil water uptake by shrub and grass species in zones where there were absorbing roots of both vegetation groups provides evidence of a strong competitive exploitation of this resource. These results show that the two-layer hypothesis of Walter (1954) cannot be applied to describe competitive interactions in West African moist savannas, even if it correctly describes these interactions in dry savanna environments. This conclusion is consistent with trenching experiments performed in dry and mesic savanna sites in Kenya (Belsky 1994) suggesting that savanna trees competed with herbaceous species more intensively at wetter sites.

The major constraints which could explain the common strategy of soil water withdrawal from the upper soil layer by both grass and shrub species in humid savannas must be investigated. A direct constraint is the pattern of water availability. Ehleringer et al. (1991) showed that herbaceous and woody perennials were dependent on the same water source in relatively deep soil layers during drought periods in an arid area. On the contrary, a strategy of water uptake in the top soil layer would be favoured where water occurred mainly in this horizon. Small precipitation events can account for a relatively large proportion of the total precipitation at a given location, and could have ecological importance as shown in a Patagonian steppe (Sala and Lauenroth 1982; Sala et al. 1992). These authors showed that events of less than 10 mm accounted for 41% of the total annual rainfall and 83% of the number of events at their study site. This leads to a shallow distribution of soil water which could favour plant species able to use this resource (Sala et al. 1992).

In Lamto, relatively small rainfalls account for a smaller part of total precipitation. Events of less than 10 mm account only for 20% of the total annual rainfall and 69% of the number of events. Furthermore, interception by canopy probably strongly reduces their relative contribution. High rainfall events are not rare and allow significant recharge of deep soil layers. Soil water content in these layers exhibited a weak seasonal pattern relative to the upper 60 cm soil layer (Le Roux 1995). Thus, precipitation and soil water availability patterns cannot explain the common strategy of soil water withdrawal from the upper soil layer by both grass and shrub species in this humid savanna.

However, nutrient availability is another strongly limiting factor for primary production in these environments (Medina et al. 1978; Le Roux and Mordelet 1995). In humid savannas, water is less limiting than in drier savannas and it can thus be assumed that nutrient availability becomes a strong constraint which influences both structure and function. Mordelet et al. (1993) showed that soil fertility and microbial activity were increased in the upper soil layer under shrub clumps in Lamto. This could explain why woody root extension is limited to the upper soil layer under or near shrub crowns (Mordelet 1993) where soil fertility is high, and where strong competition between shrub and grass roots may thus occur. The difference of tree/grass competitive interactions observed in dry and mesic savanna sites recently led Belsky (1994) to a similar hypothesis.

Important ecological implications arise from these results. One of the most fundamental hypothesis of savanna function has been spatial partitioning of water resource between shallow rooted perennial grasses and deep rooted woody species. This study shows that niche overlap is significant in West African humid savannas where shrubs and bunch grasses both acquired water from the upper soil layer. It is widely recognized that the grass layer may outcompete the woody species for water in savannas, thereby restricting growth and/or abundance of woody species. This study shows that the deciduous woody species acquire most of their water from the top soil in West African humid savannas and can thus potentially outcompete grass species. In fact, rates of water extraction can strongly influence the competitive ability of plants as shown in arid areas (Eissenstat and Caldwell 1988). Thus, more information about the relative soil water uptake rates (or the transpiration rates) of grass and shrub species in these environments are necessary to assess the actual competitive effects of each component on the other. Furthermore, water is not the only resource determining the competitive balance between grasses and shrubs. It was assumed that limiting nutrient availability could be a more efficient constraint than water in humid savanna environments. Thus, studies of the differential competitiveness for other limiting below-ground resources in savanna environments, such as nitrogen and phosphorus (Caldwell et al. 1985), are warranted. This information is necessary to model the functioning of these ecosystems, to understand the coexistence of shrub and grass components, and to predict the response of these components within the savanna plant community to any change in precipitation patterns as anticipated by Ehleringer et al. (1991) for desert plants.

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