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Seasonal variations in soil, grass and shrub water status in a West African humid savanna

Received: 11 May 1997 / Accepted: 30 September 1997

Abstract Despite their overwhelming influence on (1) variations in the physiological activity of vegetation (2) plant phenology, and (3) potential competitive interactions between coexisting species, comprehensive information on water relations and soil water uptake patterns is still lacking for grasses and shrubs in African humid savannas. Over 2 years, seasonal variations in plant water status were measured with the pressure bomb technique for two deciduous shrub species (*Cussonia barteri* and *Crossopteryx febrifuga*) and a perennial grass species (*Hyparrhenia diplandra*) in a humid savanna. Concurrently, soil moisture was surveyed with the neutron probe technique in grassy areas and under shrub clumps. Absence of transpiration at dawn was assessed by surveys of the leaf water isotopic signal, and plant water relations were characterized during rainy and dry periods with the pressure-volume curve technique. The seasonal changes in predawn and minimum shoot water potentials were pronounced for the grass species and the shrub *C. febrifuga*, but weak for the shrub *C. barteri*. Relationships between plant and soil water status showed that both the grass species and the shrub *C. febrifuga* did not maintain high water potentials when soil moisture in the upper soil layers decreased. In contrast, the shrub *C. barteri* exhibited a predawn water potential around -0.5 MPa when the 0 to 60-cm soil layer was at the permanent wilting point. During the early dry season, leaf dehydration was observed for *C. febrifuga*, but not for *C. barteri*. We conclude that the grass *H. diplandra* and the shrub *C. febrifuga* had very poor

and limited access to deep soil layers (below 60 cm), respectively while the shrub *C. barteri* was able to access this water resource. The relatively low osmotic potential and tissue elasticity measured for *C. febrifuga* as compared to *C. barteri* were consistent with the use of water from upper soil layers by this species, since these characteristics could help water withdrawal and promote turgor maintenance at lower shoot water potentials. Different water uptake patterns could explain the contrasted leaf shedding patterns reported for the two shrub species. These results emphasize that the water economy of deciduous shrub species of African humid savannas can differ significantly and that both grasses and some shrub species acquire water from the upper soil layers even during dry spells. These findings will aid understanding of interspecific competition and modelling ecosystem function in this kind of humid savanna.

Key words Guinea savanna · Competition · Water relations · Soil moisture · Leaf shedding pattern

Introduction

Savannas are defined as tropical seasonal ecosystems with continuous herbaceous cover and a discontinuous cover of trees or shrubs (Frost et al. 1986). These ecosystems generally experience strongly contrasting climatic conditions within a year. The coexistence and close interactions of the herbaceous and woody layers makes savannas unique. Along with fire regime, grazing intensity, and nutrient availability, soil water availability is recognized as a key factor affecting ecosystem function and balance between grass and woody species in tropical (Walker and Noy-Meir 1982; Eagleson and Segarra 1985; Goldstein and Sarmiento 1987) and subtropical (Brown and Archer 1990) savannas. Thus, the characteristics of soil water uptake by the different grass and tree species encountered in a given savanna ecosystem are of paramount importance to understanding potential competitive interactions between (and the actual coex-

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istence of) these life forms (Polley et al. 1997; Scholes and Archer, 1997). Moreover, the seasonality of tree water status is a major determinant of their phenology in tropical environments (e.g., Borchert 1994).

Generally, three major life forms in humid savanna ecosystems are identified as far as soil water use and seasonality of plant water status are concerned: perennial grasses, evergreen trees, and deciduous trees (e.g., Sobrado 1986; Goldstein and Sarmiento 1987). Perennial grasses grow during the rainy season and dry out during the dry season since they extract water essentially from the upper soil layers. In contrast, evergreen savanna trees have deep and extensive root systems and use water from deep soil layers. Deciduous trees are assumed to have access predominantly to upper soil layers. Many studies largely support this view. For instance, in neotropical humid savannas, both native and introduced African grasses exhibit a strong seasonality of leaf water potentials and transpiration or photosynthetic rates (Goldstein and Sarmiento 1987; Baruch and Fernandez 1993). Concurrently, evergreen tree species generally maintain relatively high shoot water potentials and relatively high transpiration and photosynthetic rates during the dry season (Medina 1967; Sarmiento et al. 1985; Goldstein et al. 1986; Goldstein and Sarmiento 1987; Medina and Francisco 1994; Sobrado 1996). This suggests a marked spatial partitioning of the soil water resource between shallow rooted grasses and deep-rooted evergreen trees which probably use groundwater (Vareschi 1960; Goldstein and Sarmiento 1987). In contrast, deciduous tree species encountered in South America exhibit marked seasonal variations of relative leaf water content and shoot water potential (Sobrado 1986; Medina and Francisco 1994). These deciduous species are shallow rooted and thus run out of water as soon as the water in the upper soil layers is depleted (Sobrado and Cuenca 1979). Compared to deciduous species, the relatively low osmotic potential at full turgor and reduced water transport efficiency leading to a reduced occurrence of embolism may be key features which allow evergreen species to maintain leaf turgor during the dry season (Sobrado 1986, 1993). These studies allow a useful classification of water economy for humid savanna shrub species based on their phenological strategies. However, the term 'deciduous shrubs' only refers to phenological aspects and can encompass different strategies of soil water uptake and different types of water relations. Furthermore, results reported for humid savanna deciduous shrub species were only obtained in South American ecosystems, and generally in dry forests since most tree species are evergreen in neotropical savannas. Comprehensive information on the seasonal variations in shrub water status and patterns of soil water uptake is still lacking for shrubs of African humid savannas, which are mainly deciduous.

In a previous study (Le Roux et al. 1995), isotopic signals of soil water and plant stem water and variations of soil moisture profile were used to assess patterns of water uptake by two shrub and a grass species in a West

African humid savanna. Only deciduous shrub species were present in this savanna. Both shrubs and grasses were found to acquire most of their water from the top soil layer during the rainy season. During the dry season, stem water isotopic signals showed that grasses still used water from upper soil layers. A shift in water uptake pattern toward deeper horizons was only observed at the end of the dry season when grass transpiration rates were low. However, it was noted that isotopic results obtained for the shrub species during the dry season were ambiguous. Due to the vertical variations in the isotopic signal of soil water, oxygen-18 and deuterium values of shrub stem water could be explained either by water withdrawal from a mean depth of 30 cm or from the deeper soil layers (below 150 cm). Variations in soil water content profiles under shrub clumps suggested that the first hypothesis was more realistic. Such water uptake patterns were consistent with root profiles since both shrubs and grasses were shallow rooted (Le Roux et al. 1995; Mordelet et al. 1997). However, variations in soil water content profiles under shrub clumps integrate water uptake patterns of different species. Thus, significant differences in soil water economy among deciduous shrub species in this humid savanna cannot be excluded. Information on patterns of water use by grass and shrub species is needed since these patterns influence plant water status and ensuing physiological activity and phenology.

The objectives of this work were (1) to analyze the seasonal changes of water status and water relations of grass and shrub species previously studied by Le Roux et al. (1995) at the same West African humid savanna site, and (2) to determine if all these species actually extract most of their water from the upper soil layers (0–60 cm). Plant water relations were assessed during rainy and dry periods by the pressure-volume curve technique for the two deciduous shrub species *Cussonia barteri* and *Crossopteryx febrifuga* and the grass species *Hyparrhenia diplandra*. Seasonal variations in plant water status were measured by the pressure bomb technique for these species over two annual cycles. Soil moisture was surveyed concurrently by the neutron probe technique in open (i.e., grassy) areas and under shrub clumps. Relationships between plant and soil water status were analyzed.

Material and methods

Study site

The study was carried out at the Lamto Réserve (6°13' N, 5°02' W), in a typical Guinea savanna of the Côte d'Ivoire. The Guinea savanna domain is defined as a zone of dense and high grass with scattered isolated trees or tree clumps, where the annual precipitation exceeds 1,000 mm and where the dry season lasts less than 2 months. Annual precipitation measured at the Lamto Station averages 1,200 mm (Fig. 1). 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 in December and January. Temperatures (annual mean 27°C) are

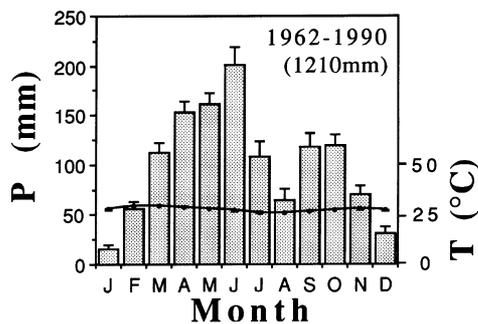


Fig. 1 Seasonal variations in monthly precipitation P (columns) and monthly mean temperature T (line) for the 1962–1990 period at Lamto. Bars are standard errors

quite constant through the year (Fig. 1). Savanna fires occur each year during the dry season, generally in January, and destroy the grass layer. Grass species regrow from February to July, flower at the end of the rainy season (September to November) and dry out during the long dry season. Leaf fall occurs during the dry season for deciduous shrub species.

The study took place in an open shrubby savanna from January 1991 to December 1992. Granites and derived sands have produced a tropical ferruginous soil, with a low clay content (e.g., Abbadie et al. 1992). The herbaceous layer consisted mainly of C_4 bunch grass species dominated by *Hyparrhenia* spp. and *Andropogon* spp. *H. diplandra* (Hack.) Stapf. was the dominant grass on the study site. The woody layer (height < 6 m) consisted of deciduous shrubs dominated by *C. barteri*, *C. febrifuga* and *Bridelia ferruginea*. This layer covered 15% of the study site area when fully developed. Although isolated trees were encountered, most trees were gathered into clumps. Detailed ecological site description may be found in Menaut and César (1979). Annual precipitations in 1991 (1,180 mm) and 1992 (990 mm) were close to and lower than the long-term mean, respectively.

Methods

Climatic data

Measurements of photosynthetic photon flux density (PPFD; Skye Instruments SKP215 quantum sensor at 2 m height in an open area) and air temperature and humidity (Vaisala HMP 35A sensor at 2 m in a climatic screen) were obtained at the study site by an automatic station controlled by a data logger (Campbell CR10). Sample measurements at 30-s intervals were used to provide 20-min average values. Precipitation was measured at the site with a standard rain collector.

Soil water content

From October 1991 to October 1992, soil moisture was surveyed using a neutron probe (Solo 25S, Nardeux Humisol, France) with seven access tubes in open areas, and with three access tubes located under three different shrub clumps. In open areas, soil moisture was measured at 10-cm intervals down to 170 cm while most of the measurements under shrub clumps were made down to 60 cm only. In open areas, neutron probe measurements were supplemented with gravimetric determinations for the 0- to 5-cm and 5- to 10-cm layers. Following the results reported by Mordelet et al. (1993) and preliminary results obtained from the study site, the water content of the 0- to 10-cm soil layer under shrub clumps was assumed to be equal to the water content measured in open areas. The methodology and calibration procedure used was described in Le Roux et al. (1995). In addition, soil moisture in the 0- to 60-cm layer was measured by the gravimetric method with five replicates from March 1991 to September 1991 in open areas.

For each 15-cm soil layer and down to 60 cm, water content at field capacity (W_{fc}) was measured with four replicates. Undisturbed soil cores were collected in the field and slowly saturated with water from the bottom. Drained weight was measured by covering the top of each core with a plastic sheet (to prevent evaporation) and allowing the core to drain for a few hours. For the same soil layers, water content at wilting point (W_{wp}) was measured with four replicates by equilibration of a soil sample with an ionic solution (saturated with ammonium oxalate, i.e., potential of 1.6 MPa). All the soil samples were oven-dried to constant weight at 105°C. W_{fc} and W_{wp} were also deduced from neutron probe surveys, assuming they were equal to maximum and minimum observed water contents, respectively.

Leaf or twig water status and water relations

During the 1991 and 1992 vegetation cycles, the water status of the perennial grass *H. diplandra* and of the two deciduous shrubs *C. barteri* and *C. febrifuga* was measured generally once a month, in clear-sky conditions when possible. At dawn, and then at 2-h intervals, shoot water potential was measured with the pressure chamber technique (Scholander et al. 1965; Ritchie and Hinckley 1975) on four to five randomly selected individuals per species. More intensive measurements were performed during a diurnal cycle in the rainy season (4 May 1992) and during the early dry season (9 November 1991). Shrubs were selected in shrub clumps on the test site while grass tufts were chosen in open areas (i.e., more than 10 m from shrub clumps). Since a stratification of leaf water potential occurs along grass stems (Le Roux and Mordelet 1995), water potential was measured only on the youngest fully expanded grass leaves. Similarly, only mature twigs were used for the shrub species. Because vertical gradients of water potential (Hellkvist et al. 1974) and exposure effects (Klepper 1968) are expected for woody species, the twigs were taken from similarly exposed branches at 2 m height between 1 and 2 m from the trunk. To test if results obtained for *H. diplandra* were representative of the grass layer, paired measurements of leaf water potential for *H. diplandra* and the other major grass species at the study site (*Andropogon schirensis*) were performed throughout a diurnal cycle during the rainy season. Paired measurements were also performed around midday during the dry season.

To facilitate analysis of the seasonal trends in water status of the three species selected here, their osmotic potential at full turgor (Π_{100}), osmotic potential at zero turgor (Π_0), turgid/dry weight ratio (TW/DW), relative water content at incipient plasmolysis (RWC_0), and modulus of elasticity near full turgor (ϵ) were deduced from pressure-volume curves. Briefly, pressure-volume curves (Tyree and Hammel 1972; Richter 1978) were determined for the three species during two periods representative of the rainy season (April to May 1992) and the dry season (November to December 1991). A method similar to that described by Cheung et al. (1975) was used. Plant material was collected at around 2100 hours (i.e., when plants were largely rehydrated in situ). Youngest fully expanded leaves were used for the grass species, and twigs with 5–8 leaves for the shrub species. Leaves and twigs were recut under water and hydrated to near maximum turgor pressure during the night. Pressure-volume curves were conducted on wiped leaves or twigs enclosed in a plastic bag to prevent transpiration. The pressure in the chamber was increased in steps of about 0.3 MPa over the previous balance pressure up to 4 MPa. A period of 25, 20, and 10 min was used to extract sap at each pressure for *C. barteri*, *C. febrifuga*, and *H. diplandra*, respectively. TW/DW was obtained by weighing the material at full turgor before the experiment, weighing after the experiment, and then drying to constant weight at 80°C. Although the method used to obtain pressure-volume curves can slightly influence the values of derived parameters (Parker and Colombo 1996), parameters observed with a given method are useful to compare water relations between several species or between contrasting seasons for a given species and to discuss their ecological significance.

Leaf water isotopic composition

At Lamto, dew generally occurs at night and prevents plant transpiration. In order to assess such transpiration restriction and to document the time of transpiration recovery in the morning, leaf water isotopic composition was measured for the grass species *H. diplandra* and one shrub species throughout a diurnal cycle during the rainy and dry seasons. The shrub species *C. febrifuga* and *C. barteri* were sampled during the rainy and dry seasons, respectively. Leaf samples were collected between 0600 and 1900 hours at 30-min intervals. Shrub leaves were collected from the same clump, and grass leaves were sampled 3 m beyond the shrub clump canopy. All the leaf 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, and 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 . The methods used for isotope analysis are detailed in Le Roux et al. (1995). Results were expressed in δ units, by reference to the international standard V-SMOW for the oxygen isotope, and in the V-SMOW-SLAP scale for the hydrogen isotope (Gonfiantini 1978):

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

where $R = {}^{18}\text{O}/{}^{16}\text{O}$ or ${}^2\text{H}/{}^1\text{H}$. The unit δ is expressed in parts per 1,000.

Results

Diurnal variations of plant water status

On 4 May 1992, values of air water vapour pressure deficit (VPD) at screen level were typical for the rainy season, i.e., very low in the early morning and reaching 2.5 kPa at midday (Fig. 2). At this time, the soil water content in the 0- to 60-cm soil layer was 59.1 mm. Shrub and grass species exhibited predawn shoot water potentials around -0.2 MPa (Fig. 2). Diurnal minimum water potential was about -0.5 , -0.9 , and -1.3 MPa for *C. barteri*, *C. febrifuga*, and *H. diplandra*, respectively. Plant rehydration was rapid, and predawn water potential was recovered by 1900 hours. On 9 November 1991 (early dry season), VPD was very low in the early morning and reached 3 kPa at midday (Fig. 3). At this time, the soil water content in the 0- to 60-cm soil layer was 47.5 mm. *C. barteri*, *C. febrifuga*, and *H. diplandra* exhibited predawn shoot water potentials around -0.2 , -0.3 and -0.5 MPa, respectively. Around midday, water potential reached about -0.7 , -1.6 , and -1.9 MPa for these species, respectively. At 1900 hours, shoot water potential remained lower than the predawn potential for *C. febrifuga* and *H. diplandra*.

During the rainy season, a change of the isotopic signal of leaf water occurred after 0630 hours for the shrub *C. febrifuga*, while no isotopic enrichment, and thus no significant transpiration, was observed before 0830 hours for the grass *H. diplandra* (Fig. 4). During the dry season, no significant transpiration was observed before 0700 hours and 0800 hours for the shrub *C. barteri* and the grass *H. diplandra*, respectively (Fig. 4).

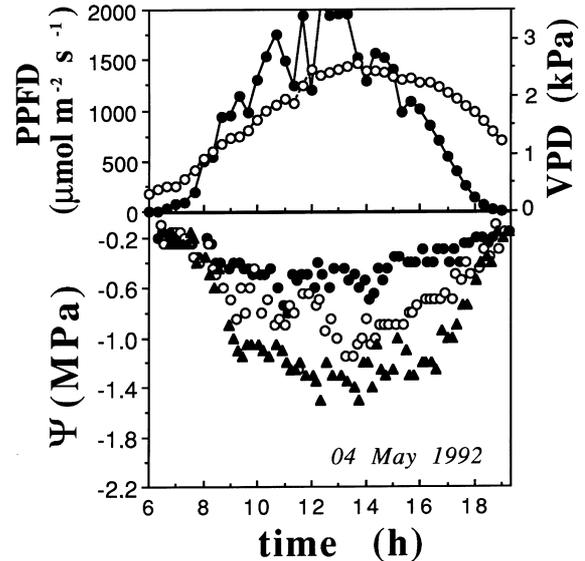


Fig. 2 Typical diurnal course of shoot water potential Ψ for the grass species *H. diplandra* (\blacktriangle), and the two shrub species *C. febrifuga* (\circ) and *C. barteri* (\bullet) during the rainy season (4 May 1992). Concurrent variations of photosynthetic photon flux density PPF (\bullet) and air water vapour pressure deficit VPD (\circ) are presented. At Lamto, local time is GMT

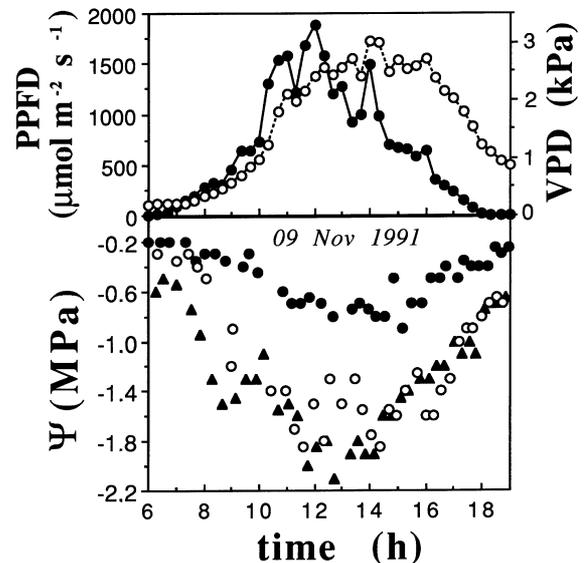


Fig. 3 Typical diurnal course of shoot water potential Ψ for the grass species *H. diplandra* (\blacktriangle), and the two shrub species *C. febrifuga* (\circ) and *C. barteri* (\bullet) during the early dry season (9 November 1991). Concurrent variations of photosynthetic photon flux density PPF (\bullet) and air water vapour pressure deficit VPD (\circ) are presented

Differences in the isotopic signal of leaf water observed between shrub and grass species were due essentially to the different VPD experienced by grass and shrub leaves, and to a lesser extent to differences in the isotopic signal of extracted water (see Le Roux et al. 1995).

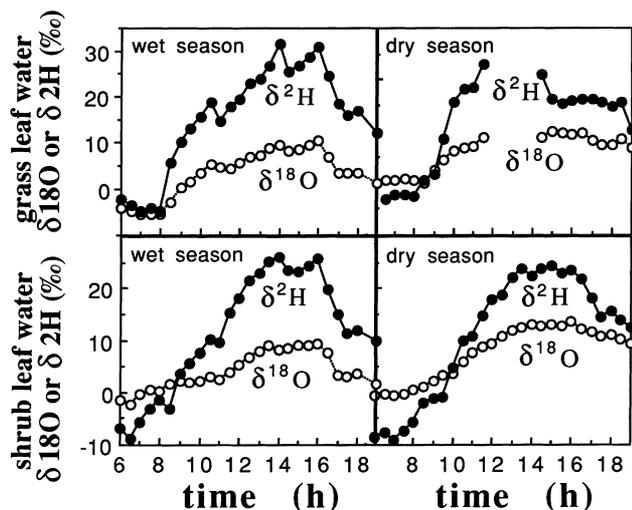


Fig. 4 Diurnal variations in the isotopic (oxygen-18 and deuterium) composition of leaf water for the grass species *H. diplandra* and the shrub species *C. febrifuga* during the wet season on 4 May 1992, and for the grass *H. diplandra* and the shrub species *C. barteri* during the dry season on 9 November 1991

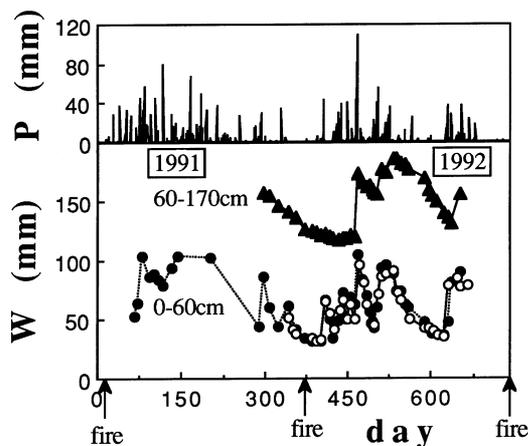


Fig. 5 Seasonal variations in daily precipitation *P* and soil water content *W* during two annual vegetation cycles. Water content is presented for the 0- to 60-cm soil layer in open areas (●) and under shrub clumps (○), and for the 60- to 170-cm soil layer in open areas (▲). Day numbers are computed from 1 January 1991

Seasonal variations in soil and plant water status

Seasonal variations in soil moisture

The seasonal variations in daily precipitation and soil moisture during the study period are presented in Fig. 5. Rain water supply was high from January to September 1991 and a marked long dry season occurred from the end of October 1991 to January 1992 (days 300 to 400). In 1992, the rainy season was interrupted by a pronounced short dry season in August 1992 (around day 600). The absolute values and seasonal dynamics of water content in the 0- to 60-cm soil layer under shrub clumps were close to values and dynamics observed in open areas (Fig. 5). In open areas, water content of the

60 to 170-cm soil layer markedly decreased during the 1991–1992 long dry season and during the short dry season in August 1992. Recharge of this deep horizon occurred during the early rainy season.

Maximum and minimum values of water content in the 0- to 60-cm soil layer in open areas were close to the water contents at field capacity and at permanent wilting point determined in the laboratory, respectively (Table 1). Furthermore, values obtained under shrub clumps were similar to values observed in open areas. Thus, the maximum water content available for plants in the 0- to 60-cm soil layer was around 70 mm, both under shrub clumps and in open areas (Table 1).

Seasonal variations of plant water status

The shrub *C. barteri* exhibited only weak variations in twig water potential (Fig. 6), and lower values were only recorded at the end of the 1991–1992 dry season. Predawn and minimum water potentials of this species always remained higher than -0.5 and -1.25 MPa, respectively. In contrast, the seasonal variations in predawn and minimum twig water potentials of the shrub *C. febrifuga* were more pronounced. Predawn and minimum water potentials reached -0.7 and -2.2 MPa, respectively. The daily predawn and minimum values of grass leaf water potential decreased steeply during the 1991–1992 dry season and during the 1992 dry spell (Fig. 6). During the rainy season, predawn and minimum values of grass leaf water potential were typically -0.2 and -1.3 MPa, respectively. At the end of the 1991 vegetation period, predawn and minimum grass leaf water potentials reached -1.3 and -3.1 MPa, respectively. On the 2 days studied, values obtained for *H. diplandra* were similar to values observed for the codominant grass *A. schirensis* (Fig. 7). Thus, we are more confident in generalizing the results obtained for *H. diplandra* to the whole grass layer.

The predawn (and minimum) shoot water potentials of the shrub *C. barteri* observed in clear-sky conditions

Table 1 Soil water contents of the 0- to 60-cm and 60- to 170-cm soil layers at field capacity (*W_{fc}*) and at the permanent wilting point (*W_{wp}*) calculated from in situ neutron probe observations or from laboratory (*Lab.*) measurements (in mm). The maximum water content available for plants (*AW*) is calculated as the difference between these two values

	<i>W_{fc}</i>		<i>W_{wp}</i>		<i>AW</i>	
	In situ	Lab	In situ	Lab	In situ	Lab
0–60 cm shrub clumps	96.6	–	31.3	–	65.3	–
0–60 cm open areas	104.6	109.4	30.9	31.1	73.7	78.3
60–170 cm open areas	185.0	–	120.9 ¹	–	64.1 ¹	–

¹ The permanent wilting point may be not reached in the deeper layers, and *AW* may thus be underestimated

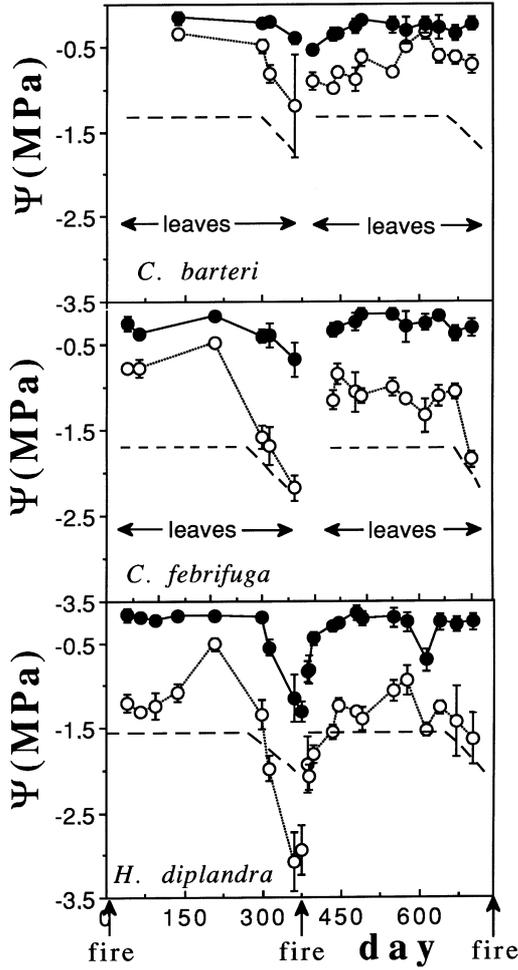


Fig. 6 Seasonal variations of predawn (●) and minimum (○) shoot water potentials Ψ ($n = 4$; means with 95% confidence intervals) for the shrub species *C. barteri*, and *C. febrifuga*, and the grass species *H. diplandra*. Broken lines roughly indicate the seasonal courses of water potential at zero turgor as reported in Table 2. Day numbers are computed as in Fig. 5

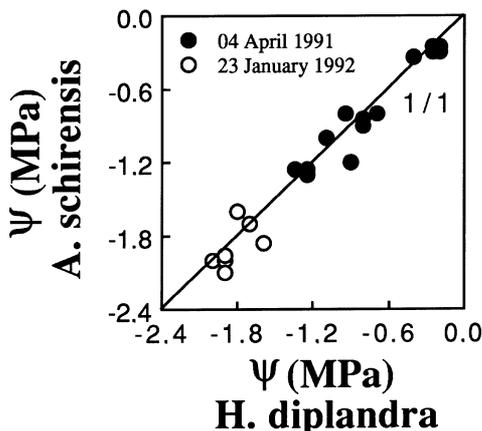


Fig. 7 Relationship between the leaf water potentials (Ψ) of the two grass species *H. diplandra* and *A. schirensis* during a diurnal cycle of the rainy season (●) and around midday during the dry season (○)

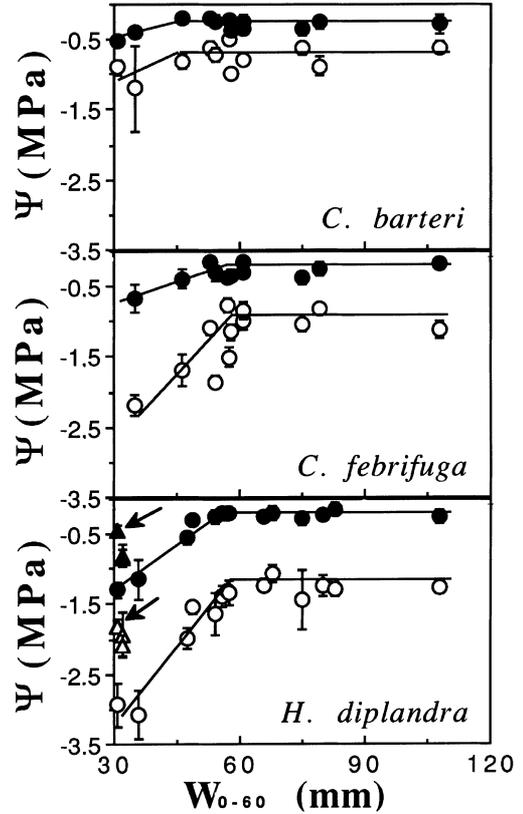


Fig. 8 Predawn (●) and minimum (○) shoot water potentials of the shrub species *C. barteri* and *C. febrifuga*, and the grass species *H. diplandra*, observed in clear-sky conditions as a function of the water content of the 0- to 60-cm soil layer (measured in open areas for the grass, and under shrub clumps for the shrubs). Values observed for young regrowing grasses at the end of the dry season are presented as triangles, and observations performed during this period after 6 mm rain are indicated by an arrow. Bars are 95% confidence intervals. Lines were fitted by eye

were weakly correlated with the water content of the 0- to 60-cm soil layer (Fig. 8). This shrub species maintained high water potentials for water contents higher than 45 mm. Furthermore, predawn water potential declined only slightly even when the water content of the upper soil layer was close to the water content at the wilting point (31 mm). In contrast, the predawn and minimum leaf water potentials of the shrub *C. febrifuga* decreased substantially when the water content of the 0- to 60-cm soil layer was lower than about 55 mm (Fig. 8). Similarly, the predawn and minimum leaf water potentials of mature stages of the grass species *H. diplandra* were strongly correlated to the water content of the 0- to 60-cm soil layer (Fig. 8). The grass species did not maintain high water potentials when the water content was lower than about 57 mm. For a given soil water availability, higher minimum leaf water potentials were observed during the early growing season after fire, particularly after 6 mm rain. A reduced leaf area index, and water supply by a perennial, extensive root system probably explained such improved grass water relations after fire. Predawn and minimum leaf water potentials of

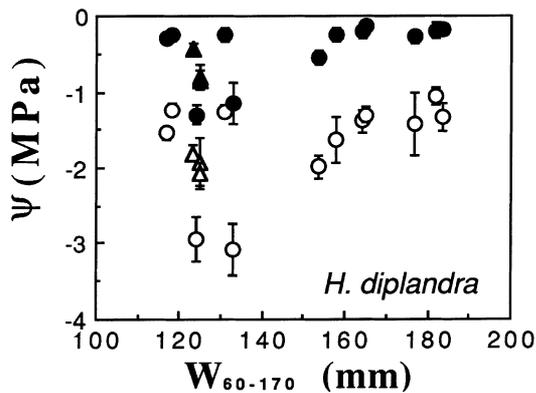


Fig. 9 Predawn (●) and minimum (○) leaf water potentials of the grass species *H. diplandra* observed in clear-sky conditions as a function of the water content of the 60- to 170-cm soil layer in open areas. Symbols as in Fig. 8. Bars are confidence intervals ($P = 0.05$)

the grass *H. diplandra* were not correlated to the water content of the 60- to 170-cm soil layer (Fig. 9). Relatively low potentials were obtained during the early dry season ($W_{0-60} = 47$ mm), and relatively high water potentials were observed during the early rainy season ($W_{0-60} = 49$ mm).

Plant water relations

The two shrub species exhibited strongly contrasting water relations (Table 2). Two-factor ANOVA showed that absolute values of osmotic potentials at full turgor and zero turgor (both $P = 0.0001$), as well as the modulus of elasticity ($P = 0.01$) were significantly lower for *C. barteri* than for *C. febrifuga*. Season effect was significant for osmotic potentials at full turgor and zero turgor (both $P = 0.0001$) but not for the modulus of elasticity ($P = 0.32$). The species \times season interaction effect was not significant for the three parameters. The lower modulus of elasticity obtained for *C. barteri* compared with *C. febrifuga* implied that a given decrease of shoot water potential corresponded to a more important dehydration for the former species. During the rainy season, incipient plasmolysis was reached at -1.37 MPa for *C. barteri*, (i.e., 10% loss of twig water content), and at -1.73 MPa for *C. febrifuga* (i.e., 13% loss of twig water content). For the grass species, incipient plasmolysis was observed at -1.55 MPa (12% loss of leaf water content).

For the three plant species, the osmotic potential at zero turgor was significantly lower during the early dry season than during the rainy season (Table 2). Furthermore, osmotic potential at full turgor was significantly lower during the early dry season than in the rainy season for the grass species and the shrub *C. febrifuga*. For the latter species, the decrease in osmotic potential was paralleled by a significant decrease in the TW/DW ratio. Leaves were fully expanded during both periods so that changes in this ratio were probably due

Table 2 Parameters deduced from pressure-volume curves performed during the rainy season (April to May 1992) and during the dry season (November to early December 1991) for the two shrub species *C. barteri* and *C. febrifuga*, and the grass *H. diplandra*. Mean values are presented with standard errors. Parameters are: osmotic potential at full turgor (Π_{100}), osmotic potential at zero turgor (Π_0), turgid/dry weight ratio (TW/DW), relative water content at incipient plasmolysis (RWC_0), and bulk modulus of elasticity (ϵ). Effect of season was assessed by analysis of variance

	Rainy season	Early dry season	Significance
<i>C. barteri</i>	($n = 7$)	($n = 5$)	
Π_{100} (MPa)	-1.00 (0.045)	-1.15 (0.075)	NS
Π_0 (MPa)	-1.37 (0.069)	-1.72 (0.073)	***
TW/DW	3.49 (0.13)	3.60 (0.22)	NS
RWC_0	0.897 (0.011)	0.842 (0.018)	*
ϵ (MPa)	3.83 (0.94)	4.65 (0.77)	NS
<i>C. febrifuga</i>	($n = 8$)	($n = 7$)	
Π_{100} (MPa)	-1.44 (0.038)	-1.67 (0.036)	***
Π_0 (MPa)	-1.73 (0.025)	2.17 (0.052)	***
TW/DW	2.72 (0.15)	2.02 (0.13)	**
RWC_0	0.870 (0.015)	0.872 (0.011)	NS
ϵ (MPa)	11.48 (1.66)	10.25 (0.95)	NS
<i>H. diplandra</i>	($n = 6$)	($n = 5$)	
Π_{100} (MPa)	-1.11 (0.069)	-1.41 (0.111)	*
Π_0 (MPa)	-1.55 (0.056)	-1.82 (0.058)	**
TW/DW	2.27 (0.45)	2.06 (0.37)	NS
RWC_0	0.882 (0.016)	0.927 (0.015)	NS
ϵ (MPa)	6.47 (1.73)	12.34 (5.57)	NS

* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$

to dehydration rather than to changes in leaf weight with leaf ageing. This would suggest that the solutes were more concentrated due to leaf dehydration rather than to active osmotic adjustment.

Discussion

This work provides comprehensive information on the seasonal variations in soil, shrub and grass water status in an African humid savanna ecosystem. Such information is available for African dry and mesic savannas (e.g., Berger et al. 1996) or humid savannas in South America (e.g., Baruch and Fernandez 1993; Medina and Francisco 1994). Verhoef et al. (1996) also documented the effect of soil moisture on stomatal conductance for a shrub species and two herbaceous species in a dry fallow

savanna in Niger. However, to our knowledge, information on the water economy of coexisting grass and shrub species has not been available to this date for African humid savannas. The shrub and grass species studied here exhibited contrasting seasonal patterns of water status. The seasonal changes in predawn and minimum shoot water potentials were pronounced for the grass species and the shrub *C. febrifuga*, but weak for the shrub *C. barteri*. The minimum grass leaf water potentials measured during this study were higher than those reported for grass species in drier savannas (Peake et al. 1975; Wilson et al. 1980) or semiarid ecosystems (Sala et al. 1981), but slightly lower than values previously reported in a Venezuelan humid savanna (-2.0 and -2.7 MPa for *H. rufa* and *Trachypogon plumosus*, respectively, according to Baruch and Fernandez 1993). The low values of water potential observed during the dry season were undoubtedly a major deterrent to grass physiological activity since the minimum potential was lower than the osmotic potential at zero turgor. During the rainy season, *H. diplandra* was found to maintain high values of stomatal conductance for leaf water potential values higher than -1.5 MPa in Lamto savannas (Mordelet 1993). A similar behavior and threshold were reported for *H. rufa* in Colombia (Jones et al. 1980). Thus, the seasonal variations in the grass water potential (Fig. 6) showed that stomatal conductance was not restricted for most of the year, but was probably strongly reduced during the dry season. In contrast, the influence of the seasonal trends in plant water status on physiological activity cannot be easily inferred for the shrubs *C. febrifuga* and *C. barteri* since the relationships between shoot water potential and leaf gas exchange have never been studied for these two shrub species. However, minimum potential values exhibited by *C. febrifuga* during the dry season were probably detrimental to shrub physiological activity since they were close to osmotic potential values at incipient plasmolysis (Fig. 6). This was not the case for *C. barteri*.

The contrasting seasonal patterns of shoot water potentials for the three species studied were probably due to different soil water uptake patterns. Linking plant and soil water status is an efficient means to assess soil water uptake pattern by plants and to define critical values of soil moisture deficit for different plant species (e.g., Redmann 1976; Sala et al. 1981). In savanna-like ecosystems, the correlation between plant predawn water potential and water potential in upper soil layers is generally much stronger for grasses than for shrubs, as documented in an East African mesic savanna (Hesla et al. 1985). Predawn potential values are used as indicators of water status of the soil layers explored by plants weighted by water uptake efficiency from each layer (e.g., Sala et al. 1981). This approach implies that (1) plants are in equilibrium with soil moisture at dawn (in particular plants do not transpire during the night), and (2) soil moisture heterogeneity does not restrict the use of bulk soil moisture as a driving variable for plant water status (Améglio and Archer 1996). In particular,

significant differences in soil moisture between shrub clumps and open areas as observed in dry savannas (Belsky et al. 1989) or in mesic savannas (Strang 1969) would make it difficult to correlate shrub water status to a soil moisture variable since shrub roots can explore upper horizons away from shrub clumps (Mordelet et al. 1997). In the present study, no significant transpiration was observed before 0630–0700 and 0800–0830 hours for the shrub species and the grass species, respectively (Fig. 4). Thus, at dawn, plants are probably in equilibrium with moisture in the explored soil profile. Furthermore, the absolute values and seasonal dynamics of water content in the 0- to 60-cm soil layer were similar under shrub clumps and in open areas (Fig. 5). This is consistent with results previously reported for the 0- to 30-cm soil layer under shrub clumps or in open areas at Lamto (Mordelet et al. 1993). A practical implication is that horizontal heterogeneity in soil moisture at the site scale is not expected to obscure relationships between predawn plant water potential and soil water content. The relationships obtained showed that the predawn water potential of the grass species strongly depended on the moisture of the 0- to 60-cm soil layer (Fig. 8). Grass water potential decreased when the water content of this layer was below about 57 mm. A similar threshold was observed for the relationship between grass transpiration rate and water content of the 0- to 60-cm soil layer (Le Roux 1997). When the water content of this layer was at the permanent wilting point, grass predawn water potential was around -1.3 MPa. Furthermore, grass predawn potential was better correlated to the water content of the 0- to 60-cm soil layer than that of the 60- to 170-cm soil layer (Figs. 8, 9). This suggests that the grass species acquired most of its water from the 0- to 60-cm soil layer. This water uptake pattern explains the high sensitivity of grass productivity to drought (Le Roux et al. 1997). The relationships obtained between shoot water potential and moisture of the upper soil layers indicated that the two shrub species exhibited different water uptake patterns. Predawn and minimum shoot water potentials of the shrub *C. barteri* were poorly correlated to the water content of the 0- to 60-cm soil layer (Fig. 8). Furthermore, this species maintained a relatively high predawn water potential (-0.5 MPa) when the water content of the upper soil layer was at the wilting point. This clearly indicates that *C. barteri* had rather good access to deeper soil layers. In contrast, shoot water potentials of the shrub *C. febrifuga* decreased significantly when the water content of the 0- to 60-cm soil layer was lower than about 55 mm (Fig. 8). When the water content of the 0- to 60-cm soil layer was 36 mm, the predawn water potential reached -0.4 , -0.7 , and -1.2 MPa for *C. barteri*, *C. febrifuga*, and *H. diplandra*, respectively. Given that these values were obtained at dawn, this implies that *C. febrifuga* had access to water in deep soil layers intermediate to those of *C. barteri* and *H. diplandra*.

The inability of *H. diplandra* and *C. febrifuga* to efficiently use water from deeper soil layers is shown

by their low predawn (-0.55 and -0.4 MPa, respectively) and minimum (-2.0 and -1.7 MPa, respectively) water potentials during the early dry season as compared to values obtained during the rainy season. Such low values were observed when the water content of the 0- to 60-cm soil layer was relatively low (47 mm) while deeper soil layers offered good water availability (soil water content of the 60- to 170-cm layer in open areas was 154 mm at this time which is only 30 mm less than field capacity). In contrast, *C. barteri* exhibited high predawn (-0.2 MPa) and minimum (-0.8 MPa) potential values at this time, which did not differ from values observed during the rainy season. These results show that the water economy of the two deciduous shrub species studied in this West African humid savanna differed significantly. Differences in soil water uptake patterns of two co-occurring shrub species in a semiarid shrubland in Argentina were previously reported by Pelaez et al. (1994). These authors showed that the water potential of one shrub species was not correlated to soil water potential of upper soil layers, while strong correlations were found for the other shrub species.

The water uptake patterns identified during this study for two species (i.e., use of water essentially in upper soil layers by *H. diplandra* and *C. febrifuga*) are consistent with the conclusion drawn from a comparison of isotopic signals of soil water and plant stem water (Le Roux et al. 1995). However, *C. barteri* was also found to acquire water from upper soil layers in this previous study. In fact, Le Roux et al. (1995) noted that isotopic results obtained for the shrub species during the dry season were ambiguous (the isotopic signal of shrub stem water could be explained either by water withdrawal from a mean depth of 30 cm or below 150 cm). In the light of the present study, it can be concluded that *C. febrifuga* actually acquires most of its water in the upper soil layers during both rainy and dry seasons. In contrast, *C. barteri* takes up water from surface soil layers during the rainy season but probably largely uses water from deep soil layers during the dry season.

Water relations of the grass and shrub species and their seasonal trends (Table 2) were consistent with these soil water uptake patterns. The validity of comparing water relations at two periods in a vegetation cycle could be questioned because of potential morphological and physiological changes associated with ontogeny (e.g., Fereres et al. 1978; Meinzer et al. 1983; Bowman and Roberts 1985). However, pressure-volume curves were obtained only for mature shrub twigs or the youngest fully expanded leaves of grasses, and ontogeny effects are assumed not to explain the observed seasonal variations in water relations. The osmotic potential was significantly lower in *C. febrifuga* than in *C. barteri* (Table 2). Furthermore, leaf dehydration and an ensuing, essentially passive osmotic adjustment were observed during the dry season for *C. febrifuga* but not for *C. barteri*. Low osmotic potential is recognized as an adaptive feature for plants growing in seasonally dry environments since it helps water withdrawal and pro-

motes turgor maintenance at low shoot water potentials (Turner and Jones 1980; Tyree and Jarvis 1982; Robichaux et al. 1984). Since *C. febrifuga* actually acquires most of its water from upper soil layers, relatively low osmotic potential values can be an important characteristic for this species since they should promote water uptake from dry soils and thus turgor-mediated physiological activity during dry spells. In contrast, relatively high osmotic potential values (Table 2) are not a deterrent for water uptake and physiological activity in *C. barteri* since this species has good access to deeper soil layers where seasonal variations of water potential are less pronounced. During the rainy season, osmotic potential at full turgor observed for *H. diplandra* (Table 2) was close to values (-0.97 and -1.55 MPa) reported for two humid savanna grass species (Baruch and Fernandez 1993). During the dry season, a weak active osmotic adjustment was observed for *H. diplandra* (Table 2). This is consistent with the fact that this species essentially explored the upper soil layers since osmotic adjustment is a potentially important process for coping with drought (Hsiao et al. 1976; Turner and Jones 1980). Osmotic adjustment was previously observed during the dry season for two humid savanna grass species in Venezuela (Baruch and Fernandez 1993). However, it is doubtful that the osmotic adjustment exhibited by *H. diplandra* could effectively maintain good water relations during most of the diurnal period at the end of the herbaceous vegetation cycle, given the very low minimum potential values recorded at this time (Fig. 6).

During both seasons, bulk moduli of elasticity observed for *H. diplandra* (Table 2) were higher than values exhibited by *H. rufa* in neotropical savannas (Baruch and Fernandez 1993), but were close to values (5.8 to 10.9 MPa) reported by these authors for another humid savanna grass species i.e., *T. plumosus*. Values of the modulus of elasticity exhibited by *C. febrifuga* were similar to values (from 7 to 10 MPa) reported by Sobrado (1986) for three deciduous species in a tropical dry forest in Venezuela. Lower values were obtained for the deciduous shrub *C. barteri* at Lamto. The high elasticity in the shrub *C. barteri* permits larger changes in cell volume with smaller changes in turgor pressure than in *C. febrifuga*. In contrast, along with low osmotic potentials, the low tissue elasticity observed for *C. febrifuga* could facilitate water uptake from drying soil since a given change in tissue water volume will result in a marked decrease in shoot water potential (Bowman and Roberts 1985). The tradeoff is that this low elasticity induces greater turgor loss during tissue dehydration.

In tropical environments, leaf shedding patterns exhibited by shrubs are strongly correlated with changes in their water status in response to increased soil water deficit (Borchert 1994; San José et al. 1995). Thus, the contrasting water uptake patterns and water relations exhibited by the two shrub species studied at Lamto could explain their different leaf-shedding patterns. For *C. febrifuga*, leaf shedding occurs rather abruptly during

the dry season, either before or after fire, according to drought intensity (Menaut 1974). This is consistent with the marked sensitivity of this shrub species to drought. In contrast, the leaf fall pattern is more continuous for *C. barteri* (Menaut 1974), which could be explained by the relatively low sensitivity to drought (i.e., maintenance of high water status) exhibited by this species. Furthermore, analysis of the spatial patterns observed for *C. febrifuga* and *C. barteri* at Lamto (Gignoux 1997) showed that these two shrub species are statistically associated. Along with seed dispersal modality and fire constraint (*C. febrifuga* is a fire-resistant species which can promote seedling recruitment of fire-sensitive species like *C. barteri* according to Gignoux 1997), the different patterns of soil water uptake identified in this study for *C. febrifuga* and *C. barteri* can be a favourable feature of this spatial association.

Conclusion

Strategies to cope with water deficits encompass drought escape and drought tolerance (Turner 1986). Among the three species studied here, two exhibited a combination of escape and tolerance strategies. Whatever the season, the grass *H. diplandra* and the shrub *C. febrifuga* acquire water essentially in the upper soil layers and have limited access to deeper soil layers (< 60cm). Thus, these species experience drought when surface soil layers are depleted (i.e., during the long dry season and even during shorter dry spells). For these two species, drought tolerance is due to the combination of low osmotic potential and high modulus of elasticity. In contrast, the shrub *C. barteri* extracts most of its water from surface soil layers during the rainy season (Le Roux et al. 1995) but has good access to deep soil layers (< 60cm) where seasonal variations in water potential are less pronounced. For this species, the combination of high osmotic potential and high elasticity allows a weak decrease in plant water potential and turgor maintenance during dehydration. The high water potentials exhibited by this species even during the dry season would prevent it from using water from drying surface soil layers. *C. barteri* probably does not experience drought before the middle of the long dry season. At this time, the three species studied exhibited a major drought escape mechanism: leaf shedding for shrub species, and leaf area reduction by leaf mortality for grasses.

The contrasting results obtained for the two shrub species, which were found to be spatially associated at Lamto, are consistent with their different leaf-shedding patterns as previously observed. Thus, the diversity of strategies of water economy exhibited by humid savanna deciduous tree species should be considered. Furthermore, the soil water uptake pattern of the shrub *C. febrifuga* is rather close to that of the grass species during both dry and rainy seasons, while *C. barteri* takes up water from upper soil layers during the rainy season (Le Roux et al. 1995). This provides evidence for po-

tentially significant competition between shrub species and grasses for the soil water resource. Thus, the two-layer hypothesis of water resource partitioning between grasses and shrubs in savanna ecosystems (see references in Le Roux et al. 1995) is a misleading simplification of actual water uptake patterns in West African humid savanna ecosystems. To better understand interspecific interactions and species coexistence in these ecosystems, models of savanna function should take into account the diversity of strategies of water economy exhibited by deciduous tree species, along with their concurrent different strategies of fire resistance (Gignoux et al. 1997).

Acknowledgements The authors are greatly indebted to P. Becker (University Brunei Darussalam, Brunei) and P. Mordelet (CESBIO Toulouse, France) for their comments on a previous version of the manuscript. We express our gratitude to R. Vuattoux, Director of the Lamto Ecological Research Station (National University of Côte d'Ivoire) and to J.L. Tireford, Director of the Lamto Geophysical Research Station for all the facilities they offered us in the field. We would particularly like to thank Konan Alexis, Konan N'Dri Alexis, Kouassi Etienne, N'Guessan François, Kouassi Guillaume, Loukou Martin, and Sawadogo Prosper for their technical assistance, and Patricia Richard for help during isotope analysis. The research was supported by the Savannas on the Long Term (SALT) IGBP-GCTE core project.

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