

Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese west Africa

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Summary

1. *Faidherbia* (*Acacia*) *albida* is a multipurpose tree widely distributed in semiarid Africa, notably in agroforestry parklands. It is in leaf during the dry season and defoliated during the rainy season, displaying therefore a peculiar reverse phenology. The related water-use strategy, including leaf water potential, sapflow, hydraulic conductance and depth of uptake, were monitored on adult trees in a Sudanese west-African parkland.

2. Despite a severe drought in the superficial soil layers, the predawn leaf water potential of *F. albida* dropped only to ca. –0.5 MPa during the end of the dry season, indicating only a moderate water stress.

3. Radial trunk growth ceased before the end of the dry season and could have been affected by the moderate drought stress. However, leafiness remained constant during the dry season. Leaf shedding occurred after the first rains and was probably independent of drought.

4. *Faidherbia albida* displayed large transpiration rates under favourable conditions but the ratio of sapflow to Penman evapotranspiration and the soil-to-leaf specific hydraulic conductance decreased severely towards the end of the dry season.

5. Roots of *F. albida* were distributed through the weathered rock, down to a depth of 7 m, and vanished in the vicinity of a permanent water-table. The isotopic composition of oxygen in the xylem sap ($\delta^{18}\text{O}$) remained very close to the values recorded in the water-table during the course of the year. Phreatophytism thus explained the maintenance of growth and transpiration during the dry season. Nevertheless, during early rains, $\delta^{18}\text{O}$ of sap switched towards the composition of the superficial soil layers, indicating facultative phreatophytism.

6. Reverse phenology, low density and depth of water uptake of *F. albida* indicated a low competition with annual crops for water; the fraction of annual rainfall used by the trees was estimated to remain below 5%.

Key-words: agroforestry, drought, oxygen isotope, phreatophyte, sapflow

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Introduction

Faidherbia albida (Del.) A. Chev. (syn. *Acacia albida*: Mimosoideae) is a leguminous tree species widely distributed in Africa. It is present in Sudanese and Sahelian zones that are affected by a long dry season. The species is distributed over territories with an annual rainfall ranging from 50 to 1500 mm (Fagg &

Barnes 1990). In eastern, central and southern Africa, it occurs naturally along riverbanks on alluvial soils. The best known peculiarity of *F. albida* is its reverse phenology (Wickens 1969). Trees are in leaf, growing and fruiting during the dry season, whereas leaves are shed after the first rains and growth resumes only at the end of the wet season. This phenology is advantageous for agroforestry, because competition with associated crops growing during the wet season is minimized. *Faidherbia albida* trees are rather vigor-

ous [heights of 15–20 m; diameter at breast height (d.b.h.) up to 1 m] and produce abundant fodder for livestock during the dry season. The species is therefore frequently used in agroforestry parklands of west Africa, where it plays an important role for the local economy (Pélissier 1980; Depommier 1996).

Little is known about the water relations of *F. albida*. In order to characterize the drought tolerance of *F. albida*, it is necessary to understand how severe the drought stress experienced by the trees was and its consequences on leaf shedding, transpiration and growth. It was hypothesized that the trees need large amounts of water, as attested by their dry season growth and their vegetative vigour. This has strong implications in terms of competition with crops and water budget of such agroforestry parklands submitted to dry conditions. The knowledge of the relative water use by the *F. albida* layer could lead to recommendations in terms of optimal tree density.

Dry season growth probably relies on uptake of water from deep soil layers or from the water-table. Deep rooting of adult *F. albida* trees has been recorded several times; for instance, down to 30 m in parklands of west Africa (Dupuy & Dreyfus 1992; T. A. Diop, personal communication). The use of ground-water may sustain growth and survival during the dry season. A phreatophytic behaviour has been frequently inferred from the observation of the deep tap root (sinker) produced by *F. albida* trees, but has never been experimentally demonstrated before now. In addition, the rooting system of *F. albida* includes lateral roots and the root-system architecture can display severe variations, depending on soil depth, nutrient availability, water reservoirs or water-table position (Alexandre & Ouedraogo 1992; Depommier 1996). Is *F. albida* phreatophytic in agroforestry parklands, as it is probably in its natural riparian communities? If so, is its transpiration only regulated by leaf area index? For instance, large rates of transpiration, limited only by leaf area, have been recorded in riparian phreatophytic tree communities of the Mojave desert floodplain (Sala, Smith & Devitt 1996).

Depth of water uptake may be assessed from the oxygen isotopic composition ($\delta^{18}\text{O}$) of sap, rain, soil and ground-water. The seasonal variability of $\delta^{18}\text{O}$ of rains, combined with the enrichment of superficial drying soil layers in ^{18}O can lead to $\delta^{18}\text{O}$ gradients between superficial and deep soil water reservoirs. The water-table itself often displays a different composition than superficial soil layers. Because water extraction by the roots does not discriminate the oxygen isotopes (White *et al.* 1985), the isotopic composition of sap water is expected to reflect the water source, or eventually the mixing of several sources (Ehleringer *et al.* 1991; Ehleringer & Dawson 1992; Flanagan, Ehleringer & Marshall 1992; Valentini, Scarascia-Mugnozza & Ehleringer 1992; Bishop & Dambrine 1995; Le Roux, Bariac & Mariotti 1995; Dawson & Pate 1996). There is strong evidence that

some trees are able to shift from one source to another, depending on the developmental stage (Dawson & Ehleringer 1991) or on season (Smith *et al.* 1991; Busch, Ingraham & Smith 1992; Thorburn & Walker 1994; Dawson & Pate 1996).

The real nature of the adaptations enabling *F. albida* to survive and to grow actively during such long dry seasons was investigated. Adult *F. albida* were monitored under agroforestry conditions and during the whole vegetation period, in the Sudanese parkland of Dossi, Burkina Faso. The following questions were addressed: (1) what are the seasonal time-courses of growth and water relations with respect to phenology and rains; (2) does *F. albida* experience drought stress during the dry season, that would affect water relations, growth and phenology; (3) what is the relative contribution of ground-water to the transpiration flow, with respect to more superficial soil layers?

Materials and methods

SITE AND CLIMATE

In Burkina Faso (west Africa), *F. albida* is present in an area where the annual rainfall ranges from 300 to 1100 mm (Depommier 1996). The parkland of Dossi (latitude, 11° 26' N; longitude, 3° 24' W; altitude, 350–450 m; nearest town, Houndé) is located close to the wettest limit of this distribution area. Mean annual rainfall from 1984 to 1993 was 924 mm with 6–7 months of drought (monthly rainfall < 50 mm). Climate was classified as south-Sudanese (Guinko 1984). In Dossi, the annual ratio of rainfall over potential evapotranspiration (P/PET) is between 0.36 (Boromo, 50 km NE) and 0.48 (Bobo-Dioulasso 110 km SW) (mean of 10 years). According to UNESCO (quoted by Pégorié 1989), areas with $0.2 < P/PET < 0.5$ display semiarid conditions.

The parkland was 340 ha in extent, surrounded by hills and plateaus. The main crops grown are pearl-millet, sorghum, maize, peanut, cotton and cowpea, using manual or draught tillage and fertilizers. The substratum is Birrimian, volcano-sedimentary (Hottin & Ouedraogo 1975), fissured and weathered over several metres depth. Soils are rich in clays (30–45% of the fraction < 2 mm) and silts (15–45%) and have a high mineral content. Their depth varies from 0 to ca. 3.5 m within the park. Wells used for water supply by cultivators show the existence of water-tables at depths of 3–19 m, generally situated at the base of the weathered rock.

The experimental stand was located on a chromic cambisol (FAO-UNESCO 1988, 'sol brun eutrophe tropical peu évolué' in the French nomenclature, Commission de Pédologie et de Cartographie des Sols 1967) 1.5 m deep, with A–B–BC–CB–C horizons. C corresponded to a highly weathered schist from 1.5 to 4.5 m. Texture was measured in the laboratory of Bunasols at Ouagadougou.

Table 1. Main features of the *F. albida* trees used in the experiments (monitored for sapflow, present in the experimental plot; 11 trees studied), compared to those present in the parkland bottom or in the whole parkland. The area of the experimental plot was fixed as the smallest disc enclosing the 11 trees (0.46 ha); parameters using this value are labelled (*) and are arbitrary. Agroforestry parkland of Dossi, Burkina Faso, west Africa, 1995–1996; d.b.h., diameter at breast height

	Trees monitored for sapflow		Experimental plot		Parkland bottom		Whole parkland	
	Tree 1	Tree 2	Mean	SD	Mean	SD	Mean	SD
Stand area (ha)			(0.46*)		90		340	
Number of trees			11		721		2522	
d.b.h. (cm)	63.7	70.5	57.8	11.2	52.2	23	50	26
Height (m)	14	18.6	13.7	2.5	12.1	2.8	11.6	3.1
Crown sheltered area (m ² tree ⁻¹)	310	155	186	101	88	74	77	72
Crown volume (m ³ tree ⁻¹)	1616	695	928	665				
Density (trees ha ⁻¹)			(23.9*)		8.0		7.4	
Basal area (m ² ha ⁻¹)			(6.3*)		1.7		1.5	
Soil cover (%)			(44.5*)		7.0		5.7	

The tree layer was mostly composed of 2500 crown-isolated *F. albida* (Table 1). Their mean age was about 40 years (Depommier & Détienne 1996). They were maintained and favoured by the cultivators and moderately pruned or debarked by pastoralists during the dry season. A 0.46 ha circular experimental plot was selected within a homogeneous soil unit that covered 26% of the total parkland area. This plot included 11 healthy trees submitted to low pruning pressure, that were monitored for growth, phenology and leaf water potential. Two neighbouring trees displaying long and straight trunks were selected for seasonal water relation studies. Measurements were conducted during the dry seasons of 1994/1995 and 1995/1996. Maize was grown by local farmers between the trees and harvested at the end of September.

GROWTH

Trees of the plot were kept unpruned during the experiment. Leaf phenology was described visually every 10–30 days, by estimating the fraction of branches still leafless, newly leafed or fully leafed. Circumference under bark was measured manually every 10–30 days, on a line drawn at breast height (three repeated measurements per tree and per date). In order to compare time-courses of radial growth among trees with different vigour, a standardized radial growth index (GI) was computed as:

$$GI = 100 (C_c - C_0) / (C_{\max} - C_0), \quad \text{eqn 1}$$

where C_c and C_0 are current and initial circumference, and C_{\max} is the maximal circumference recorded during 1995.

WATER RELATIONS AND POTENTIAL EVAPOTRANSPIRATION

Five series of water-relations measurements were conducted on two trees during the dry season from

August 1995 to July 1996. Sap flux density (F_d , kg dm⁻² h⁻¹) was measured according to Granier (1987) with 2 cm long radial flowmeters, continuously heated (0.2 W), and connected to a Data Logger (21X, Campbell Scientific, Shephed, UK). The gauges were inserted in the external sapwood. For each series of measurements, the devices were kept in place during four successive days.

Special care was provided to minimize passive thermal gradients between the reference and the heated gauge. Gauges were protected from direct sunlight and air movements with a foam–aluminium foil, and the trunk covered by a woven straw cylinder from the base up to 1.8 m. During the first day of each session, the time-course of passive thermal gradients was measured in the absence of heating. These gradients reached up to 1 °C (occasionally 2 °C) in the sun-exposed gauges. A given gauge displayed similar patterns from day to day in similar weather conditions. We therefore subtracted these passive gradients from active gradients before computing F_d . Preliminary measurements had revealed an important intra-tree azimuthal variability of F_d . Five gauges were thus inserted into each trunk, at regular intervals around the circumference. As no species-related difference in calibration factors of the Granier-sensors have yet been reported (Köstner, Garnier & Cermak 1998) we used the original values of Granier (1987):

$$F_d = 4.28 \left[\frac{\Delta T_M - \Delta T_U}{\Delta T_U} \right]^{1.231} \quad \text{eqn 2}$$

where F_d is the sapflow density (kg dm⁻² h⁻¹) and ΔT_M and ΔT_U are the maximal (recorded overnight) and current temperature difference between the two sensors (°C).

In order to compute whole-tree total sapflow (F , kg h⁻¹), the radial distribution of F_d in the sapwood was assessed. The following observations made on cut sections from adjacent trees indicated that deep within the wood in the trunk and branches, sapflow was still substantial: (1) no heartwood was visible; (2) wood

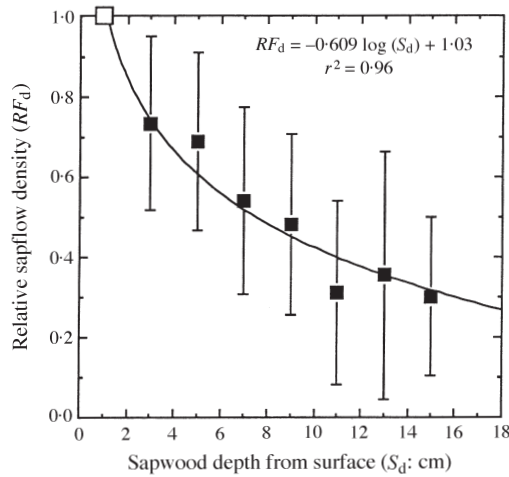


Fig. 1. Radial distribution of the sapflow density within the sapwood of adult *Faidherbia albida* trees. Relative sapflow density, $RF_d = 100 \cdot F_{di}/F_{d(\text{surface})}$. Gauges were inserted radially in the sapwood, every second cm, till 15 cm depth. Log-adjusted model ($n = 6$ trees; mean tree diameter = 54.0 ± 12 cm; mean \pm SD).

cores were wet from the surface to the centre and all vessels were open; (3) staining experiments conducted on branches showed that all vessels were functional (data not shown). The radial distribution of F_d in the sapwood was assessed on six neighbouring trees (mean d.b.h. \pm SD = 54.0 ± 12.2 cm). Two gauges were inserted close to surface, and four to eight in radial notches at depths ranging from 3 to 15 cm. Relative F_d was computed as $F_{d(\text{deep})}/F_{d(\text{surface})}$. F_d was adjusted logarithmically with depth till 15 cm (Fig. 1) and an extrapolation permitted estimation of values at larger depths. The whole-tree total sapflow, F was computed as:

$$F = \sum_i^n F_{di} \times SA_i, \quad \text{eqn 3}$$

where F is the whole tree total sapflow (kg h^{-1}), i to n represent successive 2 cm-wide sapwood layers from cambium to centre, SA_i is the sapwood area of successive layers (dm^2) and F_{di} is the sapflow density ($\text{kg dm}^{-2} \text{h}^{-1}$) in the successive layers derived from the logarithmic fit (Fig. 1).

Daily cumulative tree sapflow ($F_{24\text{h}}$) was calculated by integrating semi-hourly F over the course of the day. Assuming that surface sapflow density was independent of diameter at breast height, a rough estimate of the transpiration of the *F. albida* layer in the parkland bottom (T) was derived from the mean $F_{d(\text{surface})}$ of two trees.

$$T = D_{\text{Parkbott}} \times \sum_i^{r_{\text{Parkbott}}} (F_{di} \times SA_i), \quad \text{eqn 4}$$

where T is the transpiration of the *F. albida* layer in the parkland bottom (mm h^{-1}), r_{Parkbott} is the mean radius at breast height in the parkland bottom (Table 1), i to r are successive 2 cm-wide sapwood

layers from cambium to 26 cm, D_{Parkbott} is the mean stand density in the parkland bottom, equal to eight trees ha^{-1} (Table 1), SA_i is the sapwood area of successive layers (dm^2) and F_{di} is the sapflow density ($\text{kg dm}^{-2} \text{h}^{-1}$) in the successive layers derived from surface measurement in two experimental trees and logarithmic fit (Fig. 1).

A linear interpolation was used to estimate transpiration between measurement dates. The annual transpiration estimate was integrated over the period where leaves were present.

Leaf water potential (Ψ_w) was measured during each experimental session, with a portable pressure chamber on individual leaves (three to five leaves per tree, on 10 trees). Predawn leaf water potential (Ψ_{wp} , MPa) was measured between 04.30 and 06.00 h solar time (GMT), when sapflow was minimum. Midday leaf water potential (Ψ_m) was measured during maximum sapflow on branches fully exposed to sunlight. Soil-to-leaf sapwood-specific hydraulic conductance (g_L , $\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was computed as the slope⁻¹ of the linear regressions between Ψ and F/SA , recorded every hour during a given day (see Fig. 2 for examples), with the intercept forced through Ψ_{wp} .

Climatic variables were measured within a shelter at 1.5 m height in the stand, simultaneously with sapflow (averaged every 30 min). Global radiation (linear thermopyranometer, INRA, France), temperature and relative humidity (Vaisala HMP 31 UT, Helsinki, Finland, calibrated before each session at Direction de la Météorologie Nationale, Ouagadougou), and wind speed (IFRF Mgx 100, Birmensdorf, Switzerland) were recorded. Penman potential evapotranspiration (PET) was computed from these data, assuming a linear relationship between net and global radiation ($R_n = 0.71 R_{go} - 15$, tested under temperate climate on forest stands) and using the conventional Penman formula; the computed values are used as indexes of evapotranspiration which are sufficient to record seasonal changes but may diverge slightly from real PET.

ROOTS AND SOIL WATER CONTENT

To observe rooting and soil water profiles, a well (denoted well 1) was dug at the end of the wet season (October 1995). It was located between the two trees monitored for sapflow at a distance of 11 m from the trunks, with a 2×0.8 m cross-section and a depth of 9.5 m. Rooting profiles revealed large amounts of *F. albida* roots, and root impacts were counted on the walls facing the trees. Soil water content was recorded twice, during October 1995 and March 1996 (beginning and end of the dry season, respectively). Soil cores of 500 ml were extracted horizontally, 40 cm beyond one wall of the well. Cores were taken every 25 cm in the topsoil, and every 100 cm below 1 m depth. In order to limit evaporation from the walls between coring sessions, the coring holes

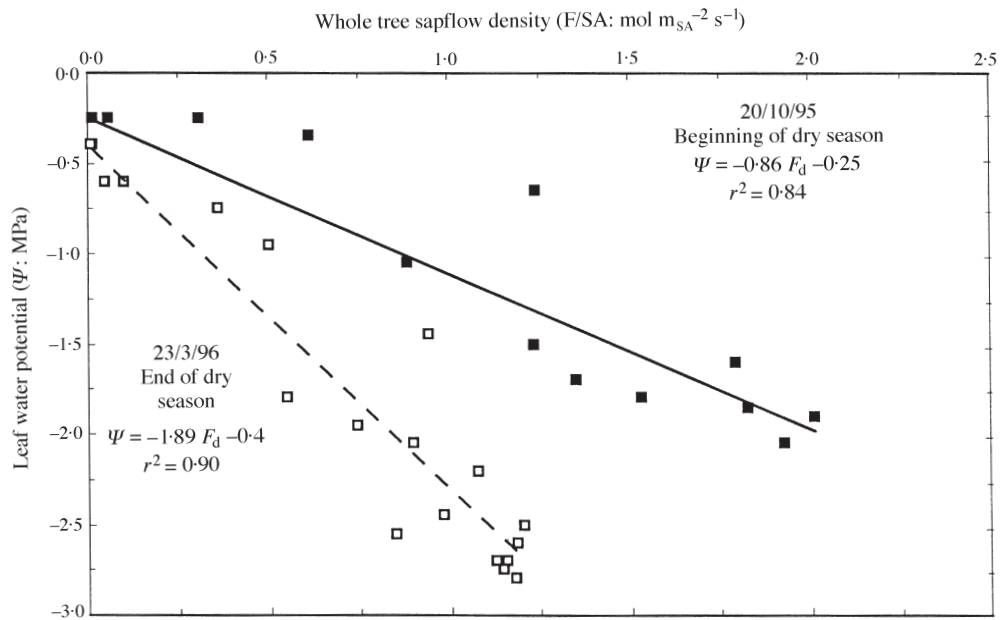


Fig. 2. Relationships between sapflow density integrated over the whole conducting sapwood (F/SA) and leaf water potential (Ψ) recorded during diurnal courses on an adult *F. albida* at the beginning (20 October 1995, black) and the end (23 March 1996, white) of the dry season. Ψ was lower in the morning than in the afternoon at a given sapflow density. Slopes⁻¹ of linear adjustments intercepted in predawn leaf water potential estimate the soil-to-leaf sapwood-specific hydraulic conductance (g_L).

were filled with dry sand, the wall covered with a plastic sheet, and the well closed with a cover. Gravimetric soil water content (H_G , kg kg^{-1}) was measured down to the bottom of the well. Values of H_G corresponding to pF 2.5, 3.0 and 4.2 were measured (Bunasols, Ouagadougou), and used to derive soil water potential (Ψ_S) from H_G . Dry bulk density (D_{db} , $\text{g}_{\text{soil}} \text{ml}^{-1}$) was measured using replicated steel rings with a volume of 100 ml. D_{db} and pF were not measured below 4.25 m, owing to rock resistance. Volumetric soil water content (H_V , $\text{m}^3 \text{m}^{-3}$), soil water storage (R , mm), extractable soil water (EW, mm) and relative extractable soil water (REW, %) were derived as follows for each layer and summed over the profile:

$$H_V = H_g \times D_{db}, \quad \text{eqn 5}$$

$$R = H_V \times z, \quad \text{eqn 6}$$

$$\text{EW} = R_{\text{pF3}} - R_{\text{pF4.2}}, \quad \text{eqn 7}$$

$$\text{REW} = \left(\frac{R - R_{\text{pF4.2}}}{\text{EW}} \right), \quad \text{eqn 8}$$

where z is the thickness of soil layer.

Root impacts were counted on each transverse wall by layer and grouped by diameter classes. Seasonal changes in the level of the water-table were monitored in the experimental well (well 1) and in a deeper one (well 2, at a distance of 200 m) after the first one had dried out during late March.

isotope composition ($\delta^{18}\text{O}$) were measured in well 1 during the experiments: about 200 ml of soil was cored horizontally, 40 cm beyond the wall and every 50 cm down to the bottom. During October 1996, a new well was dug (well 3), at 50 m distance, in an open field without trees. Water-table samples were collected deeply below the surface in well 2 with a hosepipe. Rain water was sampled on a daily basis with a raingauge: 62% of rainfall events were sampled during 1996, and 86% during 1997. All trees sampled for sapwater were located in the 0.46 ha experimental plot. About 100 ml sapwood were rapidly collected at breast height with a hatchet at 20.00 h.

Sapwood and soil samples were sealed immediately in glass vials and frozen (-20°C). The vials were equipped with a tap, directly connectable to the water extraction line. Sample water was totally extracted during a 24 h cryogenic vacuum distillation, and shipped to the 'Centre de Recherches Géodynamiques' (Thonon-les-Bains, France) in sealed vials. The ^{18}O content of water samples was measured using the equilibration method with CO_2 (Epstein & Mayeda 1953). The relative abundances of ^{18}O and ^{16}O were determined using a mass spectrometer (FINIGAN MAT CH7) and results expressed using δ , as per mil (‰):

$$\delta^{18}\text{O} = \left(\frac{R_e - R_s}{R_s} \right) \times 1000, \quad \text{eqn 9}$$

where R_e and R_s refer to the $[^{18}\text{O}]/[^{16}\text{O}]$ ratio in the sample and the SMOW standard (Standard Mean Ocean Water), respectively. The method has a precision of $\pm 0.1\text{‰}$.

Monthly or annual means of rain water were weighted, that is each individual rain isotopic measurement was multiplied by the amount of the corresponding rain volume, and their sum divided by the total rain amount.

Results

PHENOLOGY AND RADIAL GROWTH

Annual rainfall in 1995 and 1996 was 919 and 1065 mm, respectively (Fig. 3a). The maximum levels of leafiness and defoliation of the *F. albida* trees occurred during the middle of the dry and wet season, respectively, as expected from the the reverse phenology of this species (Fig. 3b). The variability between trees was larger during the transient periods.

Leaf growth started during the last rains. Leaf shedding never started during the dry season, but always about 1 month after the first rains. During 1996, rain events began 1 month earlier than during 1995, and leaf shedding also started earlier. However, first rains of 1996 were scarce and leaves were shed far more gradually than during 1995. On the contrary, the important rains of September 1996 resulted in a delay and a slow-down of leaf initiation. Leafiness therefore

appeared inversely related to the distribution of rain events.

Radial growth started on 15 October 1996, i.e. after leaf initiation (Fig. 3b). The mean annual radial increment was 0.71 ± 0.25 cm ($n = 11$ trees). A slow-down of growth occurred during mid-February 1996, which was about 2 months before the beginning of leaf shedding. Radial growth was nil during the defoliated period, as expected, and trunk shrinkage was even observed.

REGULATION OF TRANSPIRATION

Predawn leaf water potential (Ψ_{wp}) was hardly affected during the severe dry period (Fig. 3a). Ψ_{wp} was close to optimal on 10 October 1996 (-0.25 MPa) and diminished slowly to -0.5 MPa (3 March 1996). Thus the trees experienced only moderate water stress. After the first rains, Ψ_{wp} recovered to -0.3 MPa (5 July). Leaf shedding occurred during this recovery phase and was thus independent of water stress. Accordingly, the midday leaf water potential (Ψ_m) remained quite stable over the entire dry season, within the range -2.0 to -2.7 MPa. The high value recorded during 5 July 1996, was obtained on trees

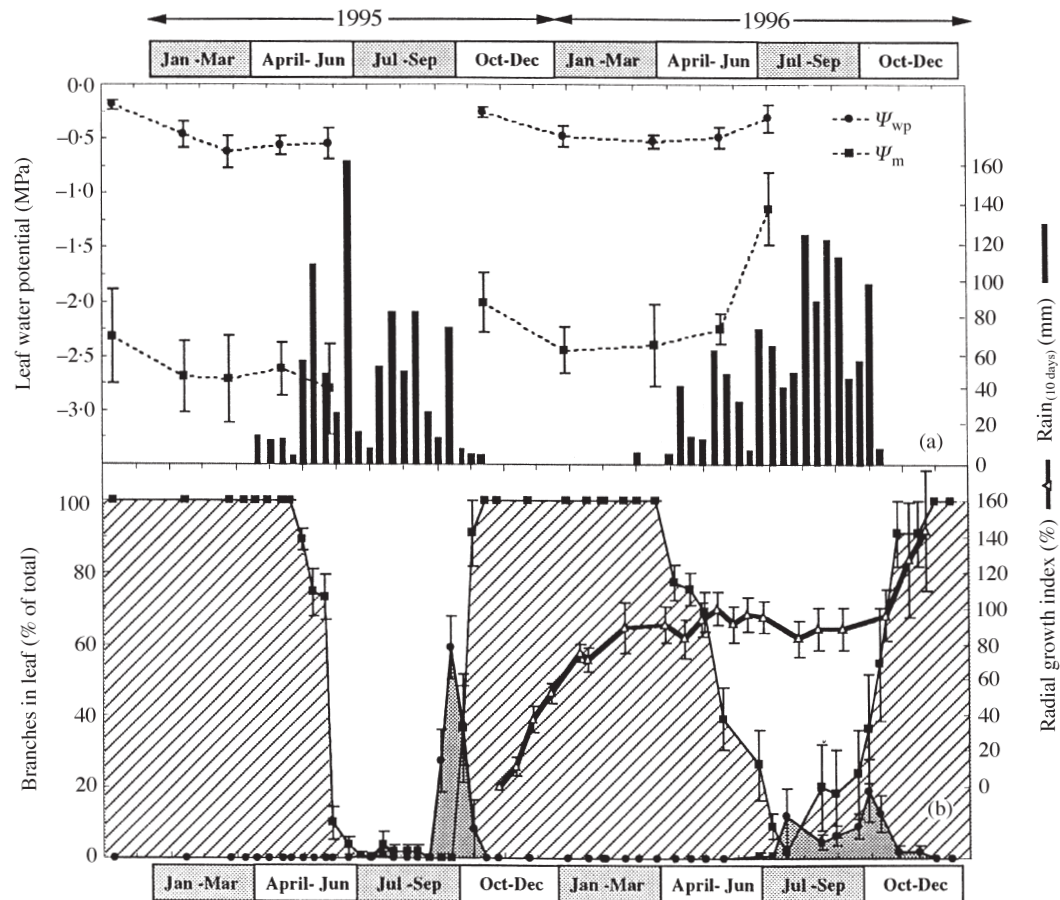


Fig. 3. Rain, water potential, phenology and radial growth of *F. albida* during the course of two successive years. (a) Rainfall (cumulated over 10 day periods), predawn (Ψ_{wp}) and midday (Ψ_m) leaf water potential (mean \pm SD). (b) Fraction of branches bearing newly formed (grey area), or mature leaves (hatched area) and relative radial growth index (mean \pm SE). $n = 11$ trees.

displaying newly formed leaves, which transpired less than the older ones (based on sapflow data), and therefore maintained high values of Ψ .

Transpiration was moderately affected by drought, at the daily and seasonal scales. An example of a daily time-course of sapflow density (F_d , $\text{kg dm}^{-2} \text{h}^{-1}$) is presented in Fig. 4. It was measured during the period of high predawn water potential (October 1995). Minimum sapflow was recorded before dawn and maximum was observed after noon. F_d increased very early in the morning, as compared to the course of Penman Evapotranspiration (PET). This was owing to the lateral interception of irradiance by the isolated tree crown in the morning. F_d was still significant after sunset, revealing a very slow internal re-equilibration between crown and soil, and possibly the maintenance of some transpiration, owing to a high

vapour pressure deficit in the atmosphere. No midday decrease of F_d occurred.

Table 2 presents daily cumulative whole tree sapflow ($F_{24\text{h}}$) values on a daily and annual basis. Maximum levels of sapflow were recorded during October 1995. $F_{24\text{h}}$ thereafter decreased moderately, reaching 75%, 71% and 62% of this maximum, during the measurement days of December, March and May, respectively. $F_{24\text{h}}$ then displayed a drastic reduction during leaf shedding in July. The annual transpiration of the *F. albida* layer of the stand was coarsely computed from these data: it represented only ca. 4% of the annual rain input.

Global radiation, vapour pressure deficit (VPD) and Penman evapotranspiration (PET) increased during the dry season and were highest during the hottest period (21 March 1996, Fig. 5a). Meanwhile, the percentage branches in leaf was stable, and total leaf area still increasing as a result of twig growth (Fig. 5b). However, the ratio $F_{24\text{h}} \text{ PET}^{-1}$ decreased from 80 to 35 $\text{kg mm}^{-1} \text{ tree}^{-1}$ during the dry season. After the first rains, VPD diminished and $F_{24\text{h}} \text{ PET}^{-1}$ partially recovered, despite a 50% reduction in leafiness. Leaf shedding then resulted in a complete cessation of transpiration.

The soil-to-leaf, sapwood-specific hydraulic conductance (g_L) was computed from diurnal changes in Ψ and in F_d (Fig. 2). The relationship between the two parameters was almost linear, with a hysteresis between morning and afternoon values (lower sapflow at a given leaf water potential in the morning than in the afternoon). In addition, g_L was lower during the late dry season. The seasonal changes of g_L are reported in Fig. 5b, showing a decrease from 1 to 0.62 $\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ between October and December, and a more gradual one down to 0.46 $\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ till the end of May. During July, there were not enough leaves left for water potential measurements.

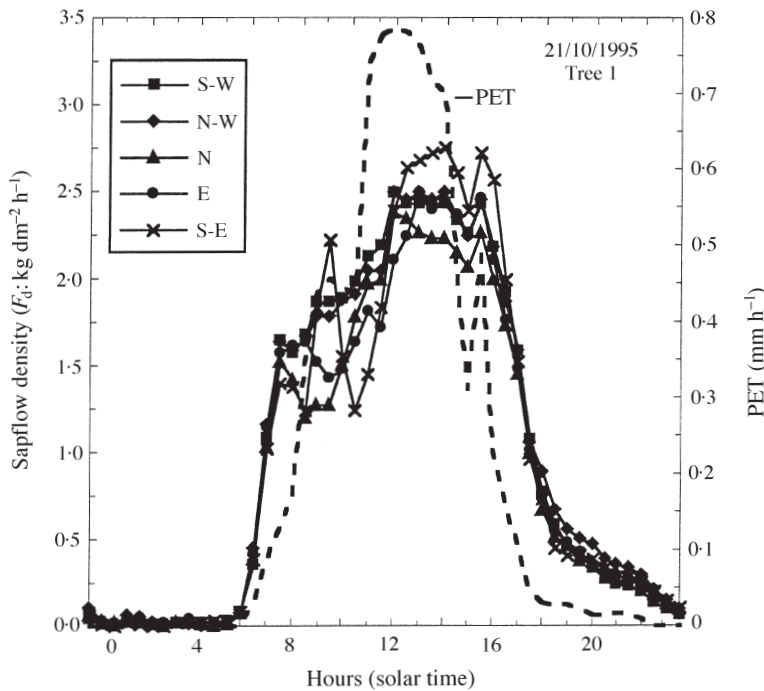


Fig. 4. Example of diurnal time-course of sapflow density (F_d) measured at breast height in the superficial sapwood of an adult *F. albida* tree (d.b.h. = 64 cm) and of Penman Evapotranspiration (PET). Five gauges inserted at breast height in five different azimuths (orientation in the insert).

DEPTH OF WATER UPTAKE

Soil moisture and rooting depth

The soil profile was described from the surface down to 4.25 m (Fig. 6). The texture was clayey-sand from

Table 2. Seasonal changes of the daily whole tree sapflow ($F_{24\text{h}}$) of adult *F. albida* (mean value for two trees, with 5 repetitions per tree); estimated transpiration of the trees from the parkland bottom (T, see eqn 4); estimated fraction of annual rain input transpired by the trees. Agroforestry parkland of Dossi, Burkina Faso, west Africa, 1995–1996

	Cumulative daily values					Cumulative annual values
	20 Oct. 1995	16 Dec. 1995	20 Mar. 1996	25 May 1996	5 Jul. 1996	
Mean sapflow of experimental trees ($F_{24\text{h}}$, kg tree^{-1})	386	290	275	239	52	67112
Estimated daily transpiration of the <i>F. albida</i> layer (T, mm)	0.213	0.160	0.151	0.131	0.028	37
T as a fraction of annual rainfall						4%

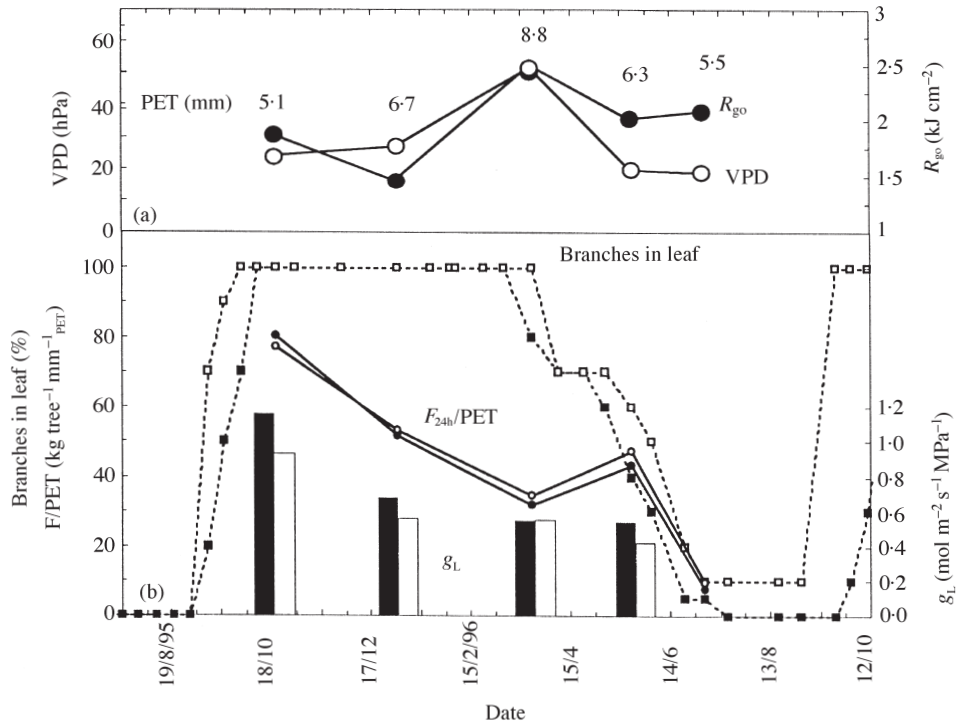


Fig. 5. Seasonal time-course of climate variables and regulation of transpiration in *F. albida*. (a) Diurnal mean vapour pressure deficit (VPD, white), daily cumulated global radiation (R_{go} , black) and potential-evapotranspiration (PET, Penman). (b) Fraction of branches in leaf, sapflow-to-potential evapotranspiration ratio (F_{24h}/PET), and soil-to-leaf sapwood-specific hydraulic conductance (g_L). In Fig. 5b, values from two adult *F. albida* trees (black and white) measured during five sessions.

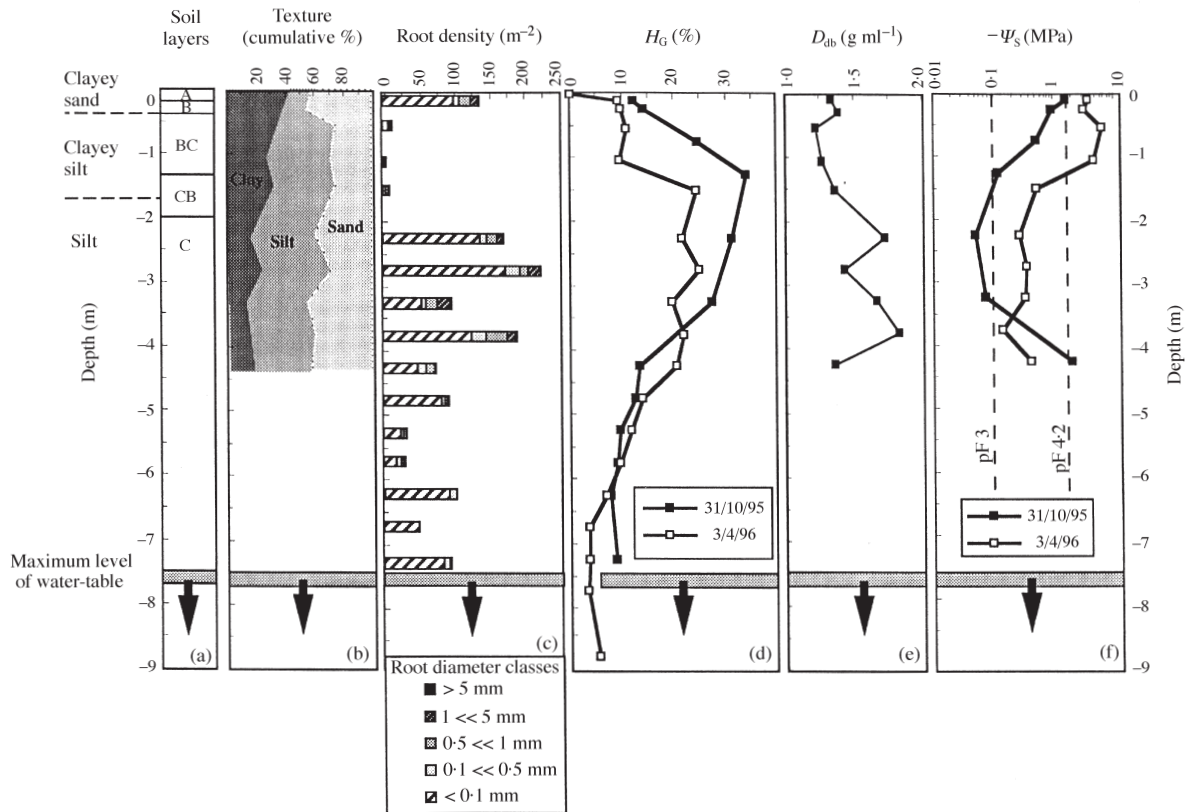


Fig. 6. Soil water availability in well 1, dug among the trees. (a) Soil layers; (b) texture (cumulative percentage of clay, silt and sand in the fraction of soil < 2 mm); (c) root density at the beginning of the dry season on the lateral walls; (d) gravimetric soil water content (H_G) at the beginning (black) and at the end (white) of the dry season; (e) dry bulk density, D_{db} ; (f) soil water potential (Ψ_s) at the beginning and the end of the dry season. Well dug during October 1995 between the two adult *F. albida* trees monitored for sapflow (distance to trunks, 11 m; length, 2 m; width, 0.8 m; depth, 9.5 m). Each value corresponds to one single measurement, root densities and D_{bd} to the mean of two measurements.

zero to 0.4 m, clayey-silt down to 1.7 m, and silt below this limit. This indicates a high water storage capacity. However, the fraction of coarse elements (> 2 mm) was large and increased downwards.

The vertical distribution of roots was described at opening of the well during October 1995 (Fig. 6c). Roots were recorded down to 7.25 m. Fine roots were numerous in the A-layer (0 to -0.20 m). Only a few roots were observed in the 0.4–1.7 m clayey-silt layer. They were very numerous again from 2 to 3.75 m, and scarce below, mainly located in cracks of the weathered rock. Rooting stopped in the vicinity of the water-table, the level of which fluctuated from 7.5 m (November, end of wet season) to ca. 11 m (end of dry season).

The vertical distribution of gravimetric soil water content (H_G) and of dry bulk density (D_{db}) is illustrated in Fig. 6d,e. Sampling for D_{db} was abandoned at a depth of 4.25 m, owing to low accuracy induced by the large fraction of coarse elements below this limit. Profiles of soil water potential (Ψ_S , Fig. 6f) were computed from soil water retention curves. From 1.5 to 3.5 m, the soil layers presented the largest values of H_G throughout the dry season and constituted a major water reservoir. The extractable water computed from 0 to 4.5 m was close to 780 mm (174 mm m⁻¹ of soil) during October. Roots were very abundant around 3.0 m. The relative extractable water (REW) of the soil layers between 0 and 4.5 m was estimated to be 93% in October and 36% in April. Cumulated water losses were ca. 450 mm, i.e. about half the annual rain

amount, during a period where annual crops were absent. However, the seasonal variations of soil humidity could not be solely attributed to extraction by *F. albida* roots. The superficial soil layers (0 to -1.5 m) dried severely after October; all annual plants dried out and roots of *F. albida* degenerated. In these layers, water loss during late dry season may be attributed mainly to direct soil evaporation. In the major soil water reservoir (1.5–3.5 m), water depletion may have originated from root extraction. Nevertheless, occurrence of drainage probably explains the observed water gain in the layers between 3.5 and 5.75 m during April, and depleted the 1.5–3.5 m layers concurrently with extraction by *F. albida* roots.

Throughout the dry season, predawn leaf water potential (Ψ_{wp}) of the trees declined from -0.28 to -0.46 MPa, indicating that they equilibrated overnight with soil layers ranging from 2 to 4.25 m (curve of 3 April 1996, Fig. 6f). Rooting densities and soil water features suggest that *F. albida* could have absorbed water from the reservoirs between 1.5 and 4.25 m during a large part of the dry season. However, soil water potential was not recorded below 4.25 m, and trees were likely to have equilibrated as well with deeper layers, closer to the water-table.

Oxygen isotopes

Isotopic composition of oxygen ($\delta^{18}\text{O}$) of rain water displayed seasonal variations during the 1996 and 1997 wet seasons, with similar patterns during the 2 years (Fig. 7b). $\delta^{18}\text{O}$ of rains was high at the beginning of the rainy season, decreased during the period of heaviest rains and increased again. In contrast, the ground-water composition was very steady, averaging $-4.4 \pm 0.3\text{‰}$ ($n = 31$). Interestingly, the annual weighted average of rain $\delta^{18}\text{O}$ was -4.2‰ during 1996 and -3.4‰ during 1997, that is very similar to ground-water. $\delta^{18}\text{O}$ of xylem sap extracted from the trunks was generally close to -4‰ (Fig. 7c), i.e. to the values recorded in ground-water. Significant deviations of xylem sap to higher values were recorded only during the beginning of the rainy season (June–July 1996), corresponding to a transiently higher value in rain water.

Soil water $\delta^{18}\text{O}$ profiles measured at the beginning and the end of the dry season 1995/1996 in a well close to the trees (well 1: Fig. 8a) and in a second one (1996/1997: well 3, Fig. 8b) under a tree-free area displayed dissimilar profiles, indicating a probably large lateral and annual variability of $\delta^{18}\text{O}$ profiles in the soils. Each profile exhibited a rather complex pattern. In the superficial soil layers, $\delta^{18}\text{O}$ was generally less negative, or even positive. A decrease of $\delta^{18}\text{O}$ was measured from the surface to -1 m (well 1) and to 2.25 m (well 3). Such a steep superficial gradient can be attributed mainly to direct soil evaporation. The gradient reversed below and this can correspond to the

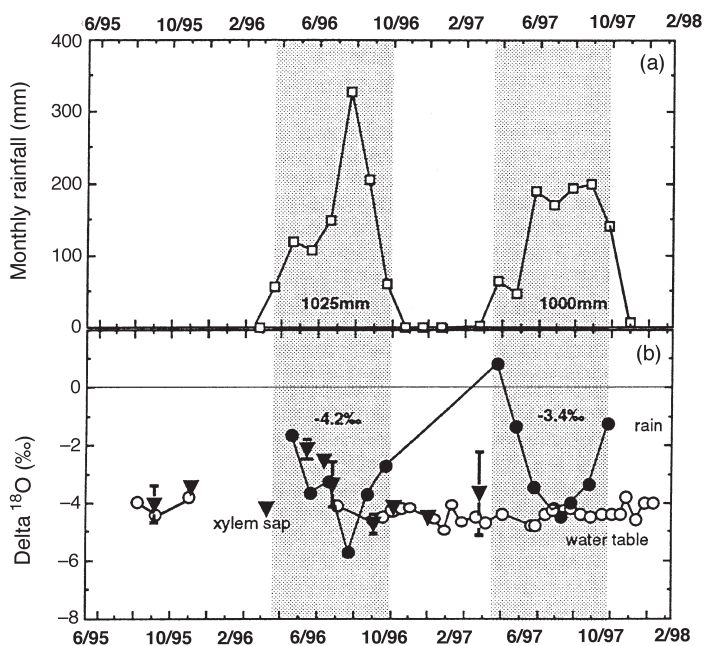


Fig. 7. Seasonal variability of the isotopic composition ($\delta^{18}\text{O}$) of water oxygen. (a) rainfall (cumulated monthly); (b) $\delta^{18}\text{O}$ of rain water (symbols, monthly mean of individual rain compositions weighted by corresponding rain amount; text, annually weighted mean), of the deep water-table (white) and of xylem sap (triangles, mean \pm SD; $N = 2\text{--}8$ trees).

signature of transitions between dry and wet season when incoming rain-water displayed lower $\delta^{18}\text{O}$ values. Another peak was recorded in the deeper layers. These vertical fluctuations in soil water $\delta^{18}\text{O}$ values were probably the signature of seasonal changes in rain water composition, the traces of which can be kept several years back in these deep soils.

During October 1995, values from the whole soil profile recorded in well 1 were lower than those of the xylem sap, except in the deepest layers. This evidences that the trees were extracting water mainly nearby the water-table. During March, xylem sap was close to that of soil water at 3 m and at 7 m depth, and the depth of water uptake remains ambiguous.

Discussion

INTENSITY OF THE DROUGHT STRESS EXPERIENCED BY *F. ALBIDA* TREES DURING THE DRY SEASON

Despite the long-lasting dry season, *F. albida* trees avoided severe drought stress in these Sudanese conditions. This lack of drought stress was probably related to the complex rooting system of the trees. Roots were distributed among three main soil compartments: (1) abundant fine roots in the superficial layers; (2) the

majority of roots between 2 and 4 m depth; (3) an appreciable number down to the zone of capillary rises from the water-table (7.5 m). The soil water content measurements revealed a large water reservoir from 2 to 4 m, the water potential of which was still above -0.5 MPa at the end of the dry season. Consistently, predawn leaf water potential, which is usually the equilibrium potential of trees with the deepest and wettest soil layers in the profile (Améglio *et al.* 1999), decreased only very slightly, to a level which could correspond to the soil water potential either in the water reservoir located between 2 and 4 m depth, or in the capillary rises in vicinity of the water-table. It was much higher than the value of -1.1 MPa reported by Ward & Breen (1983) along the Kuiseb river (Namibia), where *F. albida* was distributed in its natural riparian habitat. During late dry season, soil-to-leaf sapwood-specific hydraulic conductance nevertheless decreased by half, revealing probably a slight water stress. In a temperate sessile oak stand, on a soil with fine texture, Bréda *et al.* (1993) found a similar reduction which they attributed to changes in the hydraulic conductance between soil and roots.

Sapflow density displayed maximum values of ca. $2.5 \text{ kg dm}^{-2} \text{ h}^{-1}$, which is similar to values recorded on the temperate, ring porous, sessile oak for instance (Bréda *et al.* 1993) and much more than for *Acacia tortilis* in Sahel ($0.7 \text{ kg dm}^{-2} \text{ h}^{-1}$ in March: Do *et al.* 1997). Daily whole-tree sapflow ($F_{24 \text{ h}}$) decreased by one-third during the dry season, despite the increased Penman Potential Evapotranspiration (PET). Because $F_{24 \text{ h}} \text{ PET}^{-1}$ decreased by 50% in the meantime and before reduction in leaf area index, it is likely that canopy conductance diminished during the course of the dry season as a result of stomatal closure. *F. albida* seems to display a rather high stomatal sensitivity to soil water depletion. Rouspard, Joly, & Dreyer (1996) showed, for instance, that a complete stomatal closure was recorded in potted juveniles for a predawn water potential of -1 MPa. In addition to soil water depletion, increased vapour pressure deficit could have induced decreases in stomatal conductance. Owing to low tree density, the *F. albida* canopy is closely coupled to the atmosphere. Negative effects of vapour pressure deficit on canopy were observed in oak stands in the absence of soil drought (Bréda *et al.* 1993). Similarly, a small reduction of the ratio transpiration/PET was observed in the phreatophytic species *Prosopis* and *Salix* growing in the Mojave desert floodplain with a water-table at 3 m, when Penman evapotranspiration increased (Sala *et al.* 1996). The phreatophyte *Prosopis glandulosa* displayed no sensitivity to high vapour pressure deficits as long as the soil remained wet and a severe one during drought (Dugas, Heuer & Mayeux 1992). *Faidherbia albida* in the field probably reduced stomatal conductance in response to a combination of moderate soil water depletion and of increased vapour pressure deficit during the course of the dry season.

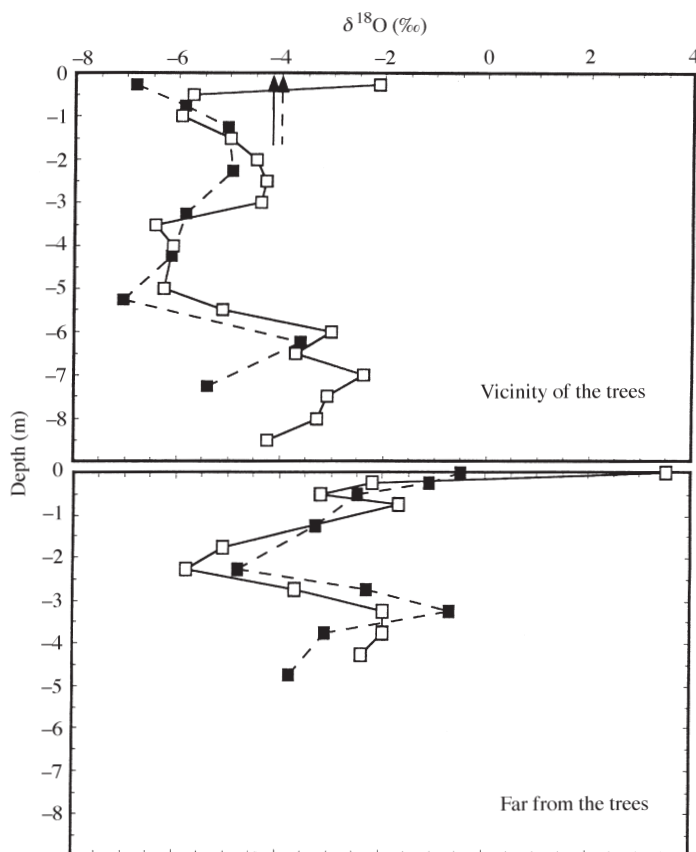


Fig. 8. Vertical profiles of the isotopic composition of water oxygen ($\delta^{18}\text{O}$) as recorded in two different wells. (a) Well 1, dug between the two adult *F. albida* trees monitored for sapflow, and sampled at the beginning (black and dotted lines) and the end (white, full line) of the dry season 1995/1996. (b) Well 3, far from the tree stand, same symbols. Arrows indicate $\delta^{18}\text{O}$ of the xylem sap at the same dates.

Altogether, these observations suggest that only a rather moderate drought stress affected *F. albida* during the dry season, which was unexpected, considering the local climate and the reverse phenology of this species, but can be explained by the rooting pattern and depth of water uptake.

EFFECTS OF DROUGHT ON PHENOLOGY AND RADIAL GROWTH

Leaf shedding started on *F. albida* trees after the first rains, when predawn leaf water potential had already recovered from the moderate dry-season decline. It was therefore not induced by an increased late dry season water stress. Duration and magnitude of leafiness were inversely related to precocity, amount and duration of rains, as shown by their interannual variability. This confirms earlier observations by Depommier (1996). The mechanisms of leaf shedding induction still remain to be understood in this species. Our results provide evidence that leaf shedding and drought are independent in this parkland, but this conclusion should not be extended to more arid zones or to juveniles during establishment growth. The question of why leaves are initiated only at the end of the wet season remains open.

Radial growth resumed when two-thirds of the branches were already fully leafed. It displayed two phases, one of rapid expansion from October to mid-February, and a second one of slow-down, and even stop from February to June. Interestingly, the slow-down occurred during the end of the dry period. It could be partly the result of drought-induced stomatal closure limiting assimilate supply. The annual diameter increment was nevertheless within the range of 0.4–1.3 cm reported for adult *F. albida* trees by Gourlay (1995) and Depommier (1996). Such an important growth rate confirms that the water and nutrient availability were favourable during a large fraction of the dry season in these Sudanese conditions. These results should be assessed in more arid conditions or during the juvenile stages.

OBLIGATE OR FACULTATIVE PHREATOPHYTE?

The ability of *F. albida* to withdraw water from deep soil layers was frequently inferred from indirect observations (Ward & Breen 1983) but not assessed experimentally. Our measurements in rain, sap, ground-water and soil support the feasibility of the isotopic method in such an environment, and points out some limitations as well.

Rains that occurred during the middle of the rainy season were depleted in heavy isotopes, as compared to early rains. This seasonal pattern was also observed by Mathieu & Bariac (1996) in Barogo, Burkina Faso, and by Smith *et al.* (1997) in Niger, and provides a useful signal. In addition, the upper soil layers were enriched in ^{18}O during the dry season. The sinuous

profiles of $\delta^{18}\text{O}$ we measured in the soil were probably induced by the seasonal variability in $\delta^{18}\text{O}$ of rains, by evaporation and by water dynamics in soil. The deep profile accumulated signatures from several (at least two) rainy seasons with a large seasonal variability visible in successive soil layers. The annual weighted average of rainfall almost corresponded to the composition of ground-water measured in this parkland, indicating that a large proportion of rainfall reached the water-table without significant evaporation

The composition of the water-table displayed a remarkable stability, similar to what had been observed by Mathieu & Bariac (1996) and Flanagan & Ehleringer (1991); its composition was very close to the one reported in Niger during 1993 (Smith *et al.* 1997). $\delta^{18}\text{O}$ of xylem sap collected from the trees remained very close to this composition during the whole dry season, except during early rainy events, when it increased significantly and revealed absorption of water by superficial roots.

The complexity of $\delta^{18}\text{O}$ profiles in the soil made any attempt to quantify the relative contribution of given soil layers *vs* that of the water-table, to transpiration flow in the tree almost impossible. Absorption from the very superficial soil layers down to 1 m was probably almost nil, as attested by the severe water depletion and the root decay that was recorded in these layers. An important contribution of the deep water-table is highly probable during a large fraction of the dry season, but deep soil layers between 2 and 4 m may have also significantly contributed to transpiration flux of the trees. The first rains were nevertheless readily absorbed by superficial roots during the beginning of the rainy season.

Faidherbia albida thus behaves like a facultative phreatophyte, like *Tamarix* sp. (Busch *et al.* 1992). *Eucalyptus camaldulensis*, a species grown in the semiarid tropics, also have the ability to use deep water (Thorburn & Walker 1994; Dawson & Pate 1996). Windbreaks of *Azadirachta indica* used ground-water during the rainy season provided the water-table was at a moderate depth in the soil (6–8 m), while the associated crop relied solely on the superficial (2–3 m) soil layers (Smith, Jarvis & Odongo 1997). In *Banksia prionotes*, Dawson & Pate (1996) observed that deep-water uptake by the sinker root was largest when rain input was lowest. During the dry period, shallow roots remained well hydrated and plants were able to take profit of the early rainy events, similarly to what we observed in *F. albida*. The superficial roots of *F. albida* were probably kept alive during the dry season, with exception to the finest ones that decayed. This would have important implications in terms of carbon budget. Though these roots have a low contribution to annual water uptake, they could have a major importance for superficial mineral uptake. Mineral nutrients are generally concentrated superficially and available when these lay-

ers are wet, that is during the wet period. The lateral roots of dimorphic plants are commonly dedicated to nutrient acquisition, notably for several phreatophytic woody plants in Mediterranean type ecosystems of south-west Australia (Jeschke & Pate 1995).

In conclusion, *F. albida* displayed efficient growth during the dry season. The trees were tapping groundwater at large depths in the soil. The root system was complex, and colonized several soil compartments, with different water dynamics. Trees were likely to exploit all compartments at different periods of the year. As a result, drought had only a moderate impact on the transpiration of this drought-avoiding species. Annual transpiration was high, like in many other phreatophytes. However, owing to the low tree density in the parkland, stand transpiration represented only about 5% of the annual rainfall. This confirmed the suitability of this species for agroforestry purposes, with respect to water use. The lack of water consumption during the cropping season (reverse phenology), the low water consumption (low densities) and the use of deep-water reserves make this tree a minor competing species for water with the associated crops. It could explain partly its success in west-African parklands. The present results are mainly valid for Sudanese conditions, and it would be worth investigating the water relations of *F. albida* in more arid conditions.

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