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Stable annual pattern of water use by *Acacia tortilis* in Sahelian Africa

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Summary Water use by mature trees of *Acacia tortilis* (Forsk.) Hayne *ssp. raddiana* (Savi) Brenan var. *raddiana* growing in the northern Sahel was continuously recorded over 4 years. Water use was estimated from xylem sap flow measured by transient heat dissipation. Concurrently, cambial growth, canopy phenology, leaf water potential, climatic conditions and soil water availability (SWA) were monitored. In addition to the variation attributable to interannual variation in rainfall, SWA was increased by irrigation during one wet season. The wet season lasted from July to September, and annual rainfall ranged between 146 and 367 mm. The annual amount and pattern of tree water use were stable from year-to-year despite interannual and seasonal variations in SWA in the upper soil layers. *Acacia tortilis* transpired readily throughout the year, except for one month during the dry season when defoliation was at a maximum. Maximum water use of about 23 l (dm sapwood area)$^{-2}$ day^{-1} was recorded at the end of the wet season. While trees retained foliage in the dry season, the decline in water use was modest at around 30%. Variation in predawn leaf water potential indicated that the trees were subject to soil water constraint.

The rapid depletion of water in the uppermost soil layers after the wet season implies that there was extensive use of water from deep soil layers. The deep soil profile revealed (1) the existence of living roots at 25 m and (2) that the availability of soil water was low (–1.6 MPa) down to the water table at a depth of 31 m. However, transpiration was recorded at a predawn leaf water potential of –2.0 MPa, indicating that the trees used water from both intermediary soil layers and the water table. During the full canopy stage, mean values of whole-tree hydraulic conductance were similar in the wet and dry seasons. We propose that the stability of water use at the seasonal and annual scales resulted from a combination of features, including an extensive rooting habit related to deep water availability and an effective regulation of canopy conductance. Despite a limited effect on tree water use, irrigation during the wet season sharply increased predawn leaf water potential and cambial growth of trunks and branches.

Keywords: deep roots, dry savanna, heat dissipation method, hydraulic conductance, rainfall, transpiration, xylem sap flow.

Introduction

The northern Sahel represents one of the driest savannas in the world (Le Houérou 1989). Potential evaporation is in excess of 2000 mm year^{-1}. The wet season lasts only three months, and rainfall averages between 200 and 400 mm year^{-1}, with high interannual variability (coefficient of variation of 37%). Groundwater is usually deeper than 30 m. *Acacia tortilis* (Forsk.) Hayne *ssp. raddiana* (Savi) Brenan var. *raddiana*, a dominant tree species in the area (Breman and Kessler 1995, Le Floc'h and Grouzis 2003), represents an efficient model of drought adaptation, but little is known about its water use and the influence of rainfall on its seasonal and annual patterns of water use. The control of water use by trees in water-limited biomes has been much debated (Eamus et al. 2000) and has important consequences for strategies of drought adaptation and optimal balance between carbon gain and water loss (Eamus and Prior 2001). Moreover, a detailed knowledge of seasonal tree water use and factors affecting its regulation is fundamental to understanding the impacts of climate change on hydrological and carbon balances at the ecosystem level.

Rainfall would be expected to have a major influence on tree water use in a water-limited biome, such that water use would be highest in the wet season, declining with soil water availability (SWA) during the dry season despite an increase in evaporative demand, thereby limiting canopy desiccation. There are few long-term studies of whole-tree water use in the seasonally dry tropics (Eamus and Prior 2001); however, several studies have shown that, contrary to expectation, tree water use in such a climate does not differ greatly (Cook et al. 1998, Roupsard et al. 1999), or at all (Meinzer et al. 1999, Eamus et al. 2000, Hutley et al. 2001), between the wet and dry seasons. Season-to-season uniformity in water use can be attributed to constancy in the balance between evaporative demand of the atmosphere and canopy conductance as determined by factors such as SWA, hydraulic conductivity of xylem, leaf area and stomatal conductance. In particular, leaf phenology, which roughly reflects seasonal changes in leaf area, is a principal driver of seasonal changes in transpiration.

Acacia tortilis ssp. raddiana is a semi-evergreen or drought-deciduous species (Breman and Kessler 1995, Le Floc'h and Grouzis 2003). In the northern Sahel, the full canopy stage of this species lasts between 6 and 8 months, including the 3-month rainy season and part of the dry season (Do et al. 2005). The ability to maintain leaf area and transpiration during the dry season may be explained by high water availability in the upper soil layers, as in the case of riparian vegetation, or a deep rooting habit that gives access to water from the subsoil or the water table, or both (Cook et al. 1998, Roupsard et al. 1999). That transpiration does not increase during the dry season in response to increasing evaporative demand, despite the availability of soil water, suggests strong stomatal regulation as reported in other dry habitats (Meinzer et al. 1999, Eamus and Prior 2001). Where deep water supply is limited, Eamus et al. (2000) and Hutley et al. (2001) hypothesize that stable dry season water use results from limited xylem conductivity associated with the ability to tolerate low water potentials without runaway xylem embolism. If this interpreation is correct, it implies that dry season conditions determine wet season water use by defining the tree's hydraulic architecture.

These studies did not consider variability within and among years, because they were conducted over short measurement periods at the end of the wet and dry seasons within a single year. Moreover, they were conducted under environmental conditions that are less dry than the northern Sahel, and where, in particular, SWA is higher during the dry season.

To investigate water use of *A. tortilis* growing in the northern Sahel, we measured sap flow in mature trees continuously over a 4-year period, with concurrent measurements of leaf water potential, SWA and climatic conditions. In addition to the natural interannual variation of rainfall, water availability in the upper soil was maximized during one rainy season by irrigation. Our objectives were, first, to quantify seasonal and annual patterns of water use by *A. tortilis*, and second, to analyze changes in water use between the wet and dry seasons and assess the effect of increased water availability during the wet season. Cambial growth was monitored concurrently. Our hypotheses were that during the full canopy stage, tree water use declines throughout the dry season, the decrease being greatest during the period of defoliation and that higher water availability during the wet season enhances seasonality and increases both water use and growth.

Materials and methods

Site

The study was carried out in northern Senegal, near the village of Souilene (16°20′ N, 15°25′ W, 5–10 m a.s.l.) located 20 km south of Dagana in the grazing land ecosystem of the sandy Ferlo. Annual rainfall averages 280 mm, mean annual temperature is 28.7 °C, and mean maximum and minimum temperatures are 41 and 22 °C for the hottest month (May), respectively and 31 and 14 °C for the coldest month (January), respectively. The sparse woody community is dominated by three species: *A. tortilis* and *Balanites aegyptiaca* (L.) Del, comprising the tree layer (90 ha^{-1}), and *Boscia senegalensis* (Pers.) Lam in the shrub layer (50 ha^{-1}). The soil is deep and sandy, with mean contents of sand, clay, organic matter, nitrogen and total phosphorus (P_2O_5) of 90%, 6%, 0.18%, 0.15‰ and 0.3‰ in the first meter of soil, respectively.

The studied population of 39 mature individuals was located in a 1-ha area that has been protected since 1989. Trunk diameter 30 cm above the soil varied from 5 to 45 cm, with 70% of the population having diameters between 15 and 30 cm. Tree height ranged from 5 to 10 m. Three trees of average diameter were chosen in a grove for the long-term study of water use. Mean tree height was 7 m, crown projected area was 30 m^2, and mean trunk diameter was 17.4 cm at a height of 1.3 m.

Sap flow measurement

Tree water use was estimated from xylem sap flow measured with a transient thermal dissipation (TTD) system (Do and Rocheteau 2002*a*), which is a modification of the continuous thermal dissipation method of Granier (1985). The modification avoids the influence of passive temperature gradients in the experimental trees (Do and Rocheteau 2002*b*). The TTD system is based on the Granier probe design, heating power and empirical response formulation, but with a cyclic schedule of heating and cooling and a specific calibration (Do and Rocheteau 2002*a*). A cycle of 45 min heating and 15 min cooling was used. Zero flux signal was determined each night assuming that sap flow was negligible at the end of the night (see details below). Total sap flow (F) was calculated as: $F = (\mathrm{SFD})A_{\mathrm{sw}}$, where SFD ($\mathrm{l\,dm^{-2}\,h^{-1}}$) is sap flow density per sapwood area and A_{sw} ($\mathrm{dm^2}$) is cross-sectional area of conducting wood at the level of the heating probe. The area of conducting wood was determined from observations of whole sections of freshly cut trees and cores. Heartwood was distinguished from sapwood by its distinct color, which was redder and duller than the sapwood. To account for cambial growth, sapwood area was calculated from the external trunk diameter based on the formula:

$$A_{\mathrm{sw}} = \pi(R_{\mathrm{w}}^2 - R_{\mathrm{h}}^2)$$

where R_{w} is wood radius (excluding bark) and R_{h} is heartwood radius. The radii were related to the external diameter (D_{ext}; cm) by following relationships based on 14 samplings of external diameters ranging from 9 to 36 cm: $R_{\mathrm{w}} = 0.49D_{\mathrm{ext}} - 0.39$ ($r^2 > 0.99$); and $R_{\mathrm{h}} = 0.48D_{\mathrm{ext}} - 5.02$ ($r^2 = 0.93$).

Probes were inserted into the trunks 1.3 m above the soil, at which height estimated mean sapwood area was 1.73 $\mathrm{dm^2}$, representing an approximate conductive radius of 4.7 cm after bark removal, which was 0.5 cm thick. Probes 2 cm in length were inserted into a hole 3 cm deep where they were fully within the conductive sapwood. To account for circumferential variation in each tree, three probes were inserted at different azimuths (North, South-East and South-West). After probe insertion, the exposed parts of the needles were coated with silicone. The trunk area containing the probes was shielded from direct sunlight. Probes were connected to a data logger. Hourly SFD were cumulated over 24 h to calculate daily SFD measurements or daily total flow. Daily total flow is an estimate of daily tree water use or transpiration, ignoring changes in tree water storage.

Estimates of tree water use from sap flow measurements are subject to various uncertainties (Köstner et al. 1998, Lu et al. 2004), one being in the estimation of the signal at zero flux. The classical method considers that the maximum value occurs each night to correspond with zero flux, and that seasonal variation in the maximum signal at night results mainly from changes in xylem water content. To test this hypothesis, we compared three methods of estimating the zero flux signal based on maximum signals recorded at the end of the night: (1) maximum value recorded each night; (2) maximum values calculated from a spline curve fitted over 10 days; (3) maximum values calculated from a spline curve fitted over 30 days. The estimates of daily maximum sap flow density based on the three methods were compared with the gradients between minimum and predawn leaf water potentials recorded on the same day, which are also related to transpiration. The first method gave the best agreement ($r^2 = 0.36$, $n = 46$) compared with the other methods ($r^2 = 0.28$ and 0.27, respectively), so we used Method 1, i.e., the classical method.

Other uncertainties concerning estimates of tree water use from sap flow measurements include the number of probes needed to account for circumferential variation in sap flow and the aging of probes during our long-term study. After 2 years, new sets of three probes were installed in each tree between the old probes at approximate azimuths East, South and West. There were no significant differences between the estimates of mean tree water use obtained with the new and old sets of probes. Within a set, probe dynamics were highly synchronous, although absolute values differed markedly and coefficients of variation ranged between 30 and 40%. Circumferential (intra-individual) variations were stable at around 30% and systematically higher than inter-individual variations. The size of the measuring tip of the probe (2 cm), compared with the estimated 4.7 cm radius of conducting xylem, allowed integration of radial variation in sap flow density.

Cambial growth

Stem diameter variation was continuously recorded to ± 0.010 mm on one main branch of each experimental tree every hour with linear displacement transducers (Enertec Sclumberger, Paris, France). Probe supports were made of INVAR. Measurement systems were shielded from direct sunlight, and probes were glued onto the bark surface. Linear transducers were cleaned and checked monthly. At the same time, measurements of each branch diameter were made at opposite axes with an electronic calliper (Sumitoyo, Tokyo, Japan).

Climatic measurements

Air temperature, relative humidity, incoming short wave radiation and rainfall were measured with automatic instruments in a field 50 m from any grove edge. A reference potential evapotranspiration (PET) was calculated according to the Penman formula (1948).

Soil water availability

A soil water profile to the water table was kindly provided by Dr. Abdoulaye Faye (Geology Department, Dakar University), which was obtained by measurements on soil samples taken with an auger every 0.5 m. In the uppermost soil layers (0–4 m), soil water content was monitored with a neutron probe (Solo 25, Nardeux S.A., Les Ulis, France). The bases of the three experimental trees in the grove approximately mark the corners of an isosceles triangle with sides of 5 m, and neutron probe access soil tubes were located in the middle of each side of the triangle. The soil wetting front rarely exceeded 1 m in depth. Soil water availability was calculated for the 0–100 cm deep layer, based on the difference between soil water content at field capacity and the lowest soil water content. Within the lowest measured soil zone, water content corresponded to a soil water potential of less than –1.6 MPa. During the wet season of 1998, irrigation was applied twice weekly during August and September to maintain soil water content in the 0–100 cm soil layer (80 mm) at field capacity, as determined by neutron probe measurements.

Phenological stages

For each tree, leaf phenology was assessed in six categories (Grouzis and Sicot 1980): 0, leafless; 1, leaf buds opening; 2, start of leaf expansion on 10–50% of branches; 3, leaves fully expanded on more than 50% of branches; 4, start of leaf senescence as indicated by color change on less than 50% of branches; 5, all leaves senescent or fallen on more than 10% of branches. These phenological stages were converted to an index of canopy fullness: 0 for Stage 0; 1 for Stages 1 and 5; 2 for Stages 2 and 4; and 3 for Stage 3. The total leaf area of three of the experimental trees was estimated in the first week of February 2000 at the end of the full canopy stage. Total leaf biomass of each tree was measured, and specific leaf area (SLA) was determined to estimate total leaf area.

Leaf water potential

Predawn leaf water potential (Ψ_{pd}) was measured with a Scholander type pressure chamber (PMS 1000, PMS Instrument Company, Corvallis, OR) between 0600 and 0645 h, and minimum leaf water potential (Ψ_{min}) was measured between 1400 and 1445 h on two randomly selected leafy twigs on each of the three experimental trees ($n = 6$). For all the days when both leaf water potentials and daily maximum SFD were available, root-to-leaf sapwood-specific hydraulic conductance (K_h; l dm^{-2} h^{-1}) was estimated as: $K_h = \mathrm{SFD}_{max}/(\Psi_{pd} - \Psi_{min})$, where SFD_{max} is daily maximum sap flow density. Predawn leaf water potential was taken as an approximation of root water potential, which was assumed to be constant throughout the day. This formula ignores capacitance and gravitational effects.

Data recording and analysis

From March 1996 to January 2000, phenological observations and measurements of soil water content and leaf water potential were carried out monthly in the dry season and twice monthly in the wet season. Characteristic values of daily water use, i.e., maximum value in the rainy season and maximum and minimum values in the dry season, were automatically selected by analyzing a moving average over a 5-day period applied to each year. To analyze annual and seasonal effects on Ψ_{pd} and daily water use, characteristic values, e.g., maximum value in the rainy season and maximum value in the dry season, were analyzed by a fixed factor analysis of variance with the factors being season, year and tree.

Results

Evaporative demand, rainfall and soil water availability

Reference PET showed seasonal variation (Figure 1a). Values were maximal (7–9 mm day^{-1}) in the hot dry season from March to May. During the wet season, from July to September, values were intermediate (5–7 mm day^{-1}). The lowest values of 4–5 mm day^{-1} were recorded in the cool dry season from December to February. Daily maximum values of vapor pressure deficit (D_{max}) ranged from 7 kPa in the hot dry season to 2 kPa in the wet season. Annual PET averaged 2260 mm with a minimum of 2181 mm in 1999 and a maximum of 2331 mm in 1997 (Table 1). Over the 4-year study, annual rainfall averaged 235 mm with a minimum of 146 mm in 1997 and a maximum of 367 mm in 1999 (Table 1, Figure 1a). The interannual variation (CV = 37%) was similar to the long-term variability for the area. Rains occurred mainly between July and September. The dates for the onset and end of rains were variable, i.e., between June and July and between September and October, respectively. August and September were the wettest months. Upper soil SWA had low and constant values and was below 5% in the hot dry season (Figure 1b). Soil water availability then increased with rainfall and with the irrigation applied in 1998. However, two months after the rainy season, SWA decreased to low values similar to those recorded in other years. The water table depth was 31 m (Figure 2). Between the uppermost soil layer and the water table, SWA was limited as shown by the actual water contents, which were equivalent to a water potential of –1.6 MPa (Figure 2). Living root fragments of *A. tortilis* were collected at depths of 6 and 25 m, confirming that these trees explored the soil profile to the depth of the water table (Figure 2).

Predawn leaf water potential, canopy phenology and cambial growth

Predawn leaf water potential may reflect SWA from either superficial or deep soil water resources. Changes in Ψ_{pd} were strongly seasonal (Figure 1c). Maximum values occurred in the wet season, varying between –1.2 MPa in 1996 and –0.4 MPa in 1998 with irrigation (year effect: $P < 0.001$). The lowest values were recorded at the end of the cool dry season and were similar in each year (–2.0 MPa, SD = 0.9). The seasonal effect, determined by comparing extreme values from the rainy season and the cool dry season, was highly significant ($P < 0.001$). There was an increase in Ψ_{pd} in the middle of the hot dry season, which reached similar values each year (–1.3 MPa, SD = 0.9).

Canopy fullness showed an annual cycle with some variation between years (Figure 1d). The dynamic was similar to the mean pattern recorded for 39 individuals studied in the protected area (Do et al. 2005). The defoliation phase was short and centered around the hot dry season. Defoliation was rarely complete, except in 1997. Leaf flushing occurred in the transition phase between the hot dry season and the rainy season and was particularly pronounced before the first rains in 1999 (Figure 1d). The full canopy stage (CF index = 3) lasted between 5 and 8 months, from July to February, and broadly included the rainy and cool dry seasons (Figure 1d).

Total leaf area of the experimental trees, estimated at the end of the full canopy stage in 2000, averaged 14 m^2 (SD = 6.2). According to the projected canopy area of 30 m^2, a low clumped leaf area index of 0.5 per tree was calculated. The ratio of xylem cross-sectional area to leaf area (Huber value) was 13.6×10^{-4}, which is in the highest range of values reviewed by Eamus and Prior (2001). Leaf density in January was less than half that at the beginning of the full canopy stage in September. However, the Huber value of 7×10^{-4} is still within the highest range of reported values.

Daily variations in branch diameter (measured at 0600 h) are shown in Figure 1e. Increases in branch diameter were observed only in the rainy season and were followed by a slight decrease in the dry season. Cambial growth of branches showed large variation between years. It was negligible in 1997 and 1999, but represented a 6% increase in diameter in 1998, i.e., diameter increased from 66.5 to 70.5 mm. Girth change measured by continuous recordings showed large variation among the three sample branches (CV = 50%), which was confirmed by manual measurements made each month (Figure 1e). The growth in trunk diameter at breast height showed a similar final increase of 5.5% (SD = 1.4), i.e., + 9.6 mm.

Seasonal water use

Daily water use measured by xylem sap flow showed a similar seasonal pattern between years where links with canopy phenology and Ψ_{pd} were evident (Figure 1d). The seasonal pattern could be split schematically into four time periods. The first period was characterized by the lowest daily water use, in the middle of the hot dry season between April and May at the time of maximum defoliation. Minimum values of daily water use, calculated over 5-day periods, averaged 8.8 l day^{-1} (SD = 1.9; Figure 3). Differences between years were significant ($P < 0.001$). The second period corresponded to the increase in water use in the dry–wet transition period, from May to July (Figure 1d). The third period was characterized by the mainte-

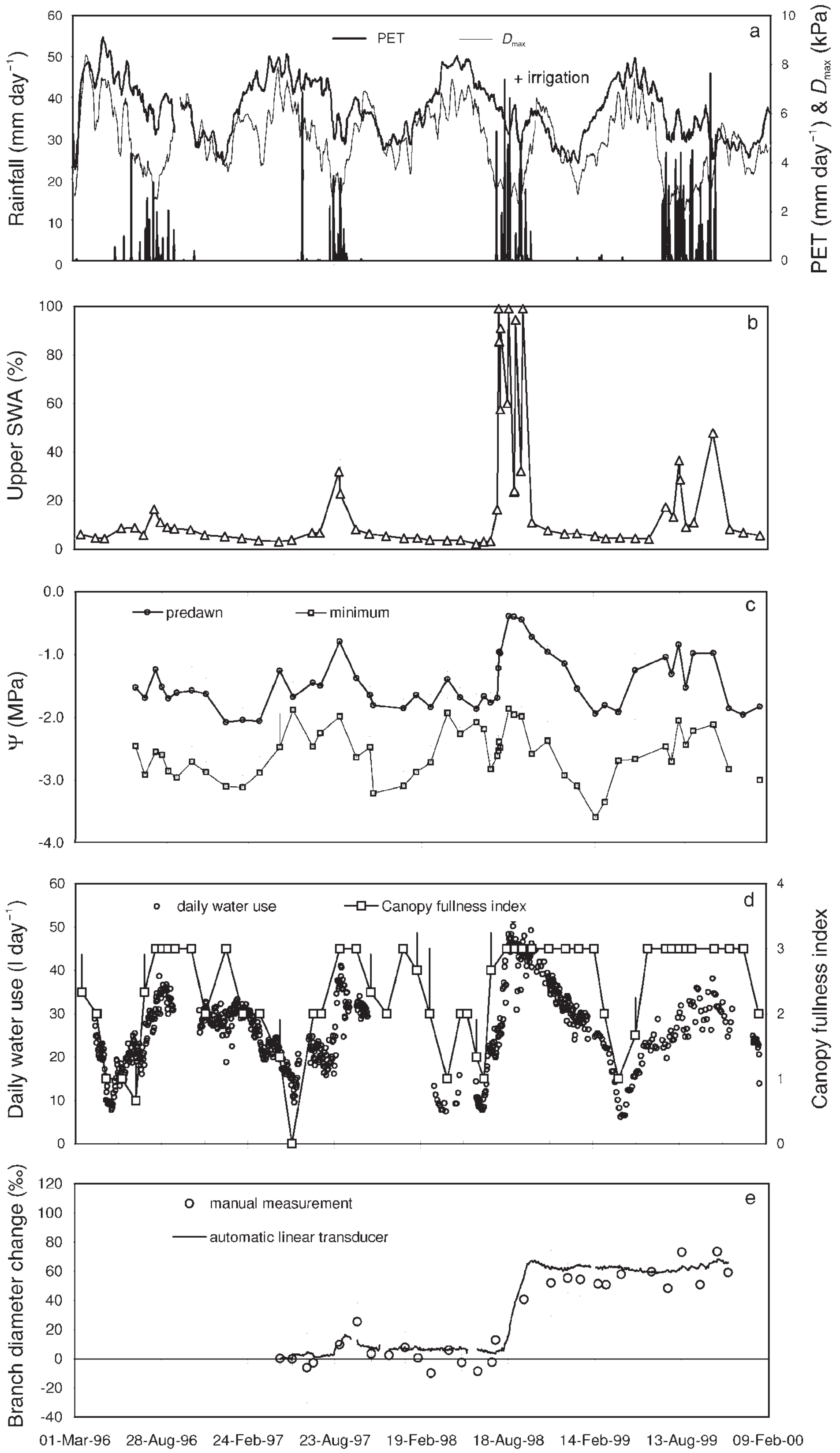

Figure 1. Seasonal variation in environmental conditions and tree water use in a natural grove of *Acacia tortilis* (three mature individuals) growing in north Senegal. (a) Daily rainfall (bars), 15-day moving mean of Penman potential evapotranspiration (PET) and maximum vapor pressure deficit of the air (D_{max}). Irrigation was provided during August and September 1998. (b) Soil water availability (SWA) in the upper layer (0–1 m) (bars are 1 SD; n = 3). (c) Predawn and minimum leaf water potentials (Ψ) (means for three trees, bars are 1 SD; n = 6). (d) Canopy fullness index (n = 3) and daily tree water use measured by sapflow sensors (n = 9). (e) Branch diameter changes, expressed in ‰ of initial diameters (66.5, SD = 1 mm; bars are 1 SD; n = 3).

Table 1. Cumulated annual Penman potential evapotranspiration (PET), annual rainfall (irrigation was provided in 1998), cumulated sap flow density per sapwood area (SFD) and cumulated total flow or tree water use based on the density of trees in the area (90 $\mathrm{ha^{-1}}$). Cumulated values were computed from July 1 to June 30 to determine the potential effect of wet season conditions (July–September) on the annual pattern of tree water use.

Year	PET ($\mathrm{mm\ year^{-1}}$)	Rainfall ($\mathrm{mm\ year^{-1}}$)	SFD ($\mathrm{l\ dm^{-2}\ year^{-1}}$)	Tree water use	
				($\mathrm{l\ year^{-1}}$)	($\mathrm{mm\ year^{-1}}$)
1996	2312	153	5576	9647	87
1997	2331	146			
1998	2212	272 (+ irrigation)	5623	10,527	95
1999	2181	367			

nance of relatively high water use (> 25 $\mathrm{l\ day^{-1}}$) for about 6 months, between August and January, corresponding to the phenological stage of full canopy development. Maximum water use (40 $\mathrm{l\ day^{-1}}$; SD = 6.0) was recorded at the end of the rainy season, between September and October, when upper SWA and Ψ_{pd} were also maximal. Differences between years were significant ($P < 0.001$), and this effect was mainly due to a value recorded in 1998, which was 20% higher than the mean (Figure 3). The maximum water use recorded in 1998 of 48 $\mathrm{l\ day^{-1}}$ for a stem with a mean diameter of 17 cm corresponded to a daily sap flow density of 28 $\mathrm{l\ dm^{-2}\ day^{-1}}$ and a maximum hourly density of 3 $\mathrm{l\ dm^{-2}\ h^{-1}}$. The fourth and last period was defined by a decrease in water use during the climatic transition between the cool dry and hot dry seasons, from February to March. Phenological cycles are identified by the year in which the rainy season occurred. Maximum daily water use in the dry season occurred at the end of the full canopy stage in January just before the period of leaf shedding. Differences between years and seasons were significant ($P < 0.001$ in each case). Values averaged 29.0 $\mathrm{l\ day^{-1}}$ (SD = 4.4), and this mean value was 27% lower than the maximum value recorded at the end of the rainy season.

Seasonal and interannual comparison of water use per sapwood area, or sap flow density (SFD), yielded the same results as water use and total flow analysis. Continuous measurement

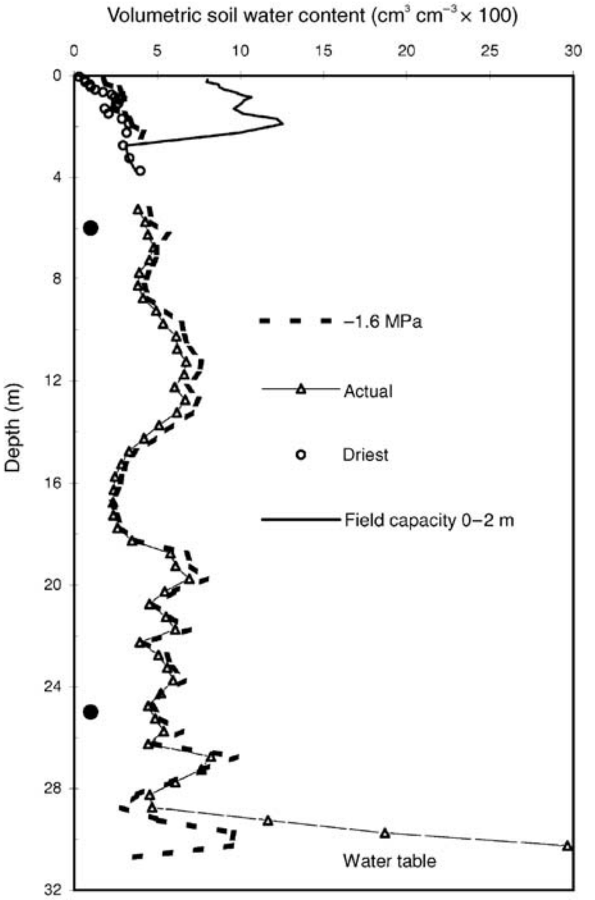

Figure 2. Deep profiles of soil water content in the experimental plot: actual soil water content and that equivalent to a water potential of –1.6 MPa ("wilting point"). Characteristic profiles used to compute soil water availability in the upper layer (0–4 m) are also shown: driest profile with soil water contents slightly lower than those equivalent to –1.6 MPa and the profile at field capacity for the 0–2 m layer. The large filled dots show the depths at which living roots of *Acacia tortilis* were found in the soil cores.

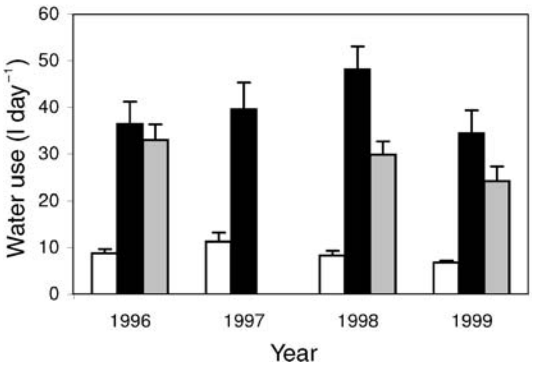

Figure 3. Characteristic values of daily water use for four annual patterns: minimum value recorded in the hot dry season (open bar), between April and May; maximum value recorded at the end of the rainy season (black bar), between September and October; and maximum value recorded in January in the cool dry season (gray bar). Phenological cycles are identified by the year in which the rainy season occurred. Values are averaged over 5-day periods ($n = 3$ sensors × 3 trees × 5 days = 45). Bars indicate confidence intervals at 95% of probability. Each annual pattern of water use is labeled by the year.

of SFD for all years permitted the estimation of annual water use for the phenological cycles of 1996 and 1998 (Figure 1d, Table 1). Calculation started on the first of July to focus on the potential influence of contrasting rainy seasons. Between 1996 and 1998, annual SFD or water use per sapwood area was stable at around 5600 l year^{-1} dm^{-2}. Total water use was close to 10,000 l year^{-1} (Table 1). The value was 9% higher in 1998 than in 1996, the difference being fully explained by the increase in conductive sapwood area. The variation in annual water use was small despite large differences in cambial growth and environmental conditions in the rainy season. A broad estimate of water use yielded 90 mm year^{-1} for an *A. tortilis* stand, assuming a stand density of 90 trees ha^{-1}.

Relationships between daily water use, canopy phenology, evaporative demand and predawn leaf water potential

As suggested by Figure 1d, daily SFD was significantly related to canopy fullness ($r^2 = 0.49$, $n = 46$; Figure 4). All measurements from the 4-year dataset were within the same range. Paradoxically, daily SFD was not zero on any measurement occasion during the period of complete defoliation (Figure 4); however, phenological assessment is qualitative and trees could have had a small proportion of green leaves, and measurement error is high when SFD values are lower than 0.5 l dm^{-2} h^{-1}. The relationship between canopy phenology and tree water use reflects the relationship between canopy fullness index and total leaf area, particularly during the period of defoliation in the hot dry season. Leaf phenology is well known as the main driver of seasonal changes in transpiration. However, the strength of the relationship is surprising, with measurements for the entire 4-year period falling within the same pattern. Canopy fullness index is derived from a qualitative phenological assessment, and the same Stage 3 of full canopy may correspond to different actual leaf areas. Moreover, in a particular season, evaporative demand varies from day-to-day and year-to-year. The relationship between canopy phenology and tree water was not improved by the use of SFD averaged over 10-day periods (data not shown, $r^2 = 0.50$) or by a normalization by Penman PET (data not shown, $r^2 = 0.54$). The relationship between water use and canopy phenology is another indication of the marked control of daily water use.

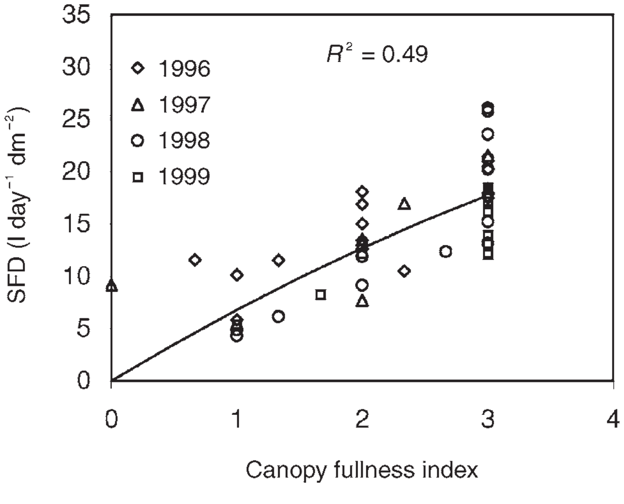

Figure 4. Relationships between daily sap flow density per sapwood area (SFD) and canopy fullness index, including four annual patterns (for labels same remark as in Figure 3), $n = 46$.

The relationships between SFD and evaporative demand were analyzed specifically for three variables: Penman PET and its main components, global radiation (R_g) and vapor pressure deficits (daily mean, minimum and maximum; D). Considering all data points and pooling values from all years, there was a weak negative correlation between SFD and PET (data not shown, $n = 812$, $r^2 = 0.19$) and D_{max} (data not shown, $r^2 = 0.15$). This relationship is largely explained by the peak in defoliation during the hot dry season (Figure 1d). No global relationships were obtained with any variable when all the data corresponding to full canopy stages were considered (data not shown; $n = 341$).

The relationship between daily SFD and Ψ_{pd} was weak but significant over all seasons and years ($r^2 = 0.40$, $n = 46$; Figure 5a). It was significantly strengthened when only the measurements corresponding to full canopy stages were considered (CF = 3, $r^2 = 0.50$, $n = 26$; Figure 5b). For large portions of the dry season, Ψ_{pd} is unlikely to be in equilibrium with SWA. The rapid increase in Ψ_{pd} of between 0.5 and 1.0 MPa, noticed at the time of maximal defoliation, supports this hypothesis. This increase in Ψ_{pd} was not explained by an increase in osmotic potential, which was 0.1 MPa at the time of maximal defoliation (data not shown). Defoliation may facilitate nocturnal rehydration. The relationship between daily SFD and Ψ_{pd} was particularly clear for 1998 (Figure 5b) and variation in SWA could largely explain the daily variation in water use for both the rainy and post-rainy seasons. For 1998, daily SFD increased twofold, from 15 to 30 l day^{-1} dm^{-2}, when Ψ_{pd} decreased from –2.0 to –0.5 MPa.

Hydraulic conductance

Daily maximum SFD versus Ψ_{pd} is plotted for full canopy stages in Figure 6a, distinguishing wet and dry seasons. In agreement with the conclusion of stable water use, the mean value in the dry season (1.7 l dm^{-2} h^{-1}, SD = 0.3) was not significantly lower than that recorded in the rainy season (1.8 l dm^{-2} h^{-1}, SD = 0.5), although Ψ_{pd} averaged –1.7 and –1.0 MPa, respectively. The gradients in water potentials were also similar between the dry season (1.3 MPa, SD = 0.3) and the rainy season (1.3 MPa, SD = 0.2; Figure 6b). Consequently, the mean hydraulic conductances did not differ between the dry season (1.4 l dm^{-2} h^{-1} MPa^{-1}, SD = 0.5) and the rainy season (1.4 l dm^{-2} h^{-1} MPa^{-1}, SD = 0.3; Figure 6c). These results were obtained when mean D_{max} values for the same period were 4.8 kPa in the dry season and 3.3 kPa in the rainy season, respectively (Figure 6d). Such results suggest a strong regulation of canopy conductance, through changes in total leaf area or stomatal conductance, or both, that compensate for the increase in evaporative demand.

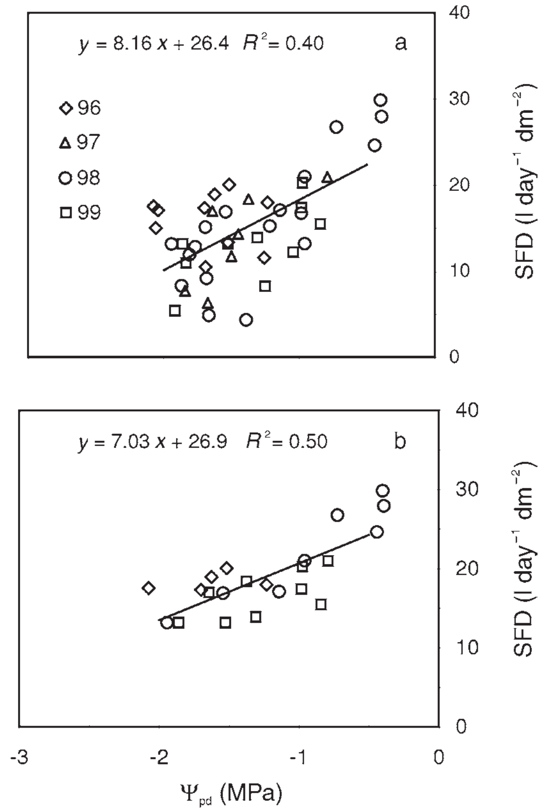

Figure 5. Relationship between daily sap flow density per sapwood area (SFD) and predawn leaf water potential (Ψ_{pd}). (a) The dataset includes all measurements of the four annual patterns, n = 46. (b) Dataset includes selected measurements corresponding to the full canopy stages, n = 26.

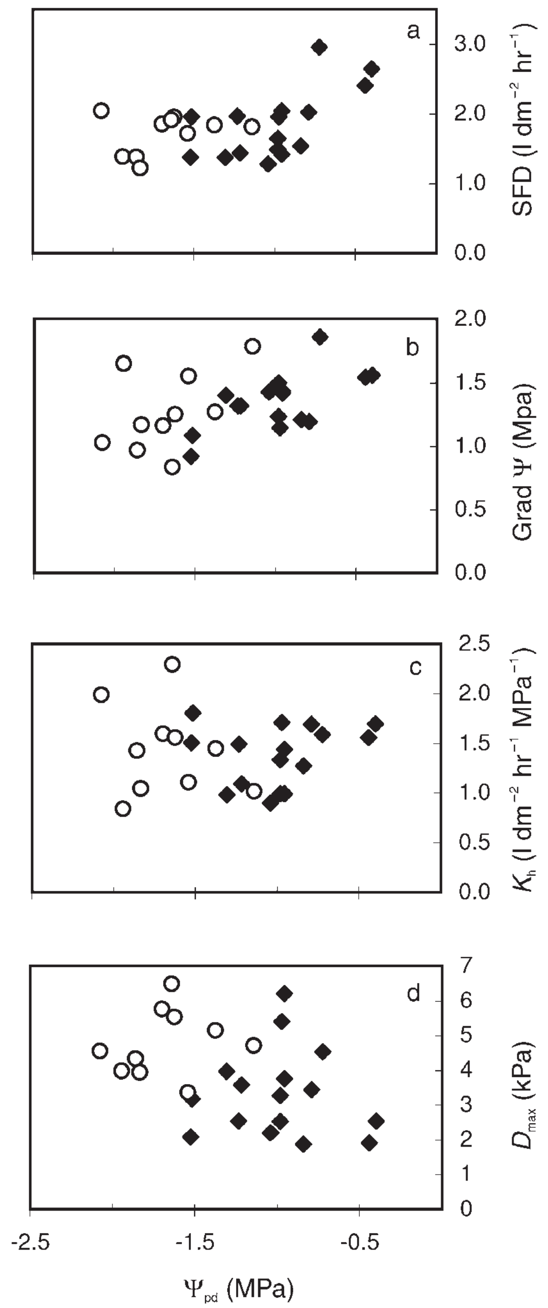

Figure 6. Plots of predawn leaf water potential (Ψ_{pd}) versus (a) daily maximum sap flow density per sapwood area (SFD), (b) maximum gradient of leaf water potential (grad Ψ), (c) whole hydraulic conductivity (K_h) and (d) maximum vapor pressure deficit of the air (D_{max}). Measurements were made for the full canopy stages during wet (◆; August–September, n = 16) and dry seasons (○; October–January, n = 10).

Discussion

Seasonal and interannual pattern of tree water use

Annual dynamics revealed that *A. tortilis* transpires readily over the whole year, except at the peak of the dry season during maximum defoliation. Throughout the dry season during the full canopy stage, there was only a modest decline in tree water use despite the exhaustion of soil water in the uppermost soil layers. An increase in SWA due to rainfall and irrigation did not greatly increase maximum daily water use or annual water use. Moreover, water use would likely have been increased more through irrigation than by natural rainfall alone, as the latter would normally be accompanied by reduced evaporative demand. The relatively uniformity in pattern and amount of tree water use despite environmental fluctuations was striking. These findings support and extend the results of recent studies showing that, in less arid environments, tree water use decreases little (Cook et al. 1998, Roupsard et al. 1999) or not at all (Meinzer et al. 1999, Eamus et al. 2000, Hutley et al. 2001, Bucci et al. 2005) during the dry season.

Daily water use during the full canopy stage ranged between 22 and 50 l day^{-1} for trees of average size (DBH =17 cm). Expressed per sapwood area, tree water use ranged from 12 to 30 l dm^{-2} day^{-1}. These values are within the range reported for other drought-tolerant species in the dry tropics, e.g., Allen and Grime (1995) for *Guiera senegalensis* JF Gmel. in Sahelian Africa, Roupsard et al. (1999) for *Faidherbia albida* (Del.) A. Chev. in Soudano–Sahelian Africa, Meinzer et al.

(1999) and Eamus et al. (2000) in the Australian savannah. More generally, our results for whole-plant water use fall within the low range given in the review by Wullschleger et al. (1998), which included trees from temperate and tropical humid zones.

Deep water uptake

One explanation for year-round water use could be that the investigated trees, like riparian vegetation, experienced no soil water constraint. Predawn water potential, which varied between –0.4 and –1.5 MPa in the wet season, depending on rainfall or irrigation, decreased to around –2.0 MPa in the dry season, indicating that SWA was limited. However, the values of predawn leaf water potential recorded in the dry season were similar to values reported for other tree and shrub species in less stressful environments (Duff et al. 1997, O'Grady et al. 1999). Furthermore, the operating range of leaf water potential is species-dependent. In the same area, Berger et al. (1996) reported in *A. tortilis* a minimum value of predawn leaf water potential that was similar to ours compared with –5.0 MPa for the co-occurring evergreen shrub *Boscia senegalensis*.

The finding that trees transpired during all but one month of the year, although water availability in the upper soil layers was extremely low during 8 to 10 months of the year, implies extensive use of deep soil water. However, the deep soil water profile showed that SWA was low all the way to the water table at a depth of 31 m. A hydrogeological study in the area has confirmed this deep soil water profile and shown a slow downward movement of soil water, which takes 50 years to reach the water table from the surface (Gaye and Edmunds 1996). This situation differs from that observed by Cook et al. (1998) and Roupsard et al. (1999) where the high availability of water in the top 10 m was clearly sufficient to maintain transpiration during the dry season. We found living roots at 25 m depth, confirming that the trees had access to deep soil water (Lhote 1961, Deans et al. 2005).

Control of water losses

Whole-tree hydraulic conductance did not differ between the wet and dry seasons during the full canopy stage, but remained at around 1.4 $l\,dm^{-2}\,MPa^{-1}\,h^{-1}$. This supports the idea that xylem conductivity, determined by dry season conditions, limits wet season water use (Eamus et al. 2000, Hutley et al. 2001). However the observed values of sapwood-specific hydraulic conductance were not particularly low relative to values reviewed by Eamus and Prior (2001) for trees in more humid environments. Moreover, our data showed that cambial growth of the trunk and branches of *A. tortilis* occurred at the end of the wet season. So in our trees, it is unclear whether the dry season conditions affect xylem architecture. However, SWA and evaporative demand during the wet season in the northern Sahel are already limiting, with upper SWA rarely exceeding 50% and D_{max} averaging 3.3 kPa.

Our observations of near uniform year-round water use and stable whole-tree conductance imply that canopy conductance is strongly regulated during the dry season to compensate for increased atmospheric evaporative demand. We can assume from the stand characteristics and the environment that a decrease in leaf area and stomatal conductance have a direct impact on tree transpiration, i.e., transpiration is strongly coupled to the atmosphere as defined by Jarvis and MacNaughton (1986). The high Huber value found at the end of the full canopy stage in the dry season demonstrates a low leaf area compared with sapwood area for these trees. This feature is a well known adaptation to high evaporative demand (Mencuccini and Grace 1994). Moreover, twig-level studies by Goudiaby (2003) and Diagne (2000) on the same trees confirmed a large decrease in both leaf area and stomatal conductance during the full canopy stage in the dry season.

Goudiaby (2003) observed pronounced inter-annual and seasonal variations in leaf area on terminal branches. Maximal leaf area occurred toward the end of the rainy season (September), with wet-year values (200 cm^2 per linear meter of leafy twigs) that were twice dry-year values. Similarly, at the end of the full canopy stage in the dry season (January), leaf area was threefold ("wet" year) or twofold ("dry" year) lower than in September, respectively. Diagne (2000) observed a wide range of stomatal conductance values during the year, with maximum values of 100–200 $mmol\,m^{-2}\,s^{-1}$ occurring during the rainy season, minimal values of 10–50 $mmol\,m^{-2}\,s^{-1}$ occurring toward the end of the full canopy stage from November to February, and intermediate values of 50–100 $mmol\,m^{-2}\,s^{-1}$ occurring at the time of maximal defoliation in the hot dry season. Such responses contribute to seasonal homeostasis of water use and water status by strong stomatal control and decreased leaf area per sapwood area, as has been described by Bucci et al. (2005) for several Cerrado woody species. In addition, for *A. tortilis*, Do et al. (2005) have shown that inter-annual variation (up to 2 months) in phenology "optimizes" the onset and duration of the full canopy stage relative to evaporative demand. Such phenological behavior contributes to the control of water use through regulation of canopy conductance. The between-year consistency in minimum Ψ_{pd} (–1.7 to –2.0 MPa), despite a wide range of environmental and growth conditions, also reflects effective regulation of water loss by *A. tortilis*, resulting from a combination of features, of which deep rooting that provides access to deep water and a strong regulation of canopy conductance are the most obvious.

Tree growth

Irrigation strongly promoted cambial growth of trunks and main branches although it had little effect on tree water use. The complete lack of cambial growth except during the year of irrigation was unexpected; however, the finding was in accordance with the dynamics of Ψ_{pd}, which exceeded –0.8 MPa only in the year of cambial growth. This result does not mean that these trees do not usually grow: a percentage of new green twigs inside the canopy was observed each year. Moreover, cambial growth may have taken place in the root system when it was absent in the branches.

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