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Responses of *Acacia tortilis* and *Acacia xanthophloea* to seasonal changes in soil water availability in the savanna region of Kenya

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Abstract

Comparative field studies were conducted on *Acacia tortilis* (Forsk.) Hyne and *Acacia xanthophloea* Benth. trees growing in a semi-arid environment in Kibwezi, Kenya, to assess root access to soil water at varying soil depths and how this may affect the expression of morphological and physiological traits developed during drought. Measurements of soil water content, leaf growth, shoot elongation, sap flow in the xylem of stems and branches, leaf water potential, leaf transpiration and stomatal conductance were carried out. Further, water use efficiency (WUE) over long-term periods was examined via carbon isotope discrimination ($\delta^{13}\text{C}$) on leaves. Whole tree and leaf specific hydraulic conductance were determined from sap flux or leaf transpiration and the water potential gradient between soil (as predawn potential) and canopy, respectively.

Leaf growth and shoot elongation depended on soil water availability (SWC) and plant tissue water status. *A. xanthophloea* showed greater (40 kg d^{-1}) water use compared to *A. tortilis* trees of comparable sizes (20 kg d^{-1}) during favorable conditions of SWC. Decline in SWC reduced water use and the onset and rate of decline in sap flux was determined by the rooting depth. *A. xanthophloea* showed earlier response (onset at $\text{SWC} = 0.24 \text{ m}^3 \text{ m}^{-3}$) to water stress than *A. tortilis* (onset at $\text{SWC} = 0.14 \text{ m}^3 \text{ m}^{-3}$). Midday depression in stomatal conductance and subsequent decline in transpiration during favorable SWC as observed in *A.*

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xanthophloea was attributed to increased hydraulic resistance and stomatal closure. Rooting patterns and root characteristics could account for the observed morphological and physiological differences between *A. tortilis* and *A. xanthophloea* as well as between small and large *A. tortilis* trees. However, seasonal responses were modified by species-inherent characteristics, which are expressed during drought. Access to deeper soil water resources and the abilities of trees to extract and efficiently transport water may explain differences in drought resistance among species and tree distribution in the arid savanna.

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1. Introduction

Savanna ecosystems are subject to alternating wet and dry seasons and occupy 65% of Africa, 60% of Australia and 45% of South America. Most of these areas receive rainfall amounts between 150 and 500 mm yr⁻¹, falling within relatively short time period and the ratio of precipitation to potential evaporation (PET) ranges from 0.05 to 0.65 (Tinley, 1982). Such areas are classified as arid and semi-arid lands (ASAL) (Walker and Noy-Meir, 1982) and are considered to experience varying degrees of heat and water stress (Mauat and McGinty, 1998), limiting the establishment, growth and distribution of trees (Kramer, 1980). Analysis of arid and semi-arid areas of Africa show potentially large losses of plant species diversity, with low landscape heterogeneity as a result of climate and land-use changes, over-exploitation and lack of tree regeneration (Rutherford et al., 1999; Climate change, 2001), leading to serious land degradation (Burley, 1982). In Kenya, ASAL occupy about 38 million ha or 60% of the total land area, most of which is under great pressure from extended drought, sedentarization of pastoralists and migration of people into these fragile ecosystems (Government of Kenya (GOK), 1986). The annual loss of woody vegetation in the Kenyan drylands currently stands at ca. 19,000 ha. This loss of forest cover and other types of woody vegetation will lead to increasing scarcity of a wide range of forest products, environmental degradation and loss of biodiversity, unless urgent measures are taken to address the situation. This calls for new hypotheses that clearly define ecosystem interactions and can predict the extent and nature of ecosystem changes and plant species geographical shifts in the event of increased drought and changes in land-use systems. Such studies must be broad-based and aimed at designing adaptive and mitigating strategies with respect to ecosystem management, biodiversity conservation and vulnerability to stress.

Soil water availability (SWC) is recognized as a key factor determining tree growth and activity, species composition and distribution as well as ecosystem functioning and long-term water, carbon and nutrient balances in the ASAL (Noy-Meir, 1973; Walker and Noy-Meir, 1982; Ehleringer, 1994; Reynolds et al., 2004). Soil moisture recharge in the ASAL is mainly through rainfall, yet precipitation in these regions

are low and very erratic, leading to different patterns of soil moisture recharge (Ehleringer, 1994; Reynolds et al., 2004). The characteristics of soil water uptake by the different plant species encountered in the arid savanna ecosystem, therefore, are fundamental to understanding ecosystem functioning and the adaptations exhibited by different tree species, which enable their growth and success. Generalized information related to root distributions and knowledge of the basic mechanisms of soil water extraction and transport by tree species are a suitable starting point in addressing differences among trees with respect to their habitat preferences and ecological potentials. Extensive and deep rooting systems with a large active surface area over which water absorption takes place will facilitate soil water uptake by trees. For trees successful in arid habitats, a greater allocation of photosynthates to the roots as compared to shoots is found, and in some cases, absolute root growth is enhanced (Jones, 1992; Scholz et al., 2002). This enables extraction of water from a large volume of soil or from a deep water table when the upper soil horizons are dry (Jones, 1992; Jackson et al., 2000). As water becomes limiting, certain trees also decrease osmotic potential of the cell sap, thus increasing the gradient between soil water and root cells, maintaining water uptake, and promoting physiological activity despite a declining soil water content (SWC) (Tyree and Jarvis, 1982). These must equally apply to the arid savanna trees.

Overall tree performance in the arid savanna, however, cannot be evaluated without considering constraints within the plant that will influence overall carbon gain (Ehleringer, 1994). For example, trees with an effective water supply system may lack specific adaptations for controlling water loss, resulting in low tissue water status that will affect overall plant performance (Levitt, 1980; Kramer, 1980). Thus, as soil water supply becomes limited due to increasing drought, high transpiration rates will result in decreases in leaf water potential (Ψ_L), leading to large gradients in water potentials between root and leaf and may reach a point at which cavitation occurs (Tyree and Sperry, 1989). Decreases in maximum stomatal conductance and increased sensitivity of stomata to changes in water status may be required to maintain leaf water potential above a critical threshold and to avoid cavitation in the xylem (Tyree and Sperry, 1989; Jones and Sutherland, 1991). In certain tree species however, stomatal conductance has been observed to decline long before any noticeable change in SWC is recorded, imposing an early restriction to CO_2 uptake (Sperry, 2000). Stomatal regulation of water loss must, therefore, balance transpiration with efficiency of water supply to the leaves so that dangerous decrease in Ψ_L is avoided without unnecessary restriction of carbon gain (Meinzer, 2002). There is growing evidence that transpirational water loss may be reduced via changes in hydraulic conductance of the water-conducting pathway (Hubbard et al., 1999; Sperry, 2000; Schultz, 2003). In this case, increased hydraulic resistance at the root surfaces will lead to steep gradients in Ψ in the soil–plant system during the day, even when soil water conditions are favorable, potentially initiating stomatal closure to avoid cavitation (Tyree and Sperry, 1989), and limiting daily water use from the soil water store. This has the ecological advantage of reducing excessive tree water use when soil water is abundant and prolonging the period with favorable soil water status, but it reduces the potential maximum stomatal conductance, hence potential

productivity. The onset of expression of the above-mentioned traits during the development of drought must depend on species differences in rooting patterns and accessibility to water at varying soil depths, root activity and water transport efficiency, and should determine success of individual tree species in the savanna habitats (Le Roux and Bariac, 1998). However, comprehensive information on seasonal variations in patterns of soil water uptake and changes in plant physiological functioning during the development of drought is lacking for indigenous tree species in the dry East African savanna.

The genus *Acacia* is currently drawing great interests for the improvement of tree cover in the Kenyan ASAL. This is due to their drought stress resistance abilities (Oba et al., 2001) and multi-purpose use-values such as fodder for animals, sources of wood and non-wood products (e.g. gums, resins and pharmaceuticals) for the local communities, provision of shade and live fencing (Noad and Birnie, 1989) and in maintaining soil fertility through nitrogen fixation (Belsky, 1984; Belsky et al., 1989). *Acacia tortilis* and *Acacia xanthophloea* have been considered for this study due to their wide range of distribution (Noad and Birnie, 1989), hence as potential candidates for reforestation processes. The two species naturally have contrasting habitat preferences, with *A. tortilis* found in the more xeric Eastern and Northern Provinces while *A. xanthophloea* dominates the mesic lowlands. This distribution pattern could be influenced by differences in abilities to cope with water stress, a fact that may be influenced by differences in rooting patterns and root water uptake. Distribution of *A. xanthophloea* is currently shifting to the increasingly dry parts of the country. This suggests an ability to adapt to environmental changes or perhaps, the result of favorable local situations such as soil quality or improved water balance through species interactions as a result of processes like hydraulic lift (Ludwig et al., 2003, 2004). In Kibwezi, a semi-arid part of Kenya, where the experiment was conducted, the two species were found growing together naturally in the same locality, providing a unique opportunity to investigate their rooting patterns and responses to changing soil water under similar natural environmental conditions.

The objectives of this study were to: (1) Assess the probable region of soil water uptake by roots of the two *Acacia* species. (2) Establish the role of root distribution pattern and root activity in species productivity, survival of stress and distribution in the arid savanna of Kenya.

2. Materials and methods

Site description: A field site with natural vegetation and co-occurrence of *A. xanthophloea* and *A. tortilis* was identified in Kibwezi, Eastern province of Kenya, approx. 250 km SE of Nairobi (37°88'E, 02°35'N) within the semi-arid area with a history of low and highly variable rainfall but with well-defined seasonality. Mean annual temperatures and rainfall over the past 10 years were 24 °C and 450 mm, respectively. The study plot was located within the Institute of Arid and Semi-Arid Research, University of Nairobi. Soils here are undisturbed except for grazing from domestic and wild animals. The vegetation was *Acacia*–*Cynodon* type with sparse

tree distribution. Table 1 indicates the mean height and diameter of trees growing within the study plot. Soils were red in color (rhodic) belonging to the ferrosols, predominantly sandy-clay-loam (45%) and the remaining is loamy sand (35%), with an average supply of nutrients (high in K^+ and Mg^{2+}) (Mbuvi, 1991). Measurements were conducted between December 2001 and June 2002.

Site climate monitoring: A climate monitoring station was established within the study plot in an open area to avoid interference from trees. Weather variables measured included rainfall (Aerodynamic gauge ARG100, Environmental Measurements Ltd., Sunderland, UK), air temperature (VAISALA HMP45A, Helsinki, Finland), soil temperature at 30 cm depth (Thermistor M841, Siemens, Germany), photosynthetic active radiation (LI-190 Quantum sensor, LI-COR, USA) and humidity (VAISALA HMP45A, Helsinki, Finland). Measurements were taken every 5 min, averaged and stored every half-hour with a data logger (Delta-T-Devices Cambridge, UK).

Soil water content: SWC in the upper soil layer was monitored using Theta probes (type ML 2 × , Delta-T-Devices, Cambridge, UK) installed at a depth of 40 cm in the soil. Data was collected every 30 min, averaged and logged every hour.

Plant growth: Trees were identified on which growth and also measurements on other morphological features were conducted. Three *A. tortilis* (*At1*, *At2* and *At3*) and *A. xanthophloea* (*Ax1*, *Ax2* and *Ax3*) trees were identified and from each tree, two newly formed (young) shoots with healthy apices from well exposed branches of each tree were selected for measurements. Monthly measurements of shoot length and leaf numbers per branch were recorded. Also for the same trees, litter was collected using traps of 30 cm diameter suspended below the crown. Tree *At2* was smaller than the rest, with stem diameter at ground level = 3.2 cm compared to $d = 14.3$ and 12.7 cm for *At1* and *At3*, respectively. *A. xanthophloea* trees selected for measurements were all relatively large and had a mean stem diameter of 23.6 cm.

Sap flux measurements: Sap flux density (SFD) was monitored on main tree stems, about 0.6 m away from the ground surface on three trees per species using the heat dissipation method (Granier, 1987). All sensor installations were made on the north-facing side of the trees and covered with a radiation shield (styrofoam cover with

Table 1

Summary of tree species, mean tree height (m) and mean tree diameter at ground level (cm) of the trees found at the study site

Tree species	Tree height (m)	Mean stem diameter at ground level (cm)	Number of individuals
<i>Acacia melifera</i>	2.7 (± 0.2)	8.3 (± 0.9)	2
<i>A. kirkii</i>	7.0 (± 4.3)	19.3 (± 11.5)	3
<i>A. senegal</i>	4.4	5.4	1
<i>A. tortilis</i>	4.4 (± 2.6)	12.4 (± 9.7)	8
<i>A. xanthophloea</i>	10.0 (± 2.7)	23.5 (± 12.6)	11
<i>Commiphora africana</i>	4.2	8.9	1
<i>Dichrostachys cinerea</i>	3.6	11.5	1

In brackets \pm S.D.

aluminum foil) to prevent thermal load on the sensors. Each sensor consisted of a pair of 2 mm diameter probes vertically aligned ca. 15 cm apart. Each probe included a 0.2 mm diameter copper–constantan thermocouple. The two thermocouples were joined at the constantan leads, so that the voltage measured across the copper leads provided the temperature difference between the heated upper probe and the lower reference. The upper probe was supplied with constant current of 120 mV (Granier, 1987). The temperature difference (T_d) between the heated and the lower unheated reference probe was measured. Heating of the upper probe was carried out along a 20 mm long winding in all cases. In cases where the tree trunk was large with sapwood radius greater than 20 mm, the radial sap flow profile was measured in order to allow observation of SFD at different depths. Second and third sensors (when used) were installed on both sides of the first one (annulus 1–20 mm radial sapwood depth). Sensors were spaced 10–15 cm circumferentially, away from the first sensor pair, but still on the same side of the stem to avoid azimuth differences. The second sensor was implanted 20–40 mm into the sapwood and the third (whenever used) 40–60 mm deep into the sapwood. To correct for natural temperature gradients in the sapwood between the heated and the reference sap flow probes, heating was turned off so that the measured temperature differences were mainly as a result of natural warming of the sapwood. This was done at different time intervals over the season. Data from sap flux probes (during heater-on) were then corrected for natural temperature gradients for the different time intervals during the season using heater-off measurements. Temperature differences were monitored every 5 min and a 30-min mean value was logged (DL-2 with LAC-1 in single ended mode, Delta-T Devices, England) for each sensor. SFD ($\text{g m}^{-2} \text{s}^{-1}$) for each sensor was calculated from T_d in accordance with Granier (1987), assuming zero SFD (T_0) late at night/early in the morning, with VPD near zero:

$$\text{SFD} = 119K^{1.231}, \quad (1)$$

where $K = (T_0 - T_d)/T_d$, and SFD is obtained in $\text{g m}^{-2} \text{s}^{-1}$. To estimate whole tree water use F (kg h^{-1}), SFD was multiplied by the total surface area over the heated needle. Sapwood area was estimated from the tree diameter measured at the sensor height, after subtracting the bark depth. Depth of the bark was determined by using increment core. Equally at the end of sap flow measurements, stem cores were taken at the sensor height of each stem measured, and xylem depth examined by physical observations, i.e. examining the depth of the wet sections of the cores. For *A. tortilis*, the conducting section of the stem was clearly visible from its light color.

Leaf water potential: On the same trees as used for sap flux measurements, diurnal measurements of leaf/shoot water potential (Ψ_L) on triplicate samples were conducted using a pressure chamber (Hayashi Denkho, Tokyo). Intensive measurements were carried out early during the season of drought (9 March 2002), during the short rain events (9 and 11 April 2002) and during intense drought (17 May and 27 June 2002) as well as during and shortly after the rainy season on 20 December 2002 and 15 January 2003, respectively. Measurements commenced early in the morning before any noticeable transpiration was recorded and proceeded throughout the day at hourly intervals. During measurements, young shoots with

2–3 leaves were cut and immediately enclosed in polythene bags to reduce further moisture loss during transfer and fixing in the chamber. Young shoots were used because of the small and delicate nature of the *Acacia* leaves, which could not be inserted through the rubber stoppers used in the pressure chamber. Green transpiring leaves were also introduced into the chamber to increase humidity and reduce water loss from the experimental sample during the measurements. Measurements were conducted on shoots obtained from exposed branches in the middle layer of the tree canopy.

Leaf transpiration and stomatal conductance: On similar trees and dates as above, parallel measurements of diurnal courses of leaf transpiration (E) and stomatal conductance (g_s) were carried out using a steady-state porometer (LI-1600, LiCOR, Nebraska, USA). On each measurement day, well-exposed leaves from each of the trees were identified and measurements conducted on the same leaves from sunrise to sunset (7.00 a.m.–6.00 p.m. local time). Alternate measurements were conducted between the two species throughout the day. At the end of each day, the measured leaves were detached and their area determined using portable Leaf Area meter (CI-202, CID Inc. USA). This was then used to correct for transpiration per unit leaf area.

Hydraulic conductance: Whole tree hydraulic conductance was calculated for individual trees on those days when plant water potentials were measured based on Wullschlegel et al. (1989) and Sperry (2000) as:

$$K_{\text{plant}} = \text{SFD}/\Delta\Psi, \quad (2)$$

where SFD is the momentary flux per unit xylem area obtained with the installed Granier sensors and $\Delta\Psi$ is the flux gradient or the driving force, which is estimated from the difference between predawn soil water potential and Ψ_L determined at any particular time of the day. Stepwise calculations on an hourly basis were carried out for the period after 10 a.m. (when water storage was assumed to no longer contribute to transpiration) until 2 p.m. (when maximum transpiration rates were observed in the trees). Specific leaf hydraulic conductance ($K_s - l$) was similarly estimated from the relationship between leaf transpiration rate (E) and leaf water potential (Ψ_L), again assuming that predawn water potential (Ψ_{pdd}) is equivalent to soil water potential

$$K_s - l = E/(\Psi_{\text{pd}} - \Psi_L), \quad (3)$$

where E is transpiration per unit leaf area measured with a porometer.

Water use efficiency: Water use efficiency (WUE) was compared between *A. tortilis* and *A. xanthophloea*. Carbon isotope composition of foliage (leaflets only), expressed as $\delta^{13}\text{C}$ was used as an index of seasonally integrated WUE (Tieszman and Archer, 1990). Leaves were collected for carbon isotope analysis on a monthly basis. Monthly samples were obtained from three trees of each species, and immediately dried in oven at 70 °C for 48 h. The samples were then ground to fine powder and 20 g obtained from each sample and sealed in plastic bags for $\delta^{13}\text{C}$ analysis. Further preparations and analysis were done in the isotope analysis lab, Plant Ecology Department, University of Bayreuth.

3. Results

3.1. Weather

Fig. 1 shows the seasonal pattern in precipitation as recorded between year 2000 and 2002. Fig. 2 shows daily weather conditions during the time when field measurements were taken. Precipitation during 2002 was above mean average for the region. More rains were received between November and December. Some significant rainfall occurred in April. Temperatures fluctuated within a fairly constant range (max = 30 °C) during the year.

3.2. Soil water content

SWC within the upper soil layer (0–40 cm) was significantly influenced by rainfall (Fig. 2). Moisture content at 40 cm depth increased within a period of 12–24 h after an event of rainfall. Highest SWC recorded at this depth was $0.34 \text{ m}^3 \text{ m}^{-3}$ and was during the rainy season (in December). There was a dry spell between January and April and this was accompanied with a decline in SWC. Rainfall events in April however led to recovery of SWC to $0.3 \text{ m}^3 \text{ m}^{-3}$. No significant rainfall occurred after April and SWC within the upper soil layers significantly declined thereafter with the lowest value of $0.11 \text{ m}^3 \text{ m}^{-3}$ observed in June.

3.3. Shoot growth, leaf initiation and shedding

Shoot extension and leaf growth occurred only during and shortly after the rainy periods except for large *A. tortilis* trees, where it continued long after rains had stopped (Fig. 3). Water stress greatly affected leaf initiation and growth as well as

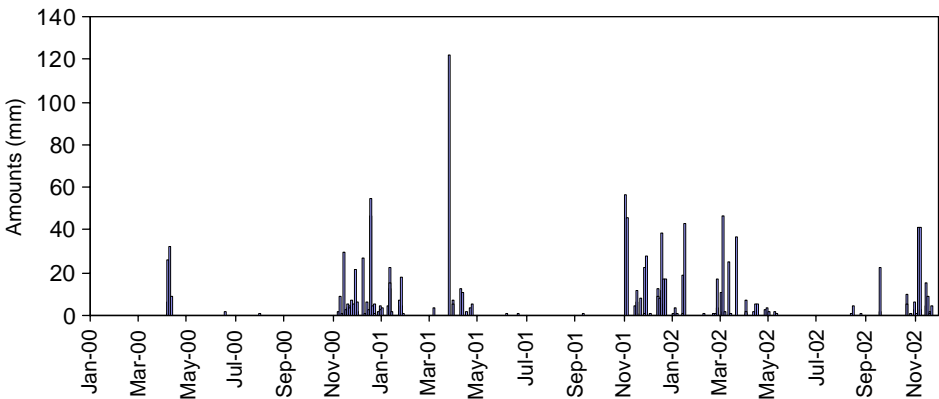


Fig. 1. Rainfall in Kibwezi between January 2000 and December 2002. Data was provided by University of Nairobi weather station, located 1 km from the study site.

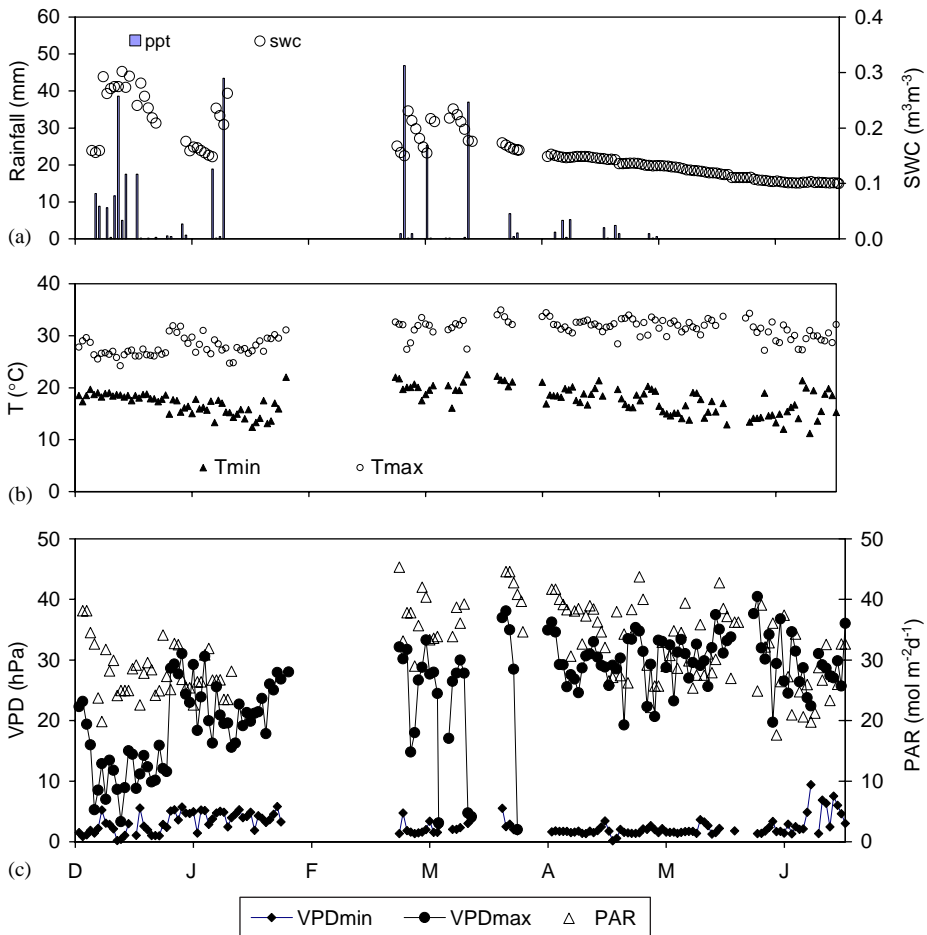


Fig. 2. (a) Precipitation and soil water content, (b) daily minimum and maximum temperatures and (c) daily minimum and maximum vapor pressure deficit (VPD) and photosynthetic active radiation (PAR) recorded at the study site between December 2001 and June 2002 when measurements were conducted. Periods when intensive field campaigns were conducted are indicated by arrows on the upper graph.

shoot extension. There was continuous leaf shedding and canopy leaf area gradually declined as drought intensified. Massive leaf fall also occurred immediately following a rain event especially after extended period of water stress, after which production of new leaves occurred. A close monitoring of representative branches showed very few leaves remaining in June and this was typical of the whole crown. Growth pattern exhibited by small *A. tortilis* resembled those of *A. xanthophloea* trees. Small *A. tortilis*, however did not show any significant growth response to the short April rainfall.

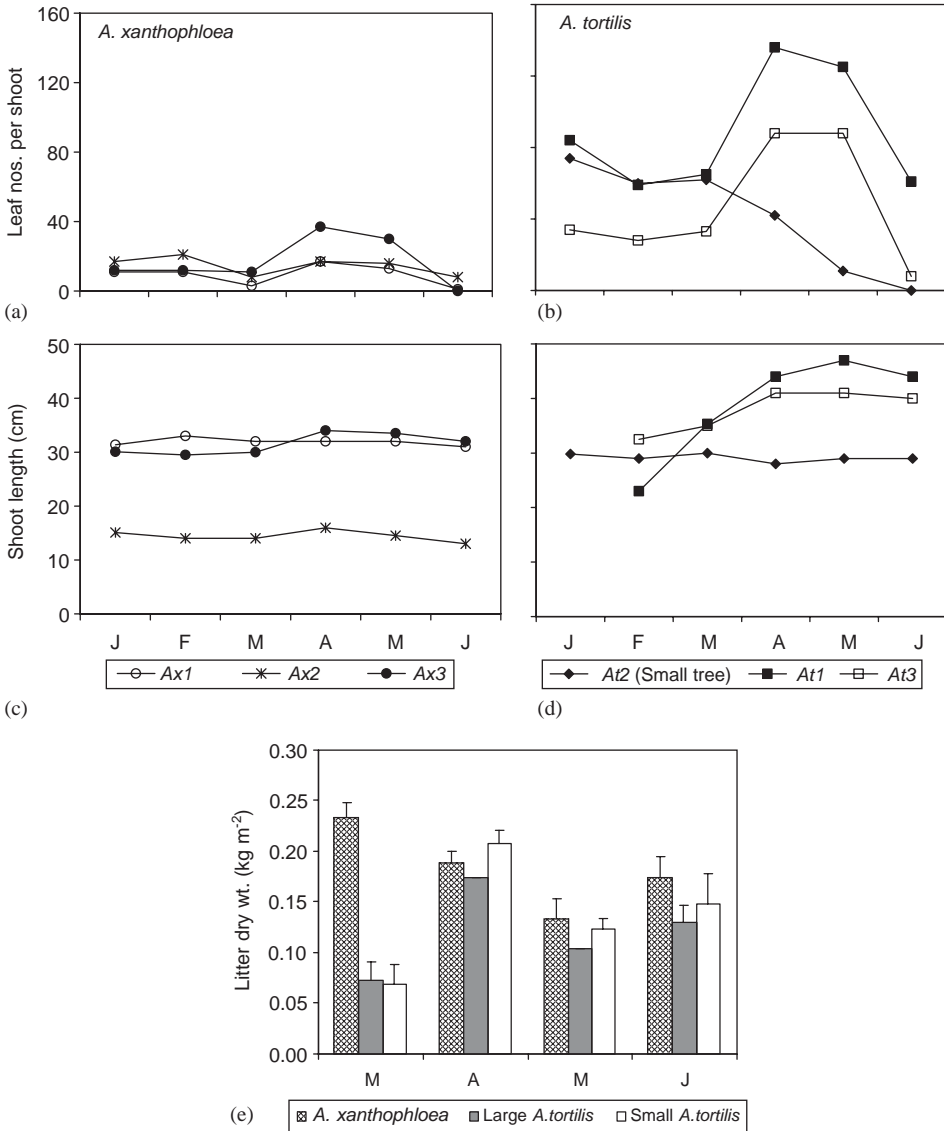


Fig. 3. Monthly records of: (a and b) shoot lengths, (c and d) number of leaves and (e) litter amounts from selected trees and branches of *A. tortilis* (At1, At2 and At3) and *A. xanthophloea* (Ax1, Ax2 and Ax3).

3.4. Seasonal changes in leaf water potential

Seasonal changes in predawn leaf water potential (Ψ_{pdd}) are shown in Fig. 4a. Highest Ψ_{pdd} were reported for all the trees during December, after successive rain events. Favorable tissue water status was also observed after the April rainfall events. Plant water status significantly declined between April and July, with *A.*

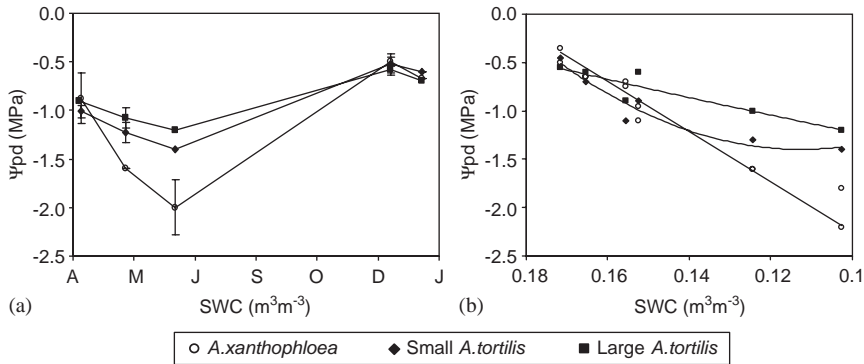


Fig. 4. (a) Seasonal changes in leaf predawn water potential (Ψ_{pdd}) for *A. xanthophloea*, small and large *A. tortilis*. Bars represent \pm S.D., $n = 3$. (b) Relationship between predawn leaf water potential for *A. xanthophloea*, small and large *A. tortilis* and soil water content (SWC) measured at 40 cm soil depth.

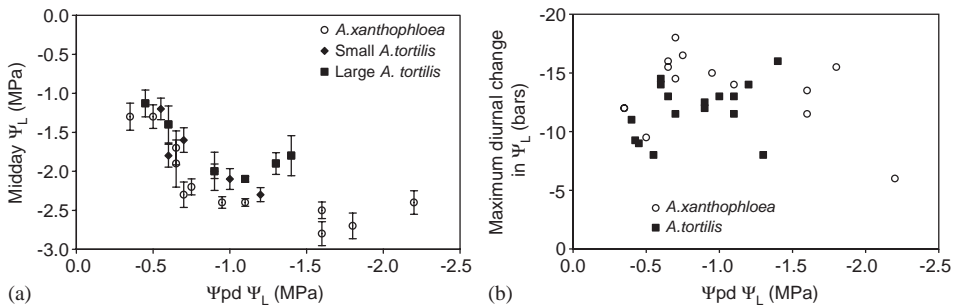


Fig. 5. (a) Relationship between midday leaf water potential (Ψ_L) and Ψ_{pdd} and (b) Relationship between maximum diurnal change in leaf water potential and Ψ_L for the measured *A. xanthophloea*, small and large *A. tortilis* trees.

xanthophloea showing the largest drop in Ψ_{pdd} (−2.0 MPa) compared to large *A. tortilis* (−1.2 MPa). Small *A. tortilis* showed intermediate response ($\Psi_{pd} = -1.4$ MPa). After November 2002 rains, all plants restored their Ψ_{pdd} to a similar value (−0.5 MPa). Decline in Ψ_{pdd} for *A. xanthophloea* corresponded with the changes in SWC observed at 40 cm soil depth and strong linear relationship existed between Ψ_{pdd} for *A. xanthophloea* and SWC measured at this depth (Fig. 4b). The weakest relationship between Ψ_{pdd} and SWC at this depth was observed for large *A. tortilis*, while that for small trees of *A. tortilis* was intermediate. Lowest Ψ_{pdd} values recorded during the study period were between May and June, a time when the SWC was $0.1 m^3 m^{-3}$. During this time, there were significant differences in Ψ_{pdd} values among the three tree classes. Similarly, midday Ψ_L also declined with increasing drought. However, for large *A. tortilis* a stable value of midday Ψ_L (around −2.0 MPa) was maintained despite the declining SWC measured at 40 cm soil depth (Fig. 5a). Fig. 5b shows that *A. xanthophloea* exercised no control on water loss during favorable soil water conditions (assuming that Ψ_{pdd} is an indicator of Ψ_s at

the rooting zone), until Ψ_{pdd} reached -0.8 MPa, after which it strongly regulated water loss. Conversely, *A. tortilis* consistently regulated water loss irrespective of soil water status, with consistent diurnal fluctuations in Ψ_L . Combining Figs. 5a and b, it appears that the differences in response as shown in Fig. 5a are due to differences in water accessibility and supply to the shoots.

3.5. Seasonal changes in sap flux

During favorable soil moisture conditions, highest flux rates of $41.8 \pm 5.4 \text{ kg d}^{-1}$ were recorded per tree for *A. xanthophloea* compared to $11.3 \pm 2.1 \text{ kg d}^{-1}$ for large *A. tortilis*. Declining soil water led to decline in daily sap flux (F) in both species but the magnitude and time at which this decline commenced varied (Fig. 6). F declined by about 40% in *A. xanthophloea* trees, 60% in small *A. tortilis* while a non-significant decline was recorded in large *A. tortilis*. For *A. xanthophloea* and small *A. tortilis*, F started to decline when SWC at 0–40 cm was around 0.1 and $0.15 \text{ m}^3 \text{ m}^{-3}$, respectively. Flux in large *A. tortilis* was less affected by changes in SWC at this

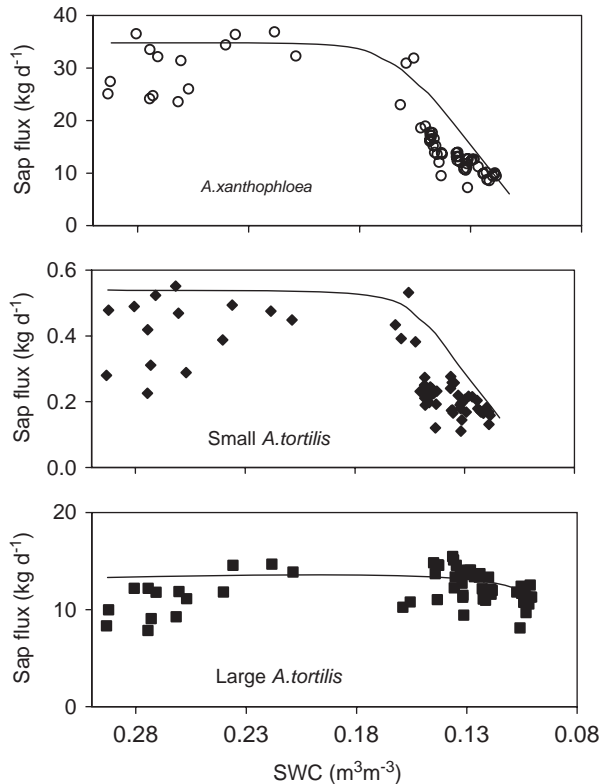


Fig. 6. Responses of sap flux (F) in *A. xanthophloea*, small and large *A. tortilis* trees to changes in soil water content (SWC) at 40 cm soil depth.

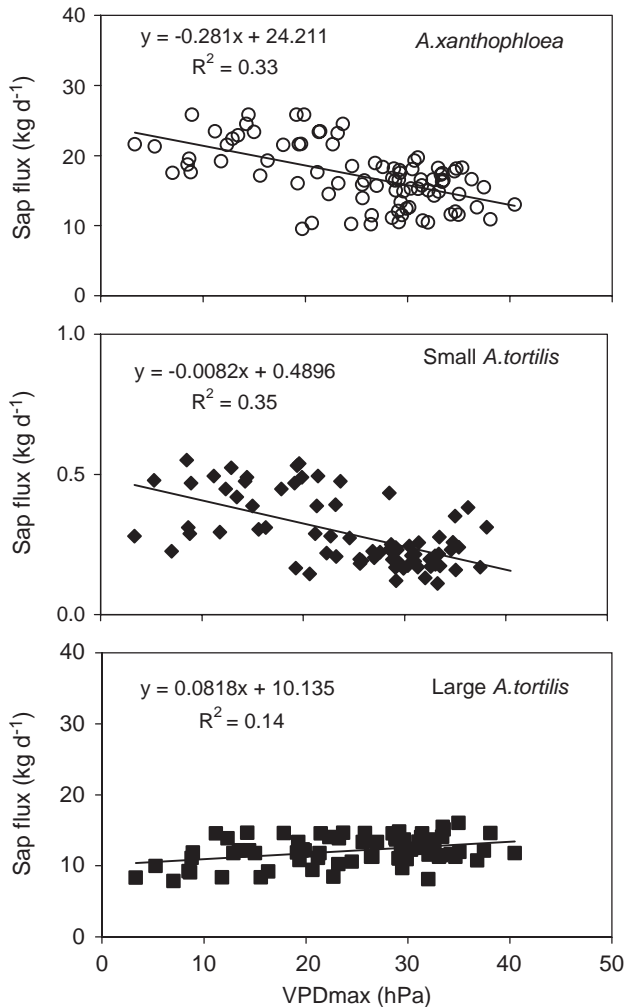


Fig. 7. Relationship between sap flux (F) and vapor pressure deficit (VPD) for *A. xanthophloea*, small and large *A. tortilis* trees.

depth. Decline was, however, more rapid in *A. xanthophloea*. Daily sap fluxes also declined as VPD increased except, in large *A. tortilis*, where no change was observed (Fig. 7).

3.6. Seasonal patterns of leaf stomatal conductance

Seasonal patterns of maximum leaf stomatal conductance ($g_{s\max}$) are shown in Fig. 8. Maximum leaf stomatal conductance was highest in both species ($350 \text{ mmol m}^{-2} \text{ s}^{-1}$) during favorable soil water conditions. Lower conductance

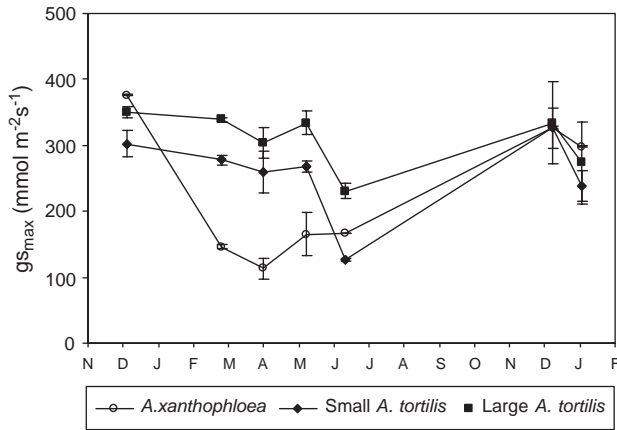


Fig. 8. Seasonal changes in maximum leaf conductance ($g_{s,max}$) measured in the sun crown of *A. xanthophloea*, small and large *A. tortilis*. Bars represent \pm S.D., $n = 3$.

rates ($300 \text{ mmol m}^{-2} \text{ s}^{-1}$) observed in small *A. tortilis* during this period were attributed to shading by the large and taller trees. Declining SWC led to a drop in stomatal conductance with significant differences between the two species. *A. xanthophloea* showed a more rapid decline in stomatal conductance, attaining a mean minimum $g_{s,max}$, of $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ at the end of the dry season. This was similar to the pattern of changes in Ψ_{pdd} . Trees of *A. xanthophloea* were more sensitive to declining SWC, and $g_{s,max}$ was at its lowest when SWC was about $0.15 \text{ m}^3 \text{ m}^{-3}$ (Fig. 9a). Large *A. tortilis* trees however, maintained $g_{s,max}$ nearly twice as high during this period (Fig. 9b). Relationship between Ψ_{pdd} and $g_{s,max}$, thus separating effects of differences in SWC at the root zone showed a similar response pattern in both small and large *A. tortilis*, Fig. 9d. It was therefore assumed that the differences observed in Fig. 9b were mainly due to differences in SWC, i.e. assuming that under similar conditions, both small and large *A. tortilis* will have similar g_s . A clear distinction appeared between the two species, with *A. xanthophloea* showing an early decline in g_s , Fig. 9c. At Ψ_{pdd} (surrogate for Ψ_s) of -1.00 MPa, when *A. tortilis* experienced stomatal conductance $>200 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Fig. 9d), $g_{s,max}$ was $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ in *A. xanthophloea* (Fig. 9c).

3.7. Diurnal changes in leaf stomatal conductance, leaf transpiration and leaf water potential

During favorable soil water conditions (December), g_s in *A. xanthophloea* rose to maximum during morning hours but declined significantly before midday with a brief resumption later in the day (Fig. 10, Panel a). For *A. tortilis* however, there was a brief decline in g_s around midday with a later return to morning values (Fig. 10, Panel a). A similar pattern was exhibited by *E*, leading to a decline in Ψ_L during the

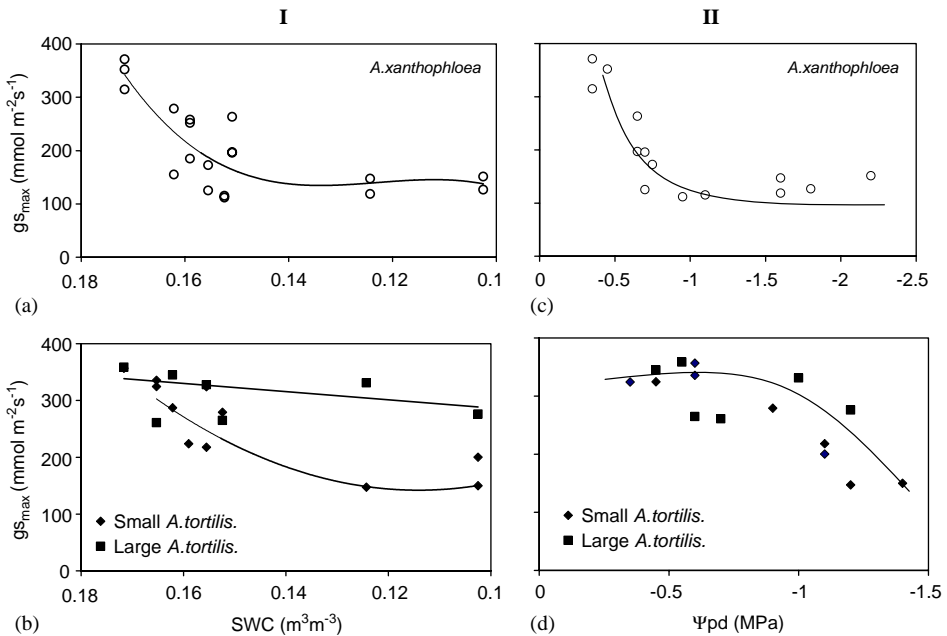


Fig. 9. (I) Responses of maximum leaf conductance ($g_{s,max}$) to changes in soil water content (SWC) at 40 cm in: (a) *A. xanthophloea* and (b) small and large *A. tortilis*. (II) Relationships between maximum leaf conductance ($g_{s,max}$) and predawn leaf water potential (Ψ_{pd}) of (c) *A. xanthophloea* and (d) Small and large *A. tortilis* trees.

morning and a recovery later in the day after E declined (Fig. 10, Panel a). Recovery of Ψ_L was, however, slower in *A. xanthophloea*. Also for *A. xanthophloea*, a brief depression in E was observed around midday, even when soil moisture was high (December). In many cases, *A. xanthophloea* experienced higher fluxes (40 kg d^{-1}) than *A. tortilis* (20 kg d^{-1}). However, when E was expressed per unit leaf area, there was no significant difference between the two species, suggesting that high daily sap flux in *A. xanthophloea* was mainly due to its large crown. With increased water stress, trees showed an early morning peak in g_s followed by a decline before noon (Fig. 10, Panels b and c—April and May). This was more pronounced in *A. xanthophloea*, which retained near zero g_s after midday. During this time, E in *A. xanthophloea* significantly dropped in the afternoon. Diurnal changes in Ψ_L were closely linked to transpiration, steeply declining when E was high and recovering when the rate declined. In the case of *A. xanthophloea*, however, it was surprising that at lower SWC, decline in E as a result of stomatal closure was not followed by recovery in Ψ_L , suggesting that there was an interruption of water supply to the leaves. This was different in *A. tortilis*, where E significantly increased over the season due to increased VPD but still fully recovered with respect to Ψ_L by dusk after the occurrence of stomatal closure (Fig. 10, Panels b and c).

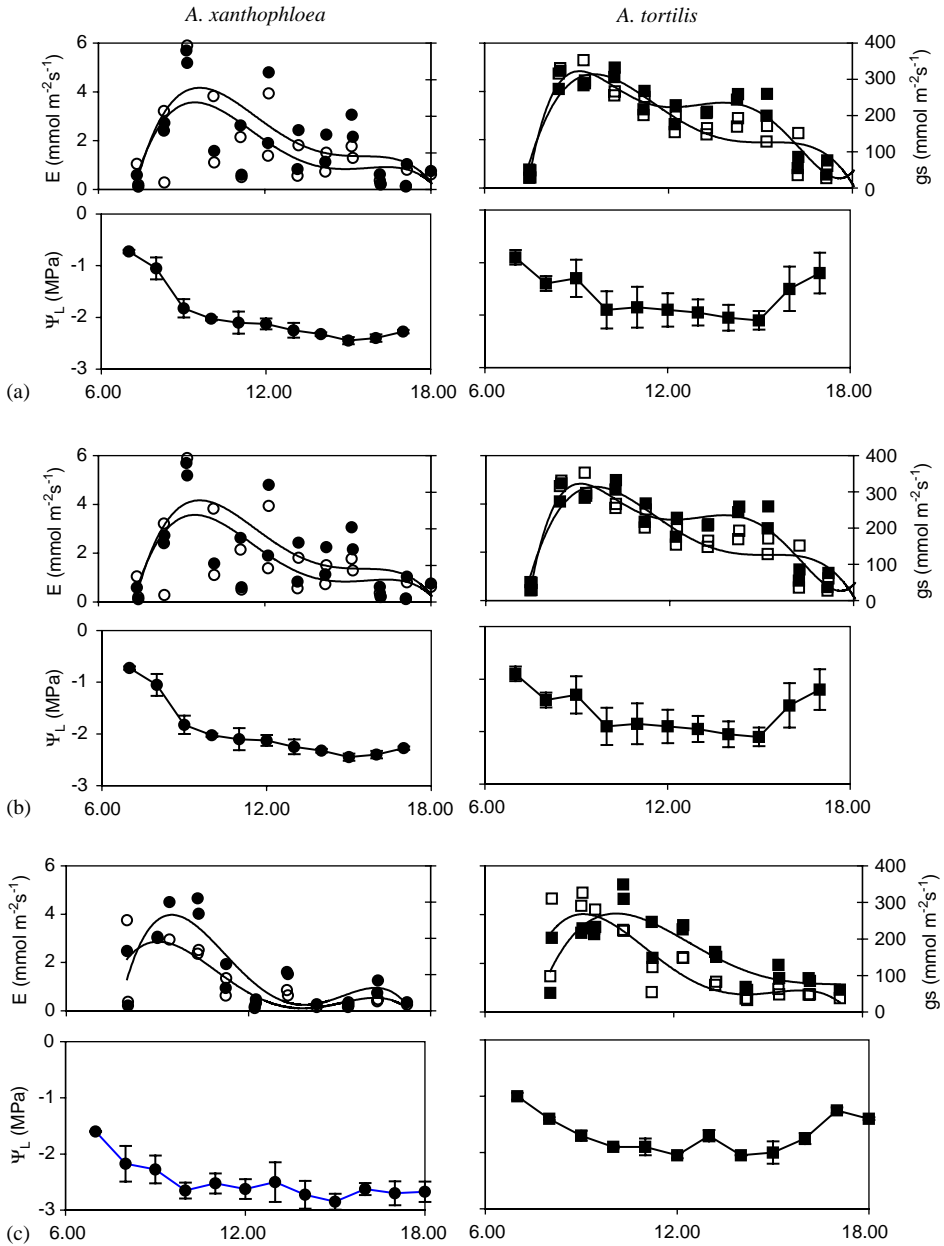


Fig. 10. Diurnal changes in leaf transpiration, E (open symbols), stomatal conductance, g_s (closed symbols) and leaf water potentials, Ψ_L (bottom) for *A. xanthophloea* (left) and *A. tortilis* (right), during three periods of the year, December (Panel A), April (Panel B) and May (Panel C), experiencing varying intensities of soil and atmospheric drought.

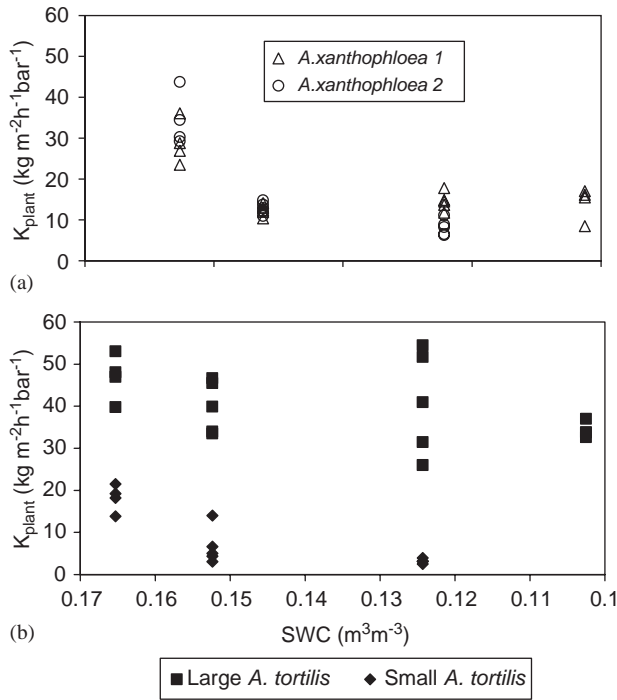


Fig. 11. Relationship between whole tree hydraulic conductance (K_{plant}) and soil water content (SWC) for: (a) *A. xanthophloea* (b) large and small *A. tortilis*.

3.8. Hydraulic conductance

Fig. 11 shows changes in whole tree hydraulic conductance (K_{plant}) in both species at different levels of SWC. During this period, K_{plant} declined by 50%, 27% and 83% in *A. xanthophloea*, large and small *A. tortilis*, respectively. Under favorable soil water conditions, significant differences occurred between large and small *A. tortilis* ($K_{\text{plant}} = 47.0$ and $18.2 \text{ kg m}^{-2} \text{ h}^{-1} \text{ bar}^{-1}$, respectively). Large *A. tortilis* also had higher hydraulic conductance compared to *A. xanthophloea* (47.0 and $28.8 \text{ kg m}^{-2} \text{ h}^{-1} \text{ bar}^{-1}$, respectively). Under similar conditions leaf specific hydraulic conductance ($K_s - l$) was 3.9 and $2.8 \mu\text{g bar}^{-1} \text{ cm}^{-1} \text{ s}^{-1}$ in *A. xanthophloea* and *A. tortilis*, respectively. A significant drop in K_{plant} occurred in trees of *A. xanthophloea* between SWC of 0.18 and $0.16 \text{ m}^3 \text{ m}^{-3}$. This coincided with the drop in g_s as well as in E .

3.9. Water use efficiency

Less negative $\delta^{13}\text{C}$ was observed for *A. xanthophloea* than for *A. tortilis* during favorable soil water condition (Table 2). $\delta^{13}\text{C}$ also increased with increasing water

Table 2
Monthly records of $\delta^{13}\text{C}$ discrimination for leaves of *A. tortilis* and *A. xanthophloea*

Month	$\delta^{13}\text{C}$ values	
	<i>A. xanthophloea</i>	<i>A. tortilis</i>
March 2002	-27.64 (± 0.5)	-27.95 (± 0.4)
April 2002	-27.42 (± 0.5)	-28.20 (± 0.6)
May 2002	-26.61 (± 0.5)	-27.59 (± 0.3)
June 2002	-26.37 (± 0.5)	-27.67 (± 0.8)
January 2003	-26.64 (± 0.4)	-28.40 (± 0.5)

In brackets \pm S.D.

stress in *A. tortilis* but no significant change occurred in *A. xanthophloea*, suggesting that *A. xanthophloea* was not able to alter water use with intensifying water stress.

4. Discussion

The study correlates the expression of morphological and physiological traits before and during the development of soil drought with tree access to soil water resources. So far, information is scanty on integrated seasonal morphological and physiological responses of the indigenous East African tree species during the development of drought. For the two *Acacia*-species studied, leaf initiation and shoot elongation were associated with water availability and started as soon as soil moisture in the root zone was favorable. Given the slow movement of water down through the soil layers (Radcliffe and Rasmussen, 2002), the rapidity and simultaneity with which leaf onset and growth responded to precipitation was an indication that they were able to access water soon after the rainfall, a sign that both species had roots located within the shallow soil layers. Fig. 2 showed that SWC at 0–40 cm depth declined rapidly soon after the rains stopped. This decline was attributed to drainage and evapotranspiration, since this is the region of greatest root biomass (Cavander-Bares and Bazzaz, 2000). If all or most of the root mass was located within the upper soil layer, it was expected that shoot elongation and leaf growth should stop soon after the rains, since trees rely solely on precipitation as their water source. This was the case with *A. xanthophloea* and small *A. tortilis* (Fig. 3). Growth in large *A. tortilis* was, however, less affected by soil drying at this depth, suggesting that water supply needed for growth was less interrupted. This was an indication that large *A. tortilis* trees also had their roots located within the deeper soil horizons with a stable water source, while *A. xanthophloea* and the small *A. tortilis* probably had most of their roots located within the upper soil layers, which dried out quickly soon after the rains.

Seasonal changes in Ψ_{pdd} and midday Ψ_{L} were more pronounced in *A. xanthophloea* compared to large *A. tortilis*, while small *A. tortilis* exhibited

intermediate responses (Figs. 4a and 5a). Similarly, relationship between Ψ_{pdd} and SWC measured at 40 cm soil depth (Fig. 4b) revealed a stronger coupling between Ψ_{pdd} and SWC for *A. xanthophloea*. Large *A. tortilis* however, showed a weak correlation, while that of the small trees was intermediate. These differences in seasonal patterns of plant water status were probably due to water uptake patterns, given that predawn water potential is an indicator of Ψ_s at the rooting zone (Ryel et al., 2004) and that plant tissue water content is in equilibrium with the soil moisture at dawn. The results indicate that root water uptake by *A. xanthophloea* was restricted to the upper soil layers and that its Ψ_{pdd} was dependent on soil moisture available within the 0–40 cm layer. Thus, Ψ_{pdd} of by *A. xanthophloea* rapidly declined to -2.0 MPa soon after the rains stopped, since soil moisture in this layer was rapidly exhausted. Ψ_{pdd} of large *A. tortilis*, however, was influenced by the upper soil layers during the rainy season and by the deeper soil layers during drought as revealed by its high Ψ_{pdd} (-1.1 MPa) during the time when SWC in 0–40 cm soil layer was relatively low and the rapid changes in Ψ_{pdd} during an event of rainfall. Certainly, the high tissue water status experienced by large *A. tortilis* during drought will not permit water uptake from the shallow soil layers, where Ψ_s is much lower. Small *A. tortilis* may have obtained water from intermediate soil layers or its behavior may reveal a superior quality in this species, such as osmotic adjustment or more effective soil water extraction by the roots and transport through the xylem, which enabled it to maintain favorable tissue water status compared to *A. xanthophloea*, despite obtaining water at the same soil layers. The results from plant tissue water status strongly supported the proposed water uptake pattern and the sensitivity of growth to SWC.

The amount of water lost through transpiration is determined by evaporative demand, SWC and plant factors, which include root and xylem characteristics and foliage quality and quantity (Turner, 1986). In this locality, the main stress was due to lack of water resulting from the variability in rainfall. Periods of water stress were associated with high temperatures and high evaporative demand (Fig. 2), both of which favor increased water loss from trees (Schulze et al., 1987). On a long-term basis, transpiration declined in both small *A. tortilis* and *A. xanthophloea*, with increasing soil and atmospheric drought, but not in large *A. tortilis*, which maintained a relatively constant transpiration rate (Figs. 6 and 7). Under such circumstances, constant or declining transpiration would mean limited water supply from the roots or restricted water loss at the leaf surface. In response to increasing soil water deficit and atmospheric demand, there was a significant reduction of the transpiring leaf surface through increased leaf shedding and reduced leaf initiation and growth. This could partially account for the decline in whole tree transpiration. Since shoot elongation and leaf initiation had long stopped, it is also suggested that photosynthetic products originating from the remaining leaves were re-directed to more important areas such as root growth to improve water uptake which, is an important adaptive mechanism to water stress (Kramer, 1980; Jones, 1992).

Stomatal conductance was also strongly influenced by declining SWC. The observed relationship between maximum stomatal conductance, Ψ_{pdd} and SWC (Fig. 9) demonstrated the dependence of stomatal conductance on SWC. Differences

in response of stomatal conductance to declining SWC between and within species (Figs. 8 and 9) could therefore serve to demonstrate the differential abilities to access water at different soil layers, root absorption and water transport. Thus, the unrestricted stomatal conductance observed in large *A. tortilis* demonstrates unrestricted access to a stable deep soil water source compared to *A. xanthophloea* and the small *A. tortilis* trees and explains its continued growth during the time when SWC at 0–40 cm soil layer was low and growth had long stopped in the latter. Changes in stomatal conductance in *A. xanthophloea*, however, followed the pattern of decline in SWC at 0–40 cm soil layer. Assuming that large *A. tortilis* would behave in a similar manner to small trees of the same species when exposed to greater water stress (Fig. 9d), it is evident that both species will, however, respond to seasonal decline in soil water by reducing stomatal conductance. Reduced stomatal conductance may, therefore, partly account for the decline in transpiration rates as observed during drought.

On a short-term basis, stomatal closure occurred in both species before noon when transpiration rate was increasing due to increasing vapor pressure deficit, thus limiting further decline in Ψ_L (Fig. 10). Through stomatal closure, trees are able to reduce water loss during the time when water supply from the soil to the leaves cannot cope with transpiration water loss and serve to avoid development of dangerous negative tissue water potentials and hydraulic failure in the soil-leaf continuum (Tyree and Sperry, 1989; Kolb and Sperry, 1999; Sperry, 2000). Trees with deep rooting system, accessing more stable soil water supplies, however, do not need to reduce transpiration as rapidly and as drastically as those with limited rooting depths (Larcher, 2003). Thus, differences in stomatal behavior between species or individuals as shown in the case of the *Acacia*-trees studied is a strong indication of their differences in rooting patterns and root water uptake.

The structure of the water-conducting system (vessel size and hydraulic architecture) determines resistance along the water flux pathway and influences water use (Ni and Pallardy, 1990). Changes in tree hydraulic conductance during progressive soil drying as shown in Fig. 11 can reveal differences among species (Abril and Hanano, 1998) and can be attributed to variation in root: leaf surface ratio or inherent absorption capacity and root permeability (Reich and Hinkley, 1989). These changes suggest a mechanism of adaptation to xeric environments that is important for drought tolerance (Abril and Hanano, 1998). Although hydraulic conductance was determined from the time when soil water potential ($\Psi_{pd} = \Psi_s$) was 0.7 MPa, it was assumed that no major differences may occur in tree responses at less negative values. A significant drop in K_{plant} in *A. xanthophloea* between $\Psi_s = -0.7$ and -1.0 MPa paralleled decreases in maximum stomatal conductance (Fig. 9). Similarly, this paralleled significant decrease in transpiration in *A. xanthophloea*. It is, therefore, suggested that the decline in g_s as well as leaf transpiration in *A. xanthophloea* was the result of a restricted flux capacity (Reich and Hinkley, 1989; Sala and Tenhunen, 1994; Sperry, 2000). This could also provide an explanation for the anomaly where stomatal closure in *A. xanthophloea* before midday did not result in improved Ψ_L later in the day and where Ψ_L did not fully recover by dusk (Fig. 10). A high hydraulic resistance between the soil and the shoot will induce relatively

lower Ψ_L in the concerned trees (Turner, 1986). Resistance to water flow could occur at two points, namely root surfaces (Boyer, 1985; Sala and Tenhunen, 1994) or in the stem and leaves (Turner, 1981). In this study, there was a marked similarity in responses between small *A. tortilis* and *A. xanthophloea* trees, a fact that was attributed to their limited rooting depth. Small *A. tortilis* also experienced similar decline in K_{plant} and this was attributed to increased resistance at the root surface as a result of rapidly declining SWC. Small *A. tortilis* were, however, able to fully recover their Ψ_L by dusk (not shown), suggesting that lack of recovery in Ψ_L in *A. xanthophloea* was an added effect of inefficient water transport system, which might have resulted in cavitation (Zimmermann, 1983; LoGullo et al., 2003). This may partly explain the observed differences in physiological responses between the two plant groups, despite having roots within similar soil layers.

Long term monitoring of tree WUE through $\delta^{13}\text{C}$ analysis (Cowan and Farquhar, 1977) showed higher WUE in *A. xanthophloea* than *A. tortilis*. High WUE is associated with increased drought tolerance hence with trees growing in dry areas (Smith and Nowak, 1990). However, high WUE would only be of any ecological significance if the conserved soil moisture were available for uptake later in the season (DeLucia and Schlesinger, 1990). For large *A. xanthophloea* trees, which showed signs of shallow rooting system, conserved moisture may not be available due to high moisture depletion from the upper soil layers through evapotranspiration as soon as the rains stop, hence no advantage derived from high WUE. Thus, despite its conservative nature, *A. xanthophloea* still experienced lower leaf water potentials in a drying soil. *A. tortilis*, with deep rooting system was able to maximize carbon gain when soil water was abundant and adjusting WUE accordingly as drought intensified, thus minimizing water loss during the progressing drought and making it available later in the season since competition for water at deeper soil layers is also limited.

Response patterns of tree growth and water use in these tree groups (*A. xanthophloea*, small and large *A. tortilis*) were according to their rooting patterns. Thus, root distribution seems to determine tree phenology and water use and must determine species distribution patterns in the arid savanna. The overall view is that most of the above-ground shoot responses, as well as whole tree behavior during the development of drought were the result of a modified soil resource base. Long term as well as short term changes associated with the root and shoot systems acted to modify plant functioning in order to accommodate changes in the soil environment. The ability of a plant species to modify its root system to optimize resource gain from the soil resource base and to maintain a balance between resource acquisition and use, therefore, ensures its success in a given savanna habitat. The final conclusion, therefore, is that the soil resource base as well as root system development and activity determine productivity, species distribution and the overall behavior of the arid savanna ecosystem. Success of *A. tortilis* in the more xeric regions of the Kenya savanna is, therefore, due to its deep rooting system and efficient root water uptake and transport while *A. xanthophloea* occupies the lowlands because of shallow rooting system. Presence of *A. xanthophloea* among of *A. tortilis* trees in the xeric environments as in the case of the current study site must

be as a result of a modified soil environment, probably through hydraulic lift by *A. tortilis* (see Ludwig et al., 2003, 2004), which improves the water status of the upper soil layers and allowing water access by shallow rooted plants. Further studies in these lines are recommended.

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