



# Tree distribution on a steep environmental gradient in an arid savanna

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## ABSTRACT

**Aim** The structure of savannas ranges from scrub to woodland over broad geographical gradients. Here we examine the hypothesis that water availability is a major determinant of these structural differences by ascertaining the relationship between water availability and tree growth across a steep moisture gradient.

**Location** The study site is a sub-tropical savanna, with a mean annual precipitation of 400 mm, located in the Phugwane river basin, Kruger National Park, Limpopo Province, South Africa.

**Methods** We determined plant moisture stress using xylem pressure potentials, stem growth using dendrometer bands, and estimated the water sources available to plants using stable hydrogen and oxygen isotope ratios. The primary objective was to understand tree growth relative to available water along an environmental gradient.

**Results** We found that *Philenoptera violacea* trees growing close to the stream have lower water stress (least negative xylem pressure potentials) and higher cumulative growth than those growing away from the stream. The stem growth of *P. violacea* was characterized by steady incremental growth and could not be related to antecedent rainfall. *Colophospermum mopane* trees experienced higher water stress, yet trees growing adjacent to the stream achieved the highest cumulative growth rates over the study period. The growth of *C. mopane* could be clearly linked to antecedent rainfall, and most growth was achieved during short growth pulses that followed rainfall events.  $\delta^{18}\text{O}$  values become progressively more enriched in the heavier isotope with distance from the stream, suggesting that access to groundwater decreases with distance from the stream side. The isotopic data suggest that *P. violacea* has access to groundwater, but that *C. mopane* does not.

**Main conclusions** Our results show that water stress increases with distance from the stream side as a result of reduced access to groundwater. Trees without access to deep water adopt an opportunistic growth strategy.

## Keywords

Arid savanna, *Colophospermum mopane*, dendrometer bands, *Philenoptera violacea*, stable oxygen isotope ratios, tree growth rates, water, xylem pressure potentials.

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## INTRODUCTION

Savannas are a tropical vegetation type in which trees and grasses co-dominate. This vegetation type covers 12% of the global land surface and some 65% of the land surface of sub-

Saharan Africa (Huntley & Walker, 1982). This extensive geographic distribution means that savannas occur over a broad climatic gradient. Throughout this broad range in climate, savanna systems are typically composed of a continuous grass layer and a discontinuous layer of shrubs

and trees (Frost *et al.*, 1986; Sankaran *et al.*, 2004). The coexistence of trees and grasses over such a wide geographic and climatic range poses an intriguing puzzle for biogeographers, elegantly captured by Sarmiento's (1984) 'savanna question'. Sarmiento asked, what is special about savanna systems that allows trees and grasses to coexist as opposed to the general pattern in grasslands and forests where either one or the other functional type dominates?

While the question of how grasses and trees coexist has intrigued ecologists for decades, equally intriguing questions are why savannas differ so fundamentally in structure, and why this vegetation type has such a wide geographic and climatic distribution (Belsky, 1990; Scholes & Walker, 1993; Sankaran *et al.*, 2004). The German biogeographer Walter (1971) noted that, although the savanna state persists over large biogeographical gradients, the structure of savannas can vary. Savanna structure ranges from scrub savanna, through grass-dominated savanna, to closed woodlands. He proposed that this structure is primarily related to water availability.

Here we explore whether the relationship between available water and tree growth across a steep environmental gradient can explain these structural differences observed in savannas (Fig. 1). For this we use the gradient along a sequence from a stream bank into the savanna upland as a mesocosm of the gradual moisture gradients that extend through savanna regions. Previous research has shown that water availability varies strongly across this gradient. Specifically, stream-side sites have higher water availability owing to deep coarse textural alluvial soils, while savanna upland sites have low water availability owing to fine-textured shallow soils (Milne, 1936; Dye & Walker, 1980; Scholes, 1999). In this study we explore how the spatial and temporal distribution of this soil water both directly and indirectly influences the growth of trees, thereby defining savanna structure.

To determine the relationship between tree growth and available water we specifically ask whether plant moisture stress changes along the gradient. We also ask whether access to water influences growth strategies. To understand how plant-available water changes across the gradient and how this influences tree growth strategies we look at plant moisture

stress (by measuring xylem pressure potentials), stem growth (measured with dendrometer bands), and estimates of water sources available to plants (estimated using stable oxygen isotope ratios).

## METHODS

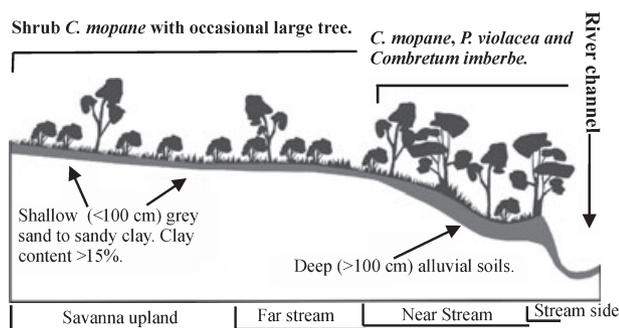
### Study area

The study site is situated at (31°29' E, 23°01' S), 21 km north-west of Shingwedzi, on the Phugwane river in the northern section of the Kruger National Park in the Limpopo Province of South Africa. The climate of the region is characterized by hot wet summers and dry mild winters. Mean monthly maximum and minimum temperatures at Shingwedzi for the 28 months of the study from April 2000 to August 2002 are, respectively, 30.2°C and 15.3°C. Rain, consisting predominantly of thundershowers from the north and north-east, or tropical cyclones from the Indian Ocean, falls primarily from October to March. Rainfall for 2000 and 2001 was above the annual average of 400 mm, at 1193 and 553 mm respectively. The abnormally high rainfall in 2000 was directly related to the tropical cyclones Eline (February 2000) and Gloria (March 2000) that originated in the Indian Ocean and moved through the Mozambique channel before swinging inland over the study area.

We have recognized four geomorphological zones along a transect from the river inland in our study area (Fig. 1). These are stream side including the river bank and levee, near stream including the alluvial terrace adjacent to the active channel, far stream including the alluvial terrace adjacent to the savanna, and savanna upland, the savanna proper. No woody plant species is common across all four zones. *Philenoptera violacea* Klotze, Schrire and *Combretum imberbe* Wawra are common in the stream-side and near-stream zones, and *Colophospermum mopane* Kirk ex J. Léonhard (Kirk ex Benth) is common in the near-stream, far-stream and savanna zones. The semi-deciduous *P. violaceae* dominates the stream-side communities of our study area. Although the stream-side vegetation is more dense than that of the other zones, the canopy remains open enough to allow a persistent grass layer. The maximum tree size and tree density are lower in the near-stream zone, and lowest in the savanna zone, which is dominated by the deciduous *C. mopane*. Each zone is relatively homogenous, and in the zone where both trees coexist (near stream), individuals of the two species grow spatially interspersed with each other.

The savanna systems of the study area are classified by Acocks (1953) as Mopane Veld. *Colophospermum mopane* is dominant on the clay-rich soils (> 15% clay), while *Combretum apiculatum* Sond. is more common on shallow gravel and sandy soils (Venter *et al.*, 2003).

The soils of the region are derived from undifferentiated metamorphic rocks and amphibolites of the Swaziland system as well as from granite (Venter, 1986; Venter *et al.*, 2003; Khomo & Rogers, 2005). The soils away from the river form shallow red clays becoming deeper with more recent alluvia



**Figure 1** Cross-section of the study site along the Phugwane River in the Kruger National Park showing the four geomorphological zones used in this study.

**Table 1** Co-ordinates for the three transects Sandpiper, Mamba and Zari along which 41 trees were investigated for this study

| Transect              | Latitude    | Longitude   |
|-----------------------|-------------|-------------|
| Sandpiper stream side | 23°01'10.2" | 31°17'37.7" |
| Sandpiper savanna     | 23°01'4.5"  | 31°17'36.8" |
| Mamba stream side     | 23°02'24.8" | 31°15'57.9" |
| Mamba savanna         | 23°02'21.9" | 31°15'57.2" |
| Zari stream side      | 23°03'17.2" | 31°12'4.4"  |
| Zari savanna          | 23°03'10.3" | 31°12'7.8"  |

adjacent to the river (Venter *et al.*, 2003; Khomo & Rogers, 2005).

We investigated 41 individual trees, 14 *P. violacea* and 27 *C. mopane*, distributed among three transects along the Phugwane River incorporating the four geomorphological zones. We call these transects Sandpiper (21 trees), Mamba (8 trees) and Zari (12 trees, Table 1). Forty trees were used for an analysis of xylem pressure potentials, and all 41 trees for stem growth, while cost implications meant that only two trees from each species for the geomorphological zones they occupied were sampled for stable-isotope analysis.

### Moisture stress

Xylem pressure potentials (XPPs) are a measure of the water status of a plant, or of plant moisture stress. XPPs indicate the demand for water in a plant by determining the tension that the water column of the plant is under. As water is transpired through the leaves it is replaced in a continuous stream from the roots through water available to the plant in the soil. The more tension on the water column in the xylem conduits, the less water is available to the plant. Plant moisture stress is therefore an integration of the amount of water available to a plant (water supply) and environmental pressures placed on the plant, such as rainfall and temperature (Scholander *et al.*, 1965; Miller *et al.*, 1984). For this study we determined XPPs using a Scholander Pressure Chamber (PMS Instrument Co., Corvallis, OR, USA).

Towards the end of the wet season in February 2002 and again towards the end of the dry season in August 2002, XPPs were measured before dawn on 40 trees from the three transects Sandpiper (13 *C. mopane* and 7 *P. violacea*), Mamba (6 *C. mopane* and 2 *P. violacea*) and Zari (7 *C. mopane* and 6 *P. violacea*; Scholander *et al.*, 1965; Miller *et al.*, 1984). These measures were repeated on each tree at hourly intervals until midday (13.00 h) on sunny, cloudless days.

### Stem growth

On 27 February 2000, dendrometer bands (Agricultural Electronics Corporation, Tucson, AZ, USA) were fitted to 41 trees, from the three transects Sandpiper (13 *C. mopane* and 8 *P. violacea*), Mamba (6 *C. mopane* and 2 *P. violacea*) and Zari (7 *C. mopane* and 6 *P. violacea*). Dendrometer bands are thin

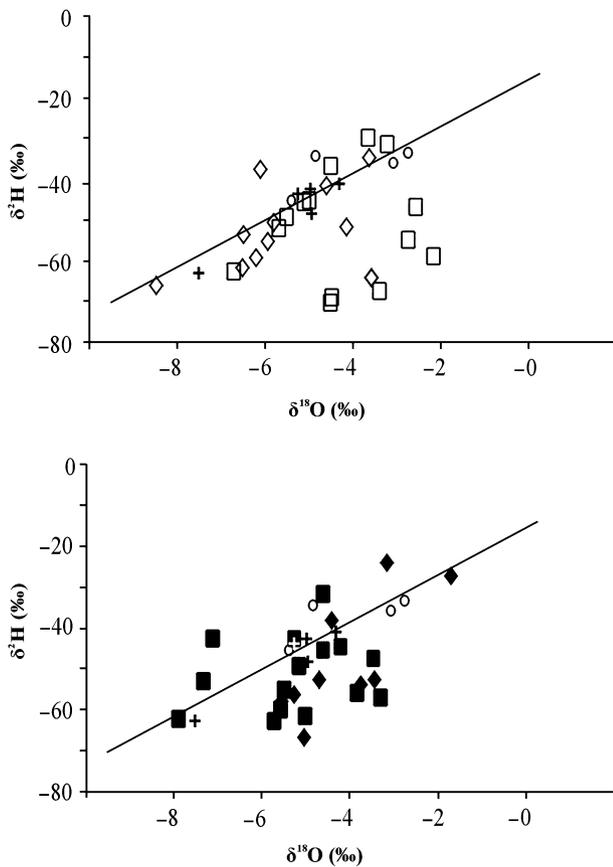
metal bands (3 mm × 75 µm) placed around the trunk of a tree; they are held in place under tension by a spring-loaded vernier gauge. The hastalloy material from which the band is constructed has a rated coefficient of thermal expansion of 11.2 µm m<sup>-1</sup> °C<sup>-1</sup>. Changes in radial diameter are read manually from the vernier gauge at a resolution of 0.1 mm. These changes may include shrinking and swelling of the stem, with changes in water content as well as increases in diameter from new wood. Bands were fitted to the stems below the height at which branching commenced, where bark damage was not apparent. Differences in the level of bark damage and the height at which branching occurred meant that the bands were fitted at different heights (typically between 0.2 and 1.8 m). Manual readings of the vernier gauge were made at the end of each month from March 2000 to the end of August 2002.

### Water source

Previous ecological research has emphasized the usefulness of stable hydrogen and oxygen isotopes in understanding the dynamics of water in atmospheric and geochemical studies (Dansgaard, 1964; Mazor, 1991). The primary assumption of the method is that within fully suberized (non-photosynthesizing) tissue the stable-isotope ratio of the water in the xylem is not different from that of the water source (White *et al.*, 1985; Ehleringer & Dawson, 1992; Thorburn & Walker, 1993; Lipp *et al.*, 1996). Therefore, stable-isotope analysis of twig xylem water should reflect the isotope ratio of the water source of the plant.

There is a linear relationship in the depletion of <sup>2</sup>H and <sup>18</sup>O in fresh water explained by the global meteoric water line (Craig, 1961). This relationship can best be described by the equation  $\delta^2\text{H} = 8\delta^{18}\text{O} + 10$ . Free evaporative processes typically describe a line with a slope that is less than 8 and an intercept that is less than 10. This shallower slope arises from the unidirectional isotopic fractionation of Raleigh distillation. The result is that evaporatively enriched water (surface water and shallow soil moisture) plots below the meteoric water line. This fractionation change is greater for oxygen than for hydrogen, leading this study to concentrate on oxygen. For plant water-source studies, in arid environments such as at our study site, these relationships are extremely useful, as deep (non-evaporatively enriched) and shallow (evaporatively enriched) moisture sources can be readily distinguished. We constructed a local meteoric water line (LMWL) for our study site using all of the stream and groundwater samples for both wet and dry seasons (Fig. 2). We also plotted our results for both *C. mopane* and *P. violacea* relative to this LMWL in both the wet and dry seasons (Fig. 2).

Ten trees (two for each species from each geomorphological zone, Fig. 1) along the Sandpiper transect were selected for analysis. As *P. violacea* does not grow outside of the riparian area, we only collected samples of this species from the stream-side and near-stream zones. Samples of *C. mopane*, on the other hand, were collected from all but the stream-side zone



**Figure 2** A plot of the relationship between hydrogen and oxygen isotope ratios for all the study samples. Open symbols are wet season and closed symbols dry season. + borehole water, O river water, ◆ *Lonchocarpus cappasa*, ■ *Colophospermum mopane*. The line (LMWL,  $y = 5.74x - 15.56$ ,  $R^2 = 0.79$ ) represents the line of best fit through all the borehole and river samples for both seasons.

(Fig. 1). From these trees, twig samples of mature wood 0.5–1 cm in diameter and 6–7 cm in length were collected twice a year (wet season and dry season) over a 3-year period (2000–02). The twigs were immediately sealed in borosilicate tubes (Kimax–Kimble, Vineland, NJ, USA.) which could then be inserted directly onto a cryogenic vacuum distillation line to extract the xylem water for stable-isotope analysis.

Water samples from the Phugwane River were collected as it flowed past the Sandpiper transect. Groundwater was collected from two boreholes in the areas Tomlinson and Sandpiper, c. 2 km west and east of the Sandpiper transect. These water samples were collected in previously unused 100-ml plastic bottles, which were sealed to prevent evaporation.

Water samples were analysed for  $^{18}\text{O}/^{16}\text{O}$  ratios using the  $\text{CO}_2$  equilibrium method of Socki *et al.* (1992).  $\text{H}^2/\text{H}$  ratios were obtained through the closed-tube zinc-reduction method of Coleman *et al.* (1982). Isotopic ratios of both  $\text{H}^2/\text{H}$  in  $\text{H}_2$  and  $^{18}\text{O}/^{16}\text{O}$  in  $\text{CO}_2$  were determined using a Finnigan Mat 252 Mass Spectrometer. Our own independently analysed internal standards were run to calibrate our results relative to Vienna Standard Mean Ocean Water (V-SMOW), as well as to

correct for drift in our reference gas. The deviation from V-SMOW is denoted by the term  $\delta$ , and the results expressed as parts per thousand or per mil (‰) through the equation:

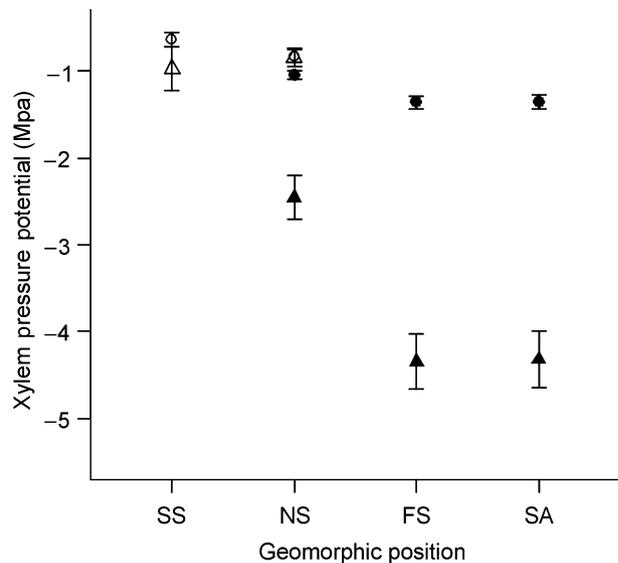
$$\delta^N\text{E} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1000,$$

where N is the heavy isotope of element E, and R is the ratio of the heavy to light isotopes ( $^2\text{H}/\text{H}$  or  $^{18}\text{O}/^{16}\text{O}$ ). Analytical uncertainty is c. 2.0‰ ( $\delta^2\text{H}$ ) and c. 0.2‰ ( $\delta^{18}\text{O}$ ).

## RESULTS

### Moisture stress

Pre-dawn XPPs for *P. violacea* were greater than  $-1$  Mpa in both the wet and dry seasons, suggesting low water stress in both seasons (Fig. 3). A repeated measures analysis of variance (using an error term with trees nested within transect) showed that pre-dawn XPPs for *P. violacea* did not differ with season (d.f. = 1,  $F = 0.70$ ,  $P = \text{NS}$ ) or geomorphological position (d.f. = 2,  $F = 0.20$ ,  $P = \text{NS}$ ). The pre-dawn XPPs for *C. mopane* suggest low water stress in the wet season ( $> -1.5$  Mpa), and high water stress in the dry season. In both seasons the far-stream and savanna trees were more water-stressed ( $< -4$  Mpa) than the near-stream trees ( $-2.5$  Mpa, Fig. 3). The pre-dawn XPPs for *C. mopane* were significantly influenced by season (d.f. = 1,  $F = 140$ ,  $P < 0.001$ ) and geomorphological position (d.f. = 2,  $F = 12.3$ ,  $P < 0.001$ ). The difference between wet- and dry-season XPPs increases as one moves from the stream-side to the



**Figure 3** Pre-dawn xylem pressure potentials in the dry and wet seasons. Open symbols are *Philenoptera violacea*, closed symbols *Colophospermum mopane*, circles wet season, and triangles dry season. Bars are standard error and points are means for all three transects (Sandpiper, Mamba and Zari). SS: stream side, NS: near stream, FS: far stream, and SA: savanna.

savanna sites, with the far-stream and savanna trees showing the greatest between-season variations (Fig. 3).

There is a gradient of noon water stress from the stream-side to the savanna positions during the wet season (Fig. 4). The diurnal cycle of XPPs in the wet season suggests that trees of both species growing further away from the stream experience earlier and more severe water stress than do trees growing closer to the stream (Fig. 4).

### Stem growth

Plots of the cumulative radial increment of stems show that *P. violacea* and *C. mopane* differ substantially in their growth strategies, and that growth responses differ with landscape position (Fig. 5). For both species, growth rates are highest closest to the stream, and lowest farthest from the stream. The highest growth rates achieved were by *C. mopane* growing in the near-stream and far-stream locations, with annual (April to April) cumulative radial increments of 3.0 mm (2001) and 1.79 mm (2002) observed for the near-stream trees (Fig. 5). Those trees growing in the far-stream zone had annual cumulative radial increments of 3.1 mm (2001) and 1.4 mm (2002). For *P. violacea*, in contrast, we detected smaller annual cumulative radial increments (1.0 mm for 2001 and 2.7 mm in 2002 in stream-side, and 1.4 mm for 2001 and 0.3 mm for 2002 in near-stream locations). The poorest-performing trees were, however, the *C. mopane* growing in savanna locations: these trees achieved annual cumulative radial increments of 0.4 mm (2001) and -0.4 mm (2002) (Fig. 5).

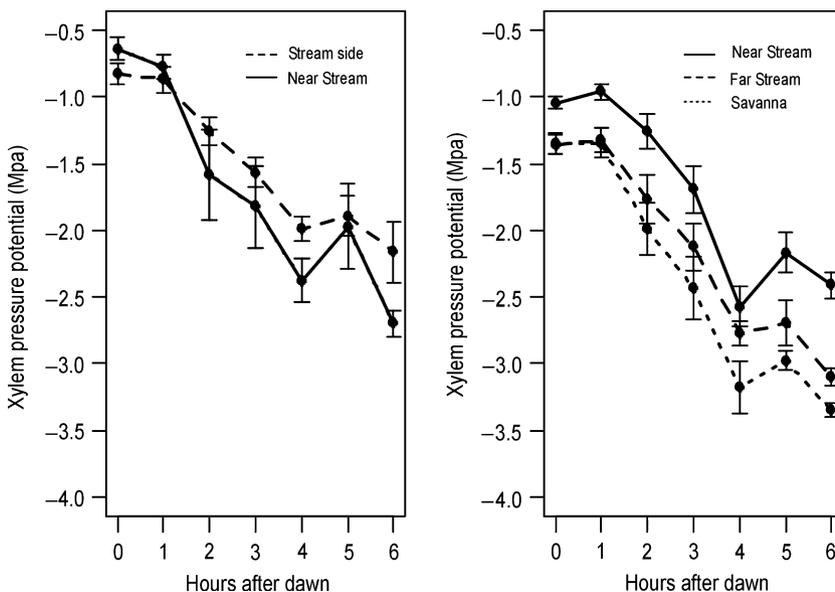
We performed linear regressions of radial increment against rainfall in the preceding two weeks for each species and geomorphological position. The results from this analysis show no relationship between radial increment and total rainfall (Table 2) for stream-side *P. violacea*. A very weak (shallow slope of the linear regression), but statistically significant,

relationship between rainfall and radial increment was detected for near-stream *P. violacea*. The relationship was strongest (steeper slopes of the linear regression) and significant for *C. mopane* in all locations (Table 2). This stronger relationship between growth rates and rainfall for *C. mopane* is further illustrated in the distribution of the growth increments recorded. This distribution has a higher variance for *C. mopane* than for *P. violacea*; that is, both higher and lower growth increments were reported for *C. mopane*.

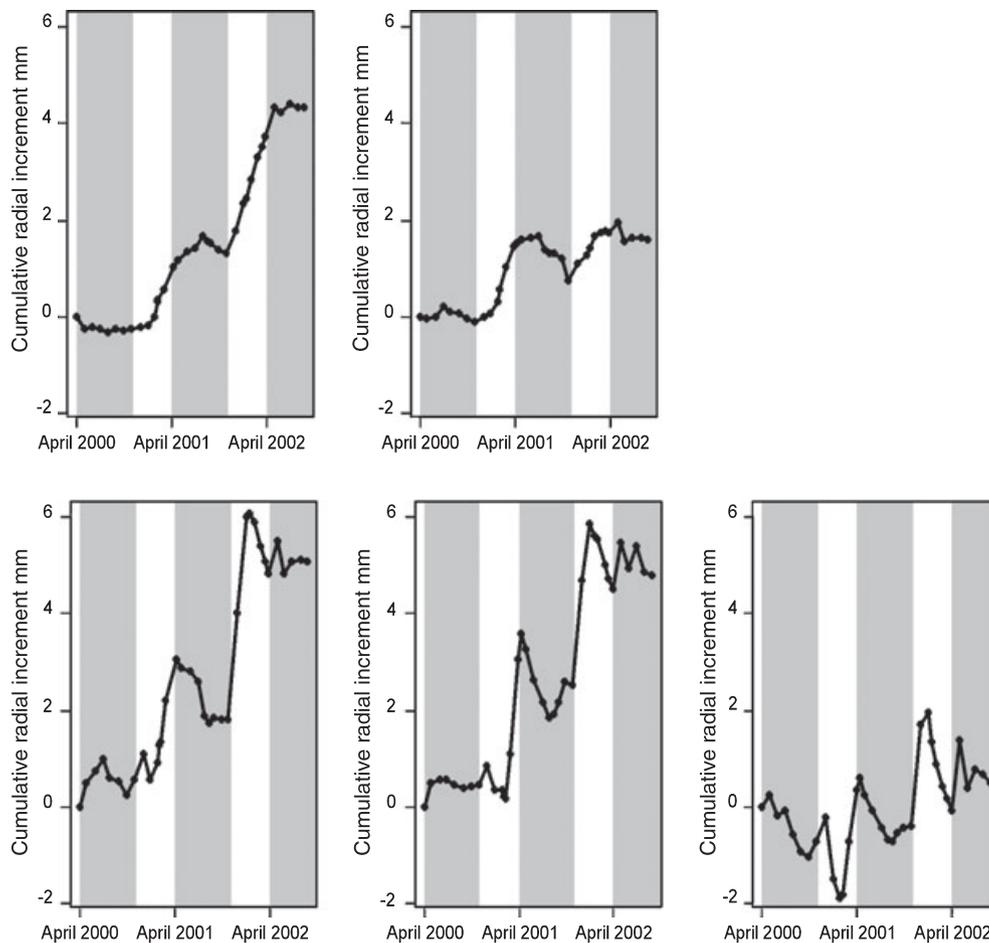
### Water source

The results for a number of water samples extracted from the trees plot below the LMWL, showing evaporative enrichment of the sample (Fig. 2). During the wet season, the  $\delta^{18}\text{O}$  values for all of the trees become progressively more enriched in the heavier isotope with distance from the stream, with the savanna trees using more enriched water than those trees closest to the stream (Fig. 6). During the wet season, which is also the growing season, *P. violacea* growing at the stream-side and near-stream zones do not use the river water. The river has a  $\delta^{18}\text{O}$  value that is more positive ( $-3.8 \pm 1.23\text{‰}$ ) than that of the deeper borehole water ( $-4.9 \pm 0.65\text{‰}$ ). *Philenoptera violacea* from the stream-side and near-stream zones have  $\delta^{18}\text{O}$  values that overlap with the value for the groundwater signal but do not overlap with that of the river-water signal (Fig. 6). In the wet season, the near-stream and far-stream *C. mopane* have  $\delta^{18}\text{O}$  values consistent with that of the groundwater, but also reflect to some extent that of the river water. The savanna *C. mopane* have  $\delta^{18}\text{O}$  values closer to that of the river water than to that of the groundwater.

During the dry season these differences are not as clear because the river and groundwater have similar  $\delta^{18}\text{O}$  values. The  $\delta^{18}\text{O}$  results for the savanna *C. mopane* are, however, still closer to the river-water than to the groundwater value (Fig. 6).



**Figure 4** Change in xylem pressure potentials in the wet season with time in hours after dawn for *Philenoptera violacea* and *Colophospermum mopane*. The different lines indicate different geomorphological positions. Bars are standard error and points are means for all three transects (Sandpiper, Mamba and Zari).



**Figure 5** Mean cumulative radial increments in stem growth for *Philenoptera violacea* and *Colophospermum mopane* in the different geomorphological positions over two growing seasons. Grey shaded areas are dry season.

**Table 2** Summary of linear regression models of rainfall in the 14 days preceding the measurement of radial increments against radial increment

| Species (location)                | Estimate | Std error | P value | Adj. $R^2$ |
|-----------------------------------|----------|-----------|---------|------------|
| <i>Philenoptera violacea</i> (SS) | 0.0268   | 0.0359    | 0.4605  | -0.0132    |
| <i>Philenoptera violacea</i> (NS) | 0.0591   | 0.0276    | 0.0393  | 0.0931     |
| <i>Colophospermum mopane</i> (NS) | 0.3083   | 0.0620    | < 0.001 | 0.4040     |
| <i>Colophospermum mopane</i> (FS) | 0.3402   | 0.0638    | < 0.001 | 0.4320     |
| <i>Colophospermum mopane</i> (SA) | 0.2782   | 0.0767    | < 0.001 | 0.2530     |

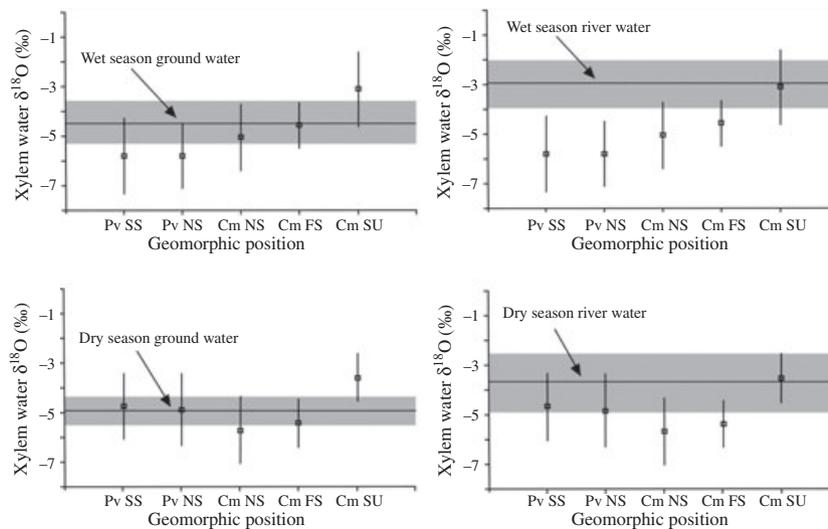
SS: stream side, NS: near stream, FS: far stream, SA: savanna.

## DISCUSSION

To explain the determinants of savanna structure we examine Walter's (1971) proposal that water availability is a major driver of these systems. We do this by evaluating the

relationship between plant water availability and tree growth for *P. violacea* and *C. mopane* across a steep environmental gradient. The three methods we use suggest that, relative to available water, *P. violacea* and *C. mopane* have different growth rates and growth strategies, which may account for the structural changes observed on moisture gradients in savannas.

Our stable-isotope analysis indicates that, in spite of the dominance of *P. violacea* at stream-side and near-stream sites, these trees do not use stream water but deeper groundwater (Fig. 6). This result agrees with the findings of Dawson & Ehleringer (1991), who were the first to show that stream-side trees do not necessarily use stream water. Access to groundwater is supported by the absence of any significant differences between the dry- and wet-season pre-dawn XPP results. Furthermore, the growth-rate data for *P. violacea* revealed no relationship between antecedent rainfall and growth increments, suggesting that *P. violacea* is not reliant on rainwater for growth (Table 2). Despite an apparent lack of reliance on either rain or stream water for growth, the growth-rate data do indicate that active growth for *P. violacea* is limited to the hot, wet summer months. Seasonal patterns of nitrogen mineralization could explain this apparent contradiction. Seasonal



**Figure 6** Mean  $\delta^{18}\text{O}$  (‰) values for the Sandpiper transect showing the change in  $\delta^{18}\text{O}$  values with geomorphological position. The shaded area covers one standard deviation of the mean  $\delta^{18}\text{O}$  values of the groundwater (left panels) and river water (right panels). Pv: *Philenoptera violacea*, Cm: *Colophospermum mopane*, SS: stream side, NS: near stream, FS: far stream, and SA: savanna.

measures of nitrogen mineralization rates in the Kruger National Park showed net mineralization in the early summer with the onset of the rains, and immobilization at other times of the year (Scholes *et al.*, 2003). Nitrogen mineralization plays a significant role in transforming nitrogen in the soils, making it available for uptake by plants. As this only occurs in the wet season, we speculate that growth of *P. violacea* is prevented in the dry season not because of a lack of moisture for transpiration but because of a lack of available nitrogen.

Our results indicate that the  $\delta^{18}\text{O}$  values of xylem water become progressively enriched in the heavier isotope with distance from the stream. This suggests an increasing dependence on shallower soil moisture, and consequently limited access to groundwater, with distance from the stream (Fig. 6; Thorburn & Walker, 1993; Dawson, 1996). *Colophospermum mopane*, although present at the near-stream sites, dominates the far-stream and savanna sites. This suggested reliance on shallow soil water (rainwater) rather than deeper groundwater by *C. mopane* is supported by the strong relationship we detected between growth increments and rainfall (Table 2) and by the large differences in dry-season and wet-season XPPs (Fig. 3).

This study shows that the two species examined have different spatial and temporal strategies of soil-water exploitation. The  $\delta^{18}\text{O}$  data suggest that *P. violacea* is a deep-rooted phreatophyte that can access groundwater. Growth-rate data suggest that this species grows conservatively, but consistently. *Colophospermum mopane*, by contrast, appears shallow-rooted (Mapaure, 1994; Smit & Rethman, 1998). The  $\delta^{18}\text{O}$  data suggest that it cannot access groundwater. *Colophospermum mopane* is, however, able to exploit rainfall and grows in rapid pulses following such events. Hence, the conservative phreatophyte strategy of *P. violacea* and the shallow-rooted opportunistic strategy of *C. mopane* appear to provide successful alternative solutions to coping with water stress. Whether these strategies are adopted by other savanna tree species remains to be tested.

Growth rates are critical for understanding the responses of savannas trees to herbivory (Smallie & O'Connor, 2000; Styles & Skinner, 2000; Baxter & Getz, 2005), fire (Higgins *et al.*, 2000) and human harvesting (Higgins *et al.*, 1999; Shackleton, 2002). Our data provide valuable empirical insights into the growth rates and growth strategies of savanna trees. Few studies have recorded growth rates of savanna trees, and fewer still have examined the seasonal pattern of growth of more than one species from the same location (Stahle *et al.*, 1999; Shackleton, 2002). The growth rates we detected are slow (*c.* 3 mm radial increment per year, Fig. 5), and typical rates may be much slower as our study was conducted in years with above-average rainfall. In an area with slightly higher rainfall Stahle *et al.* (1999) predict very similar growth rates for *P. angolensis* DC. of 3 mm at Sikumi (600 mm) and 4 mm at Mzola (700 mm) in Zimbabwe. In our savanna sites growth rates were even lower (< 0.5 mm radial increment per year); these rates may be too low to allow trees to escape the effects of recurrent fire and or herbivory and may explain the low stature of the savanna sites in our study area. The low to negative growth rates at the savanna site also suggest that density-dependent processes may be influencing the growth rates we present, and it would therefore be interesting to explore the growth rates that could be achieved in density-independent situations.

## CONCLUSION

We have shown that trees with access to reliable water supplies (deep soil water) grow slowly but steadily, and that trees that rely more directly on rainfall for their water adopt an opportunistic strategy, growing rapidly after rainfall events and with little growth between. These results indicate that at our study site water availability strongly influences tree growth rates. The suggestion is that where availability is low, growth rates are low enough to prevent trees from escaping herbivory and fire, which leads to a small structured savanna. Moisture

availability is therefore central to an understanding of savanna structure.

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## BIOSKETCHES

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## ERRATUM

Figure 5 in February *et al.* (2006) was published incomplete, with species names and geomorphological zones missing. The upper two panels show, from left to right, *P. violacea* stem growth in the Streamside and Near stream geomorphological zones. The lower three panels show, also from left to right, *C. mopane* stem growth in the Near stream, Far stream and Savanna upland geomorphological zones.

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