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## Research paper

# Seasonal changes in plant–water relations influence patterns of leaf display in Miombo woodlands: evidence of water conservative strategies

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Water availability has frequently been linked to seasonal leaf display in seasonally dry ecosystems, but there have been few ecohydrological investigations of this link. Miombo woodland is a dominant seasonally dry tropical forest ecosystem type in southern Africa; however, there are few data on the relationship between seasonal dynamics in plant–water relations and patterns of leaf display for Miombo woodland. Here we investigate this relationship among nine key Miombo woodland tree species differing in drought tolerance ability and leaf phenology. Results of this study showed that seasonal patterns of leaf phenology varied significantly with seasonal changes in stem water relations among the nine species. Leaf shedding coincided with the attainment of seasonal minimum stem water potential. Leaf flush occurred following xylem rehydration at the peak of the dry season suggesting that endogenous plant factors play a pivotal role in seasonal leaf display in this forest type. Drought-tolerant deciduous species suffered significantly higher seasonal losses in xylem hydraulic conductivity than the drought-intolerant semi-evergreen tree species ( $P < 0.05$ ). There was a significant and positive correlation between species drought tolerance index and species' seasonal loss in hydraulic conductivity ( $P < 0.05$ ), confirming the ecological role of long-distance xylem transport in this seasonally dry tropical forest. Our results reveal that water stress in seasonally dry tropical forests selects for water conservative traits that protect the vulnerable xylem transport system. Therefore, seasonal rhythms in xylem transport dictate patterns of leaf display in seasonally dry tropical forests.

**Keywords:** hydraulic conductivity, leaf phenology, Miombo woodlands, plant–water relations, xylem safety margin.

## Introduction

Miombo woodland is the most widely distributed seasonally dry tropical forest in east and southern Africa (White 1983). This seasonally dry tropical forest occurs across seven countries (Angola, Congo DR, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe) in southern Africa. As is the case with many other seasonally dry tropical forests, the long dry season is characterized by leaf shedding, suggesting that water availability controls patterns of leaf display (Borchert 1994, Williams et al.

1997, Filho and Filho 2000, Chapotin et al. 2006, Vico et al. 2015). Typically, leaf shedding occurs at the onset of the long dry season, signifying that water limitation may be the principal driver of leaf phenology (Fuller 1999).

Intriguingly, leaf flush occurs at the peak of the dry season, approximately 2 months before the onset of the summer rains (Chidumayo and Frost 1996, Guan et al. 2014, Ryan et al. 2017, Whitecross et al. 2017), suggesting that other factors

rather than water stress influence patterns of seasonal leaf display. Available evidence shows that dry season leaf flush may provide an advantage to leaves because of enhanced light availability, reduced herbivory and pathogen pressure (Ryan et al. 2017). Dry season leaf display in seasonally dry tropical forests has in the past been attributed to a number of factors including photoperiodicity (Archibald and Scholes 2007), rise in daily temperatures (Chidumayo 2001), access to deep soil water reserves (Sarmiento et al. 1985, Elliott et al. 2006) and stem water storage (Borchert 1994). Although a number of studies have acknowledged the importance of precipitation in controlling patterns of leaf display in Miombo woodland (Malaisse 1978, Chidumayo 1994, Fuller and Prince 1996, Fuller 1999), this physiological process has never been analyzed in terms of seasonal dynamics of plant–water relations.

Many authors have demonstrated a link between progressive impairment of the long-distance xylem hydraulic pathway and patterns of leaf shedding (Salleo et al. 2002, Brodribb and Holbrook 2003, Choat et al. 2012). Available evidence suggests that a plant's ability to cope with water stress is closely linked to its capacity to withstand strongly negative xylem tensions without allowing air-entry (Cochard et al. 1992, Choat et al. 2005, Barigah et al. 2013, Brodersen and McElrone 2013, Brodribb et al. 2014). Many studies have shown that plants prevent the development of runaway embolisms by limiting xylem pressures below the air-entry pressure while at the same time maximizing stomatal conductance (Tyree and Sperry 1988, Brodribb et al. 2003). Regardless of the conclusions, these studies suggest the existence of functional coordination between patterns of leaf display and species ability to maintain a safe xylem pathway in water-limited ecosystems. We hypothesized that plants' native embolism resistance influences seasonal leaf display in water-limited ecosystems. However, little is known about the relationship between native embolism and seasonal patterns of leaf display in Miombo woodlands.

In this study, the relationship between seasonal changes in plant–water relations and patterns of leaf display for nine Miombo woodland tree species differing in drought tolerance ability and leaf phenology is evaluated. The main objectives of this study were to (i) investigate the relationship between seasonal changes in stem water status and patterns of leaf display for nine principal Miombo woodland tree species; and (ii) examine the interactions between tree species drought tolerance ability and patterns of leaf display.

## Materials and methods

### Study site

The study site was Mwekera national forest number 6 (12°51'S, 28°22'E, 1295 m above sea level) located in Kitwe, Zambia. The main vegetation type was closed Miombo woodland. This

forest type is dominated by the genera *Julbernardia*, *Marquesia*, *Brachystegia* and *Isoberlinia*. The vegetation of the study site was best described as wet Miombo woodland (White 1983, Chidumayo 1987). The average diameter at breast height was around 20 cm with a canopy height of 21 m. The forest was last selectively logged in the 1950s. The study site falls within the Miombo eco-region, which has a distinct dry tropical climate in which summer rains fall between November and April (Malaisse 1978). A long dry season lasting 6 months (May–October) follows. As expected the long-term mean annual rainfall was 1200 mm. Monthly maximum temperature ranged between 25 °C and 34 °C. The soils at the study site were sandy loamy and slightly acidic with a pH of around 5.

### Choice of tree species and field sampling

We sampled nine Miombo woodland tree species representing six genera, two families and two main phenological characteristics (Table 1). The full botanical and ecological descriptions of these nine tree species have been adequately presented by many authors (Fanshawe 1962, Storrs 1979, Palgrave 2002, Smith and Allen 2004, van Wyk and van Wyk 2013). All the individuals sampled in this study came from a uniform woodland (700 ha) where they shared a common environment. The nine tree species were selected on the basis that (i) they displayed contrasting leaf phenology, (ii) they differed substantially in biogeographical distribution (Chidumayo 1987, Smith 2001, Smith and Allen 2004) and (iii) there was no substantial taxonomical difference between them.

### Monitoring of leaf phenology

A total of 225 trees of nine co-occurring species were randomly selected and tagged ( $n = 25$  trees per species) and their GPS coordinates recorded to facilitate repeat measurements. Leaf phenology was monitored in 2 years (May–August 2007 and April–December 2008). The sample trees were carefully monitored fortnightly, recording timing of leaf fall and flushing. For repeatability of the measurements, leaf shedding was taken to be the point at which leaves displayed signs of permanent water stress (leaf colour changing from green to yellow) and eventual withering. Leaf flush included both bud break and leaf emergence.

### Measurement of stem–water status

Seasonal changes in stem water status were monitored for the selected nine species on the same days as leaf phenology data collection. Pre-dawn water potential ( $\Psi_{PD}$ ) was employed to represent plant–water status. Unlike other methods (osmotic potential and water content),  $\Psi_{PD}$  is of direct relevance to the soil–plant–atmospheric continuum and is, therefore, a better approximation of soil water potential (Borchert 1994, Andrade et al. 1998, Williams and Araujo 2002). The method of determining plant water potential involved collection of three to five

twigs per individual tagged tree in the early hours of the morning (between 05:30 and 08:00 h local time) on every field visit. The harvested twigs were immediately covered in wet towels and sealed in plastic field sample bags. The twigs collected were long enough to allow for small short segments to be excised from them for water potential determination and leave a sufficient portion for hydraulic measurements. The twigs had undisturbed terminal buds. In the laboratory, small non-transpiring leaf-bearing distal twig portions were excised, and their  $\Psi_{PD}$  measured using pressure chamber method (SKPM 1405, Skye Instruments, Llandrindod Wells, UK). All segments were kept constantly under moist-dark conditions prior to  $\Psi_{PD}$  determination. Furthermore, the time difference between harvesting and actual determination of  $\Psi_{PD}$  was kept to less than 2 h.

### Determination of hydraulic conductivity and native embolism

Seasonal progression of native embolism was measured following modified methods of Sperry et al. (1988). At the laboratory, segments for hydraulic measurements were placed in distilled water and trimmed to their maximum vessel lengths plus 10% (Vinya et al. 2012, 2013). Trimmed segments were always kept submerged under distilled water until their flow rates were determined. The average segment under-bark diameter was 8 mm. Hydraulic conductivity ( $K_H$ ) was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Minimum hydraulic conductivity ( $K_{H\ min}$ ) was determined on unflushed plant segments. The segments were perfused with degassed, filtered (to 0.2  $\mu\text{m}$ ) and acidified (with HCl, pH = 2) distilled water (Sperry et al. 1988, Kolb et al. 1996). Each segment was allowed to equilibrate before initial flow rate was measured. Minimum hydraulic conductivity ( $K_{H\ min}$ ,  $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ ) was calculated as

$$K_{H\ min} = \frac{J_V}{(\Delta P/l)} \quad (1)$$

where  $J_V$  is the flow rate ( $\text{kg s}^{-1}$ ) through the segment;  $\Delta P$  is the delivery pressure (MPa); and  $l$  is the segment length (m).

Maximum hydraulic conductivity ( $K_{H\ max}$ ) was derived after flushing the segments at a pressure of 150 kPa for periods

ranging from 20 to 30 min depending on species and extent of native embolism. Seasonal loss in hydraulic conductivity (native embolism) was calculated as

$$\text{Native embolism (\%)} = (K_{H\ max} - K_{H\ min})/K_{H\ max} \times 100 \quad (2)$$

To confirm that the segments had been completely relieved of emboli, they were perfused with Safranin dye at the end of each experiment.

### Xylem safety margins

Xylem safety margins were calculated using the fitted species vulnerability curves (Vinya et al. 2013) and minimum  $\Psi_{PD}$  coinciding with leaf shedding. Xylem safety margins were calculated as the difference between  $\Psi_{PD}$  triggering leaf shedding and the water potential threshold associated with xylem air-entry ( $\Psi_e$ ) leading to a rapid loss in hydraulic conductivity calculated from the vulnerability curves. Although a number of plant water potential points have been employed in computing xylem safety margin (Meinzer et al. 2009), we chose to use  $\Psi_e$  because it is of direct physiological relevance to the process responsible for preventing runaway embolism in plants (Tyree and Ewers 1998, Tyree and Zimmerman 2002).

### Data analysis

To answer the question of whether seasonal changes in stem–water status influenced patterns of leaf display among Miombo tree species, we used a mixed-effects model (Zar 2010). Given that time-dependent data have a tendency to exhibit auto-correlation, data were, therefore, tested for serial correlation using the Durbin–Watson statistics. Where auto-correlation was detected, the Cochran–Orcutt procedure was employed to eliminate serial correlation (Ostrom 1990, Chatfield 1997, Schabenberger and Gotway 2005). A paired  $t$ -test was performed to test whether stem water potential threshold triggering leaf shedding differed from that responsible for leaf flushing. All statistical analyses were carried out in Minitab (version 16 Minitab Inc., State College, PA, USA).

Table 1. Leaf phenology of the nine Miombo woodland tree species studied.

Species	Family	Phenology
<i>Brachystegia boehmii</i> Benth	Fabaceae	Deciduous
<i>Brachystegia longifolia</i> Benth	Fabaceae	Deciduous
<i>Brachystegia spiciformis</i> Benth	Fabaceae	Deciduous
<i>Erythrophleum africanum</i> (Benth) Harms	Fabaceae	Deciduous
<i>Pericopsis angolensis</i> (Baker) Meeuwen	Fabaceae	Deciduous
<i>Brachystegia floribunda</i> Benth	Fabaceae	Semi-evergreen
<i>Isobertinia angolensis</i> (Benth) Hoyle & Brenan	Fabaceae	Semi-evergreen
<i>Julbernardia paniculata</i> (Benth) Troupin	Fabaceae	Semi-evergreen
<i>Marquesia macroura</i> Gilg	Dipterocarpaceae	Evergreen

## Results

### Leaf phenology and species classification

There was a significant ( $P < 0.05$ ) difference in patterns of leaf shedding between the two functional groups. Deciduous species shade their leaves within 7 weeks following the onset of the seasonal drought (Figure 1A). While the proportion of semi-evergreen tree species shedding leaves spread throughout the dry season, the drought-deciduous species shed their leaves at the onset of the dry season (Figure 1A).

For both functional groups, leaf flush was concentrated within 6 weeks at the peak of the dry season. However, leaf flush occurred within 4 weeks among the drought-deciduous species and spread over 6 weeks for the semi-evergreen functional group (Figure 1B).

### Stem water status

The water potential thresholds that triggered leaf shedding and flushing differed significantly (ANOVA;  $P < 0.001$ ) both between species and functional groups. On average, deciduous species dropped and flushed leaves at significantly lower water potential threshold than co-occurring semi-evergreen species (Figure 2). Average  $\Psi_{PD}$  triggering leaf shedding varied between  $-1.8 \pm 0.03$  and  $-1.3 \pm 0.06$  MPa among deciduous and between  $-1.4 \pm 0.027$  and  $-0.8 \pm 0.03$  MPa for semi-evergreen species.

Average  $\Psi_{PD}$  triggering leaf flush varied between  $-1.31 \pm 0.04$  and  $-0.7 \pm 0.03$  MPa for semi-evergreen species, and between  $-1.7 \pm 0.04$  and  $-0.8 \pm 0.07$  MPa for drought-deciduous species. All deciduous species flushed leaves at significantly (ANOVA;  $P < 0.001$ ) higher stem water potential than that triggering leaf shedding. Of the four semi-evergreen species, *Isoberlinia angolensis* and *Marquesia macroura* displayed an insignificant (paired  $t$ -

test;  $P > 0.05$ ) difference between stem water potential triggering leaf shedding and that triggering leaf flush.

### Hydraulic conductivity and embolism

There were significant ( $P < 0.05$ ) differences in seasonal losses in hydraulic conductivity among Miombo woodland tree species differing in leaf phenology and drought tolerance ability. Semi-evergreen species experienced significantly ( $P < 0.001$ ) lower seasonal losses in hydraulic conductivity than the deciduous tree species (Figure 3).

There was a significant negative correlation ( $R^2 = 0.58$ ;  $P = 0.016$ ) between hydraulic conductivity and species maximum native embolism (Figure 4). Tree species' drought tolerance ability (measured as water potential leading to 50% loss in conductivity) was negatively and significantly correlated ( $R^2 = 0.73$ ;  $P = 0.04$ ) with seasonal loss in hydraulic conductivity (Figure 5).

### Xylem safety

Xylem safety margins differed significantly (ANOVA;  $P < 0.001$ ) among co-occurring Miombo species. Deciduous tree species had wider xylem safety margins than the semi-evergreen species. Among the deciduous species, xylem safety margins ranged between  $0.6 \pm 0.06$  and  $1.4 \pm 0.03$  MPa. Xylem safety margins among semi-evergreen species ranged between  $0.09 \pm 0.03$  and  $0.5 \pm 0.05$  MPa. Among the semi-evergreen species, *M. macroura* displayed the lowest safety margin. There was a positive and significant correlation ( $R^2 = 0.63$ ;  $P = 0.011$ ) between xylem hydraulic safety margin and species seasonal loss in hydraulic conductivity (Figure 6).

## Discussion

Seasonal changes in leaf display varied significantly between the two functional groups (Figure 1). As predicted, the water poten-

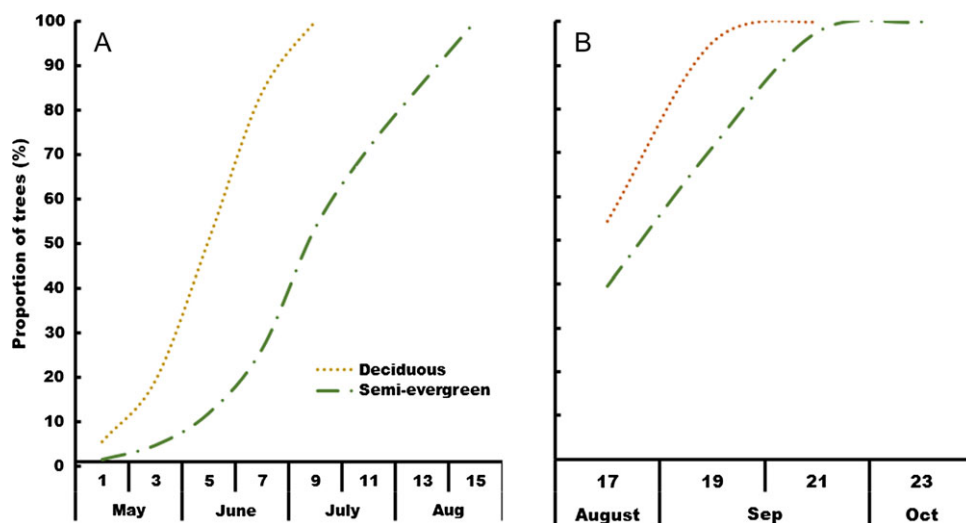


Figure 1. (A) Proportion of trees shedding leaves per functional group; (B) proportion of trees experiencing leaf flush per functional group.  $n = 225$  trees.

tial threshold triggering leaf shedding and flushing varied considerably both between species and groups despite the two functional groups growing under similar climatic conditions (Figure 2). Leaf shedding followed a pattern of steady decline in plant

water status suggesting that water is one of the decisive factors dictating patterns of leaf display in this seasonally dry tropical forest. These results are consistent with findings from other seasonally dry tropical forests (Fanjul and Barradas 1987, Borchert

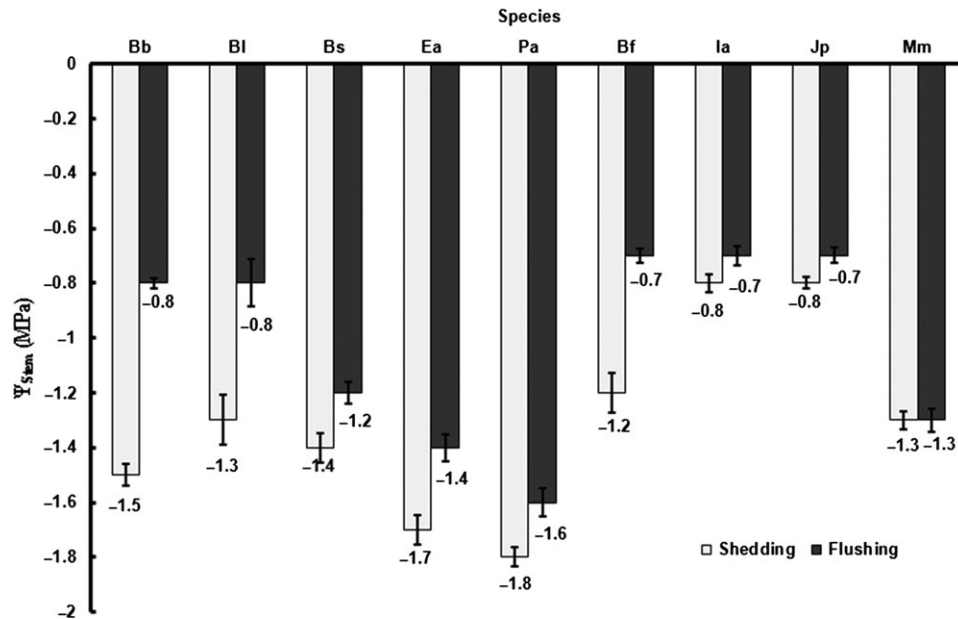


Figure 2. Tree species stem water potential triggering leaf shedding and flushing. Bb, *Brachystegia boehmii*; Bf, *Brachystegia floribunda*; Bl, *Brachystegia longifolia*; Bs, *Brachystegia spiciformis*; Ea, *Erythrophleum africanum*; Jp, *Julbernardia paniculata*; Ia, *Isoberlinia angolensis*; Mm, *Marquesia macroura*; Pa, *Pericopsis angolensis*.

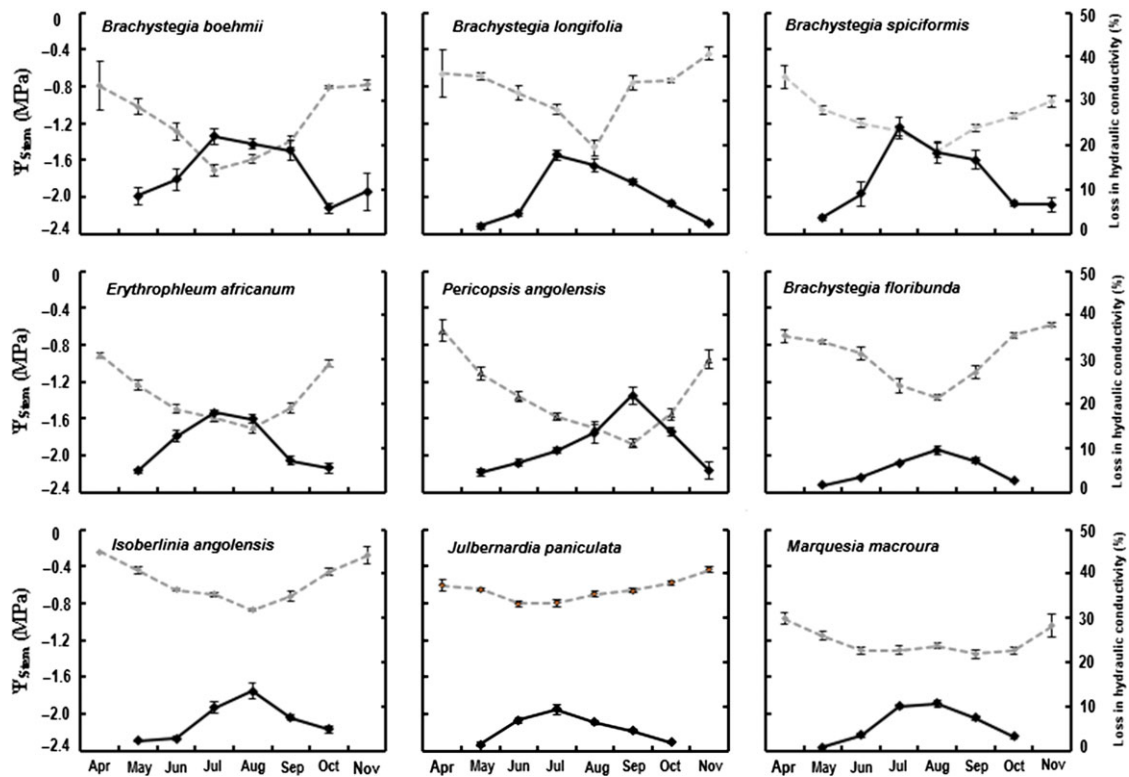


Figure 3. Seasonal dynamics in plant water relations and timing of leaf shedding and flushing in Miombo woodland (averages from May 2007 to November 2008).

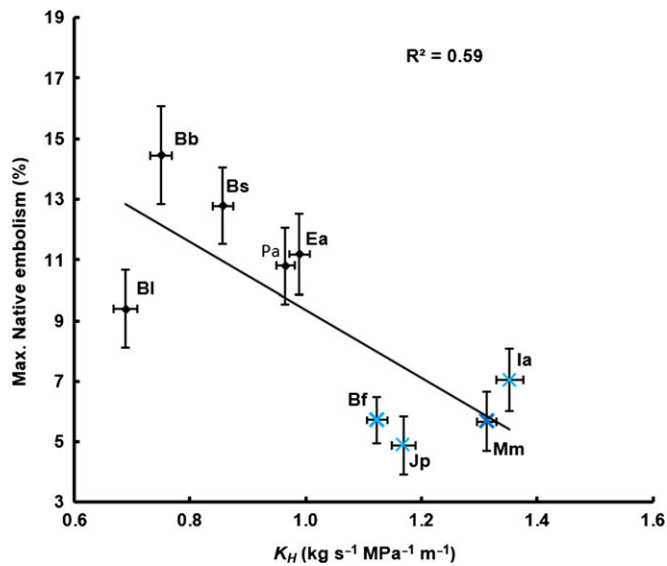


Figure 4. Relationship between tree species hydraulic conductivity and maximum native embolism. Crosses represent semi-evergreen and solid dots represent deciduous tree species. Bb, *Brachystegia boehmii*; Bf, *Brachystegia floribunda*; Bl, *Brachystegia longifolia*; Bs, *Brachystegia spiciformis*; Ea, *Erythrophleum africanum*; Jp, *Julbernardia paniculata*; Ia, *Isobertlinia angolensis*; Mm, *Marquesia macroura*; Pa, *Pericopsis angolensis*.

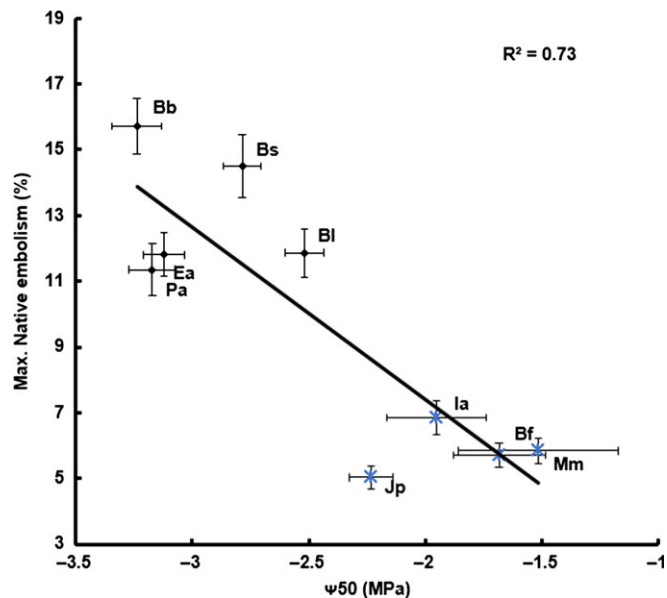


Figure 5. Relationship between tree species drought tolerance ability and seasonal loss in conductivity. Crosses represent semi-evergreen and solid dots represent deciduous tree species. Bb, *Brachystegia boehmii*; Bf, *Brachystegia floribunda*; Bl, *Brachystegia longifolia*; Bs, *Brachystegia spiciformis*; Ea, *Erythrophleum africanum*; Jp, *Julbernardia paniculata*; Ia, *Isobertlinia angolensis*; Mm, *Marquesia macroura*; Pa, *Pericopsis angolensis*.

1994, Williams et al. 1997). Results of this study render further support to the functional dependence hypothesis of leaf phenology on stem–water status (Borchert 1994, Sayer and Newbery 2003, Chapotin et al. 2006).

Interestingly, affected by similar climatic conditions, co-occurring Miombo woodland tree species differed significantly in the degree to which they suffered seasonal losses in hydraulic conductivity (Figure 3). Results of this study are consistent with studies from other seasonally dry tropical forests (Valdez-Hernández et al. 2010, Méndez-Alonzo et al. 2013). Deciduous species experienced significantly higher seasonal losses in hydraulic conductivity than co-occurring semi-evergreen species. Findings of this study suggest that co-occurring tree species are associated with different adaptive strategies for preventing catastrophic xylem failure (Urli et al. 2013, Vinya et al. 2013).

The deciduous species were observed to employ a cavitation avoidance strategy by shedding the entire canopy at the onset of the dry season to avoid permanent damage to the long-distance xylem transport (Figures 1 and 3). As expected, leaf shedding coincided with minimum seasonal stem–water status and loss in hydraulic conductivity. In stark contrast, semi-evergreen species employ cavitation avoidance strategy by maintaining high hydraulic efficiency throughout the dry season (Vinya et al. 2013). Not surprisingly, the hydraulic safety margins differed significantly between the two Miombo functional groups. Differences in cavitation avoidance strategy offer the most plausible explanation for the observed variation in hydraulic safety margins between the two functional groups. Further, the observed trade-off between tree species drought tolerance index ( $\Psi_{50}$ ) and species seasonal loss in hydraulic conductivity (Figure 4) suggests that pressure for selection in this water-stressed ecosystem favours water conservative traits that enhance species fitness (Elliott et al. 2006, Seghieri et al. 2009). The existence of a trade-off between native embolism and hydraulic conductivity supports our conclusion (Figure 5). Additionally, the observed trade-off between xylem safety and native embolism reinforces the important role that the long-distance xylem transport plays in influencing leaf display in Miombo woodland (Figure 6).

A large body of literature demonstrates the functional dependence of leaf display on plant water relations in most forest ecosystems (Nardini et al. 2001, Vilagrosa 2003). Interestingly, at the peak of a long dry season (approximately 3 months before the onset of the rainy season), both functional groups experienced leaf flush, suggesting the decoupling of environmental cues from leaf display in this seasonally dry tropical forest. Leaf flush followed a steady rise in stem water potential for all the nine species studied (Figure 3), suggesting that timing of leaf flush is primarily endogenously controlled via stem rehydration, following leaf fall during the dry season. Canny (1998) has linked dry season xylem rehydration to changes in osmotic potential mediated through starch hydrolysis. This is consistent with the observation by many authors who have demonstrated the role of Münch water in xylem repair following embolism (Bucci et al. 2003, Salleo et al. 2009).

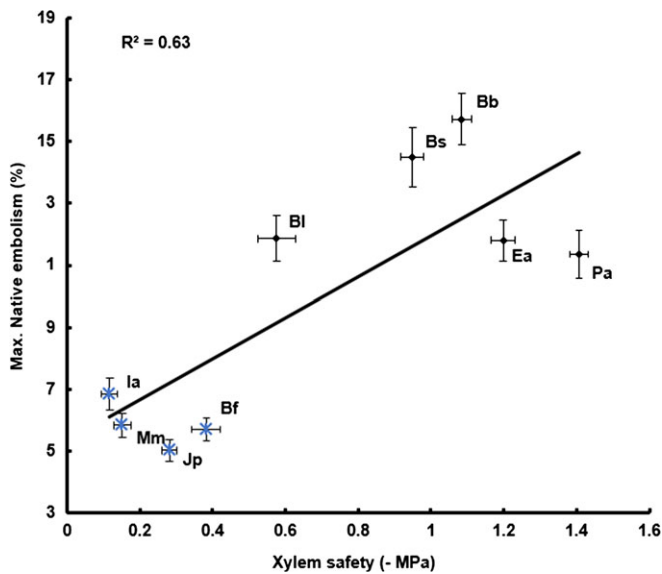


Figure 6. Correlation between xylem safety margins and tree species seasonal loss in hydraulic conductivity. Crosses represent semi-evergreen and solid dots represent deciduous tree species. Bb, *Brachystegia boehmii*; Bf, *Brachystegia floribunda*; Bl, *Brachystegia longifolia*; Bs, *Brachystegia spiciformis*; Ea, *Erythrophleum africanum*; Jp, *Julbernardia paniculata*; Ia, *Isobertlinia angolensis*; Mm, *Marquesia macroura*; Pa, *Pericopsis angolensis*.

Available evidence suggests that Miombo woodland tree species accumulate substantial quantities of organic compounds prior to leaf shedding (Ernst and Walker 1973). Therefore, the most plausible explanation for the dry season improvement in stem–water status could be the accumulation of the metabolically active compounds that hydrolyze into active sugars thereby lowering the osmotic potential of the nearby parenchyma cells (Johnson et al. 2012). In turn, localized pressure gradients are generated that aid in drawing water from the nearby parenchyma cells adjacent to the vascular bundles. Coupled with low transpiration rates and stomatal conductance in newly developed leaves, Miombo woodland canopy tree species maintain a favourable stem–water balance during the dry season (Choinski and Johnson 1993, Tuohy and Choinsk 1990). Many authors have demonstrated the accessibility of underground water sources by trees growing in water-stressed ecosystems (Meinzer et al. 1999, von der Heyden and New 2003). Although underground water sources may play a critical role in supporting leaf expansion following leaf emergence, the actual role of these water sources in xylem repair following cavitation remains not well understood.

## Conclusion

Seasonal changes in plant–water relations influence patterns of leaf shedding and flushing among nine Miombo woodland tree species. The hydraulically efficient semi-evergreen tree species with a narrow biogeographical distribution are well adapted to deal with water stress by maintaining high hydraulic supply,

consequently experiencing low hydraulic losses in the dry season. On the other hand, deciduous tree species mitigate problems of water stress by shedding leaves right at the onset of the dry season to restore the overall integrity of the long-distance hydraulic supply. Therefore, plant–water relations are a decisive factor dictating patterns of leaf display in Miombo woodland. Further, pressure for selection in this seasonally dry tropical forest favours individuals with water conservative traits.

## Conflict of interest

None declared.

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## References

- Andrade JL, Meinzer FC, Goldstein G, Holbrook NM, Cavelier J, Jackson P, Silvera K (1998) Regulation of water flux through trunks, branches, and leaves in trees of a lowland tropical forest. *Oecologia* 115: 463–471.
- Archibald S, Scholes RJ (2007) Leaf green-up in a semi-arid African Savanna-separating tree and grass responses to environmental cues. *J Veg Sci* 18:583–594.
- Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Améglio T, Cochard H (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. *Ann Bot (Lond)* 112:1431–1437.
- Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449.
- Brodribb JT, Holbrook NM (2003) Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytol* 158: 295–303.
- Brodersen CR, McElrone AJ (2013) Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Front. Plant Sci.* 4:108. [10.3389/fpls.2013.00108](https://doi.org/10.3389/fpls.2013.00108).
- Brodribb JT, Holbrook NM, Edwards EJ, Gutiérrez MV (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell Environ* 26:443–450.
- Brodribb JT, McAdam AMS, Jordan JG, Martins CVS (2014) Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proc Natl Acad Sci USA* 111:14489–14493.
- Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Sternberg LDSL (2003) Dynamic changes in hydraulic conductivity in petioles of two savanna species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant Cell Environ* 26:1633–1645.
- Canny MJ (1998) Applications of the compensating pressure theory of water transport. *Am J Bot* 85:897–909.
- Chatfield C (1997) *The analysis of time series: an introduction*. Chapman and Hall, London.
- Chidumayo EN (2001) Climate and phenology of savanna vegetation in southern Africa. *J Veg Sci* 12:347–354.

- Cochard H, Badel E, Herbette S, Delzon S, Choat B, Jansen S (1992) Methods for measuring plant vulnerability to cavitation: a critical review. *J Exp Bot* 64:4779–4791.
- Chapotin MS, Razanameharizaka HJ, Holbrook MN (2006) Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytol* 169:549–559.
- Chidumayo EN (1987) Species structure in Zambian Miombo woodland. *J Appl Ecol* 3:109–118.
- Chidumayo EN (1994) Phenology and nutrition of Miombo woodland trees in Zambia. *Trees* 9:67–72.
- Chidumayo EN, Frost P (1996) Population biology of miombo trees. In: Campbell B (ed) *The miombo in transition: woodlands and welfare*. Bogor CIFOR, Indonesia, pp 59–71.
- Choat B, Ball MC, Luly GJ, Holtum MAJ (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from North-eastern Australia. *Trees* 19:305–311.
- Choat B, Jansen S, Brodribb TJ et al. (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491:752–755.
- Choinski JS, Johnson JM (1993) Changes in photosynthesis and water status of developing leaves of *Brachystegia spiciformis* Benth. *Tree Physiol* 13:17–27.
- Elliott S, Baker PJ, Borchert R (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecol Biogeogr* 15: 248–257.
- Ernst W, Walker BH (1973) Studies on the hydrature of trees in miombo woodland in south central Africa. *J Ecol* 61:667–673.
- Fanjul L, Barradas VL (1987) Diurnal and seasonal variation in the water relations of some deciduous and evergreen trees of a deciduous dry forest of the western coast of Mexico. *J Appl Ecol* 24:289–303.
- Fanshawe DB (1962) *Fifty common trees of Northern Rhodesia*. Government Printer, Lusaka.
- Filho LJP, Filho CVM (2000) Seasonal changes in the water status of three woody legumes from the Atlantic forest, Caratinga, Brazil. *J Trop Ecol* 16:21–32.
- Fuller DO, Prince SD (1996) Rainfall and foliar dynamics in tropical southern Africa: potential impacts of global climatic change on savanna vegetation. *Climate Change* 33:69–96.
- Fuller OD (1999) Canopy phenology of some Mopane and miombo woodlands in Eastern Zambia. *Biogeography* 8:199–209.
- Guan K, Wood EF, Medvigy D, Kimball J, Pan M, Caylor KK, Sheffield J, Xu X, Jones MO (2014) Terrestrial hydrological controls on land surface phenology of African savannas and woodlands. *J Geophys Res* 119: 1652–1669.
- Johnson DM, McCulloh KA, Woodruff DR, Meinzer FC (2012) Hydraulic safety margins and embolism reversal in stems and leaves: Why are conifers and angiosperms so different? *Plant Sci* 195:48–53.
- Kolb KJ, Sperry JS, Lamont BB (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. *J Exp Bot* 47:1805–1810.
- Malaisse F (1978) *The Miombo ecosystem. Tropical forest ecosystems: a state-of-knowledge report prepared by UNESCO/UNEP/FAO*. UNESCO, Paris, p 589.
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavelier J, Wright SJ (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301.
- Meinzer FC, Johnson MD, Lachenbruch B, McCulloh AK, Woodruff RD (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Funct Ecol* 23:922–930.
- Méndez-Alonzo R, Pineda-García F, Paz H, Rosell JA, Olson ME (2013) Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. *Trees* 27:745–754.
- Nardini A, Tyree MT, Salleo S (2001) Xylem cavitation in the leaf of *Prunus laurocerasus* and its impact on leaf hydraulics. *Plant Physiol* 125:1700–1709.
- Ostrom CW (1990) *Time series analysis: regression techniques*. In: SAGE, London.
- Palgrave KC (2002) *Trees of Southern Africa*. Struik Publishers, Cape Town.
- Ryan MC, Williams M, Grace J, Woollen E, Lehmann CER (2017) Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation. *New Phytol* 213: 625–633.
- Salleo S, Nardini A, Lo Gullo MA, Ghirardelli LA (2002) Changes in stem and leaf hydraulics preceding leaf shedding in *Castanea sativa* L. *Biol Plant* 45:227–234.
- Salleo S, Trifilò P, Esposito S, Nardini A, Lo Gullo MA (2009) Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? *Funct Plant Biol* 36:815–825.
- Sarmiento G, Goldstein G, Meinzer F (1985) Adaptive strategies of woody species in neotropical savannas. *Bio Rev* 60:315–355.
- Sayer EJ, Newbery DM (2003) The role of tree size in the leafing phenology of a seasonally dry tropical forest in Belize, Central America. *J Trop Ecol* 19:539–548.
- Seghieri J, Vescovo A, Padel K et al. (2009) Relationships between climate, soil moisture and phenology of the woody cover in two sites located along the West African latitudinal gradient. *J Hydrol* 375: 78–89.
- Schabenberger O, Gotway AC (2005) *Statistical methods for spatial data analysis*. Chapman and Hall, London.
- Smith P, Allen Q (2004) *Field guide to the trees and shrubs of the Miombo woodlands*. Royal Botanical Gardens Kew, London.
- Smith P (ed) (2001) *Ecological survey of Zambia: the traverse records of C.G. Trapnell*. Royal Botanic Gardens Kew, London, pp 1932–1943.
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ* 11:35–40.
- Storrs AEG (1979) *Know your trees: some of the common trees found in Zambia*. Mission Press, Ndola, Zambia.
- Tuohy JM, Choinski JS (1990) Comparative photosynthesis in developing leaves of *Brachystegia spiciformis* Benth. *J Exp Bot* 41:919–923.
- Tyree MT, Ewers FW (1998) Tansley review no. 34: the hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360.
- Tyree MT, Sperry JS (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol* 88:0574–0580.
- Tyree MT, Zimmermann MH (2002) *Xylem structure and the ascent of sap*. Springer, Berlin, Germany.
- Urli M, Porté AJ, Cochard H, Guengant Y, Burrell R, Delzon S (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiol* 33:672–683.
- Valdez-Hernández M, Andrade JL, Jackson PC, Rebolledo-Vieyra M (2010) Phenology of five tree species of a tropical dry forest in Yucatan, Mexico: effects of environmental and physiological factors. In: *Plant Soil*, 329:pp 155–171.
- van Wyk B, van Wyk P (2013) *Field guide to trees of Southern Africa*. Struik Nature, Cape Town, South Africa.
- Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrin E (2003) Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *J Exp Bot* 54: 2015–2024.
- Vico G, Thompson SE, Manzoni S et al. (2015) Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. *Ecohydrology* 8:660–681.



- Vinya R, Malhi Y, Brown N, Fisher JB (2012) Functional coordination between branch hydraulic properties and leaf functional traits in miombo woodlands: Implications for water stress management and species habitat preference. *Acta Physiol Plant* 34:1701–1710.
- Vinya R, Malhi Y, Fisher JB, Brown N, Brodribb T, Aragao LE (2013) Xylem cavitation vulnerability influences species habitat preference in miombo woodlands. *Oecologia* 173:711–720.
- von der Heyden CJ, New MG (2003) The role of a dambo in the hydrology of a catchment and the river network downstream. *Hydrol Earth Syst Sci* 7:339–357.
- White F (1983) *The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. UNESCO, Paris.
- Whitecross MA, Witkowski ETF, Archibald S (2017) Assessing the frequency and drivers of early-greening in broad-leaved woodlands along a latitudinal gradient in southern Africa. *Austral Ecol* 42: 341–353.
- Williams LE, Araujo FJ (2002) Correlations among predawn leaf, midday leaf, and midday stem water potential and their correlations with other measures of soil and plant water status in *Vitis vinifera*. *J Am Soc Horticult Sci* 127:448–454.
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a North Australian Tropical Savanna. *Ecology* 78:2542–2558.
- Zar JH (2010) *Biostatistical analysis*. Pearson Education International, London.