

Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation

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ABSTRACT

Size-related changes in hydraulic architecture, carbon allocation and gas exchange of *Sclerolobium paniculatum* (Leguminosae), a dominant tree species in Neotropical savannas of central Brazil (Cerrado), were investigated to assess their potential role in the dieback of tall individuals. Trees greater than ~6-m-tall exhibited more branch damage, larger numbers of dead individuals, higher wood density, greater leaf mass per area, lower leaf area to sapwood area ratio (LA/SA), lower stomatal conductance and lower net CO₂ assimilation than small trees. Stem-specific hydraulic conductivity decreased, while leaf-specific hydraulic conductivity remained nearly constant, with increasing tree size because of lower LA/SA in larger trees. Leaves were substantially more vulnerable to embolism than stems. Large trees had lower maximum leaf hydraulic conductance (K_{leaf}) than small trees and all tree sizes exhibited lower K_{leaf} at midday than at dawn. These size-related adjustments in hydraulic architecture and carbon allocation apparently incurred a large physiological cost: large trees received a lower return in carbon gain from their investment in stem and leaf biomass compared with small trees. Additionally, large trees may experience more severe water deficits in dry years due to lower capacity for buffering the effects of hydraulic path-length and soil water deficits.

Key-words: carbon balance; hydraulic conductivity; population dynamics; tree dieback; xylem cavitation.

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INTRODUCTION

Tree mortality and the consequent release of carbon and nutrients are important processes that influence the structure, composition, dynamics and functioning of woody ecosystems (Franklin, Shugart & Harmon 1987). Tree dieback, the synchronized mortality of an entire population or a cohort of that population, is a phenomenon that has been documented in a variety of tree species and ecosystem types (e.g. Watt 1987; Woodman 1987; Gerrish, Mueller-Dombois & Bridges 1988; Crombie & Tippet 1990; MacGregor & O'Connor 2002; Rice *et al.* 2004). Factors contributing to tree dieback include air pollution (Woodman 1987), herbivory by insects (Haugen & Underdown 1990), fungal infection (Crombie & Tippet 1990), climate change (Watt 1987), nutrient limitation (Gerrish *et al.* 1988) and drought (MacGregor & O'Connor 2002; Rice *et al.* 2004). Frequently, death of trees is attributed to more than one triggering agent, and is the result of a combination of biotic and abiotic factors (Manion & Lachance 1992). However, dieback could also be a natural recurring phenomenon resulting from cohort senescence (Mueller-Dombois 1985) or related to reproduction (Foster 1977) rather than from diseases or environmental stresses. Dieback in Australian and African savannas has been attributed to the effects of drought (MacGregor & O'Connor 2002; Rice *et al.* 2004), but to our knowledge, no tree dieback has been reported and no studies have been done to link tree physiological processes and population dynamics for Neotropical savannas.

Since savanna ecosystems are usually characterized by strong seasonality in precipitation, plant–water relations are considered to be key determinants of their structure

and composition (Huntley & Walker 1982). Drought, in general, not only influences the water relations and hydraulic properties of plants but also negatively affects photosynthesis (Chaves *et al.* 2002), as well as resistance to herbivory (Lowman & Heatwole 1992) and infection by fungi (Gibbs *et al.* 1990). Central Brazilian savannas (Cerrado) are subjected to a pronounced dry season that may last for as long as 5 months. Water deficits play a crucial role in the growth and physiology of savanna trees because of the high atmospheric evaporative demand and the limited amount of water that trees can obtain daily from the upper soil layers during the dry season (Meinzer *et al.* 1999). Although many savanna woody species have deep root systems that access water available at depth during the dry season (Rawitscher 1948; Oliveira *et al.* 2005), the paradigm that they all have similar access to deep soil water reserves does not appear to be universally applicable (Jackson *et al.* 1999; Bucci *et al.* 2005; Goldstein *et al.* 2008; Scholz *et al.* 2008).

Water deficits are amplified in tall trees owing to increased tension in the xylem required to draw water from the soil to the canopy. Increased tension in xylem conduits in tall trees may induce embolism and hydraulic dysfunction, leading to increased water deficits, decreased stomatal conductance (g_s) and photosynthesis, lower growth rates (Ryan & Yoder 1997; Koch *et al.* 2004; Woodruff, Bond & Meinzer 2004; Ryan, Phillips & Bond 2006; Domec *et al.* 2008) and, eventually, tree mortality. In order to mitigate the effects of increased water deficits, trees may decrease g_s , down-regulate photosynthesis, intensify refilling of embolized xylem and/or modify their hydraulic architecture, in particular, the leaf area to sapwood area ratio (LA/SA) (McDowell *et al.* 2002). Recently, it has been shown that leaves are a hydraulic bottleneck in the water transport pathway of the plant, representing about 30% of whole plant resistance for a range of life forms (Sack *et al.* 2003) and that maximum leaf hydraulic conductance (K_{leaf}) decreases with increasing height (Woodruff, Meinzer & Lachenbruch 2008). The relationship between adjustment in hydraulic architecture when growing taller and whole-tree carbon balance, as well as their roles in tree mortality, however, is poorly understood.

Sclerolobium paniculatum Vog. (Leguminosae) is a dominant tall evergreen savanna species exhibiting conspicuous branch dieback and tree mortality among larger individuals. It is a fast-growing pioneer species (Pires & Marcatti 2005) and is among the few Brazilian Cerrado tree species with relatively shallow root systems (Jackson *et al.* 1999; Scholz

2006). The objective of this study was to identify potential causal relationships between size-related changes in tree hydraulic architecture, carbon allocation, growth, gas exchange, water deficits and mortality in *S. paniculatum* trees growing in a Cerrado site where fire has been excluded during the last 35 years. We investigated stem and leaf hydraulic properties, leaf water status, growth rates, gas exchange and other functional traits such as wood density and leaf mass per area (LMA) in *S. paniculatum* trees of different heights.

MATERIALS AND METHODS

Study site and plant material

This research was carried out in a savanna site at the Instituto Brasileiro de Geografia e Estatística (IBGE) reserve, a field experimental station located 35 km south of Brasília (15°56'S, 47°53'W, elevation 1100 m). Average annual precipitation in the reserve is 1500 mm with a pronounced dry season from May to September. Average relative humidity during the dry season is 55% and minimum relative humidity can drop to values as low as 10%. Mean monthly temperatures range from 19 to 23 °C. The soils are very nutrient poor, deep and well-drained oxisols. Soil bulk density is about 0.99 g cm⁻³, macroporosity is about 18% and texture fraction (silt/clay) is about 0.22 in the upper 100 cm of a typical soil profile (Bucci *et al.* 2008). The IBGE reserve contains all major physiognomic types of savannas from very open to closed savannas. *Sclerolobium paniculatum* is a dominant species in savannas with a high tree density and exhibits high chronic mortality of large trees.

A 'cerrado denso' site with relatively uniform topography and soil characteristics and intermediate tree density was chosen to minimize shading effects and increase the likelihood that small and large trees experienced similar light regimes. Fire had been excluded from the site for more than 35 years. All of the *S. paniculatum* trees inside a 200-m-long, 40-m-wide transect were surveyed and later categorized into four height classes for measurements of functional traits (Table 1). Both the height and stem diameter at 1.3 m (DBH) of the individuals used for physiological studies were determined. The percentage of dead branches per tree of each *S. paniculatum* individual was determined by counting the total number of dead branches per plant in smaller trees, or visually estimating the percentages of dead branches in the crowns of taller trees in which

Table 1. Number of individuals used for physiological measurements, height, DBH and relative abundance of trees in each size class

| Tree height class (m) | Number of individuals | Height (m) | DBH (cm) | Relative abundance (%) |
|-----------------------|-----------------------|-------------|--------------|------------------------|
| <3 | 10 | 1.74 ± 0.10 | 1.46 ± 0.07 | 13 |
| 3 to 6 | 20 | 4.60 ± 0.17 | 5.34 ± 0.43 | 13 |
| 6 to 8 | 15 | 6.89 ± 0.16 | 12.97 ± 1.05 | 32 |
| >8 | 11 | 8.95 ± 0.19 | 16.26 ± 0.88 | 42 |

The height and DBH values are means ± SE from all the sampled trees used to measure physiological variables. The relative abundance corresponds to all *Sclerolobium paniculatum* trees in the study site, even if they were dead.

branches were too numerous to accurately count from the ground.

Leaf water potential

A pressure chamber (PMS, Corvallis, OR, USA) was used to measure leaf water potential (Ψ_L) during the dry season of 2006. Six to 10 newest fully developed mature leaves from sun-exposed terminal branches of different individuals were selected to measure dawn and midday Ψ_L . Samples for dawn Ψ_L were collected between 0630 and 0730 h, while leaves for midday measurements were collected between 1230 and 1400 h. Previous studies at the IBGE reserve have shown that daily maximum (least negative) values of Ψ_L are typically attained between 0600 and 0630 h with a decline of ≤ 0.2 MPa by 0730 h (Bucci *et al.* 2003, 2004a). The top two leaflets of the large compound leaves were excised, immediately sealed in plastic bags and kept in a cooler with small amount of ice until balancing pressures were determined in the laboratory within 1 h of sample collection.

K_{leaf} , pressure-volume relationships and leaf capacitance

K_{leaf} was estimated using the partial rehydration method (Brodribb & Holbrook 2003). Samples for dawn K_{leaf} were collected between 0630 and 0730 h, while leaves for midday measurements were collected between 1230 and 1400 h. Large branches were cut, bagged and kept in the dark with slightly wet paper towels for about 30 min for water potential equilibration of leaves and leaflets. Two leaves were chosen to measure the initial Ψ_L in the two top leaflets of the compound leaf. Then, the top two leaflets of two adjacent leaves were cut from the rachis under water, and allowed to absorb water for 3 to 15 s depending on the initial water potential, after which, their rachis ends were dried carefully. The final value of Ψ_L was immediately measured using the pressure chamber. K_{leaf} was then calculated from the equation:

$$K_{\text{leaf}} = C \times \ln(\Psi_o/\Psi_f)/t \quad (1)$$

where C is the leaf capacitance, Ψ_o is the Ψ_L prior to rehydration and Ψ_f is the Ψ_L after rehydration for t seconds.

Values of leaf capacitance used to calculate K_{leaf} were derived from pressure–volume relationships (Tyree & Hammel 1972) using the method described by Brodribb & Holbrook (2003). Briefly, the Ψ_L corresponding to turgor loss was estimated as the inflection point (the transition from the initial curvilinear, steeper portion of the curve to the more linear less steep portion) of the graph of Ψ_L versus relative water content (RWC). The slope of the curve prior to and following turgor loss provided C in terms of RWC (C_{RWC}) for pre-turgor loss and post-turgor loss, respectively. Leaf area to dry mass ratios were used to normalize C on a leaf area basis. Pressure–volume curves were determined for six fully developed exposed leaves from different

individuals. Leaves for pressure–volume analyses were obtained from branches cut in the field in the early morning, re-cut immediately under water and covered with black plastic bags with the cut end in water for about 2 h until measurements began. Data were fitted by a pressure–volume program developed by Schulte & Hinckley (1985).

Leaf vulnerability curves were plotted as K_{leaf} against initial Ψ_L before rehydration. A range of Ψ_L was attained through slow bench drying of leafy branches collected from the field at dawn. Branches were dehydrated for different time periods, after which, they were enclosed in black plastic bags with slightly wet paper towels. After 0.5 to 1 h equilibration period, Ψ_L before and after rehydration, were measured.

Stem hydraulic conductivity

Hydraulic conductivity (k_h) was measured on sun-exposed terminal branches excised at dawn (0630 to 0730 h) and midday (1300 to 1400 h) from four to five individuals of each height class except the smallest (< 3 m) because their branches were few, very short and were not suitable for k_h measurement. Vessel length was estimated according to Zimmermann & Jeje (1981). Maximum vessel length of *S. paniculatum* was between 35 and 57 cm ($n = 10$ branches). Long branches, about two times longer than the maximum vessel length, were excised from the tree and then immediately re-cut under water. The other end of the stem section was also cut under water and stem sections were submerged and transported rapidly to the laboratory. Immediately after arriving at the laboratory, both ends of 60-cm-long stem segments were re-cut under water and attached to a k_h apparatus (Tyree & Sperry 1989). The downstream ends of the stems were connected to measuring pipettes and the flow rates were volumetrically monitored. Following a short equilibration period, water flow generated by a constant hydraulic head of 80 cm was measured. Distilled/de-gassed water was used as the perfusion fluid. k_h ($\text{kg m}^{-1} \text{MPa}^{-1}$) was calculated as:

$$k_h = J_v/(\Delta P/\Delta X) \quad (2)$$

where J_v is the flow rate through the stem segment (kg s^{-1} ; converted from mL s^{-1}) and $\Delta P/\Delta X$ is the pressure gradient across the stem segment (MPa m^{-1}). Specific hydraulic conductivity (k_s ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was obtained as the ratio of k_h and the cross-sectional area of the active xylem. Active xylem area was distinguished from heartwood based on dye injections in the stem as described by James *et al.* (2002). Leaf-specific conductivity (k_l ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was obtained as the ratio of k_h and the leaf area distal to the stem segment. One-sided leaf areas were obtained using a scanner and ImageJ image analysis software (Abramoff, Magelhaes & Ram 2004).

Stem vulnerability curves were determined using the bench drying method (Tyree & Sperry 1989). Large branches, about two times longer than the maximum vessel length, were excised from the tree, covered with plastic bags

and then transported to the laboratory. Different Ψ_L and percentage loss of conductivity (PLC) values were obtained by allowing excised branches to dehydrate slowly in air for different time periods. The segments used to determine branch vulnerability curves were 10 cm long. Maximum k_h was determined after initial k_h measurements by flushing the stems with the perfusion fluid (distilled and de-gassed water) at a pressure of 0.2 MPa for 15 min, to remove air from embolized vessels. The flushing solution had been passed through a 0.22 μm membrane filter to prevent particulate matter from blocking the conduits. After 15 min flushing, k_h was measured again as described above. The process was repeated until maximum conductivity (k_{max}) was achieved. The initial k_h measurement (k_i) was expressed as a percentage of k_{max} , and PLC was calculated as $(1 - k_i/k_{\text{max}}) \times 100$. Leaf water potential was measured with the pressure chamber. Stem hydraulic vulnerability curves were obtained by plotting PLC against Ψ_L .

Wood density, LMA and stem growth rate

Wood density of terminal branches was measured for six individuals of each height class. Stem section samples were taken from the terminal branches, sealed in aluminum foil and plastic bags and taken to the laboratory. The pith was removed by splitting the stem segments longitudinally and carefully excising the pith with a razor blade. After removing the bark and pith, the cores were weighed to the nearest milligram, placed in water in a small graduated cylinder to determine the volume and then oven-dried to a constant mass and weighed again to obtain the dry mass. Density was then determined by dividing the dry mass by the volume of the sample. For leaf mass per unit leaf area determinations, six newest fully expanded mature sun leaves were collected from six trees of each height class. After their areas had been measured as described above, the leaves were oven-dried at 70 °C to constant weight, and weighed. Stem growth rates of different height individuals were monitored using locally constructed stainless steel dendrometer bands installed at ~1.3 m. Irregular sections of tree stems were avoided. Data were collected monthly from July 2005 to April 2006 and then every two months from April 2006 to June 2008. Annual basal area increment ($\text{cm}^2 \text{y}^{-1}$) was calculated from the total circumference increment over the time interval from July 2005 to June 2008.

Gas exchange measurements

Net CO_2 assimilation (A) and g_s of individuals of different heights were measured during the wet season (February) of 2008 using a portable photosynthesis system (Li-6400, Li-Cor, NE, USA). Tree height was estimated from DBH using the relationship in Fig. 1 rather than separating the trees into height classes prior to measuring gas exchange. The newest fully developed mature leaves from sun-exposed terminal branches of different individuals were selected for gas exchange measurements ($n = 47$). Photosynthetic photon flux was held at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$

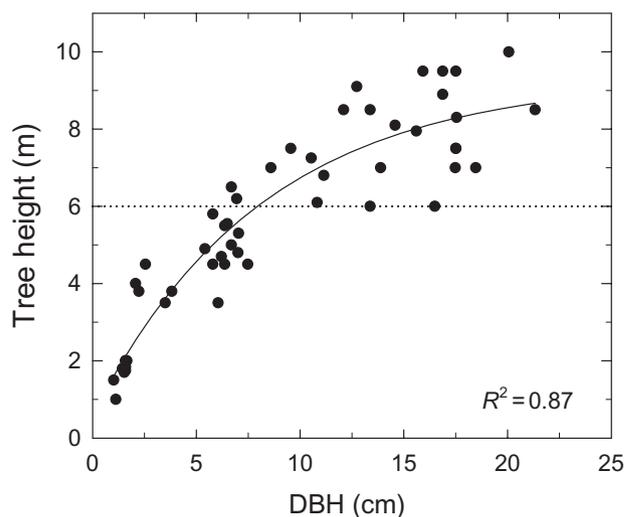


Figure 1. Relationship between tree height and stem diameter at 1.3 m (DBH) of *Sclerolobium paniculatum* trees later divided into height classes for physiological measurements. The dotted line represents the approximate height threshold at which mortality of entire trees was observed.

and ambient CO_2 at 400 ppm during the measurements. The measurements were conducted on sunny days between 0930 and 1100 h. There were no discernible time-dependent trends in A over this interval. Gas exchange measurements were made on detached shoots with their bases in water to minimize the extrinsic influence of factors such as hydraulic path-length resistance and to facilitate detection of intrinsic height-related leaf structural and physiological constraints on gas exchange. This procedure has been successfully applied to other species (e.g. Woodruff *et al.* 2009). Branches were cut with a pruner, then immediately re-cut under water and gas exchange was measured within 5 min of excision. Initial comparisons ($n = 9$) made on branches accessible from the ground indicated that mean A during the first 5 min after excision differed by <4% from pre-excision values. Gas exchange rates were expressed on a leaf mass basis using leaf area to dry mass ratios of leaves on which gas exchange was measured.

Data analysis

Height-related trends in branch dieback, basal area increment and gas exchange, and the relationship between height and DBH were evaluated by regression analysis and one-way analysis of variance (ANOVA). Four height classes were identified (Table 1) for sampling of trees and subsequent analysis of height-related trends in functional traits using general linear model ANOVA (Minitab 15, Minitab, Inc., <http://www.minitab.com>). Sigmoid functions were fitted to the leaf and stem vulnerability curves.

RESULTS

Tree height increased asymptotically with DBH to a mean maximum height of about 8.7 m in the *S. paniculatum*

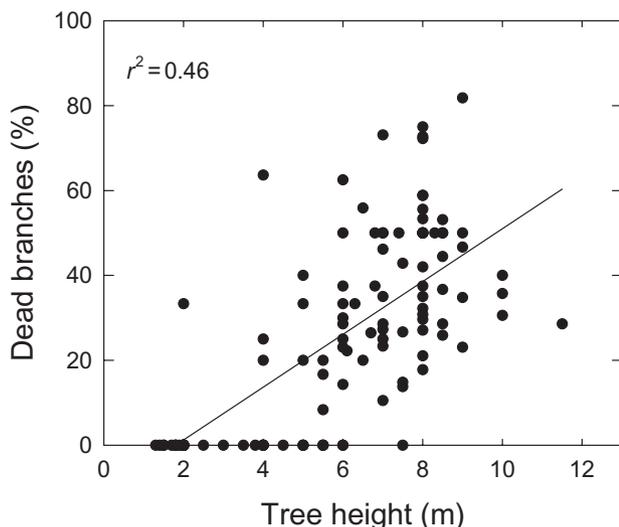


Figure 2. Percentage of dead branches per tree in relation to tree height for *Sclerobolium paniculatum* in the study site.

population studied ($P < 0.00001$, Fig. 1). Of the 120 standing trees taller than 6 m, 41% were dead, and consequently were not included in Fig. 1. No dead trees shorter than 6 m were observed. The transition from a rapid to gradual increase in tree height with DBH coincided approximately with the height threshold of 6 m at which mortality of entire trees was observed (Fig. 1, dotted line). The percentage of dead branches per tree increased significantly ($P < 0.00001$) with increasing tree height, especially in individuals greater than ~5 m tall (Fig. 2). Mean basal area increment was $8.6 \text{ cm}^2 \text{ y}^{-1}$ among 30 trees spanning a height range of 5.0 to 8.5 m and an initial diameter range of 5.7 to 18.6 cm. There was no significant height-related trend in the basal area increment, but five trees taller than 7.5 m died during the 3 year growth measurement period between July 2005 and June 2008 and were not included in the calculation of mean basal area growth.

Mean dawn and midday Ψ_L was -0.35 and -1.8 MPa, respectively, and did not differ significantly among tree size classes. The percent loss of k_h in stems increased abruptly below threshold water potential values of about -3.0 MPa (Fig. 3). K_{leaf} , on the other hand, decreased continuously with decreasing water potential. The water potential at 50% of maximum K_{leaf} (Ψ_{50}) was attained at about -1 MPa, while 50% loss of maximum stem k_h occurred at about -3.4 MPa and varied little with tree size (Fig. 3). Leaves were thus substantially more vulnerable to embolism than terminal stems. Leaves of trees >6 m tall exhibited slightly lower vulnerability to embolism than those of small trees. The Ψ_{50} was -0.8 MPa in leaves of trees <6 m tall, while leaves of trees in the two taller size classes had a Ψ_{50} of about -1 MPa. The maximum K_{leaf} (K_{leaf} at Ψ_L close to 0 MPa) was lowest in trees >8 m tall (Fig. 3). The y-intercept of the function fitted to Ψ_L versus K_{leaf} relationships (K_{leaf} at a Ψ_L of 0 MPa) was $22 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for trees >8 m tall, while it ranged from 30 to $40 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for

trees in the other height classes. Leaf turgor loss points ranged between -1.5 and -1.7 MPa, and coincided approximately with the Ψ_L at which K_{leaf} approached zero (Fig. 3).

Stem-specific hydraulic conductivity (k_s) did not change significantly between dawn and midday (Fig. 4). On the other hand, midday K_{leaf} was substantially lower compared with dawn values in trees from all size classes (Fig. 4). There was a marginally significant ($P = 0.06$) decline in dawn K_{leaf} with increasing tree height. The midday K_{leaf} values were slightly higher than the values derived from leaf vulnerability curves and midday Ψ_L , probably as a result of the equilibration between leaf and stem water potentials, while the branches remained bagged before measurements.

Since no significant difference was found between dawn and midday k_h , k_s and k_l (data not shown for k_h and k_l), the means of midday and dawn values were used in Fig. 5. There was a significant ($P = 0.003$) height-related decline in k_h (Fig. 5). k_s also decreased significantly ($P < 0.001$) with increasing tree height (Fig. 5), whereas k_l did not change significantly ($P = 0.24$) with tree height (Fig. 5). The lack of a significant height-related trend in k_l was associated with a significant ($P = 0.033$) reduction in branch LA/SA with increasing tree height (Fig. 5). LMA and wood density increased, whereas leaf size decreased ($P = 0.003$ to <0.001) with increasing tree height (Fig. 6). Daily maximum g_s and net photosynthetic rate per unit mass (A) decreased ($P < 0.00001$ and 0.0001 , respectively), while intrinsic water use efficiency (A/g_s) increased ($P < 0.0001$) linearly with increasing tree, size indicating that the relative stomatal limitation of photosynthesis increased with height (Fig. 7).

DISCUSSION

Our results suggest that *S. paniculatum* undergoes compensatory changes in its hydraulic architecture when growing taller that serve to avoid greater leaf water deficits associated with increased tree height and hydraulic path-length resistances (e.g. Koch *et al.* 2004; Woodruff *et al.* 2004). However, these adjustments appeared to incur a substantial physiological cost in terms of altered patterns of carbon allocation and their impact on growth efficiency and likely whole-tree carbon balance. The height-dependent trends in hydraulic architecture, carbon allocation and growth of *S. paniculatum* were consistent with size-dependent patterns of branch damage and tree mortality. Nevertheless, we did not assess the extent to which larger trees were carbon limited compared with smaller trees. Previous studies suggest that size-related reductions in growth of taller, longer-lived tree species are not attributable to reduced carbon availability (Ryan *et al.* 2006; Sala & Hoch 2009). Consistent with the steep decline in the slope of the tree height versus diameter relationship over a relatively small range of tree height (Fig. 1), LMA was 17% greater and wood density 14% greater in the tallest than in the shortest trees, implying a steadily declining efficiency of CO_2 uptake and volume growth per unit biomass.

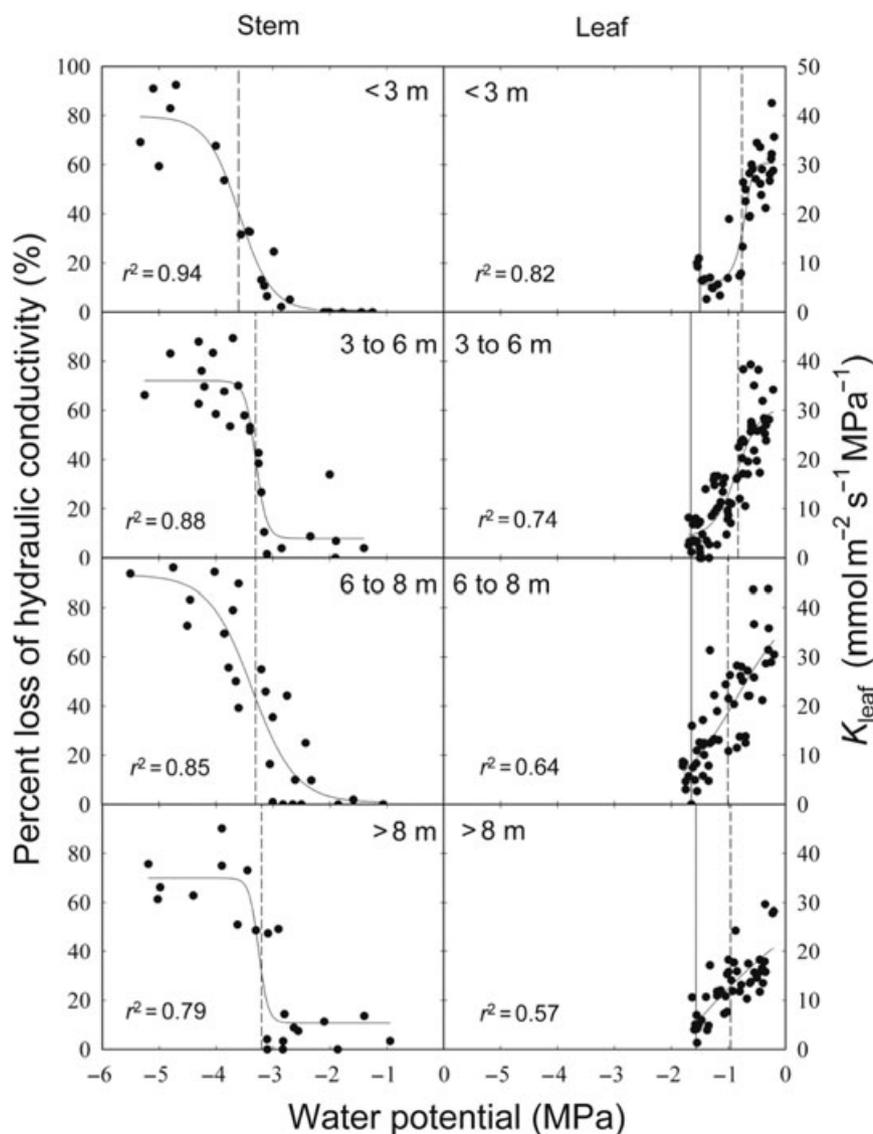


Figure 3. Leaf and stem hydraulic vulnerability curves for trees in different height classes. A sigmoid function was fitted to the data ($P < 0.001$). The dashed lines represent the water potential at 50% loss of maximum stem hydraulic conductivity, or 50% loss of maximum leaf hydraulic conductance (K_{leaf}). The solid vertical lines indicate the osmotic potential at the leaf turgor loss point, calculated from pressure–volume relationships.

Height-related trends in hydraulic architecture and stem water storage capacity

The largest size classes of *S. paniculatum* exhibited a greater frequency of branch damage and dead individuals, as well as distinct hydraulic architecture and related carbon allocation traits compared with small individuals. The absence of significant size-related decreases in dawn and midday Ψ_L may have been associated with reduced g_s in taller trees (Fig. 7). Additionally, reduced leaf area at the branch (Fig. 5) and whole-tree (Fig. 2) scales appeared to have stabilized k_1 despite size-related reductions in k_s (Fig. 5). In view of the lack of height-related differences in maximum leaf water deficits observed in this study, it seems unlikely that extreme values of Ψ_L governed the size-related hydraulic and morphological changes observed in *S. paniculatum*. The most negative minimum Ψ_L observed during the study period was higher than -2 MPa. However, minimum Ψ_L during drier years can drop to -2.3 MPa (Scholz *et al.* 2007).

Lower k_s and higher LMA in taller trees were associated with a height-related increase in wood density (Fig. 6), consistent with relationships between k_s , LMA and wood density previously observed in tropical tree species (e.g. Bucci *et al.* 2004b; Meinzer *et al.* 2008). Smaller, thicker leaves (high LMA) in taller *S. paniculatum* trees could be associated with reduced cell turgor during leaf expansion (Koch *et al.* 2004; Woodruff *et al.* 2004). Our results suggest that *S. paniculatum* leaves lose turgor at midday, with Ψ_L in trees >6 m tall falling further below the Ψ_L at turgor loss than in trees <6 m tall. For example, the difference between midday Ψ_L and the osmotic potential at turgor loss was 0.16 MPa in trees from 3 to 6 m tall, while this difference was 0.29 MPa in trees >8 m tall. In plants from arid environments, rehydration of samples for pressure–volume analysis may sometimes cause artefacts by shifting the turgor loss point to less negative values (Meinzer *et al.* 1986). However, Cerrado trees experience Ψ_L close to 0 MPa at night and

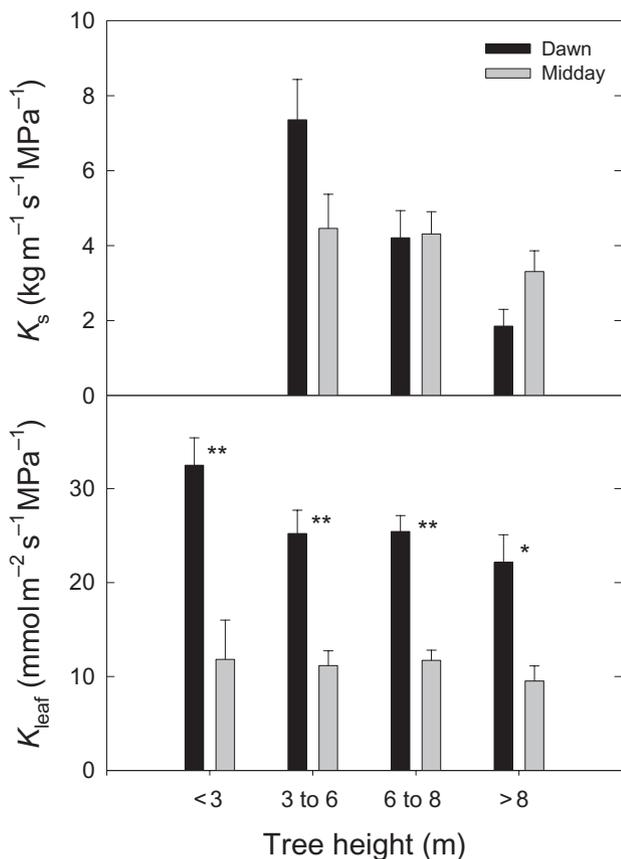


Figure 4. Dawn (black bars) and midday (grey bars) stem-specific hydraulic conductivity (k_s), and leaf hydraulic conductance (K_{leaf}), of trees from different height classes. k_s of trees shorter than 3 m was not measured (see methods). Bars are means \pm SE for $n = 4$ to 6. Significant differences between dawn and midday K_{leaf} were found (** $P < 0.001$, * $P < 0.05$).

we limited the rehydration period to 2 h to avoid rehydration artefacts.

A strong negative relationship between sapwood hydraulic capacitance and wood density has been found in several Neotropical tree species (Scholz *et al.* 2007; Meinzer *et al.* 2008). In Cerrado trees, species-specific values of wood density largely determine stem water storage capacity, and high water storage capacity helps to maintain an adequate water balance by improving delivery of water to leaves, particularly during the dry season (Scholz *et al.* 2007). *Sclerolobium paniculatum* had the highest wood density and the lowest capacitance among all the Cerrado species for which data are available (Scholz *et al.* 2007). Capacitance of *S. paniculatum* was less than $40 \text{ kg m}^{-3} \text{MPa}^{-1}$, whereas the capacitance of *Vochysia thyrsoidea*, the species with the least dense wood among savanna trees (0.42 g cm^{-3}), was $160 \text{ kg m}^{-3} \text{MPa}^{-1}$. Thus, *S. paniculatum*, with a low intrinsic water storage capacity, is at a comparative disadvantage in terms of buffering diurnal and seasonal variation in Ψ_L and minimizing the amount of time plant tissues remain at their daily minimum values of Ψ . Furthermore, the increase in wood density with increasing tree size (Fig. 6) suggests that the largest individuals have an even lower capacity for buffering the effects of hydraulic path length and soil water deficits than smaller trees. Therefore, in exceptionally dry years, tall trees may experience more severe or prolonged water deficits, which could result in reduced growth, branch damage and even mortality of the whole tree.

Comparative xylem vulnerability of stems and leaves

Sclerolobium paniculatum leaves were more vulnerable to embolism than terminal stems. Leaves were 50% embolized

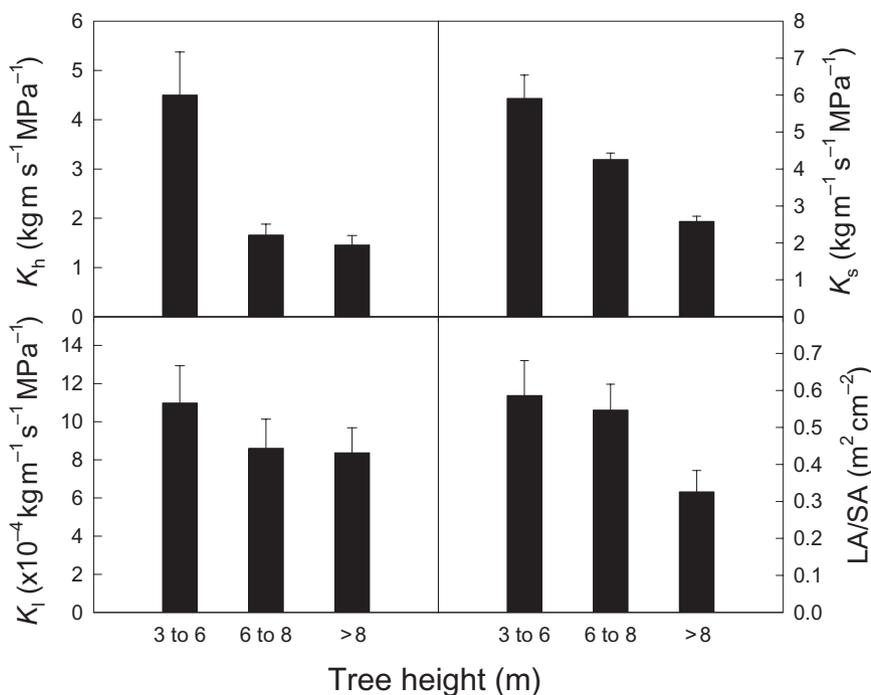


Figure 5. Hydraulic conductivity (k_h), specific hydraulic conductivity (k_s), leaf-specific hydraulic conductivity (k_l) and ratio of leaf area to sapwood area (LA/SA) of terminal branches of trees in different height classes. Bars are means \pm SE of four or five individuals.

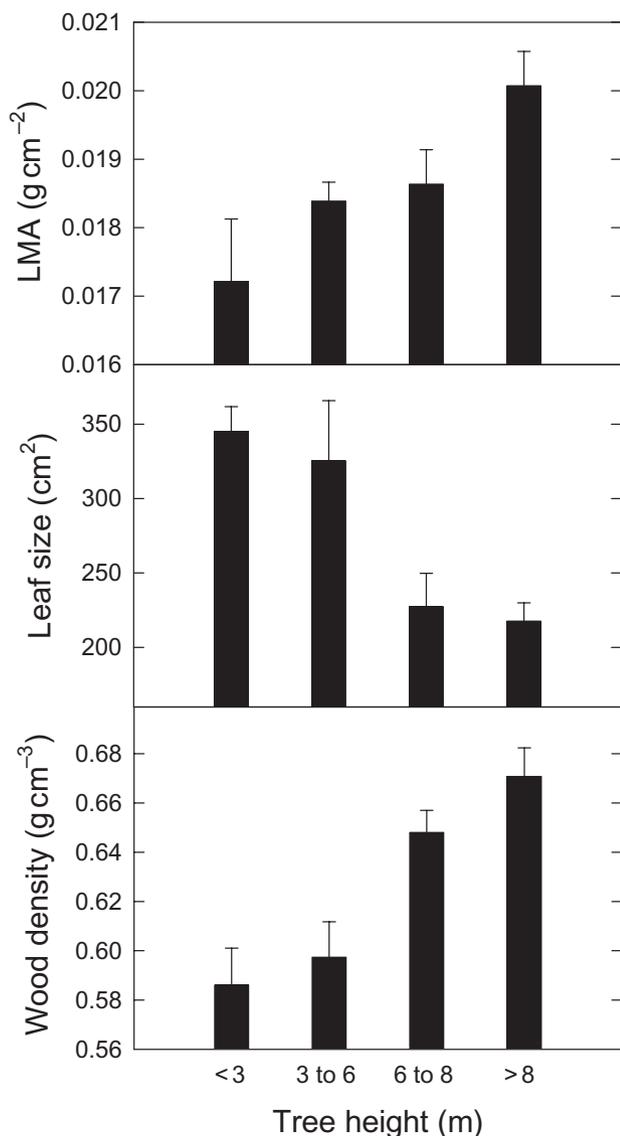


Figure 6. Leaf mass per area (LMA), leaf size and wood density of trees in different height classes. Bars are means \pm SE of six individuals.

at about -1 MPa, whereas stems were 50% embolized below -3.2 MPa (Fig. 3). Stem xylem was operating far from the point of catastrophic dysfunction *sensu* Tyree & Sperry (1988), and therefore terminal stems had a wider safety margin in terms of water deficits than leaves. Leaf water potentials at which K_{leaf} reached minimum values were close to their turgor loss points. The mortality of *S. paniculatum* trees is not likely to result from catastrophic stem xylem dysfunction during periods of drought because minimum stem water potentials in the field were not only well above those corresponding to P_{50} , but also well above the water potential threshold at which cavitation starts to increase according to the stem xylem vulnerability curves. On the other hand, Ψ_L in the field and leaf vulnerability curves suggest that embolism in leaves occurred regularly. Lower maximum K_{leaf} in taller *S. paniculatum* trees may

reflect height-related trends in xylem structure associated with reduced leaf expansion (Woodruff *et al.* 2008).

Leaves of *S. paniculatum* showed a consistent daily pattern of depression and recovery of K_{leaf} (Fig. 4). Daily changes in K_{leaf} could be partially explained by embolism formation during the morning when Ψ_L decreased as evaporative demand and transpiration increased. In the afternoon or at night, K_{leaf} increased, consistent with daily embolism repair. Results of dye experiments by Bucci *et al.* (2003) support the hypothesis that diel variation of petiole k_h of savanna trees was associated with embolism formation and repair. Dye experiments are difficult to perform with the leaf lamina, but results obtained with other techniques,

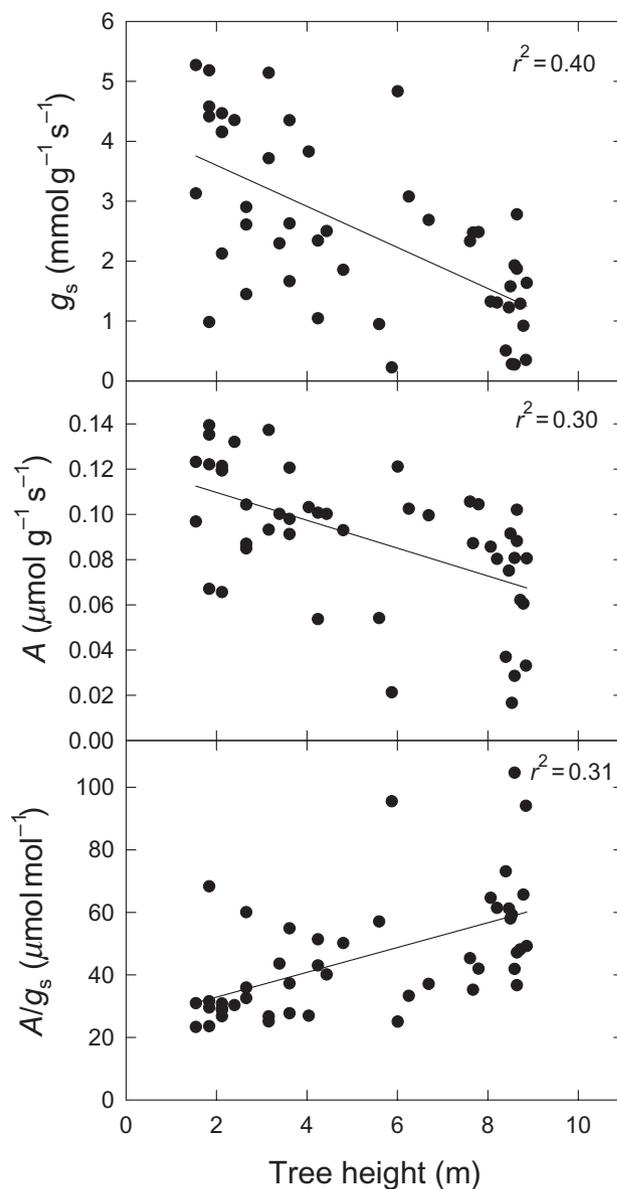


Figure 7. Stomatal conductance (g_s), net assimilation rate (A) and intrinsic water use efficiency (A/g_s) in relation to height of *S. paniculatum* trees. The lines are linear regressions fitted to the data.

such as cryoscanning electron microscopy (Canny 2001; Woodruff *et al.* 2007) and acoustic emission (e.g. Lo Gullo *et al.* 2003; Johnson *et al.* 2009), indicate that cavitation commonly occurs in leaves of many species. Cochard *et al.* (2004), on the other hand, suggested that diurnal variations in K_{leaf} of conifers could be partially explained by changes in conduit dimensions under cycles of tension increase and tension release, reversibly constricting the water flow through the leaf.

Regardless of the mechanism governing diurnal changes in K_{leaf} , the reversible loss of hydraulic conductance in the leaf lamina may be an adaptive means of amplifying the evaporative demand signal to the stomata in order to expedite a stomatal response (Brodribb & Holbrook 2004). Although we did not find daily changes in k_s of stems in our study, diurnal depression and recovery of stem k_s has been observed in other species (Zwieniecki & Holbrook 1998; Melcher *et al.* 2001). Embolism formation and refilling is probably of limited significance for stems of woody plants at most times because of the high energetic costs of refilling a large volume of tissue that is distant from the sites of carbohydrate synthesis in the leaves. Compared with stems, diurnal refilling in leaves may be less energetically costly and may involve simpler mechanisms (Bucci *et al.* 2003; Brodribb & Holbrook 2004). *Sclerobium paniculatum* stems were less vulnerable to cavitation than leaves on one hand, and also were protected by regulation of transpiration through diurnal depression and recovery of K_{leaf} . Due to the high safety of *S. paniculatum* stems, and the effective regulation of K_{leaf} and g_s , the dieback of tall individuals could not be explained by catastrophic xylem dysfunction when experiencing drought but may be related to changes in whole-tree water and carbon balance resulting from size-related structural changes, as discussed below.

Carbon balance in relation to hydraulic architecture and carbon allocation

Trees adjusted their branch hydraulic architecture with increasing height, resulting in lower LA/SA in taller trees and a relatively constant k_i , so the amount of water that could be delivered by the vascular system per unit leaf area was similar in different size trees despite a sharp reduction in branch k_s with increasing tree size. These relationships were not directly characterized at the whole-tree level, but size-dependent increases in branch dieback and similar values of dawn and midday Ψ_L across size classes were consistent with maintenance of whole-tree leaf-specific conductance. Seasonal adjustments in leaf area of Cerrado trees have been shown to reduce seasonal variation in midday Ψ_L and whole-plant leaf-specific conductance (Bucci *et al.* 2005). Other studies have shown compensatory adjustments in tree allometry and stand structure that contribute to homeostasis of minimum Ψ_L (Whitehead, Jarvis & Waring 1984; Williams & Cooper 2005). Nevertheless, adjustments that maintain an adequate water balance could result in an unsustainable situation in terms of whole-tree carbon balance in *S. paniculatum*. The largest *S. paniculatum*

trees are likely to receive a substantially lower return in carbon gain from their investment in stem and leaf biomass compared with smaller trees as explained in the following exercise based on our data on size-dependent changes in allometry, carbon allocation and gas exchange.

For a given investment in sapwood area, the largest trees (>8 m tall) display only 55% as much leaf area compared with 3 to 6-m-tall trees (LA/SA = 0.33 and 0.60 m² cm⁻² in trees >8 m tall and 3 to 6 m tall, respectively). When the differences above are normalized by the difference in branch wood density and LMA between the largest trees and smaller trees (an estimate of the amount of leaf mass developed per biomass invested), then the largest trees developed only 54% as much leaf mass per biomass invested in stem tissue. Furthermore, according to the linear relationship between A (mass based net CO₂ uptake) and H (tree height) ($A = 0.122 - 0.0062H$), A in trees 10 m tall would be about 64% of that in trees 3 to 6 m tall. Thus, large trees may only get 35% as much carbon return per biomass invested as small trees do. It is noteworthy that A of detached shoots declined by ~50% between 1 and 10 m (Fig. 7), suggesting that this height-related change was associated with inherent leaf structural and physiological constraints on gas exchange (e.g. Niinemets 2002; Woodruff *et al.* 2009) rather than extrinsic effects of hydraulic path-length resistances. Gas exchange of attached shoots is likely to decline more steeply with increasing height because of hydraulic constraints (Schäfer, Oren & Tenhunen 2000; McDowell, Licata & Bond 2005).

Sclerobium paniculatum is a fast-growing pioneer species with a relatively short life cycle. These species should have allocation patterns that favour survival and growth of young trees, even if the performance of the same tree is compromised when older (Williams 1957). In *S. paniculatum*, patterns of hydraulic architecture adopted early in development appear to constrain water and carbon relations late in development. High adult mortality has also been found in monocarpic species (Stearns 1992), a life history strategy in which individuals reproduce only once and subsequently die. Several species of *Tachigali*, a genus now considered synonymous with *Sclerobium* (Lewis 2005), are monocarpic (Foster 1977; Poorter *et al.* 2005), an extremely rare characteristic for tropical trees. If the observed patterns of hydraulic architecture and carbon imbalance represent more general characteristics of the *Sclerobium-Tachigali* clade, this suggests that hydraulic constraints may have resulted in the life-history trade-off responsible for the monocarpy in some *Tachigali* species.

The height of tall *S. paniculatum* trees may confer an advantage in competition for light and establishing dominance, particularly in dense Cerrado physiognomies, but may also carry the risk of greater water deficits in exceptionally dry years. Compensatory adjustments in leaf and branch hydraulic architecture with increasing tree height appeared to carry a large physiological cost: a poor return in carbon gain for a given investment in stem and leaf biomass compared with small trees, which eventually could lead to dieback of the whole tree. Our results provide a potential

explanation for the mass mortality in large *S. paniculatum* trees, as well as insights into the physiological costs of size-related changes in carbon allocation patterns.

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