

Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant

S. J. BUCCI,¹ G. GOLDSTEIN,^{2,3} F. C. MEINZER,⁴ F. G. SCHOLZ,² A. C. FRANCO⁵ and M. BUSTAMANTE⁶

¹ Department of Biology, University of Miami, Coral Gables, FL 33124, USA

² Laboratorio de Ecología Funcional, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Núñez, Buenos Aires, Argentina

³ Corresponding author (goldstein@bio.miami.edu)

⁴ USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331, USA

⁵ Departamento de Botânica, Universidade de Brasília, caixa postal 04457, Brasília, DF 70919970, Brazil

⁶ Departamento de Ecologia, Universidade de Brasília, caixa postal 04457, Brasília, DF 70919970, Brazil

Received August 11, 2003; accepted March 8, 2004; published online June 1, 2004

Summary Functional convergence in hydraulic architecture and water relations, and potential trade-offs in resource allocation were investigated in six dominant neotropical savanna tree species from central Brazil during the peak of the dry season. Common relationships between wood density and several aspects of plant water relations and hydraulic architecture were observed. All species and individuals shared the same negative exponential relationship between sapwood saturated water content and wood density. Wood density was a good predictor of minimum (midday) leaf water potential and total daily transpiration, both of which decreased linearly with increasing wood density for all individuals and species. With respect to hydraulic architecture, specific and leaf-specific hydraulic conductivity decreased and the leaf:sapwood area ratio increased more than 5-fold as wood density increased from 0.37 to 0.71 g cm⁻³ for all individuals and species. Wood density was also a good predictor of the temporal dynamics of water flow in stems, with the time of onset of sap flow in the morning and the maximum sap flow tending to occur progressively earlier in the day as wood density increased. Leaf properties associated with wood density included stomatal conductance, specific leaf area, and osmotic potential at the turgor loss point, which decreased linearly with increasing wood density. Wood density increased linearly with decreasing bulk soil water potential experienced by individual plants during the dry season, suggesting that wood density was greatest in individuals with mostly shallow roots, and therefore limited access to more abundant soil water at greater depths. Despite their taxonomic diversity and large intrapopulation differences in architectural traits, the six co-occurring species and their individuals shared similar functional relationships between all pairs of variables studied. Thus, rather than differing intrinsically in physiological responsiveness, the species and the individuals appeared to have distinct operating ranges along common physiological re-

sponse curves dictated by plant architectural and structural features. The patterns of water uptake and access to soil water during the dry season appeared to be the main determinant of wood density, which constrained evolutionary options related to plant water economy and hydraulic architecture, leading to functional convergence in the neotropical savanna trees studied.

Keywords: cerrado, hydraulic conductivity, sap flow, soil water potential, water transport, wood density.

Introduction

Recognition of functional convergence in physiological and morphological characteristics of plants can be obscured by ambiguities concerning the scale at which measurements are made. The relevant scale for characterizing responses of plants to environmental factors is often the individual because it is the integration of activities and processes in the entire plant that contributes to features such as survival, growth and reproductive success. For example, photosynthetic rates of individual leaves are often assumed to represent a property uniquely linked to a species under certain environmental conditions when in reality it may not because changes in total leaf surface area per plant as a result of defoliation or experimental manipulations often result in very rapid changes in stomatal aperture and carbon assimilation in the remaining leaves (Meinzer and Grantz 1990, Whitehead et al. 1996). Thus, information on total leaf surface area per plant, leaf dynamics and hydraulic architecture is often required to interpret variation in leaf-level properties such as stomatal conductance and photosynthesis. The use of appropriate variables, strongly related to overall plant fitness, to scale variation in physiological traits among species may reveal functional similarities that cannot be detected with single-leaf measurements alone (Meinzer 2003).

Because selective pressures operate on the plant as a whole organism, coordination of resource allocation between the different levels of organization from cell to whole plant is a prerequisite for achieving optimum fitness. Resource allocation patterns often result in enhancement of a particular function at the expense of another, particularly in resource-limited environments, such as those with low water and nutrient availability. Examples of these trade-offs include enhancement of water-use efficiency at the expense of nitrogen-use efficiency (Field and Mooney 1983), and the negative association between leaf life span and nitrogen content (Reich et al. 1997, Cordell et al. 2001). Conflicts in resource allocation tend to constrain the number of possible combinations of functional traits in a particular individual and among species, leading to functional convergence across a broad range of species (Schulze et al. 1994, Reich et al. 1997, Meinzer 2003).

Variation in wood density is a strong predictor of concomitant variation in a suite of characteristics related to stem water storage capacity, the efficiency of xylem water transport, regulation of leaf water status, and avoidance of turgor loss (Bucci 2001, Meinzer 2003, Gartner and Meinzer 2004). The widely reported inverse relationship between sapwood density and saturated water content implies that sapwood water storage, or capacitance, diminishes with increasing density (Stratton et al. 2000, Bucci 2001, Meinzer 2003). Moreover, it seems likely that the gain in xylem embolism resistance associated with increasing wood density (Hacke et al. 2001) is traded off against a cost in terms of reduced sapwood hydraulic conductivity (Stratton et al. 2000). If both sapwood water storage capacity and water transport efficiency are negatively correlated with wood density, it is reasonable to postulate that species with greater wood density experience larger daily fluctuations in leaf water status, requiring them to allocate more resources to osmoregulation to maintain turgor than species with low wood density. Consistent with this postulate, a strong positive correlation was found between wood density and the magnitude of daily fluctuations in leaf water potential among 27 species with wood densities ranging from 0.14 to 0.9 g cm⁻³ (Meinzer 2003), and in another survey of 12 species, the leaf turgor loss point declined from about -1.2 to -4.5 MPa over a range of wood density from 0.16 to 0.90 g cm⁻³ (Gartner and Meinzer 2004). Because wood density is a fundamental trait that appears to constrain physiological options related to plant water relations and hydraulic architecture (Meinzer 2003), it may prove useful for scaling physiological properties and behavior within and across species.

In the present study, we assessed several ecophysiological traits of six Brazilian savanna woody species. The savannas of central Brazil (Cerrado), characterized by a 4- to 5-month dry season, oligotrophic soils and frequent fires, are the second most extensive plant formation in South America after the lowland tropical rain forests (Eiten 1972). The Brazilian savannas are composed of deeply rooted trees and grasses and other herbaceous species with relatively shallow roots. Trees tend to be relatively small (usually less than 12 m tall) and have stems with thick bark and large internal water storage capacity (Coradin 2000). The consequences of seasonal drought

for physiological activity of woody Cerrado plants have been studied for only a limited number of species and the results appear to be contradictory. It was assumed initially that most Cerrado woody species transpired freely throughout the year (Ferri 1944). The explanation offered to account for this putative weak stomatal control of transpiration in Cerrado tree species is continuous access to deep soil water (Goodland and Ferri 1979). Many Cerrado woody species have root systems at least 10 m deep (Sarmiento 1983). However, rooting depth is species-dependent, with deciduous species often having deeper root systems than evergreen species (Jackson et al. 1999). More recently Meinzer et al. (1999) and Bucci (2001) observed strong stomatal limitation of transpiration before midday in tree species during both the dry and wet seasons.

The main objectives of this study were to: (1) determine whether functional convergence in hydraulic architecture and water relations is observed among savanna tree species when appropriate scaling variables are used; (2) identify potential trade-offs in resource allocation to traits related to rooting depth, stem water-transport efficiency, water storage capacity and leaf osmoregulation; and (3) identify the functional significance of selected architectural, anatomical and structural characteristics of savanna trees. Several individuals of six dominant savanna tree species with diverse phylogeny, architecture, and leaf phenology were studied. Wood density, wood saturated water content, branch hydraulic architecture, stem sap flow, stomatal conductance, leaf water potential, specific leaf area, and leaf pressure-volume relationships were measured at the peak of the dry season.

Materials and methods

Study site and plant material

The study was conducted in savanna sites at the Instituto Brasileiro de Geografia e Estatística (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasília (15°56' S, 47°53' W, altitude 1100 m). In the IBGE Reserve, mean annual precipitation is about 1500 mm with a pronounced dry season from May to September. The months of June, July and August are often devoid of precipitation. Mean monthly temperature ranges from 19 to 23 °C, with diurnal temperature ranges of 20 °C being common during the dry season. The soils are deep oxisols consisting of about 72% clay. Despite their high percentage of clay, the soils behave as coarser-textured soils and are extremely well drained. The study was carried out during August and September 2000 and 2001.

At least six individuals from each of six dominant woody species with different leaf phenology were selected for the study: *Schefflera macrocarpa* (C. & S.) Seem (Araliaceae), *Styrax ferrugineus* Ness et Mart. (Styracaceae), *Ouratea hexasperma* (St. Hil.) Baill. (Ochnaceae), *Caryocar brasiliense* Camb. (Caryocaraceae), *Erythroxylum suberosum* St. Hil. (Erythroxylaceae), and *Kielmeyera coriacea* (Spr.) Mart. (Guttiferaceae). The first three species are evergreen, the last one is deciduous (leafless for about a month) and *C. brasiliense* and

E. suberosum are brevideciduous. In August 2000, mean height (m) and diameter at breast height (DBH; cm) of the selected individuals of each studied species (means $\pm$ SE) were: *S. macrocarpa* 4.4 ± 0.3 m and 8.8 ± 0.7 cm; *O. hexasperma* 1.8 ± 0.1 m and 9.5 ± 0.6 cm; *S. ferrugineus* 4.2 ± 0.3 m and 11.3 ± 0.6 cm; *K. coriacea* 2.8 ± 0.2 m and 7.0 ± 0.5 cm; *E. suberosum* 1.8 ± 0.1 m and 7.5 ± 0.7 cm; *C. brasiliense* 3.7 ± 0.1 m and 11.1 ± 1.1 cm.

Leaf water potential and stomatal conductance

Leaf water potential (Ψ_L) was measured with a pressure chamber (PMS, Corvallis, OR). Typically, six to seven sets of measurements were obtained during the course of a day for each individual (three different leaves per individual and six individuals per species). Leaves were excised and immediately sealed in plastic bags and kept in a cooler until balancing pressures were determined in the laboratory within 1 h of sample collection. A steady-state porometer (Model LI-1600, Li-Cor, Lincoln, NE) measured stomatal conductance (g_s) on the new, fully expanded leaves from sun-exposed areas. Six to seven complete sets of measurements were obtained during the course of a day. Cerrado trees tend to have crowns with low LAI and therefore there is little self-shading among leaves within the crown.

Sap flow

Sap flow was measured, during 2 to 3 consecutive days in each individual per species, with the heat dissipation method described by Granier (1985, 1987). Briefly, a pair of 20-mm long, 2-mm diameter probes (UP GmbH, Munich, Germany) was inserted into the sapwood near the base of the main stem in each plant. The upper (downstream) probe contained a copper-constantan thermocouple and a heating element of constantan, which was continuously heated at a constant power, while the unheated upstream probe served as a temperature reference. Temperature differences between the upstream and downstream probes were recorded every 10 s and 10-min means were stored in solid-state modules (SM192, Campbell Scientific, Logan, UT) connected to data loggers (CR 10X, Campbell Scientific). Sapwood depth in the stems of the individuals studied ranged from 3 to 6 cm, and consequently the 20-mm probes used spanned a large fraction of the hydroactive portion of the xylem.

Sap flux was calculated from the temperature difference between the two probes based on an empirical calibration (Granier 1985, 1987) recently revalidated for tropical trees (Clearwater et al. 1999). Mass flow of sap per individual was obtained by multiplying flux by sapwood cross-sectional area. The relationship between sapwood cross-sectional area and stem diameter was obtained by injecting dye near the base of the main stem for several individuals of each species representing a range of stem diameters. After 2 h, the plants were decapitated a few cm above the point of dye injection and the area of conducting tissue was determined from the pattern of staining by the dye as it moved in the transpiration stream. Transpiration per unit leaf area was obtained by dividing mass sap flow by the total leaf surface area per plant. Total leaf area

per plant was obtained by multiplying the number of leaves per plant by the mean area per leaf determined from a subsample of 10 to 50 leaves per plant, depending on the total number of leaves per plant.

Pressure–volume relationships

Pressure–volume curves were determined for three, fully developed exposed leaves from each individual. The leaves were cut in the field, recut immediately under water and covered with black plastic bags with the cut end in water for 2 h until measurements began. After each determination of balancing pressure with the pressure chamber, leaves were immediately weighed to the nearest 0.001 g and, until the next measurement, left to transpire freely on the laboratory bench. After all balancing pressure–weight measurements were completed, the branches were oven-dried at 70 °C to a constant mass and weighed (Tyree and Richter 1981). Pressure readings, fresh mass at each reading, saturated mass and dry mass for each leaf were entered into a pressure–volume relationship analysis program developed by Schulte and Hinckley (1985).

Wood density and specific leaf area

The density and saturated water content of stem sapwood were measured for three stem cores per individual. Sapwood was distinguished from heartwood based on dye injections in the stem as described by James et al. (2002). Samples were taken with an increment borer, sealed in aluminum foil and plastic bags, and taken to the laboratory. After removing the bark, the cores were weighed to the nearest mg, placed in water in a small graduated cylinder to determine the volume, and allowed to equilibrate overnight in deionized water. The cores were reweighed after being lightly blotted with tissue paper, and then oven-dried to a constant mass and weighed again to obtain the dry mass. Saturated water content was determined by dividing the saturated mass minus the dry mass by the dry mass. Density was determined by dividing the dry mass by the volume of the sample. For specific leaf area (area/dry mass) determinations, ten fully expanded sun leaves were collected from each of three trees per species. After their areas had been measured, the leaves were oven-dried at 70 °C and weighed.

Hydraulic conductivity

Hydraulic conductivity (k_h) was measured on three branches or petioles excised before dawn from six individuals of each species. A small portion of the branch or petiole cut end was then immediately removed by recutting under water. The leaves were then tightly covered with black plastic bags and transported to the laboratory with the cut ends of the branches or petioles under water. Immediately after arriving at the laboratory, stem or petiole segments were cut under water and attached to a hydraulic conductivity apparatus (Tyree and Sperry 1989). Water exuding from the open end of the stem or petiole drained into test tubes containing damp paper towels touching the segment ends. Following a short equilibration period, water flow, generated by a constant hydraulic head of 50 cm, was measured gravimetrically. Hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was calculated as:

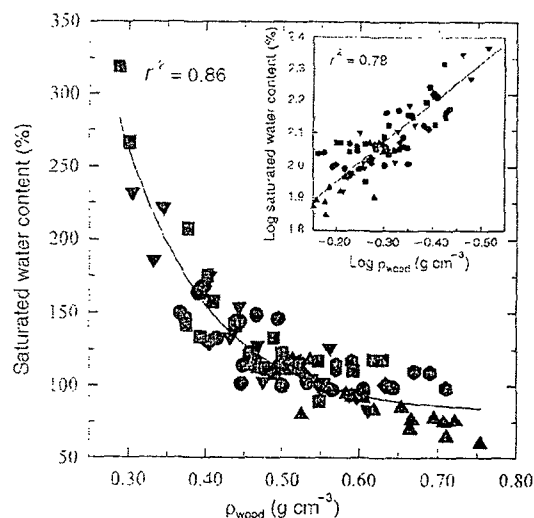


Figure 1. Wood saturated water content in relation to wood density (ρ_{wood}) for six co-occurring savanna species: $\blacktriangle$ = *Schefflera macrocarpa* ($n = 21$); $\bullet$ = *Styrax ferrugineus* ($n = 21$); $\blacksquare$ = *Kielmeyera coriacea* ($n = 21$); $\blacktriangledown$ = *Ouatea hexasperma* ($n = 6$); $\blacklozenge$ = *Caryocar brasiliense* ($n = 6$); and $\bullet$ = *Erythroxylum suberosum* ($n = 6$). Each value represents one individual. The curve is a negative exponential function fitted to the data ($y = 81.39 + 2628\exp(-8.9x)$). The insert depicts the relationship between the same two variables using log transformation of the data ($\log y = 1.71 - 1.21\log x$).

$$k_h = J_v \frac{\Delta P}{\Delta X} \quad (1)$$

where J_v is the flow rate through the stem or petiole segment (kg s^{-1}) and $\Delta P/\Delta X$ is the pressure gradient across the 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. 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 or petiole segment. Distilled/de-gassed water was used as perfusion fluid.

The apparent leaf area specific hydraulic conductance of the soil/root/leaf pathway (G_t) was determined as:

$$G_t = \frac{E}{\Delta \Psi} \quad (2)$$

where $\Delta \Psi$ is the difference between the current Ψ_L and the Ψ of the soil, and E is the mean transpiration rate per unit leaf area determined from sap flow measurements at the time of the Ψ_L measurements. Soil Ψ was estimated by extrapolating to $E = 0$ and the $\Psi_L - E$ relationships obtained by simultaneous measurements of Ψ_L and E throughout the day, for each individual (Sperry et al. 2002, Bucci et al. 2004a). A morphological index of potential transpirational demand relative to water transport capacity was obtained for each individual fitted with sap flow sensors, by dividing the total leaf area by the sapwood area (LA/SA) near the base of the main stem.

Results

Variation in sapwood saturated water content was associated with variation in wood density (Figure 1). A single negative exponential relationship was fitted to all data, indicating that saturated water content decreased with increasing wood density in a similar manner across all individuals and species. Log transformation of the data resulted in a linear relationship between the two variables (see insert in Figure 1). Wood density was also a good predictor of minimum (midday) leaf water potential and total daily transpiration (Figure 2). Midday Ψ_L and daily transpiration decreased linearly with increasing wood density in a similar fashion across all individuals and species. Daily transpiration increased 9-fold with a 50% decline in wood density from 0.71 to 0.37 g cm^{-3} . Relative variation in specific hydraulic conductivity (k_s), leaf specific hydraulic conductivity (k_l) and leaf area to sapwood area ratios was also

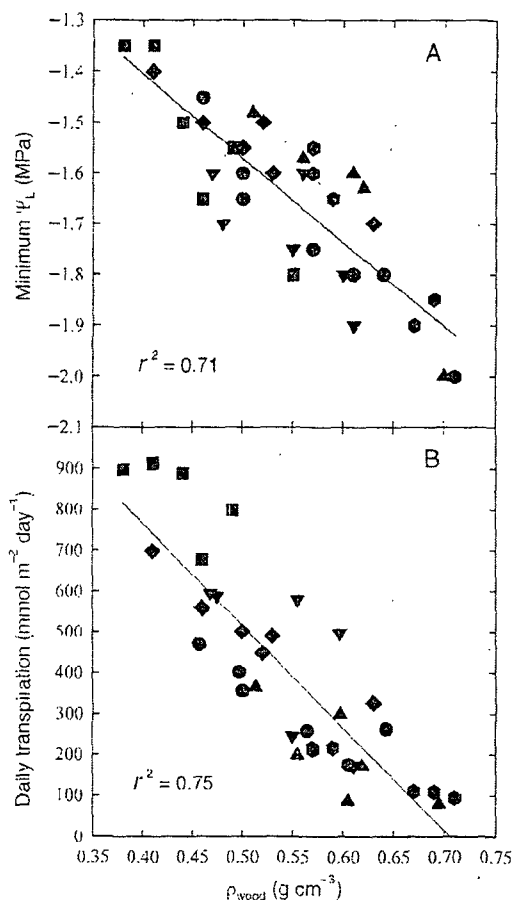


Figure 2. (A) Minimum (midday) leaf water potential (Ψ_L) and (B) total daily transpiration in relation to wood density (ρ_{wood}) for six savanna species. Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Styrax ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouatea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\bullet$ = *Erythroxylum suberosum* ($n = 6$ for each species). Each value represents one individual. The lines are linear regressions fitted to the data: $y = -0.74 - 1.66x$ for (A); and $y = 1769 - 2506x$ for (B).

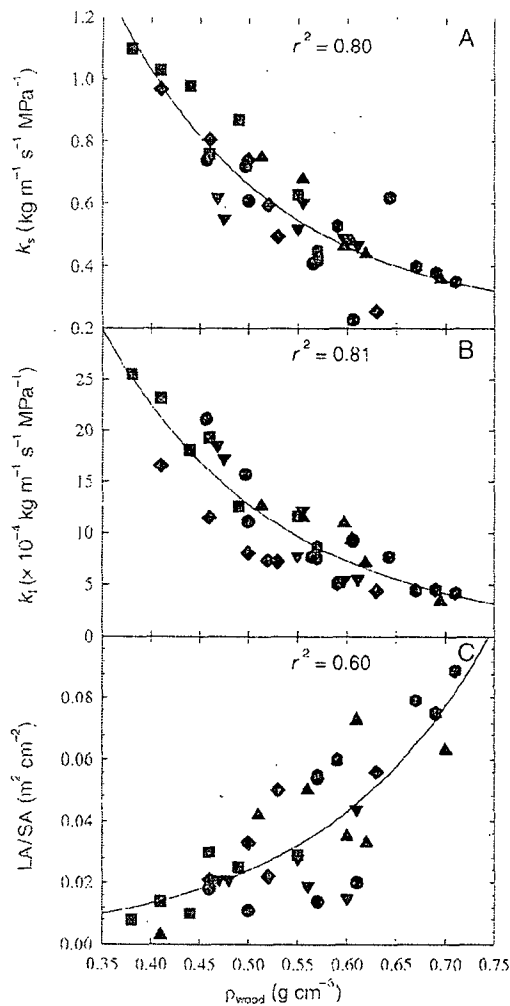


Figure 3. (A) Specific hydraulic conductivity (k_s), (B) leaf specific hydraulic conductivity (k_l) and (C) leaf area per unit of sapwood area (LA/SA) in relation to wood density for six savanna species. Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Styrax ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouratea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\bullet$ = *Erythroxylum suberosum* ($n = 6$ for each species). Each value represents one individual. The curve in (A) is a negative exponential function fitted to the data ($y = 0.22 + 9.22 \exp(-6.10x)$), the curve in (B) is a negative exponential function fitted to the data ($y = 5.61 \exp(-212x)$), and the curve in (C) is a positive exponential function fitted to the data ($y = 0.001 \exp(5.85x)$).

large in relation to the total variation in wood density among all individuals and species (Figure 3). Maximum whole-plant hydraulic conductance (G_{max}), calculated as maximum sap flow divided by the difference between soil Ψ and midday leaf water potentials, was positively correlated with k_l (Figure 4), suggesting that these two aspects of hydraulic architecture provided information of similar functional significance for long distance water transport in savanna tree species.

In addition to the strong relationships between wood density and hydraulic architecture, leaf water balance, sapwood water

storage capacity and total daily water flux, wood density was a good predictor of the temporal dynamics of water flow in stems of the study species (Figure 5). When concurrent time courses of sap flow during clear days were available, it was observed that both the time of onset of sap flow in the morning and the time of maximum sap flow tended to occur progressively earlier in the day as wood density increased. These relationships were individual and species-independent, because a single function provided an adequate fit to all the data, despite the potential influence of confounding factors such as day-to-day variation in the environmental conditions. Wood density increased linearly with decreasing bulk soil Ψ experienced by individual plants (Figure 6). Because all estimates of soil Ψ were obtained during the same portion of the dry season, differences in soil Ψ (the x-intercept of the Ψ_L -E relationships) reflected differences in patterns of soil water uptake, with more negative values of Ψ indicating that root systems were tapping shallow soil layers where soil water availability was relatively low.

Several additional leaf properties were associated with wood density. Mean stomatal conductance and specific leaf area decreased linearly with increasing woody density in a similar fashion independent of individual and species (Figure 7). The leaf osmotic potential at the turgor loss point decreased at lower SLA (Figure 8). Species and individuals with thicker leaves (lower specific leaf area) thus lost turgor at more negative values of Ψ_L than species and individuals with thinner leaves. Because specific leaf area and wood density were linearly related (Figure 7B), species and individuals with denser wood tended to have leaves with lower turgor loss points. A

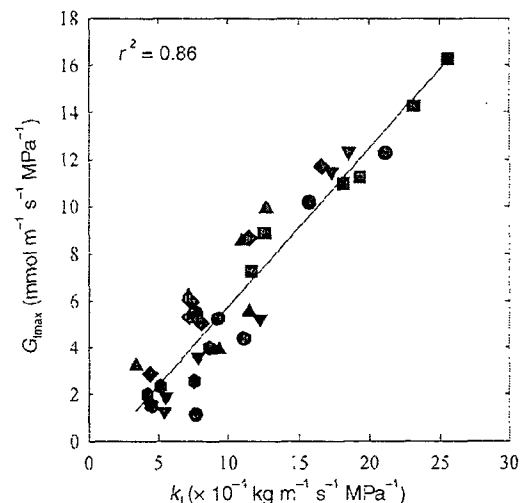


Figure 4. Maximum apparent leaf area-specific hydraulic conductance of the soil/root/leaf pathway (G_{max}) in relation to leaf specific hydraulic conductivity (k_l) for six savanna species. Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Styrax ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouratea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\bullet$ = *Erythroxylum suberosum* ($n = 6$ for each species). Each value represents one individual. The line is a linear regression fitted to the data ($y = -1 + 0.67x$).

linear function fitted to the relationship between wood density and leaf turgor loss point yielded an $r^2 = 0.57$.

Discussion

Traditionally, species are placed along a continuum from drought avoidant to drought tolerant on the basis of operating ranges of leaf water status. Although a particular species may be either more or less tolerant of water deficits than another, this classification according to discrete functional groups may conceal the existence of substantial convergence in leaf and whole-plant physiological responses and traits related to water-transport efficiency, regulation of water loss and stem water-storage capacity. The six co-occurring neotropical savanna species that we studied shared similar functional relationships between wood density and leaf- and whole-plant level traits,

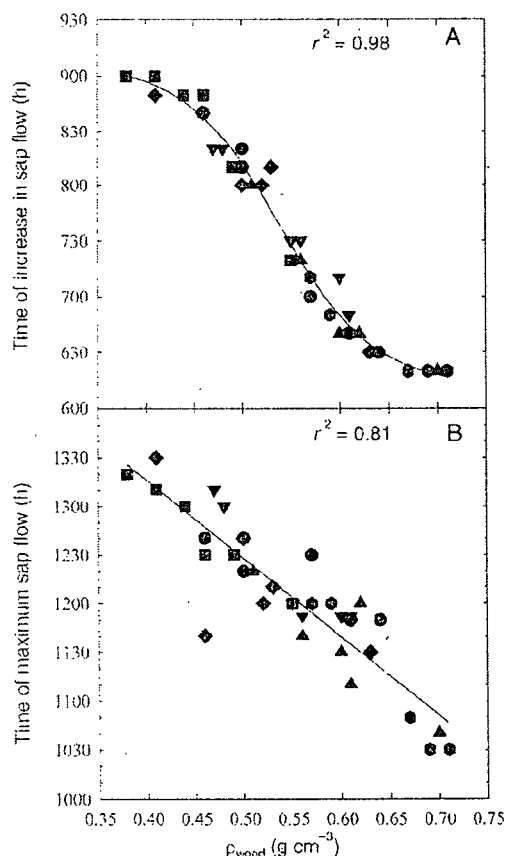


Figure 5. (A) Time at which basal sap flow begins to increase in the early morning and (B) time at which maximum basal sap flow is attained in relation to wood density (ρ_{wood}). Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Styrox ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouratea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\bullet$ = *Erythroxylum suberosum* ($n = 6$ for each species). Each value represents one individual. The curve in (A) is a sigmoid function fitted to the data: $y = 6.2 - (2.91 / (1 + \exp(-((x + 0.5) - 0.05))))$, and the line in (B) is a linear regression fitted to the data ($y = 16.49 - 8.05x$).

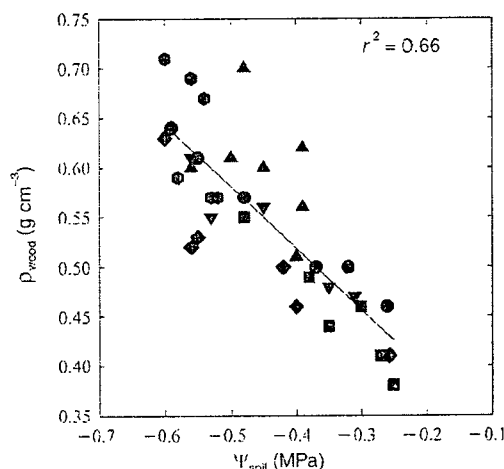


Figure 6. Wood density (ρ_{wood}) in relation to individual-specific soil water potential (Ψ_{soil}) predicted from sap flow versus the leaf water potential of freely transpiring leaves extrapolated to the x-axis (zero flow). Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Styrox ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouratea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\bullet$ = *Erythroxylum suberosum* ($n = 6$ for each species). The line is a linear regression fitted to the data ($y = 0.27 - 0.6x$).

despite their taxonomic diversity and the fact that these species are not phylogenetically related. Thus, rather than differing intrinsically in physiological responsiveness to the Cerrado environment, the study species appeared to have operating ranges along common physiological response curves, defined by variation in wood density, a fundamental trait. Shared functional relationships based on wood density were adequate for scaling variations in several aspects of whole-tree performance, both within and among species. Both individual- and species-specific variation in physiological and morphological traits thus appear to be subjected to similar selective pressures, resulting in general functional convergence in plant hydraulic architecture and water relations characteristics. The coordination of suites of traits from the leaf- to whole-plant level would result in a multidimensional physiological response surface common to all species and individuals. These findings suggest that Cerrado tree species may possess a limited number of physiological and morphological solutions for coping with seasonal drought.

In a recent study, Enquist et al. (1999) derived an allometric model to predict growth rates of tropical trees using wood density as an independent variable and found that there was a trade-off between growth rate and allocation of biomass to tissue density, with species that allocate less biomass to their stems (light woods) increasing in basal diameter faster than species that allocate more biomass to stems (dense woods). The model highlights the central roles of allometric scaling and wood density in predicting life history traits and growth rates of trees. Wood density is frequently cited as being a main determinant of life history variation in woody plants (Denslow 1980, Fearnside 1997). An important question is why wood density alone explains an important percentage of variation in

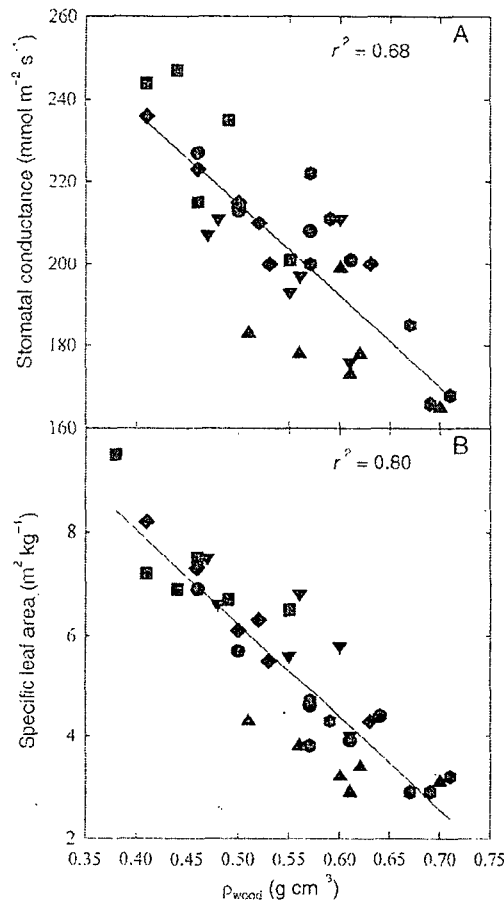


Figure 7. (A) Mean daily stomatal conductance and (B) specific leaf area as a function of wood density (ρ_{wood}). Symbols: $\blacktriangle$ = *Schefflera macrocarpa*; $\bullet$ = *Syzygium ferrugineus*; $\blacksquare$ = *Kielmeyera coriacea*; $\blacktriangledown$ = *Ouratea hexasperma*; $\blacklozenge$ = *Caryocar brasiliense*; and $\circ$ = *Erythroxylum suberosum* ($n = 6$ for each species). Each value represents one individual. The lines are linear regressions fitted to the data (A: $y = 326 - 223x$; B: $y = 15.35 - 18.29x$).

growth rates and life history traits of woody plants? It is likely that the basis of these relationships is the correlation of wood density with stem water storage and transport capacity (Enquist et al. 1999), both of which have an important impact on leaf and whole-plant physiological performance.

We found that wood density was a good predictor of the temporal dynamics of water flow in stems as well as sapwood saturated water content. Consistent with this, both the time of onset of sap flow in the morning and the time at which maximum flow was observed became progressively earlier with increasing wood density (Figure 5). A relatively large lag, between increases in evaporative demand in the early morning and increases in basal sap flow, suggests that a substantial amount of water being lost by transpiration is obtained initially from stem water storage. Only after part of the stem water store is depleted, does sap flow increase near the base of the tree as a result of absorption of soil water by the roots. Wood

saturated water content was also correlated directly with the temporal dynamics of sap flow. Although the correlation coefficients of the relationships between saturated water content and time courses of sap flow were significant ($P < 0.01$), the r^2 values were smaller than those obtained with wood density as the independent variable. It is possible that wood density was a better predictor of storage capacity than saturated water content, because it reflects biophysical properties of the sapwood related to the efficiency of recharge and utilization of stored water as well as the potential maximum amount of stem water storage.

Leaf-specific hydraulic conductivity (k_l), an in-vitro measurement of water-transport efficiency obtained with detached sections of terminal stems or petioles, was strongly correlated with apparent soil-to-leaf hydraulic conductance (G_l), an in vivo estimate of whole-plant water-transport efficiency. Both measurements of transport efficiency thus provided information on hydraulic architecture of similar functional significance for long-distance water transport in savanna tree species. There was no trade-off between water-transport efficiency, represented by k_s or k_l , and water storage capacity, represented by sapwood saturated water content, because these variables were greatest in individuals with the lowest wood density. However, a pronounced trade-off between water transport efficiency and wood density was evident (Figure 3). Similar associations between wood density and water storage and transport capacity were observed in Hawaiian dry forest tree species (Stratton et al. 2000) and in Panamanian forest canopy tree species (Meinzer et al. 2003). Hacke et al. (2001) reported a highly significant correlation between wood density and the xylem pressure threshold for 50% loss of hydraulic conductivity by cavitation among several species exhibiting a broad

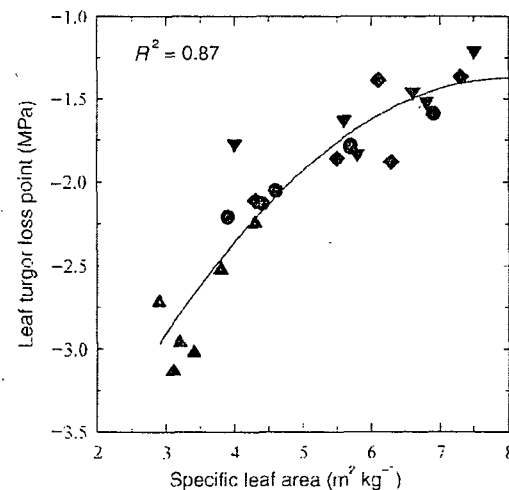


Figure 8. Leaf osmotic potential at turgor loss point in relation to specific leaf area. Each value represents one individual and each symbol type represents a different species: $\blacktriangle$ = *S. macrocarpa*; $\bullet$ = *S. ferrugineus*; $\blacktriangledown$ = *O. hexasperma*; and $\blacklozenge$ = *C. brasiliense* ($n = 6$ for each species). The line is a quadratic function fitted to the data ($y = -5.27 + 0.97x - 0.06x^2$).

range of wood densities. Although the relationships were distinct for angiosperms and conifers, all species within each group shared a common relationship between density and xylem resistance to cavitation. If Cerrado trees conform to the same functional relationship between wood density and xylem resistance to cavitation, the gain in cavitation resistance with increasing wood density would be associated with a cost in terms of reduced hydraulic conductivity.

Reliable estimates of soil water potential are key to calculating the driving forces for water movement along the soil-plant-atmosphere continuum. Negligible or low nocturnal transpiration is assumed to allow leaf and soil water potential to equilibrate before dawn, permitting use of predawn leaf water potential as a surrogate for soil water potential (Ritchie and Hinckley 1975, Hinckley et al. 1978, Richter 1997). However, if processes such as nighttime transpiration prevent equilibration along the soil-to-leaf continuum, predawn leaf water potential may be significantly more negative than the water potential of the soil accessed by the roots (Donovan et al. 1999, 2001). Nocturnal transpiration can be substantial in Cerrado trees because of high nocturnal stomatal conductance and relatively high vapor pressure deficit at night during the dry season (Bucci et al. 2004b). In our study, when the linear relationships between sap flow and Ψ_L were extrapolated to the x-axis (flow = 0), the predicted values of soil Ψ were substantially less negative than the measured values of predawn Ψ_L , suggesting that substantial soil-leaf disequilibrium persisted as a result of nighttime transpiration.

Because the Ψ_L -sap flow relationships in our study were obtained at the peak of the dry season during a short period when no precipitation occurred, the estimates of soil water potential obtained provide a relative index of differences in the patterns of water uptake among the different individuals. The strong correlation between wood density and individual-specific soil water potential, a surrogate measure of rooting depth, suggests that the pattern of water uptake and access to soil water during the dry season could be one of the main determinants of wood density.

The potential causal relationship between wood density and the degree of water deficit that the plant experiences during the dry season needs to be better established with studies carried out under controlled conditions. Wood density, as was shown in this study, appears to be a surrogate for water-transport efficiency and storage capacity. Selective pressures should operate more on the water relations processes that maximize the plant's fitness rather than on the xylem anatomy itself. Wood density appears to be an anatomical correlate of these processes. Wood density integrates many years of environmental conditions and consequently it may be seen as a long-term indicator of "operating limits." However, it has been suggested that, on an evolutionary time scale, selection is virtually absent except during extreme events such as long droughts (Gutschick and BassiriRad 2003). Regardless of the role that extreme events may have on shaping the physiology of plants, this study shows the potential links between soil water availability, hydraulic conductivity and storage capacity of the in-

ternal water circulation pathway in the plant, and average wood properties (density) of the active xylem.

Overall, our results imply that allocation of resources to the production of wood of high density constrains other patterns of resource allocation. Individuals with dense wood had thick leaves (low specific leaf area), relatively shallow root systems and tended to experience more negative midday Ψ_L during the dry season. This is consistent with their negative osmotic potentials at the turgor loss point which are required for osmoregulation, turgor maintenance and leaf expansion during the dry season. In individuals with high wood density, and consequently relatively inefficient water transport systems, a larger driving force, and therefore more negative Ψ_L , will be required to transport a given amount of water to the leaves. On the other hand, Cerrado trees with low wood density and high stem water storage capacity exhibited high daily transpiration rates and high stomatal conductance. In addition, individuals with low wood density tended to tap water from deeper soil layers with high soil water availability during the dry season (Franco 1998, Meinzer et al. 1999, Bucci 2001). Access to deep soil water will help in water storage recharge during the night. Taken together, our results suggest that variation in wood density is a strong predictor of variation in a suite of characteristics related to water transport properties, regulation of leaf water deficits and avoidance of turgor loss. The patterns of water uptake and access to soil water during the dry season appeared to be the main determinant of wood density, which constrained evolutionary options related to plant water economy and hydraulic architecture, leading to functional convergence across a broad range of woody species and their individuals in the savanna ecosystem studied.

Acknowledgments

This work was supported by grants from Inter-American Institute for Global Change Research, the National Science Foundation (USA) Grant No. 0296174 to G. Goldstein and F.C. Meinzer, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and PRONEX (Brazil). We thank the Reserva Ecológica do IBGE and in particular I. Gonzalez for logistic support. We are grateful to P. Campanello and M. Saraceno for help with field work.

References

- Bucci, S.J. 2001. Arquitectura hidráulica y relaciones hídricas de árboles de sabanas neotropicales: efectos de la disponibilidad de agua y nutrientes. Ph.D. Diss., Universidad de Buenos Aires, Argentina, 189 p.
- Bucci, S.J., F.G. Scholz, G. Goldstein, F.C. Meinzer, J.A. Hinojosa, W.A. Hoffmann and A.C. Franco. 2004a. Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. *Tree Physiol.* In press.
- Bucci, S.J., G. Goldstein, F.C. Meinzer, A.C. Franco, P. Campanello and F.G. Scholz. 2004b. Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plants in Neotropical savanna trees. *Trees*. In press.
- Clearwater, M.J., F.C. Meinzer, J.L. Andrade, G. Goldstein and N.M. Holbrook. 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiol.* 19:681–687.

- Coradin, V.T. 2000. Formação de anéis de crescimento e sazonalidade da atividade cambial de dez espécies lenhosas do Cerrado. Ph.D. Diss., Universidade de Brasília, Brazil. 125 p.
- Cordell, S., G. Goldstein, F.C. Meinzer and P.M. Vitousek. 2001. Regulation of leaf life-span and nutrient use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. *Oecologia* 127:198–206.
- Denslow, J.S. Gap partitioning among tropical rain forest trees. 1980. *Biotropica* 12:47–55.
- Donovan, L.A., D.J. Grisé, J.B. West, R.A. Pappert, N.M. Alder and J.H. Richards. 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. *Oecologia* 120: 209–217.
- Eiten, G. 1972. The Cerrado vegetation of Brazil. *Bot. Rev.* 38: 201–341.
- Enquist, B.J., G.B. West and J.H. Brown. 1999. Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In *Scaling in Biology*. Eds. J.H. Brown and G.B. West. Oxford University Press, Oxford, pp 167–199.
- Fearnside, P.M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. *For. Ecol. Manage.* 90:59–87.
- Ferri, M. 1944. Transpiração de plantas permanentes dos cerrados. *Bol. Fac. Fil. Ciênc. Letr. USP* 41, Botânica 4:159–224.
- Field, C. and H.A. Mooney. 1983. Leaf age and season effects on light, water and nitrogen use efficiency in a California shrub. *Oecologia* 56:348–355.
- Franco, A.C. 1998. Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen species. *Plant Ecol.* 136:69–76.
- Gartner, B.L. and F.C. Meinzer. 2004. Structure–function relationships in sapwood water transport and storage. In *Long-Distance Transport Systems in Plants: Integration and Coordination*. Eds. N.M. Holbrook and M. Zwieniecki. Academic Press, New York. In press.
- Goodland, R. and M.G. Ferri. 1979. *Ecologia do Cerrado*. Editora da Universidade de São Paulo, São Paulo, Brazil. 193 p.
- Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurement. *Tree Physiol.* 3:309–320.
- Gutschick, V.P. and H. BassiriRad. 2003. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytol.* 160: 21–42.
- Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. Davis and K.A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461.
- Hinckley, T.M., R.G. Aslin, R.R. Aubuchon, C.L. Metcalf and J.E. Roberts. 1978. Leaf conductance and photosynthesis in four species of the oak-hickory forest type. *For. Sci.* 24:73–84.
- Jackson, P.C., F.C. Meinzer, M. Bustamante, G. Goldstein, A.C. Franco, P.W. Rundel, L. Caldas, E. Iglar and F. Causin. 1999. Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiol.* 19:717–724.
- James, S.A., M.J. Clearwater, F.C. Meinzer and G. Goldstein. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol.* 22:277–283.
- Meinzer F.C. 2003. Functional convergence in plants responses to the environment. *Oecologia* 134:1–11.
- Meinzer, F.C. and D.A. Grantz. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13:383–388.
- Meinzer, F.C., G. Goldstein, A.C. Franco, M. Bustamante, E. Iglar, P. Jackson, L. Caldas and P.W. Rundel. 1999. Atmospheric and hydraulic limitations on transpiration in Brazilian Cerrado woody species. *Funct. Ecol.* 13:273–282.
- Meinzer, F.C., S.A. James, G. Goldstein and D. Woodruff. 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant Cell Environ.* 26:1147–1155.
- Reich, P.B., M.A. Walters and D.S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci.* 94:13,730–13,734.
- Ritchie, G.A. and T.M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. *Adv. Ecol. Res.* 9:165–254.
- Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. *J. Exp. Bot.* 48: 1–7.
- Sarmiento, G. 1983. The savannas of tropical America. In *Tropical Savannas, Ecosystems of the World*. Vol 13. Ed. F. Bourlière. Elsevier, Amsterdam, pp 245–288.
- Schulte P.J. and T.M. Hinckley. 1985. A Comparison of pressure–volume curve data analysis techniques. *J. Exp. Bot.* 36:590–602.
- Schulze, E.-D., F.M. Kelliher, C. Körner, J. Lloyd and R. Leuning. 1994. Relationships among maximum stomatal conductance, carbon assimilation rate and plant nitrogen nutrition: a global ecology scaling exercise. *Annu. Rev. Ecol. Syst.* 25:629–660.
- Sperry, J.S., U.G. Hacke, R. Oren and J.P. Comstock. 2002. Water deficit and hydraulic limits to leaf water supply. *Plant Cell Environ.* 25:251–263.
- Stratton, L., G. Goldstein and F.C. Meinzer. 2000. Stem water storage and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell Environ.* 23:99–106.
- Tyree, M.T. and H. Richter. 1981. Alternative methods of analyzing water potential isotherms: some cautions and clarifications. *J. Exp. Bot.* 32:643–653.
- Tyree, M.T. and J.S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Mol. Biol.* 40:19–48.
- Whitehead, D., N.J. Livingston, F.M. Kelliher, K.P. Hogan, S. Pepin, T.M. McSeveny and J.N. Beyers. 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. *Plant Cell Environ.* 19:949–957.