

# Regulation of water flux through tropical forest canopy trees: Do universal rules apply?

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**Summary** Tropical moist forests are notable for their richness in tree species. The presence of such a diverse tree flora presents potential problems for scaling up estimates of water use from individual trees to entire stands and for drawing generalizations about physiological regulation of water use in tropical trees. We measured sapwood area or sap flow, or both, in 27 co-occurring canopy species in a Panamanian forest to determine the extent to which relationships between tree size, sapwood area and sap flow were species-specific, or whether they were constrained by universal functional relationships between tree size, conducting xylem area, and water use. For the 24 species in which active xylem area was estimated over a range of size classes, diameter at breast height (DBH) accounted for 98% of the variation in sapwood area and 67% of the variation in sapwood depth when data for all species were combined. The DBH alone also accounted for  $\geq 90\%$  of the variation in both maximum and total daily sap flux density in the outermost 2 cm of sapwood for all species taken together. Maximum sap flux density measured near the base of the tree occurred at about 1400 h in the largest trees and 1130 h in the smallest trees studied, and DBH accounted for 93% of the variation in the time of day at which maximum sap flow occurred. The shared relationship between tree size and time of maximum sap flow at the base of the tree suggests that a common relationship between diurnal stem water storage capacity and tree size existed. These results are consistent with a recent hypothesis that allometric scaling of plant vascular systems, and therefore water use, is universal.

**Keywords:** *allometric relationships, sap flow, sapwood, stem water storage.*

## Introduction

Stand-level estimates of water use by forest trees are often obtained using micrometeorological approaches such as the Bowen ratio energy balance and eddy flux methods (Köstner et al. 1992, Herbst 1995, Berbigier et al. 1996). Alternatively, estimates of water use by individual trees can be scaled to the

stand level if the size distribution and density of trees within the stand are known (Wullschlegel et al. 1998). Although micrometeorological methods can provide reliable estimates of stand-level evapotranspiration, knowledge of whole-tree transpiration rates and the ability to scale them up are advantageous because they can yield insights concerning the physiological regulation of water use at the stand level. Recent refinements and simplification of techniques have made it economically feasible to measure whole-tree sap flow as a surrogate for transpiration in a relatively large number of trees simultaneously (Granier 1987). However, several important constraints may arise in attempting to scale from sap flow measurements to stand-level transpiration. First, most methods rely on multiplying sap flux density or sap velocity by sapwood area to obtain mass flow of sap. Extrapolation from tree-to stand-level transpiration is therefore limited by the accuracy with which sapwood or functional xylem area can be determined in individual trees and by variability in the relationship between sapwood area and tree size (DBH). Second, sap flow in whole trees is typically measured over a relatively narrow range of sapwood depth, usually close to the vascular cambium where sap flow is near maximal. If sap velocity diminishes rapidly with increasing depth, large errors in estimates of whole-tree mass flow can result when sap flux density or sap velocity is multiplied by sapwood area. Finally, in multi-species stands, inter-specific variation in regulation of sap flow must be characterized.

Scaling of water use in monospecific stands can be reasonably straightforward if the first two constraints are overcome by accurate determination of sapwood area–tree size relationships and representative measurements of sap flow in relation to tree size and sapwood depth (Čermák et al. 1995, Vertessy et al. 1995). In species-rich stands, on the other hand, the problem of scaling transpiration could become intractable if regulation of whole-tree sap flow is species-specific. However, it has recently been hypothesized that allometric scaling of plant vascular systems, and therefore water use, is universal (Enquist et al. 1998, West et al. 1999). If this hypothesis proves to be valid, then the problem of scaling from tree sap

flow to stand transpiration in species-rich stands may not be as daunting, but a comprehensive test of the hypothesis has yet to be undertaken.

In the present study, we report results of sap flow measurements in 23 tree species growing in a lowland tropical forest on Barro Colorado Island, Panama, where a 1-ha stand can contain as many as 100 tree species represented by individuals with DBH greater than 10 cm (Foster and Hubbell 1990). Our objectives were to characterize relationships between functional xylem area and tree size, sap flux density and tree size, and daily courses of sap flow and tree size to determine whether universal constraints on regulation of water use were applicable across a range of taxonomically and ecologically diverse species. In addition to their relevance for the practical problem of scaling from sap flow to transpiration, our results have broader implications with regard to universal evolutionary constraints on relationships between tree size and hydraulic architecture that lead to convergence in physiological regulation of water use at the whole-tree scale.

## Materials and methods

### *Study site and plant material*

The study was carried out from January 1996 through May 1998 in a tropical moist forest on Barro Colorado Island (BCI), Panama (9°09' N, 79°51' W) and on the nearby Gigante Peninsula. The site on BCI was located on the plateau area near a 50-ha permanent plot established in 1980 (Hubbell and Foster 1983). Mean annual rainfall is 2600 mm with a pronounced dry season from mid-December through April, during which only about 8% of the total rainfall is received (Windsor 1990). On BCI, 15 circular plots were established in 1996 in which all trees > 20 cm diameter at breast height (DBH) were marked, identified and their DBH recorded. A subset of these trees was used for the measurements of sap flow and sapwood area ( $A_s$ ) reported here. On the Gigante Peninsula, additional trees > 20 cm DBH were identified, their DBH recorded and  $A_s$  determined as described below. A list of the 27 species studied and the number and size range of individuals used for  $A_s$  and sap flow measurements are presented in Table 1. Sap flow was measured in 23 of the species in which  $A_s$  was determined.

### *Sap flow and environmental variables*

Sap flow was measured by the constant heating method described by Granier (1985, 1987). Pairs of 20-mm-long, 2-mm-diameter temperature probes were installed at about 1.5 m height. The upper (downstream) probe was continuously heated with a constant-current power supply (UP GmbH, Munich, Germany) while the lower unheated probe measured the reference temperature of the wood. The measurements reported in Figures 3 to 6 were made in the outer 2 cm of the sapwood, but occasionally additional measurements were made with the probe tips installed to depths of 3.4 and 4.2 cm (e.g., Figure 7). The protruding portions of the probes were insulated with a layer of foam rubber surrounded by an outer shield of reflective material and transparent plastic. Probe

temperatures were recorded continuously with a data logger (CR21X, Campbell Scientific, Logan, UT) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and 10-min means were stored in a solid-state storage module (SM192, Campbell Scientific). Sap flux density was calculated from the temperature difference between the two probes based on an empirical relationship developed by Granier (1985) and recently revalidated by Clearwater et al. (1999). Although sap flux density has velocity units ( $\text{m h}^{-1}$ ), it is not a true velocity because it represents volume flow per unit sapwood cross-sectional area rather than conducting xylem lumen area. Measurements reported here were made between January 1996 and May 1998.

Environmental variables were recorded as 10-min means with an automated weather station installed on the 40-m canopy tower on BCI. Photosynthetic photon flux density (PPFD) was measured with a quantum sensor (LI190SB, Li-Cor, Inc., Lincoln, NE) and atmospheric saturation deficit (ASD) was calculated from measurements of air temperature and relative humidity made with shielded sensors (HMP35C, Campbell Scientific).

### *Sapwood area and depth*

Sapwood cross-sectional area at about 1.3 m height was determined by injecting dye (0.1% indigo carmine) into the bole through holes made by a 5-mm increment borer. After 1–2 h, a core was taken 2–4 cm above each dye injection point and the area of the conducting tissue was determined from the thickness of the wood colored by the dye as it moved up in the transpiration stream. Preliminary measurements using cores taken about 10–20 cm above the dye injection point yielded similar results but several cores were often required to locate the dye. The shorter distance between dye injection and core extraction was used to minimize damage to the trees.

In a few species, the relative magnitude of sapwood depths determined with the dye method was confirmed independently with specially constructed thermal dissipation probes (Burns and Holbrook 2000). Two, 2-mm-diameter holes separated vertically by 10 cm were drilled to 7 to 8 cm depth in the xylem at about 1.3 m height. The temperature difference between the heated downstream probe and the reference upstream probe was monitored as the probes were incrementally withdrawn and inserted into the xylem. The probes were allowed to remain at each depth until the temperature difference stabilized. The temperature difference corresponding to zero flow was determined by using a hole saw to isolate the upper, heated probe from the influence of water moving through the xylem. The temperature difference at zero flow was subtracted from the temperature difference measured at each depth to obtain a relative radial profile of water movement through the xylem.

## Results

All of the study species appeared to share a common relationship between functional xylem area and tree size (Figure 1).

Table 1. Tree species in which sapwood area and sap flow were measured.

Species	Family	Sapwood area		Sap flow	
		Individuals	DBH (cm)	Individuals	DBH (cm)
<i>Alseis blackiana</i> Hemsl.	Rubiaceae	5	20–43	5	22–38
<i>Anacardium excelsum</i> (Bertero & Balb.) Skeels	Anacardiaceae	7	52–102	1	32
<i>Apeiba membranacea</i> Spruce ex Benth.	Tiliaceae	2	42–52	1	41
<i>Cecropia insignis</i> Liebm.	Cecropiaceae	3	19–28	0	–
<i>Cecropia longipes</i> Pitt.	Cecropiaceae	3	13–25	0	–
<i>Cecropia peltata</i> L.	Cecropiaceae	2	15–18	1	24
<i>Cordia alliodora</i> (R. & P.) Cham.	Boraginaceae	3	25–48	1	40
<i>Dipteryx panamensis</i> (Pitt.) Rec. & Mell	Fabaceae	0	–	2	41–118
<i>Eugenia coloradensis</i> Standl.	Myrtaceae	2	22–33	1	31
<i>Ficus insipida</i> Willd.	Moraceae	9	19–100	1	122
<i>Guapira standleyanum</i> Woods.	Nyctaginaceae	3	41–56	1	69
<i>Guatteria dumetorum</i> Fries	Annonaceae	5	27–69	2	46–69
<i>Hura crepitans</i> L.	Euphorbiaceae	0	–	3	60–107
<i>Jacaranda copaia</i> (Aubl.) D. Don	Bignoniaceae	6	22–57	2	73–86
<i>Lonchocarpus latifolius</i> (Willd.) HBK	Fabaceae	7	25–43	2	25–33
<i>Luehea seemannii</i> Tr. & Planch.	Tiliaceae	7	27–53	3	38–40
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urban	Bombacaceae	3	23–49	1	51
<i>Platymiscium pinnatum</i> (Jacq.) Dug.	Fabaceae	0	–	4	39–64
<i>Prioria copaifera</i> Griseb.	Fabaceae	5	25–71	1	68
<i>Pseudobombax septenatum</i> (Jacq.) Dug.	Bombacaceae	3	32–95	2	98–130
<i>Quararibea asterolepis</i> Pitt.	Bombacaceae	4	23–48	3	28–50
<i>Simarouba amara</i> Aubl.	Simaroubaceae	4	27–69	0	–
<i>Spondias radlkoferi</i> Donn. Sm.	Anacardiaceae	4	26–50	1	60
<i>Sterculia apetala</i> (Jacq.) Karst.	Sterculiaceae	5	30–72	0	–
<i>Trichilia tuberculata</i> C. DC.	Meliaceae	4	23–27	4	24–27
<i>Virola surinamensis</i> (Rol.) Warb.	Myristicaceae	7	22–60	3	28–77
<i>Zanthoxylum belizense</i> Lund.	Rutaceae	4	29–68	3	55–68

Tree size (DBH) accounted for 98% of the variation in  $A_s$  over a diameter range from about 0.2 to 0.8 m when the relationship was linearized by scaling both variables on a log-log plot (Figure 1, inset). The dependence of  $A_s$  on DBH conformed closely

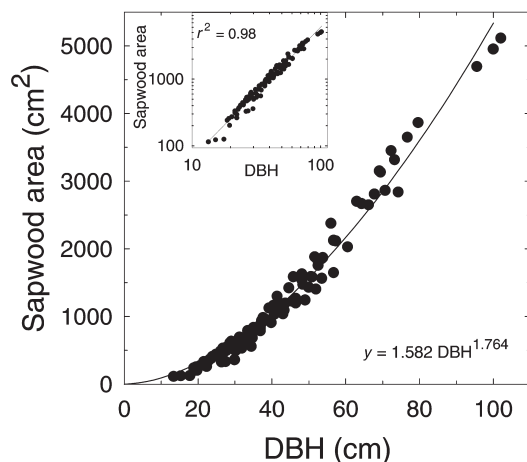


Figure 1. Sapwood area in relation to DBH for 107 individuals of 24 co-occurring Panamanian forest canopy tree species. The inset shows sapwood area and DBH plotted on a log scale. The species, numbers of individuals of each, and their size range are listed in Table 1.

with a power function of the form  $y = y_0 \text{DBH}^b$  when the y-intercept was taken to be zero (Figure 1, curve). Sapwood area and DBH are strongly autocorrelated (Oren et al. 1998) because DBH is used to convert sapwood depth ( $d_s$ ) to  $A_s$ . Therefore,  $d_s$  was plotted directly against DBH (Figure 2a) to evaluate further the universality of the relationship between tree size and functional xylem among the study species. Although there was considerably more scatter in this relationship than in the dependence of  $A_s$  on DBH, DBH accounted for at least 67% of the observed variation in  $d_s$ . An additional analysis was conducted to assess the relative influence of marginal changes in  $d_s$  and DBH on  $A_s$  over the range of DBH observed. Sapwood depth estimated from the relationship in Figure 2a was used to calculate the sensitivity of  $A_s$  to a marginal change in  $d_s$  ( $dA_s/dd_s$ ) and also the sensitivity of  $A_s$  to a marginal change in DBH ( $dA_s/d\text{DBH}$ ) at a given DBH. The ratio of these sensitivities is an index of the relative influence of marginal changes in  $d_s$  and DBH on  $A_s$  (Figure 2b). In the smallest trees (10–20 cm DBH), the relative influence on  $A_s$  of a small change in DBH was about three times greater than that of an equivalent change in  $d_s$ , whereas in the largest trees (80–100 cm DBH) the relative influences of changes in  $d_s$  and DBH on  $A_s$  were similar. Thus, the influence of autocorrelation between  $A_s$  and DBH on estimates of  $A_s$  diminished with increasing tree size.

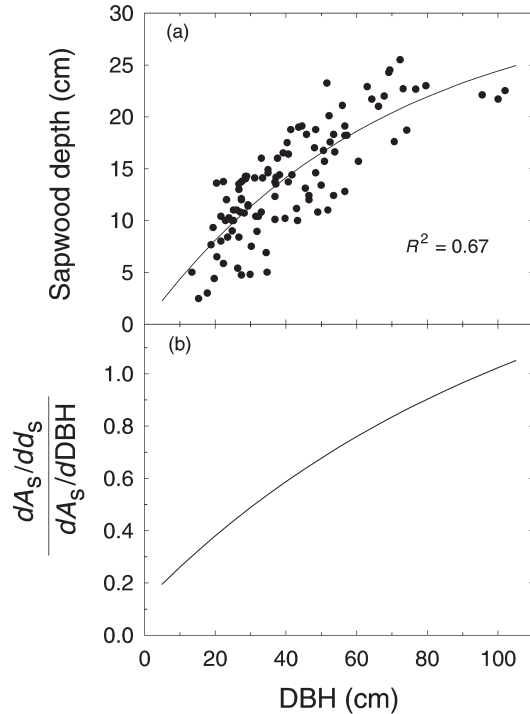


Figure 2. Sapwood depth in relation to DBH for co-occurring Panamanian forest canopy tree species (a), and the ratio of the sensitivity of sapwood area ( $A_s$ ) to a marginal change in sapwood depth ( $dA_s/dd_s$ ) and the sensitivity of  $A_s$  to a marginal change in DBH ( $dA_s/dDBH$ ) as a function of DBH (b). The ratio of sensitivities is an index of the relative influence of marginal changes in  $d_s$  and DBH on  $A_s$  at a given DBH.

Consistent with the relationship between  $A_s$  and tree size, all of the species studied shared a common relationship between maximum sap flux density measured in the outermost 2 cm of the sapwood, and DBH (Figure 3). Maximum sap flux density declined sharply with increasing DBH from about  $0.25 \text{ m h}^{-1}$  in 20-cm-DBH trees to about  $0.05 \text{ m h}^{-1}$  in 120-cm-DBH trees (Figure 3). The coefficient of determination for the curvilinear relationship between sap flux density and DBH was 0.85 and increased to 0.90 when the relationship was linearized by plotting the log of sap flux density against DBH (Figure 3, inset). The maximum size of individuals available for sap flow determinations in the plots on BCI was greater than that of the individuals of the same species in which  $A_s$  was determined on Gigante peninsula nearby (cf. Figures 1 and 3). The common relationship between sap flow and DBH persisted when integrated total daily sap flux density was plotted against DBH (Figure 4). The coefficient of determination for the relationship between total daily sap flux density and DBH increased to 0.91 when both variables were plotted on a log scale (Figure 4, inset). Uniformity of the evaporative demand and PPFD regimes on the measurement days selected for evaluation contributed to the ability of DBH alone to account for such a large percentage of the variation in sap flow. The decline in sap flux density with increasing DBH does not imply a corresponding decline in whole-tree water use. If sap flux density does not

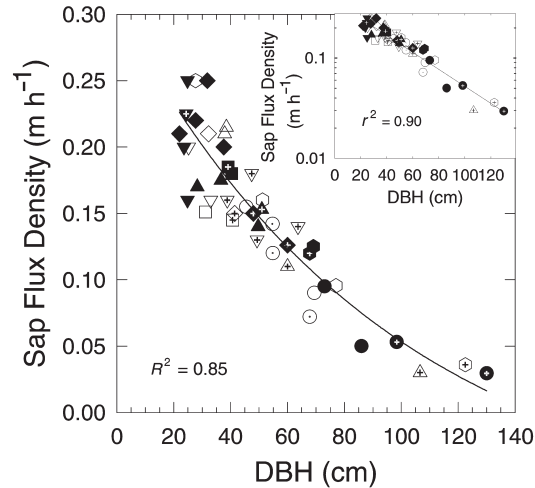


Figure 3. Maximum sap flux density in relation to DBH for co-occurring Panamanian forest canopy tree species. The fitted curve is:  $y = -0.084 + 0.39e^{(-0.0105x)}$ . The inset shows linearization of the relationship by plotting sap flux density on a log scale. The  $r^2$  value for a linear relationship was 0.79 when the log of DBH was also taken. Each type of symbol represents a different species. Species are listed in Table 1.

decline precipitously with increasing depth in the sapwood, the increase in  $A_s$  with DBH is more than sufficient to compensate for the decrease in sap flux density. Whole-tree water use was not estimated because radial profiles of sap flux density were not known in sufficient detail.

Tree size also influenced the daily course of sap flow, particularly the time at which maximum sap flux density was attained. When concurrent daily courses were available for individuals representing a wide range of DBH, it was observed

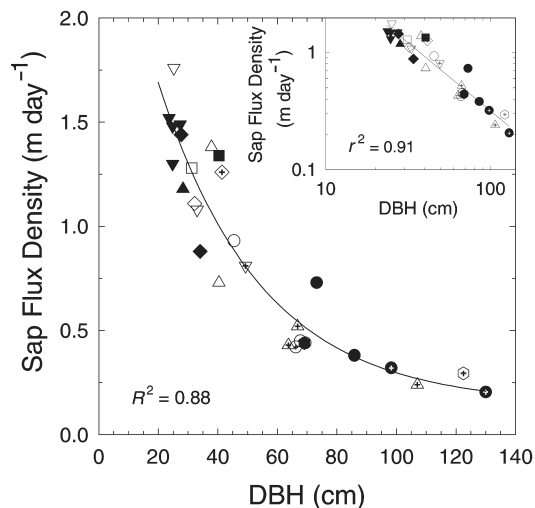


Figure 4. Total daily sap flux density in relation to DBH for co-occurring Panamanian forest canopy tree species. The fitted curve is:  $y = 0.145 + 2.759e^{(-0.029x)}$ . The inset shows sap flux density and DBH plotted on a log scale. Each type of symbol represents a different species.



that maximum sap flow tended to occur progressively later in the day as tree size increased (Figure 5). When data for several measurement days were pooled, it was clear that the time at which maximum sap flow was attained increased with increasing DBH, despite the influence of confounding factors such as day-to-day variation in the course of evaporative demand and PPFD (Figure 6).

Substantial radial variation in sap flux density was observed when simultaneous measurements at three ranges of depth near the periphery of the sapwood were compared (Figure 7). Sap flux density did not vary consistently with depth and was often greatest at the intermediate depth and was either higher or lower at 1.0 cm than at 3.2 cm mean depth, depending on the species and individual. The probe design restricted measurements of absolute sap flux density to the outer 4 cm of the sapwood. However, radial profiles of relative sap velocity, inferred from the temperature difference between specially constructed heated and unheated probes (see methods) inserted in one individual each of *Alseis blackiana*, *Platymiscium pinnatum* and *Quararibea asterolepis*, indicated that the functional xylem extended to a depth of at least 7 cm (data not shown), the maximum depth to which these probes could be inserted. These results were qualitatively consistent with those obtained with the dye injection and coring method, which yielded sapwood depths ranging from 7 to 27 cm in individuals ranging from 25 to 100 cm DBH.

## Discussion

The 27 phylogenetically diverse tropical forest tree species studied exhibited pronounced allometric convergence with re-

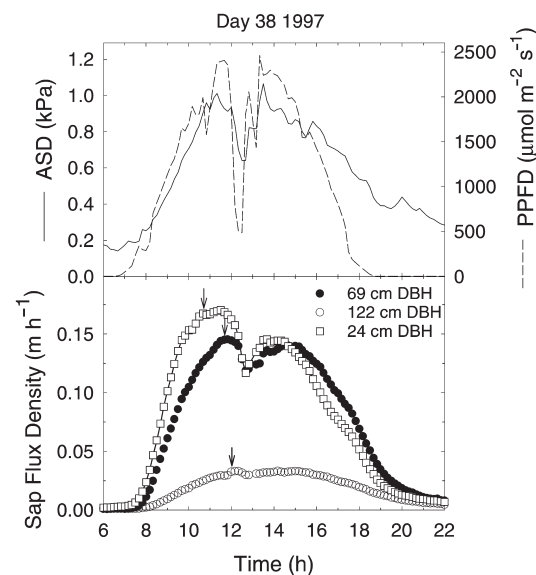


Figure 5. Daily courses of air saturation deficit (ASD), photosynthetic photon flux density (PPFD) and sap flux density for three trees representing different size classes. Arrows indicate the time at which the initial maximum sap flux density was observed. Symbols:  $\square$  = *Trichilia tuberculata*;  $\bullet$  = *Guapira standleyanum*;  $\circ$  = *Ficus insipida*.

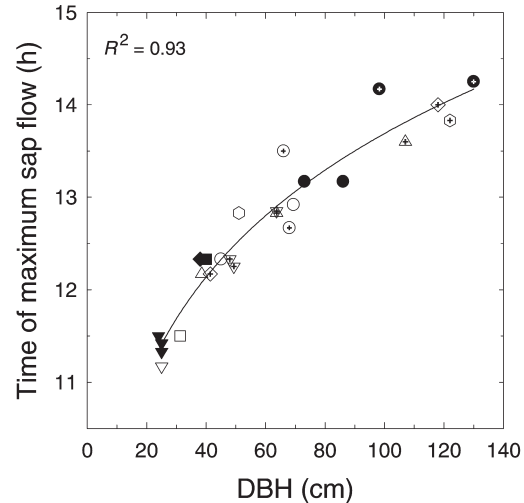


Figure 6. Time at which maximum sap flow was attained in relation to DBH for co-occurring Panamanian forest canopy tree species. The fitted curve is:  $y = 7.48x^{0.131}$ . Each type of symbol represents a different species.

spect to the relationship between tree size and the amount of xylem functional in water transport. Although autocorrelation between  $A_s$  and DBH may have dominated the relationship between  $A_s$  and DBH in smaller trees, its influence diminished with increasing tree size. Regardless of the geometric relationship between  $A_s$  and DBH,  $d_s$  appeared to vary with DBH in a similar manner among all of the study species.

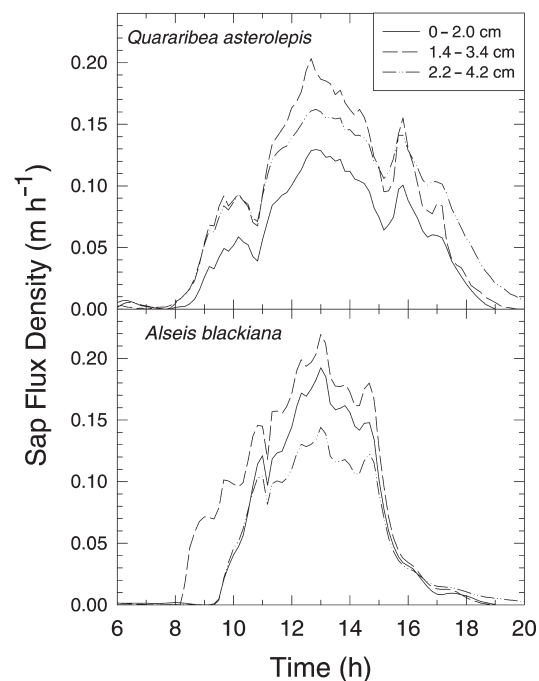


Figure 7. Time courses of sap flux density at different depths in the sapwood measured on different days for an individual of *Quararibea asterolepis* and an individual of *Alseis blackiana*.

Convergence in physiological regulation of water transport was also pronounced. For example, there were common relationships between tree size and maximum and total daily rates of sap flow per unit  $A_s$ , and between tree size and daily courses of sap flow, specifically, the time at which the maximum rate of sap flow was attained. The ability of a single variable, DBH, to account for 91% of the variation in total daily sap flux density in the outermost 2 cm of sapwood among several of the most abundant species in the study area suggests that scaling tree water use to a land area basis in this species-rich forest could be relatively straightforward, provided radial profiles of sap flux density are known and do not vary substantially among species. Nevertheless, considerable variation among reported relationships between sap flux density and tree size suggests that considerable background information is required for reliable scaling of tree water use to a land area basis. For example, both Granier et al. (1996) and Oren et al. (1999) found that sap flux density increased rather than decreased with increasing tree size, and Phillips et al. (1999) found no consistent relationship between sap flux density and tree size.

The cause of the sharp decline in maximum and total daily sap flux density with increasing tree size was not clear. If the overall leaf area:sapwood area ratio decreased with increasing size, then sap flux density would be expected to diminish in response to the reduction in transpiring leaf area relative to functional xylem area. Consistent with this, a tendency for the leaf area:sapwood area ratio to be lower in taller trees has been noted (Schäfer et al. 2000; N.G. McDowell, Oregon State University, Corvallis, OR, unpublished data), and we have observed that maximum sap flux density increased sharply with decreasing stem diameter, and correspondingly higher leaf area:sapwood area ratios, within individual trees of a subset of the species studied here (Andrade et al. 1998). Alternatively, the inverse relationship between sap flux density and DBH may reflect a direct hydraulic constraint on sap flux density associated with increasing tree height. If it is assumed that height varied essentially linearly with DBH over the range of size studied, then application of a simplified hydraulic model in which sap flux density varies inversely with height (Schäfer et al. 2000) yields a curve nearly identical to that shown in Figure 4.

The shared relationship between time of maximum sap flow and tree size probably reflects a common relationship between diurnal stem water storage capacity and tree size (Goldstein et al. 1998), because the lag between sap flow measured at the base of the tree and transpiration from the crown is attributable to water being transiently removed from storage compartments above the point of sap flow measurement. This interpretation is consistent with the results of a resistance-capacitance analysis applied to the lag between transpiration and sap flow in *Pinus taeda* L. (Phillips et al. 1997). However, the lag between transpiration and sap flow in *P. taeda* did not vary with stem diameter, presumably because hydraulic resistance and capacitance changed in a compensatory manner with increasing tree size (Phillips et al. 1997). The marked size-dependence of the time at which maximum sap flow was observed in

the present study thus points to an increase in relative capacitance with increasing tree size, most likely associated with an increase in the sapwood volume per unit leaf area.

The allometric and functional convergences reported here are consistent with predictions of recent models describing universal,  $\frac{3}{4}$  power allometric scaling of plant vascular systems based on plant mass (Enquist et al. 1998, West et al. 1999). When DBH was converted to approximate above-ground dry mass ( $M$ ) based on the relationship  $\text{DBH} \propto M^{0.412}$ , given by Enquist et al. (1998), the exponent shown in Figure 1 became 0.740. Similarly, in a previous study involving a subset of five of the species studied here, we found that contrasting patterns of regulation of water use at the leaf level converged when an appropriate tree architectural scaling factor, the branch leaf area:sapwood area ratio, was applied (Andrade et al. 1998). Similarly, Reich et al. (1997) reported that relationships among leaf traits such as photosynthesis, nitrogen content, life span and specific leaf area appeared to be constrained in a similar manner among hundreds of diverse species from tropical, temperate and arctic biomes. Taken together, these findings suggest that comparable functional constraints may apply across a wide range of conditions leading to inevitable tradeoffs among fundamental plant traits. Thus, apparent intrinsic differences in physiological behavior and responsiveness may actually reflect different operating regions on the same physiological response surface common to a large group of species.

Conclusions about inter-specific differences in regulation of transpiration and carbon assimilation are often based on bodies of data describing the behavior of individual leaves rather than entire individuals. However, inferences about species-specific behavior drawn from these data sets can be misleading in the absence of knowledge of whole-plant architectural and structural features contributing to the individual leaves behaving as they do. The divergence among species of regulation of transpiration at the single leaf scale and its convergence after normalization by appropriate scaling factors point to the potential pitfalls of not considering multiple scales in comparative studies of physiological regulation of water use among trees. For example, if individuals of two co-occurring species tend to be restricted to distinct diameter classes, then contrasting diurnal courses of sap flow could mistakenly be taken to represent species-specific rather than size-specific behavior.

The convergence in regulation of whole-plant water transport observed in the present study seems remarkable given that the species and individuals studied undoubtedly represent a broad range of xylem vessel diameters and lengths, wood anatomy, and crown leaf area to basal sapwood area ratios. Recognition of this shared scaling facilitates the explicit examination of questions concerning the ecological significance of inter-specific differences in crown architecture. Species experiencing similar transpiration rates, and possibly  $\text{CO}_2$  assimilation rates, on a sapwood area basis can have dramatically different rates of gas exchange per unit leaf area. For example, in a previous study, a sevenfold greater transpiration

rate in *Ficus insipida* than in *Anacardium excelsum* on a leaf area basis was associated with a fourfold greater branch leaf area:sapwood area ratio in *A. excelsum* than in *F. insipida* (Andrade et al. 1998). Consistent with this, CO<sub>2</sub> assimilation rates and leaf N concentration on an area basis were 2.5 times greater in *F. insipida* than in *A. excelsum* (J. Cavelier et al., Universidad de los Andes, Bogota, Colombia; unpublished observations). Clearly, differential investment in leaf area to conduct similar amounts of gas exchange on a whole-tree basis has multiple implications for relative construction costs, nutrient allocation and leaf life span as well as processes such as decomposition and herbivory.

Despite the relatively large number of published studies on sap flow in trees (Wullschlegel et al. 1998), there is insufficient information to determine whether the dependence of  $A_s$  and sap flux density on DBH for temperate and other tropical tree species is similar to that shown in Figures 1 and 3. Sapwood area–DBH relationships for the temperate species *Pinus pinaster* Ait. (Loustau et al. 1996) and *P. radiata* D. Don (Teskey and Sheriff 1996) do not appear to differ significantly from that shown in Figure 1, whereas *Larix gmelinii* (Rupr.) Rupr. ex Kuzen. growing in Siberia (Arneth et al. 1996) and *Eucalyptus regnans* F.J. Muell growing in southern Australia (Vertessy et al. 1995) seem to maintain a substantially smaller functional xylem area for a given diameter class. The extent to which variation in published  $A_s$ –DBH relationships among and within species is attributable to the use of different criteria to assess  $A_s$  is not known. For example, appearance alone has been used to assess functional xylem depth in some studies, whereas more quantitative criteria such as dye travel and measurements of sap flow at different depths in the stem have been employed in other studies. Even though  $A_s$  may scale differently with DBH in some species, corresponding variation in sap flux density could result in total water use scaling universally with tree size under a given regime of evaporative demand. Confirmation of the universality of scaling of plant vascular systems and water use (Enquist et al. 1998, West et al. 1999) awaits the use of comparable methods to assess these relationships in a broader range of species.

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