

# Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees

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Received October 23, 2003; accepted February 15, 2004; published online June 1, 2004

**Summary** In large trees, the daily onset of transpiration causes water to be withdrawn from internal storage compartments, resulting in lags between changes in transpiration and sap flow at the base of the tree. We measured time courses of sap flow, hydraulic resistance, plant water potential and stomatal resistance in co-occurring tropical forest canopy trees with trunk diameters ranging from 0.34–0.98 m, to determine how total daily water use and daily reliance on stored water scaled with size. We also examined the effects of scale and tree hydraulic properties on apparent time constants for changes in transpiration and water flow in response to fluctuating environmental variables. Time constants for water movement were estimated from whole-tree hydraulic resistance ( $R$ ) and capacitance ( $C$ ) using an electric circuit analogy, and from rates of change in water movement through intact trees. Total daily water use and reliance on stored water were strongly correlated with trunk diameter, independent of species. Although total daily withdrawal of water from internal storage increased with tree size, its relative contribution to the daily water budget (~10%) remained constant. Net withdrawal of water from storage ceased when upper branch water potential corresponded to the sapwood water potential ( $\Psi_{sw}$ ) at which further withdrawal of water from sapwood would have caused  $\Psi_{sw}$  to decline precipitously. Stomatal coordination of vapor and liquid phase resistances played a key role in limiting stored water use to a nearly constant fraction of total daily water use. Time constants for changes in transpiration, estimated as the product of whole-tree  $R$  and  $C$ , were similar among individuals (~0.53 h), indicating that  $R$  and  $C$  co-varied with tree size in an inverse manner. Similarly, time constants estimated from rates of change in crown and basal sap flux were nearly identical among individuals and therefore independent of tree size and species.

**Keywords:** allometric relationships, hydraulic architecture, hydraulic capacitance, hydraulic resistance, scaling, time constants.

## Introduction

In trees, reliance on stored water to temporarily replace tran-

spirational losses is an important homeostatic mechanism, constraining leaf water deficits and maintaining photosynthetic gas exchange as increases in hydraulic path length increase hydraulic resistance with tree height (Goldstein et al. 1998, Phillips et al. 2003). Daily withdrawal of water from internal storage compartments close to the sites of evaporative water loss transiently uncouples leaf water status from resistances associated with water movement through the soil, roots and portions of the stem (Meinzer 2002). Thus internal water storage confers elasticity to an otherwise inelastic hydraulic system. The relative contribution of stored water to daily transpiration has been estimated for a number of species and varies widely from as little as 10–20% (Loustau et al. 1996, Goldstein et al. 1998, Kobayashi and Tanaka 2001, Maherali and DeLucia 2001) to as much as 30–50% (Waring and Running 1978, Holbrook and Sinclair 1992). Relative water storage capacity is determined by the moisture release characteristics of the principal storage compartment tissues and components of the hydraulic architecture such as the leaf area:sapwood area ratio, provided the sapwood constitutes a significant storage compartment.

Despite the increasing availability of estimates of water storage capacity in trees, relatively little is known about the daily dynamics of discharge and recharge of stored water and their consequences for stomatal regulation of gas exchange and leaf water status. In a few recent studies, Williams et al. (1996) attributed the afternoon decline in  $\text{CO}_2$  uptake in a *Quercus–Acer* stand to partial stomatal closure in response to depletion of stored water. Goldstein et al. (1998) showed that larger tropical trees with greater storage capacity maintained maximum rates of transpiration for a greater fraction of the day than smaller trees with a smaller storage capacity, and Phillips et al. (2003) showed that use of stored water in coniferous and angiosperm species was concentrated in the morning and early afternoon when conditions were most conducive for photosynthesis. However, the extent to which observed behavior is species-specific or dependent in a universal manner on variables such as tree size, architecture and allometry, is unknown.

The elasticity or capacitance associated with the release of stored water into the transpiration stream results in time lags between changes in transpiration and changes in liquid water movement through the xylem of leaves, stems and roots. In intact trees, use of stored water is often assessed from the lag between changes in sap flow measured in the upper crown and near the base of the tree (Loustau et al. 1996, Goldstein et al. 1998). However, this approach, which assumes that sap flow in upper branches is a surrogate for transpiration, does not account for the water storage capacity of stem and leaf tissue distal to the uppermost point where sap flow is measured. Using an Ohm's Law analogy, time constants associated with lags between changes in environmental variables that affect transpiration and changes in water flow within the plant can be estimated as the product of its hydraulic resistance and hydraulic capacitance ( $RC$ ) between the soil and a reference point within the plant, usually the leaves. If either hydraulic resistance or capacitance varies throughout the day, the whole-tree time constant for environmentally-driven changes in water flow may be a dynamic rather than static property of water transport along the soil-to-atmosphere continuum.

The objectives of the present study were to determine how total daily water use and daily reliance on stored water scaled with size among four co-occurring tropical forest canopy tree species, and to examine the effects of scale and tree hydraulic properties on apparent time constants for changes in water flow in response to fluctuations of the driving environmental variables. We employed a general electric circuit analogy to assess overall patterns of water use, water storage and apparent time constants among the four species studied rather than attempting to apply a specific  $RC$  model to describe their dynamic behavior. We predicted that scaling of both water use and water storage capacity would be species-independent, and that compensatory variation in hydraulic resistance and capacitance would result in similar time constants across a large range of tree sizes.

## Materials and methods

### Field site and plant material

The study was carried out in a seasonally dry tropical forest in the Parque Natural Metropolitano, Panama City, Republic of Panama (09°10' N, 79°51' E, elevation 50 m), at the site of the Smithsonian Tropical Research Institute canopy crane. Mean annual rainfall at the site is ~1800 mm, of which less than

150 mm falls during the dry season between January and April. One individual each of *Cordia alliodora* (Ruiz. & Pav.) Oken (Boraginaceae) and *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin (Araliaceae) was studied during the dry season (February to April) of 2000, and one individual each of *Anacardium excelsum* (Bentner & Balb. ex Kunth) Skeels (Anacardiaceae) and *Ficus insipida* Willd. (Moraceae) was studied during the dry season of 2001 (Table 1). The mean maximum canopy height was ~35 m and numerous gaps were present, resulting in nearly complete exposure of the crowns of the study trees. The crane's gondola provided access to the crowns and upper trunks of the study trees.

### Sap flow, transpiration and water storage

Variable length heat dissipation sap flow probes with a heated and reference sensor measuring length of 10 mm at the probe tip (James et al. 2002) determined sap flux at different radial depths and vertical positions in the four trees. Two replicate sets of probes were installed on opposite sides of the trunk near the base of each tree. Pairs of sensors were placed in an upward spiral around the trunk, 10 cm apart vertically and 5 cm apart circumferentially at five successive depths at a height of 3.1 m for *A. excelsum*, 3.5 m for *F. insipida* and 1.5 m for *S. morototoni*, and at four depths at 1.5 m height for *C. alliodora*. Sensor depths were 1.5, 4, 10, 17 and 24 cm for *A. excelsum* and *F. insipida*, 1.3, 3.6, 7.6, 13.6 and 18 cm for *S. morototoni*, and 1.7, 4, 7 and 11 cm for *C. alliodora*. A pair of sensors was also installed at a sapwood depth of approximately 1.3 cm in each of three (2001) or five (2000) replicate branches in the upper crown (branch diameter about 5 cm).

For probe installation, two 38-gauge (2.58-mm-diameter) holes, separated axially by 10 cm, were drilled into the sapwood. The sensors were coated with thermally conductive silicone heat sink compound prior to insertion. All probes were protected from direct sunlight and rainfall by reflective insulation and foam insulation in the branches. Concurrent differential voltage measurements across the copper thermocouple leads were converted to a temperature difference between the heated and reference sensor ( $\Delta T$ ). Signals from the sap flow probes were scanned every minute and 10-min means were recorded with a data logger (CR10X or CR21X, Campbell Scientific, Logan, UT) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and stored in a solid-state storage module (SM192, Campbell Scientific). About 55–67 days of data were recorded for each tree, except the *A. excelsum* individual for which intermittent sensor failure resulted in only

Table 1. Characteristics of the individual representative trees studied. Whole-tree resistance values ( $R$ ) were calculated from data presented in Meinzer et al. (2003). Using an electric circuit analogy, the time constant ( $\tau$ ) is the product of resistance and capacitance ( $C$ ) (Phillips et al. 1997).

Species	Diameter (m)	Height (m)	$R$ (h MPa kg <sup>-1</sup> )	$C$ (kg MPa <sup>-1</sup> )	$\tau$ (h)
<i>Anacardium excelsum</i>	0.98	38	0.0042	131.4	0.55
<i>Ficus insipida</i>	0.65	28	0.013	43.4	0.56
<i>Schefflera morototoni</i>	0.47	22	0.014	35.7	0.50
<i>Cordia alliodora</i>	0.34	26	0.16	3.2	0.51

22 days of data being recorded.

The temperature difference between the heated and reference sensors ( $\Delta T$ ) was converted to sap flux ( $v$ ;  $\text{g m}^{-2} \text{s}^{-1}$ ) based on the calibration of Granier (1985). The mass flow of sap corresponding to each trunk probe ( $F$ ;  $\text{g s}^{-1}$ ) was calculated as:

$$F = vA \quad (1)$$

where  $A$  ( $\text{m}^2$ ) is the cross-sectional area of the sapwood calculated as the ring area centered on the 10-mm-long sensor and extending to midway between two sensors of successive depth. The innermost sensor was considered to measure the sap flux to the estimated depth of heartwood as determined from wood cores (James et al. 2002, 2003). Sapwood area was calculated with the assumption of radial symmetry. Whole-tree daily water use ( $\text{kg day}^{-1}$ ), calculated from radial profiles of sap flow near the base of the tree, was assumed to be equal to total daily transpiration. Branch sap flow was used as a surrogate for whole-crown transpiration, which assumes that lags between change in rate of water vapor loss and change in branch sap flow were negligible compared with lags for change in basal sap flow. For each 10-min measurement, the mean sap flow of three to five branches was calculated and divided by the daily maximum to obtain an estimate of normalized whole-crown transpiration. Sap flow measured at the two outermost depths near the base of the trunk was normalized in a similar manner. Daily use of stored water for transpiration was estimated from lags between normalized crown and basal sap flow, as described by Goldstein et al. (1998). Positive values of crown minus basal sap flow indicate that water is being withdrawn from storage compartments located between the upper branches and the base of the trunk.

#### Hydraulic resistance, stomatal resistance and capacitance

Species-specific values of soil-to-terminal branch hydraulic resistance ( $R$ ) were calculated from the inverse of hydraulic conductance data reported by Meinzer et al. (2003) for the same individuals. Determinations of  $R$  were restricted to periods when the lag between upper branch and basal sap flow was negligible indicating that the influence of capacitance on apparent resistance was minimal. In *S. morotoni* and *C. alliodora*, leaf hydraulic resistance ( $R_L$ ) was determined as:

$$R_L = \frac{\Delta\Psi_L}{E} \quad (2)$$

where  $\Delta\Psi_L$  is the difference in water potential between exposed transpiring leaves and covered non-transpiring leaves, and  $E$  is the corresponding transpiration rate per unit leaf area determined from values of upper branch sap flow normalized by the total leaf area distal to the sap flow probes. Branch transpiration was measured continuously (see above) and  $\Delta\Psi_L$  was measured at 1–2 h intervals throughout the morning and early afternoon (0800 to 1300 h). The water potential of covered leaves was assumed to be equivalent to branch water potential ( $\Psi_{br}$ ) at the point of leaf attachment (Begg and Turner 1970).

Therefore,  $\Delta\Psi_L$  should represent the transpiration-induced drop in  $\Delta\Psi_L$  across the total hydraulic resistance of the leaf (Melcher et al. 1998). Leaf water potential was measured with a pressure chamber. Non-transpiring leaves were covered with aluminum foil and enclosed in plastic bags during the early evening preceding the measurement day. Stomatal resistance ( $r_s$ ) of *S. morotoni* and *C. alliodora* was measured with a steady state porometer (Model 1600, Li-Cor, Lincoln, NE) in order to determine whether there was an association between dynamic variation in  $r_s$  and  $R_L$ .

Whole-tree capacitance ( $\text{kg MPa}^{-1}$ ) was determined as total daily withdrawal of water from storage, calculated from the cumulative differences between crown and basal sap flow (Goldstein et al. 1998), divided by the difference between  $\Psi_{br}$  at the time withdrawal of water from storage ceased, and early morning values of  $\Psi_{br}$  measured prior to the onset of sap flow. In addition, sapwood water release curves determined for the same individuals in a previous study (Meinzer et al. 2003) were used to estimate inflection points corresponding to the sapwood water potential ( $\Psi_{sw}$ ) at which the capacitance, or slope of the curve ( $\text{kg m}^{-3} \text{MPa}^{-1}$ ), changed from a nearly linear phase to a distinctly nonlinear phase.

#### Time constants and time lags

Using an electric circuit analogy, the time constant ( $\tau$ ) for changes in crown transpiration is the product of the soil-to-leaf hydraulic resistance and the total capacitance ( $RC$ ; Phillips et al. 1997). Whole-tree time constants (Table 1) were estimated by applying this model to the values of whole-tree capacitance and hydraulic resistance determined as described above. Time constants for changes in water flow were also estimated from time courses of sap flux in terminal branches and near the base of the main stem during the morning when irradiance and vapor pressure deficit were increasing steadily. The time constants for changes in crown and basal sap flux were estimated as the time required for sap flux to attain 63% of its daily maximum steady state value. This procedure was expected to overestimate the true time constants because environmental drivers of transpiration were changing in a continuous rather than stepwise fashion. Nevertheless, application of the same procedure to all of the trees was expected to reveal possible trends related to size and species.

## Results

#### Stored water use

Total daily water use and stored water use for the four tropical tree species remained relatively constant during the dry seasons of 2000 and 2001 (Figure 1) with the exception of *A. excelsum*, in which total daily water use increased by about 20% ( $P < 0.01$ ) during the study as a consequence of bud flushing and leaf expansion. Mean daily water use increased with tree size from 42  $\text{kg day}^{-1}$  in the 0.34-m-diameter *C. alliodora* tree to 785  $\text{kg day}^{-1}$  in the 0.98-m-diameter *A. excelsum* tree (Figure 2A). Daily withdrawal of water from storage followed a similar trend with increasing tree size (Fig-

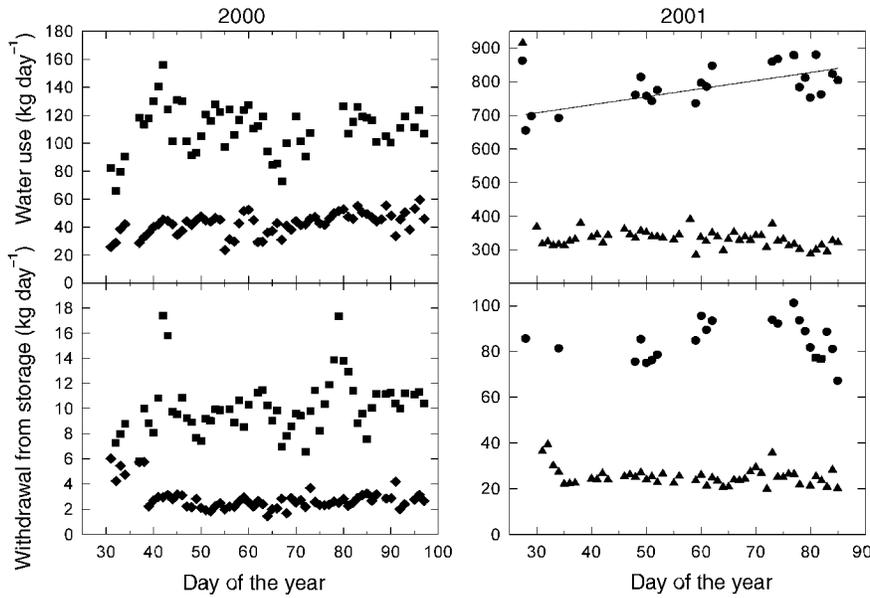


Figure 1. Seasonal course of daily water use and use of stored water for *Schefflera morototoni* (■) and *Cordia alliodora* (◆) during the 2000 dry season and *Anacardium excelsum* (●) and *Ficus insipida* (▲) during the 2001 dry season.

ure 2B), and the rankings of the trees according to total water use and stored water use were identical. Nevertheless, the relative contribution of stored water to total daily transpiration remained nearly constant at about 10%, independent of total water use, tree size and species, as indicated by the slope of a highly significant ( $P < 0.01$ ) linear regression fitted to the

pooled seasonal data for all four trees (Figure 3). Daily courses of use and recharge of stored water determined from the difference between crown and basal sap flow indicated that, in all four trees, stored water use increased abruptly shortly after sunrise, peaked at about 0800–0830 h, and ceased at 1000–1100 h (Figure 4). Thus, about 10% of total daily water use had been withdrawn from storage by 1000 to 1100 h in all individuals, and varying amounts of recharge occurred during the remainder of the day and night (Figure 4, negative values).

At least three independent lines of evidence suggest that none of the trees experienced progressive depletion of stored water, which would have resulted in increasing water deficits over the course of the dry season. First, no seasonal decline in total daily water use was observed in either year (Figure 1). Second, no seasonal increase in the nighttime maximum tem-

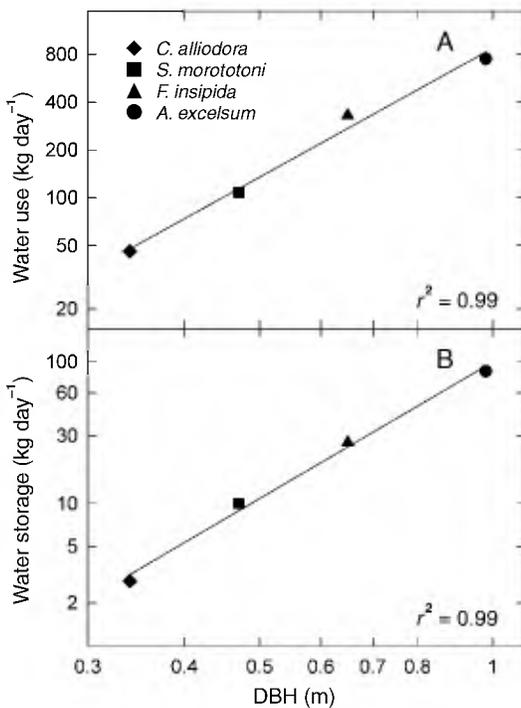


Figure 2. Log-log plots of total daily water use and use of stored water in relation to tree diameter at breast height (DBH) for four tropical canopy trees. Values are means of 55–67 days of measurements. Standard errors are smaller than symbols.

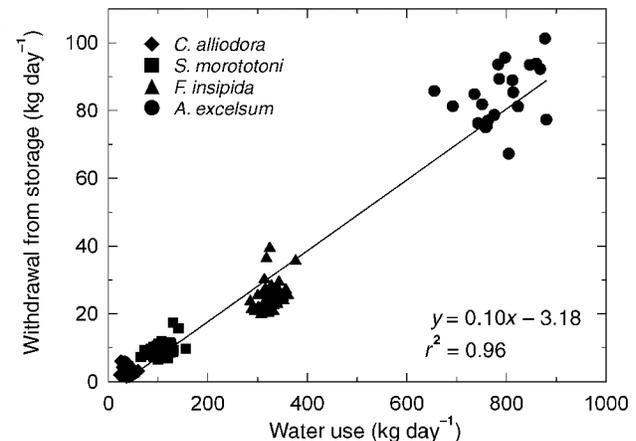


Figure 3. Daily use of stored water in relation to total daily water use for four tropical canopy trees. The slope of the line is 0.10, indicating a contribution of 10% stored water to total daily transpiration, regardless of tree size or species.

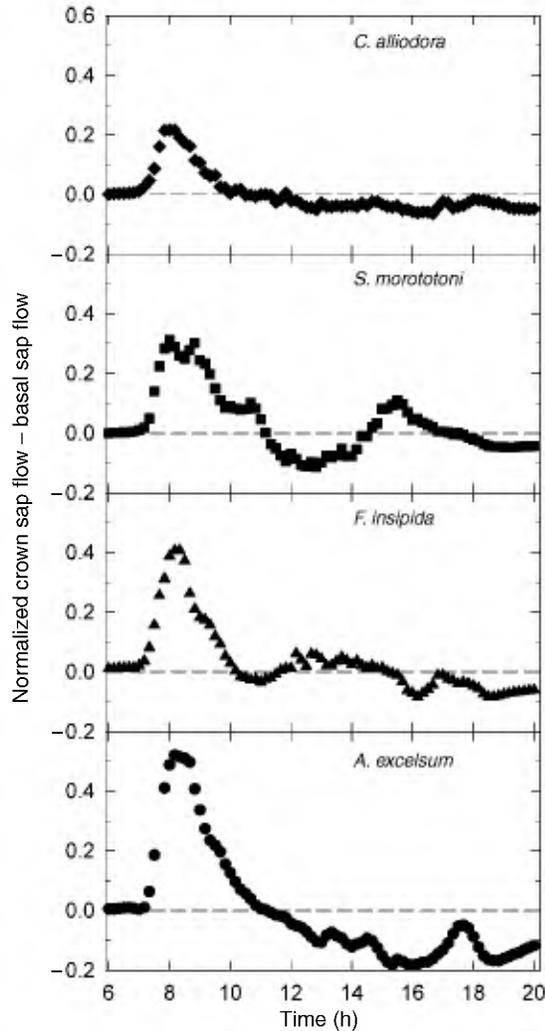


Figure 4. Representative time courses of the difference between crown and basal sap flow normalized with respect to their daily maximum values. Positive values represent withdrawal of water from internal storage and negative values represent recharge of storage compartments.

perature difference between heated and reference sap flow sensors was observed (data not shown). If sapwood water content had declined, sensor heat dissipation would have become slower, leading to seasonal increases in the temperature difference between sensors when flow was at or near zero. Third, the sums of 24-h time courses of the difference between crown and basal sap flow were never significantly different from zero, consistent with no net withdrawal of water from storage over 24-h cycles.

To identify potential regulatory mechanisms contributing to the similar timing of stored water use and relative reliance on stored water among the four species representatives, sapwood water potentials ( $\Psi_{sw}$ ) from sapwood water release curves determined in a previous study (Meinzer et al. 2003) were compared with branch water potentials ( $\Psi_{br}$ ) corresponding to the times at which daily use of stored water ceased. Values of  $\Psi_{sw}$

at which sapwood water release curves showed a transition from a nearly linear phase to a distinctly nonlinear phase ranged from  $-0.54$  MPa in *S. morototoni* to  $-1.3$  MPa in *C. alliodora* (Figure 5). When these values were plotted against intact tree  $\Psi_{br}$  values at the time daily use of stored water ceased (1000–1100 h), a linear relationship not significantly different from a 1:1 relationship was obtained (Figure 6). Thus about 10% of daily water use had been withdrawn from storage at the time  $\Psi_{br}$  attained a value corresponding to the  $\Psi_{sw}$  at which further withdrawal of water from sapwood would have caused  $\Psi_{sw}$  to decline precipitously (cf. Figures 5 and 6).

#### Dynamics of transpiration and sap flow

When upper crown sap flow was substituted for transpiration, the relative rates of the morning increase in transpiration for 2 days with similar time courses of solar radiation were found to be nearly identical among the four individuals studied (Figure 7). Therefore, dynamic changes in transpiration in response to changes in the irradiance regime appeared to be independent of tree size, rates of whole-tree water use and water storage capacity. The preceding observation suggested that time constants for dynamic responses of transpiration to changes in environmental variables such as irradiance were similar. To evaluate this possibility, whole-tree time constants were estimated as the product of soil-to-branch hydraulic resistance obtained from an earlier study (Meinzer et al. 2003) and whole-tree capacitance calculated as described above (Table 1). Consistent with similar dynamic responses to changing irradiance (Figure 7), whole-tree time constants were nearly identical, ranging from 0.50–0.56 h.

Relationships between tree size and the initial slope of the morning increase in sap flow near the base of the tree were strongly dependent on the scale at which they were assessed

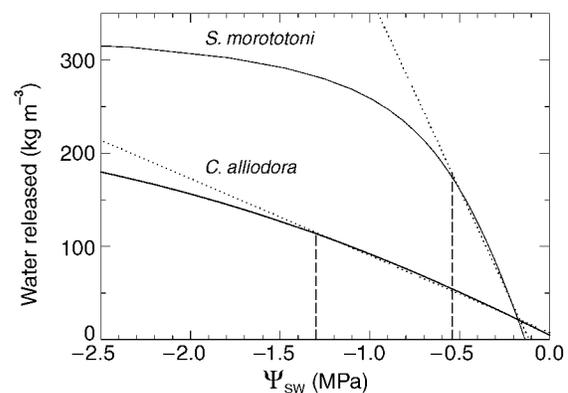


Figure 5. Sapwood water release curves for *S. morototoni* and *C. alliodora*. The dotted lines are linear regressions fitted to the nearly linear portions of the curves and the dashed lines indicate inflection points at which the relationship between water released and sapwood water potential ( $\Psi_{sw}$ ), determined psychrometrically, becomes distinctly nonlinear. Water release curves for *A. excelsum* and *F. insipida* were intermediate between those of *C. alliodora* and *S. morototoni*. Inflection points were  $-1.3$  MPa for *C. alliodora*,  $-0.90$  MPa for *F. insipida*,  $-0.70$  MPa for *A. excelsum* and  $-0.55$  MPa for *S. morototoni*. Data were obtained from Meinzer et al. (2003).

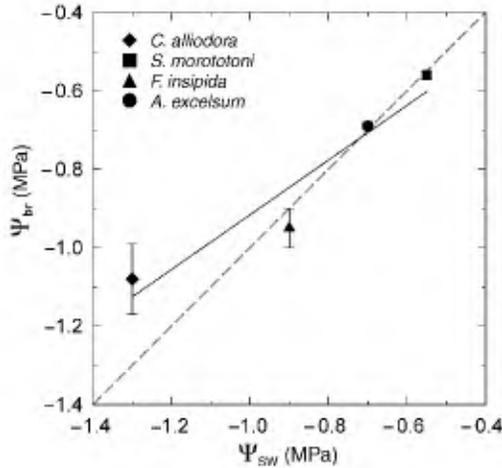


Figure 6. Relationship between branch water potential ( $\Psi_{br}$ ) at the time net daily withdrawal from internal storage ceased and sapwood water potential ( $\Psi_{sw}$ ) corresponding to inflection points on sapwood water release curves (see Figure 5). The solid regression line did not differ significantly from a 1:1 relationship (dashed line).

(Figure 8). The relative rate of increase in basal sap flow decreased with increasing tree size (Figure 8A). In contrast to normalized flow, the rate of increase in whole-tree water use was greatest for larger trees (Figure 8B). Thus, despite the slower relative increase of sap flow in larger trees, the absolute increase was greater. However, the rate of increase in sap flux averaged over the entire basal sapwood area to remove the influence of differences in total sapwood area among trees, was

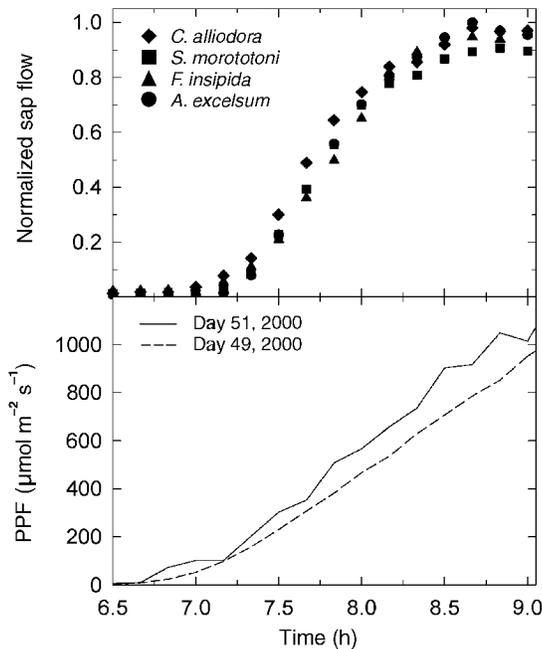


Figure 7. Time courses of normalized crown (upper branch) sap flow on days with similar morning time courses of solar radiation (PPF) from the 2 years of measurement.

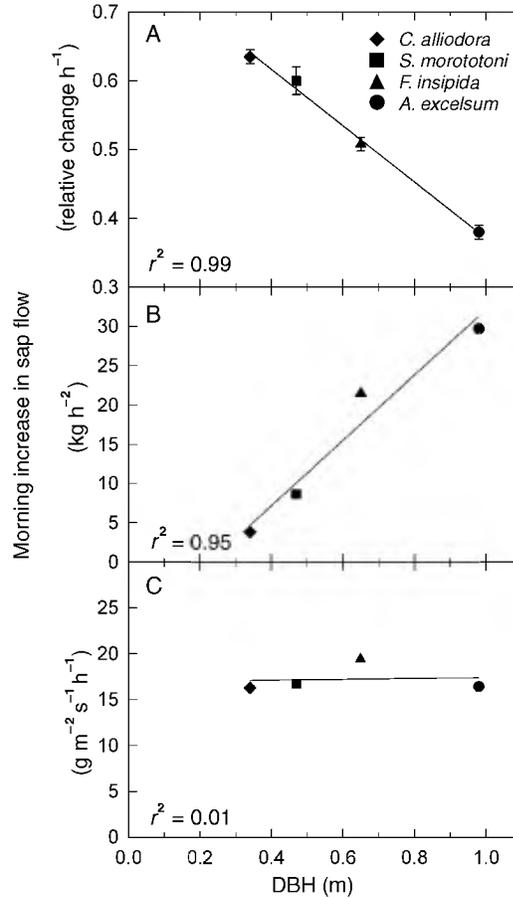


Figure 8. Rates of the initial morning increase in sap flow (~0700 to 0900 h) calculated with (A) flow normalized with respect to the daily maximum, (B) whole-tree water use and (C) sap flux per unit of sapwood area.

similar among the four individuals (Figure 8C), implying that the time constants for changes in basal sap flux were similar among all individuals and independent of tree size or wood properties.

Because the slopes of the initial morning increase in sap flow were similar among individuals when sap flow was expressed per unit of sapwood area (sap flux), mean time courses of crown and basal sap flux were calculated to examine the characteristics of the lag between changes in crown and basal sap flow (Figure 9). The morning lag between crown transpiration and basal sap flow increased from about 0.25 h shortly after sunrise to about 0.75 h when crown transpiration first attained its maximum value as stomata began to restrict transpiration. The increasing lag time was indicative of the differences in time constants for changes in crown and basal sap flow. Once stomata began to restrict transpiration, the lag quickly diminished and had disappeared by 0900 h (Figure 9). As both irradiance and atmospheric saturation deficit increased in the morning, stomatal limitation of transpiration was associated with increasing leaf hydraulic resistance ( $R_L$ ) during the same time period. Data obtained for *C. alliodora* and *S. morototoni* showed that stomatal resistance ( $r_s$ ) more than

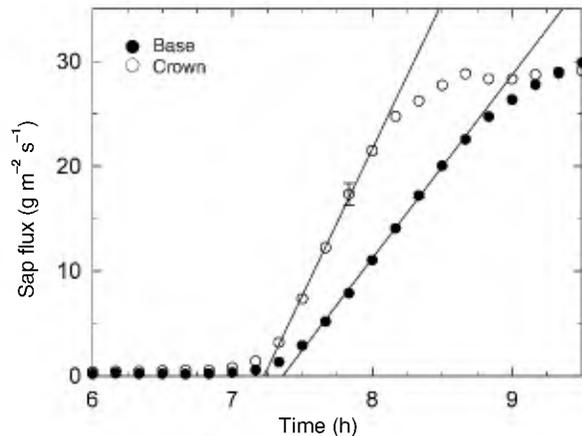


Figure 9. Mean time courses of crown and basal sap flux on representative clear days for *A. excelsum*, *F. insipida*, *C. alliodora* and *S. morototoni*. Crown sap flux was obtained by normalizing mean upper branch sap flux with respect to its maximum value for the day, then using the dimensionless values and corresponding values of total daily water use, determined from the basal sap flow probes, to calculate the time course of whole-crown transpiration ( $\text{g s}^{-1}$ ), which was normalized by basal sapwood area ( $\text{m}^2$ ). This procedure allowed both fluxes to be expressed at the same time scale.

doubled between 0800 and 1300 h as  $R_L$  increased by an order of magnitude (Figure 10).

## Discussion

Plant size played a dominant role in determining the water use and water storage characteristics of the four individuals studied (Figure 2). Although total daily withdrawal of water from internal storage increased with tree size, and therefore total daily water use increased, the relative contribution of stored water to the daily water budget remained constant at about 10% (Figure 3). Similarly, Maherali and DeLucia (2001) re-

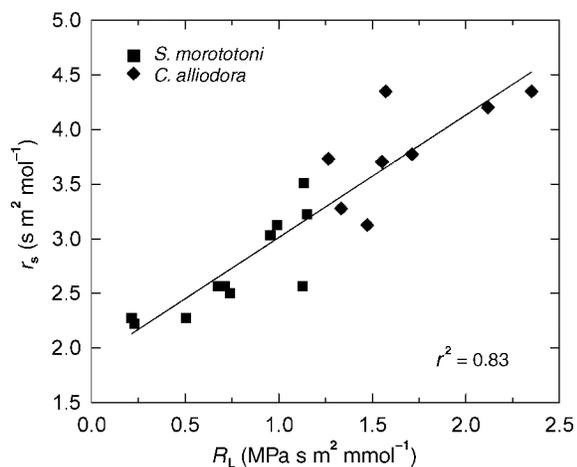


Figure 10. Relationship between stomatal resistance ( $r_s$ ) and leaf hydraulic resistance ( $R_L$ ) for *C. alliodora* and *S. morototoni*. Data were pooled from 2–3 days of measurements for each species.

ported little site-specific and seasonal variation in relative water storage capacity of ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws.) trees growing in desert and montane environments. In contrast, Phillips et al. (2003) reported that daily reliance on stored water increased with tree size in two temperate coniferous and one temperate angiosperm species. Nevertheless, the relative reliance on stored water reported here and by Phillips et al. (2003) is within the range of estimates obtained in earlier studies (Loustau et al. 1996, Kobayashi and Tanaka 2001).

The mechanisms that govern the extent to which transient withdrawal of water from internal storage is relied upon to replace daily transpirational losses are uncertain. However, in the present study, a relationship was found between the timing of stored water use (Figure 4), sapwood water release characteristics (Figure 5), and values of  $\Psi_{br}$  at which net withdrawal of water from storage ceased (Figure 6). By the time approximately 10% of the total daily water use had been withdrawn from storage,  $\Psi_{br}$  had fallen to values that corresponded to inflection points on sapwood water release curves where  $\Psi_{sw}$  began to decline precipitously with further withdrawal of water (cf. Figures 5 and 6). Although these threshold values of  $\Psi_{sw}$  were substantially less negative than values of  $\Psi_{br}$  associated with 50% loss of hydraulic conductivity from embolism, which ranged from  $-1.6$  MPa in *A. excelsum* to  $-3.0$  MPa in *C. alliodora* (Meinzer et al. 2003), it is possible that conservative stomatal regulation of  $\Psi_{br}$  at a setpoint corresponding to the point of “diminishing returns” on the sapwood water release curve dampened daily fluctuations in the fraction of dysfunctional xylem in stems.

Stomata thus played a key role in limiting use of stored water to a nearly constant fraction of total daily water use independent of species and tree size. Rapid increases in  $r_s$  from early morning minimum values at 0800 h (data not shown) strongly limited transpiration, causing crown and basal sap flux to converge (Figure 9), thereby preventing further withdrawal of water from storage (Figure 4). Rapid increases in  $r_s$  during the morning were associated with corresponding increases in  $R_L$  (Figure 10). Marked diel fluctuations in  $R_L$  have been noted in earlier studies (Zwieniecki et al. 2000, Bucci et al. 2003) and can be expected to strongly influence stomatal regulation of leaf water potential, and therefore  $\Psi_{br}$ , because  $R_L$  is often the dominant resistance in the soil-to-leaf pathway (Meinzer 2002). Recent work has shown that diel fluctuations in  $R_L$  reflect diel cycles of embolism and refilling of xylem conduits (Bucci et al. 2003, Nardini et al. 2003). Thus, it appears that the dynamics of embolism formation and repair in the terminal portions of the water transport pathway (i.e., leaves) may govern stomatal regulation of the water status of woody transport tissue to which the leaves are attached. In other words, dynamic responses of stomata to daily fluctuations in leaf embolism and hydraulic resistance suggest that a sensitive regulatory system exists that provides early warning of changes in evaporative demand. Failure of stomata to “anticipate” rapid increases in transpiration could result in sharp increases in stem xylem tension and loss of conductivity, especially if the capability for buffering through capacitive discharge of water from sapwood storage has already been ex-

hausted. Moreover, reliance on transient xylem dysfunction in leaves to regulate the water status and degree of embolism in stems could be advantageous if embolism repair processes in woody stems are not as vigorous as those observed in leaves (Hacke and Sperry 2003).

The data presented here suggest that time constants for changes in transpiration and sap flow in response to changing environmental conditions were similar among individuals of four tropical forest canopy tree species comprising a substantial range of tree sizes. Similar time constants for changes in transpiration estimated from sap flow in upper branches (Figures 7 and 9) were associated with an inverse relationship between whole-tree hydraulic resistance and capacitance (Table 1 and Meinzer et al. 2003). Whole-tree hydraulic resistance and capacitance thus appeared to co-vary in a predictable manner that resulted in their product ( $RC$ ), an estimate of the time constant, remaining similar and therefore independent of tree size as proposed earlier (Hunt et al. 1991, Phillips et al. 1997, 1999). The mean time constant of 0.53 h for changes in transpiration (Table 1) is consistent with estimates of 0.5 to 0.7 h reported for two *Pinus* species (Phillips et al. 1997). An independent estimate of the mean time constant for the four study trees based on the linear portion of the increase in crown sap flux shown in Figure 9, and assuming a maximum sap flux of  $30 \text{ g m}^{-2} \text{ s}^{-1}$ , yielded a value of about 0.7 h. Although this value was within the 0.5–0.7 h range cited above, it was about 30% greater than the estimate of 0.53 h obtained from Table 1. Step changes in environmental drivers of transpiration were implicitly assumed in calculating the time constants in Table 1, whereas slower, continuous changes in environmental variables, namely irradiance and vapor pressure deficit, led to the behavior depicted in Figure 9.

A key assumption involved in estimating both the amount of water withdrawn daily from internal storage and time constants for changes in transpiration was that water storage capacity distal to the locations of branch sap flow measurements was negligible. Significant daily discharge and recharge of storage tissues distal to the uppermost sap flow sensors would have resulted in additional undetected lags between changes in transpiration and sap flow, and therefore underestimates of total daily storage capacity and overestimates of time constants for changes in transpiration. However, technical and logistical constraints associated with sampling an adequate fraction of the crown prevented measurements of water flux in the smallest branches. Although porometric measurements of stomatal conductance can be used to measure leaf transpiration inside ventilated chambers, previous studies have shown that they often provide unreliable estimates of transpiration from unenclosed leaves because the impact of leaf and canopy boundary layers on transpiration are ignored (Meinzer et al. 1995, 1997).

Apparent time constants for changes in sap flow near the base of the tree were strongly dependent on how the data were normalized and the scale at which they were expressed (Figure 8). Normalizing sap flow with respect to its daily maximum value yielded a negative relationship between tree size and the relative rate of change in sap flow (Figure 8A), whereas, the rate of change in whole-tree sap flow increased sharply with increasing tree size (Figure 8B). However, when mean

sap flow per unit of basal sapwood area was considered, its rate of change was independent of tree size and nearly constant (Figure 8C), suggesting uniform time constants for changes in basal sap flux among the four trees. The pattern in Figure 8C was consistent with the mean time course of basal sap flux shown in Figure 9.

## Conclusions

Homeostatic mechanisms involving compensating adjustments in whole-tree capacitance and hydraulic properties over a range of tree sizes appeared to contribute to the stability of time constants for responses of transpiration and sap flow to changes in environmental variables. Additional homeostatic mechanisms were involved in the stomatal regulation of tree water status that limited withdrawal of water from internal storage compartments to about 10% of total daily water use independent of tree size and species. The four individuals studied showed a common relationship between tree size and total daily water use.

## Acknowledgments

This research was supported by National Science Foundation Grant IBN 99-05012 to F. Meinzer and G. Goldstein. We thank the Smithsonian Tropical Research Institute for providing facilities, logistical support and the expertise of the canopy crane operators.

## References

- Andrade, J.L., F.C. Meinzer, G. Goldstein, N.M. Holbrook, J. Cavellier, P. Jackson and K. Silvera. 1998. Regulation of water flux through trunks, branches and leaves in trees of a lowland tropical forest. *Oecologia* 115:463–471.
- Begg, J.E. and N.C. Turner. 1970. Water potential gradients in field tobacco. *Plant Physiol.* 46:343–346.
- Bucci, S.J., F.G. Scholz, G. Goldstein, F.C. Meinzer and L. Sternberg. 2003. Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant Cell Environ.* 26: 1633–1645.
- Goldstein, G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavellier, P. Jackson and A. Celis. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ.* 21:397–406.
- 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.
- Hacke, U.G. and J.S. Sperry. 2003. Limits to xylem refilling under negative pressure in *Laurus nobilis* and *Acer negundo*. *Plant Cell Environ.* 26:303–311.
- Holbrook N.M. and T.R. Sinclair. 1992. Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and stem water storage. *Plant Cell Environ.* 15:401–409.
- Hunt, E.R., S.W. Running and C.A. Federer. 1991. Extrapolating plant water flow resistances and capacitances to regional scales. *Agric. For. Meteorol.* 54:169–195.
- 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.

- James, S.A., F.C. Meinzer, G. Goldstein, D. Woodruff, T. Jones, T. Restom, M. Mejia, M. Clearwater and P. Campanello. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134:37–45.
- Kobayashi, Y. and T. Tanaka. 2001. Water flow and hydraulic characteristics of Japanese red pine and oak trees. *Hydrol. Proc.* 15: 1731–1750.
- Loustau, D., P. Berbigier, P. Roumagnac, C. Arruda-Pacheco, J.S. David, M.J. Ferreira, J.S. Pereira and R. Tavares. 1996. Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. *Oecologia* 107:33–42.
- Maherali, H. and E.H. DeLucia. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* 129:481–491.
- Meinzer, F.C. 2002. Co-ordination of liquid and vapor phase water transport properties in plants. *Plant Cell Environ.* 25:265–274.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavellier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia* 101: 514–522.
- Meinzer, F.C., J.L. Andrade, G. Goldstein, N.M. Holbrook, J. Cavellier and P. Jackson. 1997. Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. *Plant Cell Environ.* 20: 1242–1252.
- Meinzer, F.C., S.A. James, G. Goldstein and D. Woodruff. 2003. Whole-tree water transport scales with sapwood biophysical properties in tropical forest canopy trees. *Plant Cell Environ.* 26: 1147–1155.
- Melcher, P.J., F.C. Meinzer, D.E. Yount, G. Goldstein and U. Zimmermann. 1998. Comparative measurements of xylem pressure in transpiring and non-transpiring leaves by means of the pressure chamber and the xylem pressure probe. *J. Exp. Bot.* 49:1757–1760.
- Nardini, A., S. Salleo and F. Raimondo. 2003. Changes in leaf hydraulic conductance correlate with leaf vein embolism in *Cercis siliquastrum* L. *Trees* 17:529–534.
- Phillips, N., A. Nagchaudhuri, R. Oren and G.G. Katul. 1997. Time constant for water uptake in loblolly pine trees estimated from time series of stem sap flow and evaporative demand. *Trees* 11: 412–419.
- Phillips, N., R. Oren, R. Zimmermann and S.J. Wright. 1999. Temporal patterns of water flux in trees and lianas in a Panamanian moist forest. *Trees* 14:116–123.
- Phillips, N.A., M.G. Ryan, B.J. Bond, N.G. McDowell, T.M. Hinckley and J. Čermák. 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiol.* 23: 237–245.
- Waring R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon the water conductance through the stems of old-growth Douglas-fir. *Plant Cell Environ.* 1:131–140.
- Williams, M., E.B. Rastetter, D.N. Fernandes et al. 1996. Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ.* 19: 911–927.
- Zwieniecki, M.A., L. Hutyra, M.V. Thompson and N.M. Holbrook. 2000. Dynamic changes in petiole specific conductivity in red maple (*Acer rubrum* L.), tulip tree (*Liriodendron tulipifera* L.) and northern fox grape (*Vitis labrusca* L.). *Plant Cell Environ.* 23: 407–414.