

# Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees

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## ABSTRACT

The present study examines the manner in which several whole-tree water transport properties scale with species-specific variation in sapwood water storage capacity. The hypothesis that constraints on relationships between sapwood capacitance and other water relations characteristics lead to predictable scaling relationships between intrinsic capacitance and whole-tree behaviour was investigated. Samples of sapwood from four tropical forest canopy tree species selected to represent a range of wood density, tree size and architecture, and taxonomic diversity were used to generate moisture release curves in thermocouple psychrometer chambers, from which species-specific values of sapwood capacitance were calculated. Sapwood capacitance was then used to scale several whole-tree water transport properties determined from measurements of upper branch and basal sap flow, branch water potential, and axial and radial movement of deuterated water (D<sub>2</sub>O) injected into the base of the trunk as a tracer. Sapwood capacitance ranged from 83 to 416 kg m<sup>-3</sup> MPa<sup>-1</sup> among the four species studied and was strongly correlated with minimum branch water potential, soil-to-branch hydraulic conductance, daily utilization of stored water, and axial and radial movement of D<sub>2</sub>O. The species-independent scaling of several whole-tree water transport properties with sapwood capacitance indicated that substantial convergence in plant function at multiple levels of biological organization was revealed by a simple variable related to a biophysical property of water transport tissue.

*Key-words:* capacitance; deuterated water; hydraulic conductance; plant water potential; sap flow.

## INTRODUCTION

Tropical forests are notable for their high diversity of tree species, tree architecture and phenology. In tropical trees growing in regions characterized by marked seasonality of

rainfall, features related to regulation of water utilization and water balance are key components of adaptation to the environment. Comparative studies of plant–water relations frequently rely on leaf level measurements of variables such as stomatal conductance, transpiration and water potential, which often differ markedly among co-occurring species. However, inferences drawn from leaf level measurements concerning species-specific physiological differences at the whole-plant level can be confounded by interactions among unrecognized variables operating at other scales (Meinzer & Goldstein 1996; Andrade *et al.* 1998; Meinzer 2003). It is becoming increasingly apparent that physiological behaviour is constrained by trade-offs among traits related to plant size, architecture, allometry and tissue biophysical and chemical properties (Reich, Walters & Ellsworth 1997; Enquist, Brown & West 1998; Enquist *et al.* 1999; Roderick *et al.* 1999; Enquist 2002). When variation in these traits is used to scale physiological responses and processes, considerable convergence in plant function is often revealed (Reich, Ellsworth & Bowman 1999; Meinzer 2003). For example, it has been proposed that scaling of plant vascular systems, and therefore water use, with plant size is universal (Enquist *et al.* 1998; West, Brown & Enquist 1999). Consistent with this, Meinzer, Goldstein & Andrade (2001) reported common relationships between stem diameter, sapwood area, and maximum sap flow among more than 20 co-occurring tropical forest tree species. Here we examine how several whole-tree water transport properties scale with species-specific variation in sapwood water storage capacity.

Water stored in plant tissues has long been recognized as an important factor in plant–water relations. In large trees, seasonal courses of discharge and recharge of water stored in sapwood have been measured and modelled (Waring & Running 1978; Waring, Whitehead & Jarvis 1979). Estimates of the contribution of stored water to daily transpiration vary widely, ranging from 10 to 20% (Lostau *et al.* 1996; Goldstein *et al.* 1998; Kobayashi & Tanaka 2001) to as much as 30–50% (Waring *et al.* 1979; Holbrook & Sinclair 1992). Capacitance, typically defined as the ratio of change in water content to change in water potential of a tissue, has been formally incorporated into Ohms law ana-

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logue models of water transport along the soil–plant–atmosphere continuum (Cowan 1972; Phillips *et al.* 1997). However, specific relationships between short-term cycles of capacitive discharge and recharge and the daily dynamics of stomatal behaviour, transpiration and plant water balance have not been studied until relatively recently. Capacitive exchange of water between storage compartments and the transpiration stream leads to daily fluctuations in apparent soil-to-leaf hydraulic conductance, provoking dynamic stomatal responses that maintain the balance between transpiration and hydraulic conductance, thereby limiting daily fluctuations in leaf water potential (Andrade *et al.* 1998; Meinzer 2002). Consistent with this, Williams *et al.* (1996) attributed the afternoon decline in CO<sub>2</sub> uptake in a mixed *Quercus–Acer* stand to partial stomatal closure in response to depletion of stored water, Goldstein *et al.* (1998) reported that tropical forest trees with greater water storage capacity maintained maximum rates of transpiration for a substantially longer fraction of the day than trees with smaller water storage capacity, and Lo Gullo & Salleo (1992) concluded that the amount of water stored in twigs of *Populus deltoides* was sufficient to dampen diurnal fluctuation in leaf water deficits when stress was moderate.

Estimates of capacitance obtained from *in situ* measurements on intact trees range from approximately 0.4–2 kg MPa<sup>-1</sup> for a number of coniferous and angiosperm species (Wronski, Holmes & Turner 1985; Tyree 1988; Milne 1989; Takizawa *et al.* 1996; Kobayashi & Tanaka 2001). However, it is unclear whether this range of values largely reflects intrinsic differences in the biophysical properties of the storage tissues involved or merely differences in the size of the storage compartment because none of the estimates was normalized for differences in the total volume of tissue. The present study was undertaken to assess differences in the intrinsic capacitance of sapwood among four tropical forest canopy tree species selected to represent a range of wood density, tree size and architecture, and taxonomic diversity. Our ultimate objective was to determine the extent to which tissue level differences in water

storage capacity were reflected in whole-tree water transport properties. We hypothesized that constraints on relationships between sapwood capacitance and other water relations characteristics lead to predictable scaling relationships between intrinsic capacitance and whole-tree behaviour.

## 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 a canopy crane operated by the Smithsonian Tropical Research Institute. The mean annual rainfall at the site is about 1800 mm, of which less than 150 mm normally falls during the dry season between January and April. A single individual of *Anacardium excelsum* (Bentner & Balb. ex Kunth) Skeels (Anacardiaceae), *Cordia alliodora* (R. & P) Oken. (Boraginaceae), *Ficus insipida* Willd. (Moraceae), and *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin (Araliaceae) was studied during the dry seasons (February to April) of 2000 and 2001 (Table 1). *Ficus insipida* and *S. morototoni* are evergreen, *A. excelsum* is brevideciduous and rapidly renews all of its leaves early in the dry season, and *C. alliodora* is gradually deciduous with peak leaf fall occurring between April and June. The gondola of the crane was used to gain access to the crowns and upper trunks of the study trees. Logistical constraints and the presence of only one individual each of *C. alliodora* and *S. morototoni* within the area accessible from the gondola prevented the inclusion of additional species and individuals of different sizes within a species.

### Sapwood biophysical properties

Cylinders of sapwood were obtained at about 1.2 m height with a 5-mm-diameter increment borer and sealed in glass

**Table 1.** Characteristics of the four study trees

Species	Diameter (m)	Height (m)	Basal sapwood area (m <sup>2</sup> )	Water use (kg d <sup>-1</sup> )	Sap flux density (g cm <sup>-2</sup> d <sup>-1</sup> )	Wood density (g cm <sup>-3</sup> )	$\Psi_{br}$		$P_{50}$ (MPa)
							Predawn (MPa)	Minimum (MPa)	
<i>Anacardium excelsum</i>	0.98	38	0.66	750 ± 11	114	0.39 ± 0.02	-0.39 ± 0.03	-0.74 ± 0.04	-1.56
<i>Ficus insipida</i>	0.65	28	0.31	331 ± 3	107	0.29 ± 0.04	-0.46 ± 0.05	-1.10 ± 0.02	-1.66
<i>Schefflera morototoni</i>	0.47	22	0.15	108 ± 3	72	0.28 ± 0.07	-0.33 ± 0.02	-0.61 ± 0.02	-1.68
<i>Cordia alliodora</i>	0.34	26	0.07	46 ± 1	66	0.52 ± 0.03	-0.49 ± 0.02	-1.37 ± 0.06	-3.00

Diameter and sapwood area were measured at the height of the basal set of sap flow probes. Values of whole-tree water use are means and standard error of 56–66 d of measurement. Sap flux density was calculated from water use and sapwood area values. Wood density values are means ± SE of four determinations and branch water potentials are means ± SE of measurements made on three to five leaves at each measurement time on three different days. Branch xylem pressure corresponding to 50% loss of hydraulic conductivity ( $P_{50}$ ) was estimated from Weibull functions fitted to plots of percentage loss of conductivity against xylem pressure.

vials for transport to the laboratory where they were allowed to hydrate overnight in distilled water. The following morning, the cylinders were cut into 10 mm segments, quickly blotted to remove excess water, placed in caps of thermocouple psychrometer chambers (83 series; JRD Merrill Specialty Equipment, Logan, UT, USA), weighed, and then sealed inside the rest of the chamber for determination of water potential isotherms. Each chamber contained three sapwood cylinders. The psychrometer chambers were placed in an insulated water bath and allowed to equilibrate for at least 2 h before measurements were started using a 12-channel digital psychrometer meter (85 series; JRD Merrill Specialty Equipment) operating in the psychrometric mode. Measurements were repeated at approximately 30 min intervals until the water potential values stabilized. The psychrometer chambers were then removed from the water bath and reopened to allow the sapwood to partially dehydrate. The samples were then reweighed in the psychrometer caps, resealed inside the psychrometer chambers, and allowed to equilibrate for another determination of water potential. This procedure was repeated six to seven times until the sapwood water potential reached approximately  $-2.5$  to  $-7$  MPa depending on the species. Each psychrometer was calibrated against salt solutions of known water potential. Sapwood moisture release curves were generated by plotting water potential against relative water content (Fig. 1). Data points from four to seven replicate curves per species were pooled. Sapwood relative water content (RWC) was calculated as

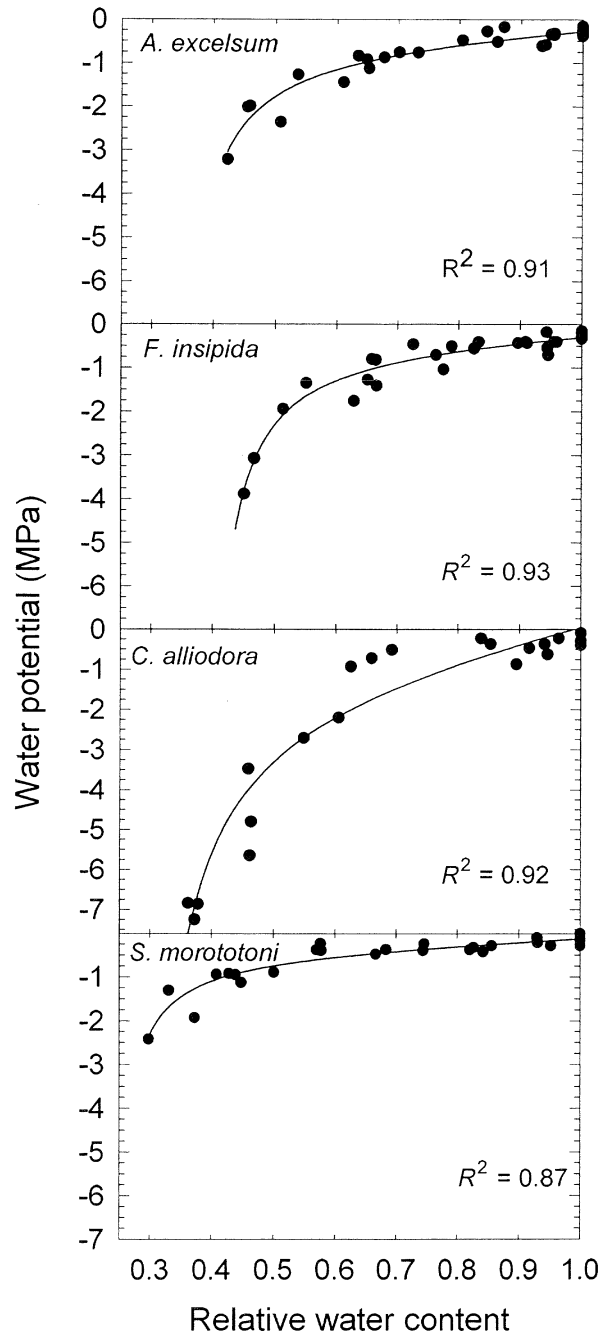
$$\text{RWC} = \frac{W_f - W_d}{W_s - W_d}$$

where  $W_s$  is the saturated weight determined after overnight hydration and blotting of excess water,  $W_f$  is the fresh weight, and  $W_d$  is the dry weight determined after oven-drying at  $70^\circ\text{C}$  for 24 h. Curves fitted to the relationships between sapwood water potential ( $\Psi_{\text{sw}}$ ) and RWC were used to calculate sapwood capacitance as described below.

Capacitance was normalized on a sapwood volume basis to facilitate comparison of absolute amounts of water released per unit decline in  $\Psi_{\text{sw}}$ . Sapwood capacitance ( $C$ ;  $\text{kg m}^{-3} \text{MPa}^{-1}$ ) was calculated as

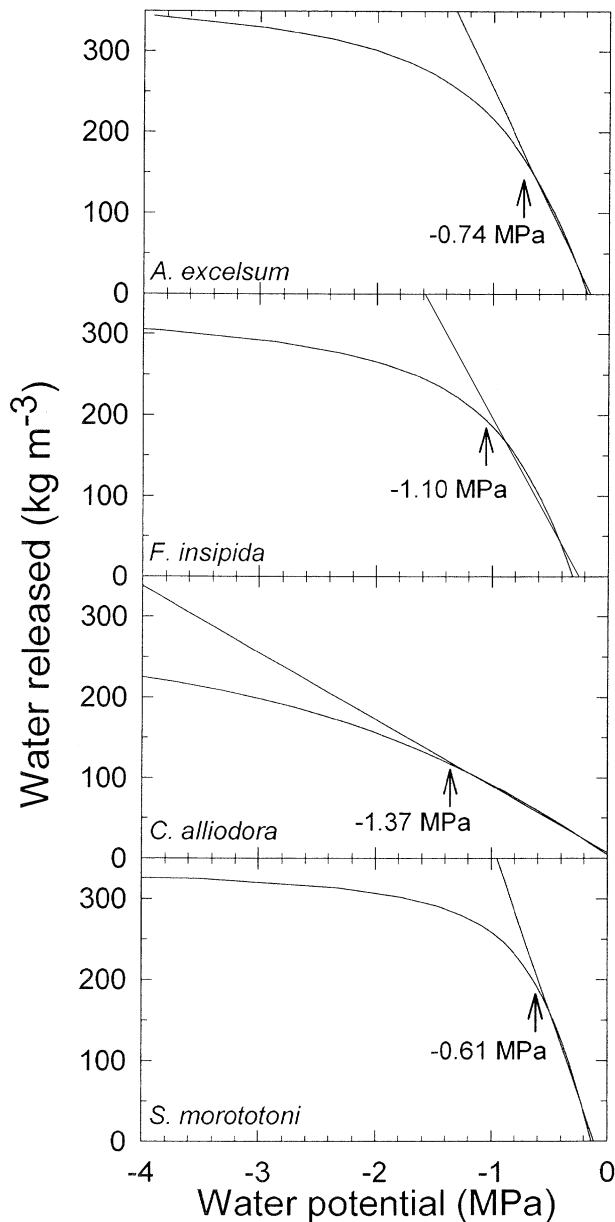
$$C = \frac{dW}{d\Psi_{\text{sw}}}$$

where  $W$  is weight of water per unit volume of sapwood. Weight of water per unit sapwood volume at saturation ( $\text{kg m}^{-3}$ ) was calculated by multiplying the saturated/dry weight ratio by sapwood density ( $\text{kg m}^{-3}$ ) and subtracting sapwood density. The cumulative weight of water released per unit sapwood volume was then calculated by multiplying the sapwood relative water deficit ( $1 - \text{RWC}$ ) at a given value of  $\Psi_{\text{sw}}$  by the weight of water per unit sapwood volume at saturation. Density was determined for small cylinders of sapwood collected as described above. Volume displacement was determined for samples of saturated tis-



**Figure 1.** Relationship between sapwood water potential and relative water content in four tropical forest canopy tree species. Curves were fitted using a hyperbolic function of the form  $y = (ax/b + x) + cx$ .

sue, which were then oven-dried. Capacitance values were determined from instantaneous slopes of plots of cumulative weight of water released against  $\Psi_{\text{sw}}$ . These plots exhibited a clear initial phase in which cumulative water release increased in a nearly linear fashion as  $\Psi_{\text{sw}}$  declined followed by a marginal increase in cumulative water released as  $\Psi_{\text{sw}}$  declined precipitously (Fig. 2). Species-specific values of



**Figure 2.** Cumulative amount of water released per unit sapwood volume as a function of sapwood water potential. Water release curves were determined from wood densities and the data presented in Fig. 1 as described in the text. Values of sapwood capacitance were estimated from the slopes of the lines fitted to the nearly linear portions of the water release curves. The arrows indicate mean daily minimum water potential of terminal branches ( $\Psi_{br}$ ) estimated from balance pressures of non-transpiring leaves.

capacitance were taken as the slope of linear regression fitted to the initial phase of each water release curve.

Vulnerability of terminal branch xylem to cavitation was determined with the air dehydration method (Tyree & Sperry 1989). The xylem pressure corresponding to 50% loss of hydraulic conductivity ( $P_{50}$ ) was estimated by fitting Weibull functions to plots of percentage loss of conductivity against xylem pressure to generate vulnerability curves.

### Whole-tree sap flow, hydraulic conductance and water storage

Sap flow was measured near the base of the trunk and in the crown of each tree with variable length heat dissipation sensors as described by James *et al.* (2002). Basal flow was measured at heights of 1.5–3.5 m with probes installed at five depths in the sapwood ranging from 1.5 to 24 cm in *A. excelsum* and *F. insipida* and 1.3–18 cm in *S. morototoni*, and four depths ranging from 1.7 to 11 cm in *C. alliodora*. The cross-sectional area of sapwood corresponding to each probe was estimated according to James *et al.* (2002). Sap flow measured with probes installed in four to six branches in the crown of each tree was taken as a surrogate for transpiration (Goldstein *et al.* 1998).

Soil-to-terminal branch hydraulic conductance per unit basal sapwood area ( $K_{sa}$ ) was calculated as

$$K_{sa} = \frac{J_s}{\Delta\Psi_{br}}$$

where  $J_s$  is mean sap flux density over the entire sapwood depth and  $\Delta\Psi_{br}$  is the difference between predawn and daily minimum water potential of terminal branches estimated with a pressure chamber from balance pressures of covered, non-transpiring leaves. The influence of capacitive exchange of water between internal storage compartments and the transpiration stream on estimates of  $K_{sa}$  was minimized by calculating  $K_{sa}$  only when lags in sap flow between the crown and the base of the tree were negligible (e.g. 1100–1400 h; see Fig. 5). Expressing hydraulic conductance on a unit sapwood area basis compensated for large differences in total sapwood area among trees (Table 1) and determining  $\Psi_{br}$  rather than  $\Psi$  of transpiring leaves eliminated the influence on tree hydraulic conductance of differences in leaf hydraulic resistance among species.

Daily utilization of stored water for transpiration was estimated from lags between crown and basal sap flow as described by Goldstein *et al.* (1998). To facilitate comparison among individuals differing in their total daily water utilization, crown and basal sap flow were first normalized with respect to their daily maximum values (e.g. Fig. 5). Initial relative utilization of water from storage during the morning was then estimated by determining the area corresponding to the lag between curves representing the initial morning rise in sap flow in the crown (transpiration) and near the base of the tree (Fig. 5). Mean initial relative utilization of stored water for four representative clear days was then further normalized by tree height for comparison with values of sapwood capacitance calculated as described above.

### Transport of deuterated water

Deuterium oxide (99.9 atom percentage D  $D_2O$ , Aldrich Chemical CO., Milwaukee, WI, USA) was injected into the base of the four trees as described by James *et al.* (2003) to assess the rate of xylem sap flow to the crown and the extent of radial water movement. Holes (5-mm-diameter, 50-mm-



deep) were drilled at an angle of 30° from horizontal down and into the trunk, 30–40 cm above ground level at 4–6 cm intervals around the circumference of the trunk. The volume of D<sub>2</sub>O was evenly distributed between the holes. D<sub>2</sub>O was injected into the trunk immediately after drilling and the holes were sealed with wood putty. Injections were initiated and completed between 0900 and 1100 h.

The presence of the D<sub>2</sub>O tracer in transpired water was detected by collecting five leaves from different regions of the crown, which were sealed within clear plastic bags and left in direct sunlight for about 30 min. Approximately 30 µL of condensed water was then collected with a 100 µL micropipette capillary and the ends were rapidly sealed with a gas torch. The baseline D<sub>2</sub>O signal in transpired water was determined by collecting samples of transpired water for 4 d prior to D<sub>2</sub>O injection. After the injection of D<sub>2</sub>O (day 0), transpired water was collected daily for 10 d, with additional collections up to 27 d after injection. In all cases, leaves were collected at 1200 h.

Xylem tissue samples were collected from all four trees to assess the radial movement of D<sub>2</sub>O during the measurement period. Samples were collected 1 d prior to injection, and on post-injection days 1 and 8. Two 5-mm-diameter wood cylinders were obtained using an increment borer at about 1.2 m. The total core length was approximately the radius of the stem, and wood segments of 2–6 cm were immediately placed in a glass vial, sealed with a rubber stopper and Parafilm, and stored at 0 °C to prevent evaporative fractionation.

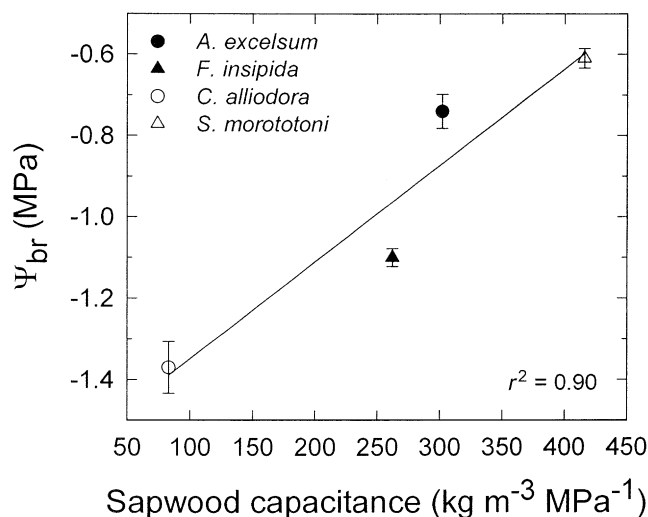
All transpired water and xylem samples were sent to Mountain Mass Spectrometry (Evergreen, CO, USA) for preparation and analysis. For each transpired and xylem water sample, two subsamples were analysed and an average value was calculated. The velocity of D<sub>2</sub>O transport was estimated as the tree height divided by the number of days required to detect the D<sub>2</sub>O tracer in transpired water.

## RESULTS

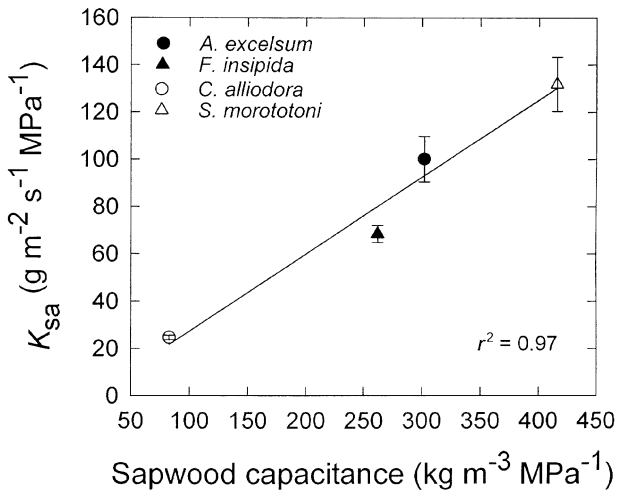
Total daily water use increased sharply with tree size from 46 kg d<sup>-1</sup> in the 0.34-m-diameter individual of *C. alliodora* to 750 kg d<sup>-1</sup> in the 0.98-m-diameter individual of *A. excelsum* (Table 1). The relative increase in daily water use with tree size was substantially greater than that of sapwood area, indicating that flow per unit sapwood area also increased as a result of changes in tree allometry (e.g. leaf area/sapwood area) or stomatal regulation of water loss. Consistent with this, total daily sap flux density was about 70% greater in *A. excelsum* than in *C. alliodora*. Although predawn  $\Psi_{br}$  was similar among the four species, daily minimum  $\Psi_{br}$  ranged from -0.61 MPa in *S. morototoni* to -1.37 MPa in *C. alliodora*. The branch xylem pressure causing 50% loss of hydraulic conductivity by cavitation was similar among *A. excelsum*, *F. insipida* and *S. morototoni*, but substantially more negative in *C. alliodora*. In all species, minimum values of  $\Psi_{br}$  were well above the threshold associated with 50% loss of xylem conductivity.

The rate of decline in  $\Psi_{sw}$  with declining RWC differed markedly among species (Fig. 1). At the extremes were *S. morototoni* and *C. alliodora*, in which a 50% reduction in sapwood RWC caused  $\Psi_{sw}$  to fall to -0.8 and -3.3 MPa, respectively. When wood density was used to normalize water release curves on a sapwood volume basis, all of the curves exhibited a clear initial phase in which cumulative water release increased in a nearly linear fashion as  $\Psi_{sw}$  declined to a threshold range of  $\Psi_{sw}$  (Fig. 2). Beyond the threshold range of  $\Psi_{sw}$ , cumulative water release increased marginally as  $\Psi_{sw}$  declined precipitously. Daily minimum  $\Psi_{br}$  for each species fell within the transition region of its sapwood water release curve where the cumulative amount of water released stopped increasing linearly and began to increase asymptotically. Therefore, sapwood capacitance was estimated as the slope of a line fitted to the initial phase of the water release curve in order to obtain a value representative of the normal physiological operating range of each species. This procedure yielded capacitance values ranging from 83 kg m<sup>-3</sup> MPa<sup>-1</sup> in *C. alliodora* to 416 kg m<sup>-3</sup> MPa<sup>-1</sup> in *S. morototoni*.

The four species shared a number of common functional relationships defined by variation in sapwood capacitance. Daily minimum  $\Psi_{br}$  increased with sapwood capacitance (Fig. 3). As a result, smaller diel fluctuations in  $\Psi_{br}$  occurred when capacitance was greater because all species had similar values of predawn  $\Psi_{br}$ . In all species, values of minimum  $\Psi_{br}$  were substantially less negative than those corresponding with P<sub>50</sub> (cf. Fig. 3 and Table 1). In contrast to the strong relationship between  $\Psi_{br}$  and sapwood capacitance, no significant relationship between the  $\Psi$  of transpiring leaves and capacitance was observed (data not shown). Soil-to-terminal branch hydraulic conductance per unit basal sapwood area ( $K_{sa}$ ), an estimate of whole-tree water transport



**Figure 3.** Mean daily minimum water potential of terminal branches ( $\Psi_{br}$ ) in relation to sapwood capacitance. Water potentials are means of four measurements on each of three days. Vertical bars represent standard errors.



**Figure 4.** Soil-to-terminal branch hydraulic conductance per unit basal sapwood area in relation to sapwood capacitance. Vertical bars represent standard errors ( $n = 3$ ).

efficiency, increased linearly with sapwood capacitance (Fig. 4). Estimates of  $K_{sa}$  were obtained when lags between crown and basal sap flow, and presumably capacitive discharge of water from sapwood storage, were minimal.

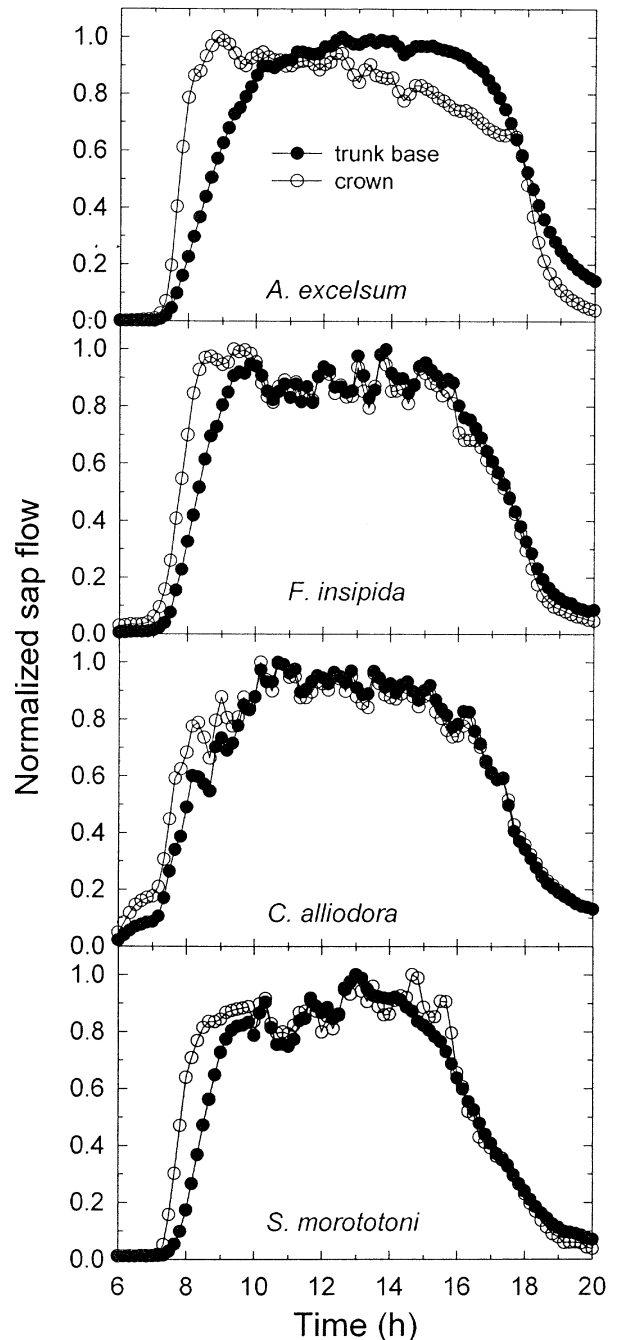
Sap flow data were normalized with respect to their maximum values to allow direct comparisons between branch and basal flow and among species. In all of the trees studied, a noticeable lag was observed between the onset of sap flow in the crown and at the base of the tree in the morning (Fig. 5). Sap flow in the crown was taken as a surrogate for transpiration in order to utilize the morning lag between crown and basal sap flow as a relative index of utilization of stored water. When the areas corresponding to the initial lags between crown and basal sap flow were further normalized by tree height, a strong positive correlation between normalized utilization of stored water and sapwood capacitance was observed (Fig. 6).

Movement of deuterated water injected into the trees as a tracer was also strongly correlated with sapwood capacitance. Tracer velocity, estimated from the tree height divided by the time elapsed between injection and detection of the tracer in the upper leaves, ranged from approximately 26–5 m d<sup>-1</sup> and declined linearly with increasing sapwood capacitance (Fig. 7). Radial penetration of D<sub>2</sub>O beyond the 5 cm injection depth was zero in *C. alliodora*, the species with the lowest sapwood capacitance, and >16 cm in *S. morototoni*, the species with the greatest capacitance.

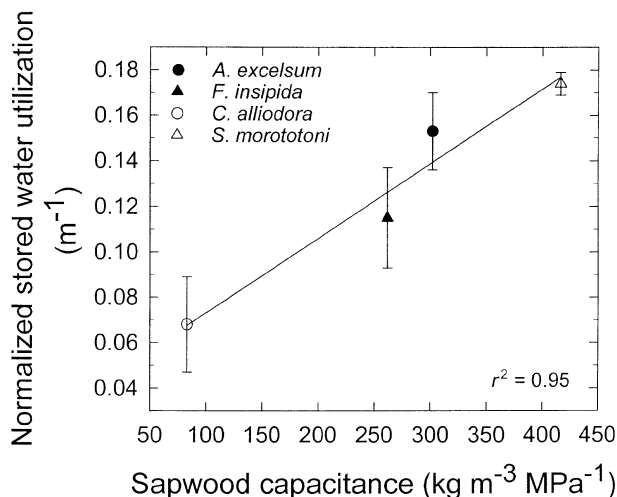
## DISCUSSION

Our results showed that several whole-tree water transport properties scaled with sapwood capacitance among the four species studied. Although strong linear relationships between sapwood capacitance and features such as branch water status, whole-tree hydraulic conductance, sap veloc-

ity and radial water movement do not necessarily imply direct mechanistic linkages, it is notable that based on the four species studied here, the scaling of these features with capacitance appeared to be species-independent. Therefore, it is possible that fundamental tissue biophysical traits such as wood density and capacitance are linked to suites



**Figure 5.** Typical daily courses of sap flow in the crown and near the base of the four study species on 21 February 2001 (*A. excelsum*), 3 March 2001 (*F. insipida*), 19 February 2000 (*C. alliodora*), and 8 February 2000 (*S. morototoni*). Crown sap flow was used as a surrogate for transpiration (see text).

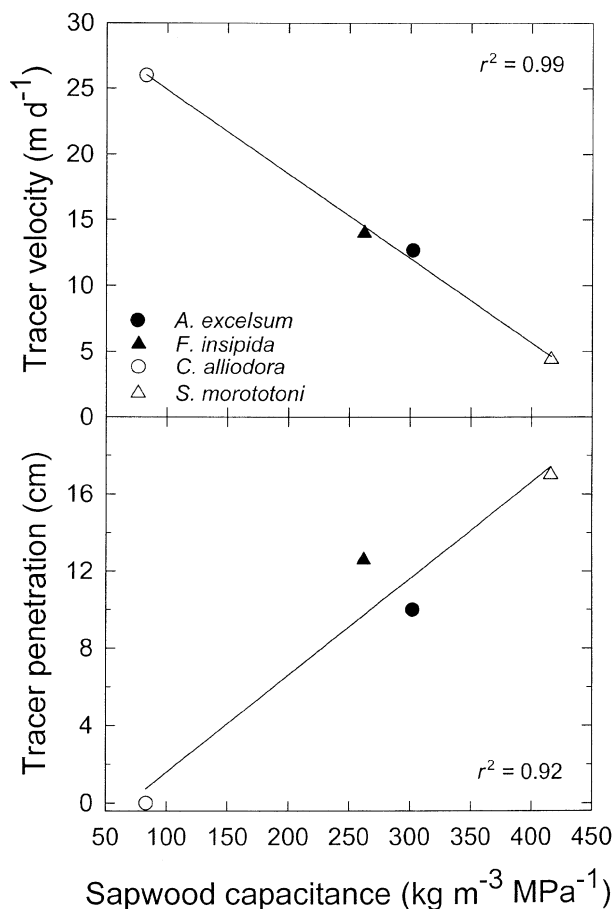


**Figure 6.** Relationship between sapwood capacitance and relative daily utilization of stored water normalized by tree height (see text for details). Vertical bars represent standard errors ( $n = 4$ ).

of other characteristics whose possible combinations are constrained by a limited number of compatible physiological solutions to a given problem of plant adaptation to the environment. In the present study, for instance, the species with the highest sapwood density, *C. alliodora* ( $0.52 \text{ g cm}^{-3}$ ), also exhibited the lowest sapwood capacitance, the least reliance on internal water storage to offset daily transpirational loss, essentially no movement of water radially through the sapwood, the lowest soil-to-branch apparent hydraulic conductance, the lowest daily minimum terminal branch water potential, and the lowest xylem vulnerability to cavitation. On the other hand, the species with the lowest wood density, *S. morototoni* ( $0.28 \text{ g cm}^{-3}$ ), exhibited the opposite extremes of the preceding suite of characteristics, implying that obligatory trade-offs may exist between wood density and a number of functional traits. Given the patterns observed, the likelihood of encountering a co-occurring species with wood density similar to that of *S. morototoni*, but water transport properties similar to those of *C. alliodora* seems low. Conversely, a co-occurring species with dense wood is unlikely to behave similarly to *S. morototoni*. However, it should be noted that the water transport properties characterized here scaled more consistently with sapwood capacitance than wood density. Appropriate variables can thus reveal convergence in functioning among taxonomically and architecturally diverse species because obligatory trade-offs and resulting constraints on suites of functional traits lead to predictable behaviour at successively higher levels of organization and integration in the plant.

The preceding interpretation is consistent with findings recently reported by a number of researchers. For example, Reich *et al.* (1997, 1999) demonstrated that universal trade-offs among fundamental leaf traits such as nitrogen content, life-span, photosynthetic capacity, dark respiration rate and leaf mass per area apply across hundreds of species

native to a wide range of biomes from the tropics to the tundra. Similarly, wood density has been shown to be an important correlate of xylem vulnerability to cavitation (Hacke *et al.* 2001), xylem hydraulic conductivity (Stratton, Goldstein & Meinzer 2000), diel variation in leaf water potential (Stratton *et al.* 2000; Meinzer 2003), and growth rates (Enquist *et al.* 1999) across a broad range of woody species. It thus appears that the greater mechanical strength and resistance to xylem cavitation associated with higher wood density may be traded off against overall water transport efficiency, internal water storage capacity to buffer diurnal fluctuations in leaf water status, and the ability to grow rapidly. In this context, it is interesting to note that fast-growing tropical forest pioneer tree species tend to have lower wood density than slower-growing mature forest species and thus should differ with regard to whole-tree water transport properties. However, *S. morototoni* and *C. alliodora*, the two species exhibiting extremes of wood density, sapwood capacitance and water transport properties in the present study, have both been classified as pioneers characteristic of young forests (Foster & Brokaw 1990). Apparent ecological groupings may thus partially conceal



**Figure 7.** Axial transport rate of  $\text{D}_2\text{O}$  tracer and radial penetration of the tracer in relation to sapwood capacitance.

convergence in functional relationships governed by plant structural and architectural traits.

The tissue storage compartments responsible for release of water during determination of sapwood moisture release curves were not identified. Water released from both elastic compartments such as parenchymatous tissue and inelastic compartments such as apoplastic capillary spaces and vessel lumens during cavitation can contribute to sapwood capacitance (Holbrook 1995). If the xylem vulnerability to cavitation of trunk sapwood was similar to that of branches (Table 1), the data shown in Fig. 2 suggest that the water released over the initial, linear portions of the moisture release curves may have been derived largely from elastic storage compartments and capillary spaces rather than cavitated vessels because the curves become distinctly non-linear at values of  $\Psi_{sw}$  well above those associated with  $P_{50}$  in branches. However, it is possible that sapwood in the trunk may have been considerably more vulnerable to cavitation than branch sapwood (Domec & Gartner 2001).

The mechanisms responsible for the striking correspondence between daily minimum branch water potential and the transition between the nearly linear and asymptotic phases of the sapwood water release curve are not known. Below these minimum values of  $\Psi_{br}$ , additional release of water from storage is marginal as  $\Psi_{sw}$  continues to decline. The nature of the internal signal involved in causing stomata to regulate minimum leaf  $\Psi$  at a value that results in  $\Psi_{br}$  falling within the transitional region of the sapwood moisture release curve is unclear. It has been suggested that cavitation may generate a hydraulic signal to which stomata respond (Salleo *et al.* 2000), but this seems unlikely under the conditions of the present study because  $\Psi_{br}$  remained well above levels corresponding to  $P_{50}$ . If elastic parenchymatous tissue represents a significant sapwood water storage compartment, it is possible that dehydration of this tissue to a critical turgor or volume threshold may generate or release a chemical signal that enters the transpiration stream, causing a stomatal response. However, this scenario remains to be evaluated.

Although the decline in  $D_2O$  tracer velocity and the increase in its radial penetration with increasing sapwood capacitance seemed intuitively reasonable (Fig. 7), their anatomical and structural bases were not clear. More efficient radial hydraulic communication in sapwood with higher capacitance may have been associated with more abundant pit pairs in tangential vessel walls or with the arrangement and abundance of ray tissue. With regard to axial water movement, the Hagen–Poiseuille law predicts that maximum sap velocity should increase sharply with vessel diameter if the driving force for water movement remains constant. In *C. alliodora* and *S. morototoni*, the two individuals in which tracer velocity was highest and lowest, respectively, mean vessel lumen diameter was similar (approximately 150  $\mu\text{m}$ ) near the base of the trunk, but twice as great in *C. alliodora* at a height of 16 m (James *et al.* 2003). Furthermore, the overall driving force for water movement was roughly three times greater in *C. alliodora* than in *S. morototoni* (Table 1). However, the apparent

qualitative agreement between tracer velocity and the Hagen–Poiseuille law does not preclude a direct effect of sapwood capacitance on tracer velocity mediated via transient sequestering of  $D_2O$  in and its subsequent release from tissue storage compartments. The tracer velocity of 26  $\text{m d}^{-1}$  in *C. alliodora* points to the difficulty of estimating maximum sap velocity from rates of sap flow measured with common techniques such as heat dissipation (Granier 1987) and heat pulse (Marshall 1958). For example, when total daily sap flux density in *C. alliodora* (Table 1) is expressed as a volume per area then divided by the fraction of vessel lumen area in relation to total sapwood area (approximately 0.1–0.25; James *et al.* 2003) to estimate sap velocity, the resulting value is still less than one-third of the measured tracer velocities. The range of maximum sap velocity inferred from tracer measurements implies that a chemical signal travelling from the roots to the crown in the transpiration stream would have arrived in 1 d or less in *C. alliodora*, 2 d in *F. insipida*, 3 d in *A. excelsum*, and 5 d in *S. morototoni*. Given the rate at which variables such as soil water deficit are expected to change, the magnitude of sap velocity in the trees studied seems sufficient to allow chemical signalling, along with hydraulic signalling, to contribute to integration of leaf physiology with changes in the soil environment.

The results of the present study suggest that a simple variable related to tissue biophysical properties can reveal substantial convergence in plant function at multiple levels of biological organization. Comparative studies of whole-plant behaviour would therefore benefit from consideration of the constraints that tissue anatomical, structural and biophysical features place on physiological functioning. At a minimum, it would be useful for comparative studies of plant performance to include simultaneous measurements over a range of scale, and sufficient information on plant size, allometry and tissue biophysical properties to allow the observed responses and behaviour to be normalized to facilitate comparisons across species both within and among independent studies.

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