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Regulation of water flux through trunks, branches, and leaves in trees of a lowland tropical forest

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Abstract We studied regulation of whole-tree water use in individuals of five diverse canopy tree species growing in a Panamanian seasonal forest. A construction crane equipped with a gondola was used to access the upper crowns and points along the branches and trunks of the study trees for making concurrent measurements of sap flow at the whole-tree and branch levels, and vapor phase conductances and water status at the leaf level. These measurements were integrated to assess physiological regulation of water use from the whole-tree to the single-leaf scale. Whole-tree water use ranged from 379 kg day^{-1} in a 35 m-tall *Anacardium excelsum* tree to 46 kg day^{-1} in an 18 m-tall *Cecropia longipes* tree. The dependence of whole-tree and branch sap velocity and sap flow on sapwood area was essentially identical in the five trees studied. However, large differences in transpiration per unit leaf area (E) among individuals and among branches on the same individual were observed. These differences were substantially reduced when E was normalized by the corresponding branch leaf area:sapwood area ratio (LA/SA). Variation in stomatal conductance (g_s) and crown conductance (g_c), a total vapor phase conductance that includes stomatal and boundary layer components, was closely associated with variation in the leaf area-specific total hydraulic conductance of the soil/leaf pathway (G_t). Vapor phase conductance in all five trees responded similarly to variation in G_t. Large diurnal variations in G_t were associated with diurnal variation in exchange of water between the transpiration stream and internal stem storage compartments. Differences in stomatal regulation of transpiration on a leaf area basis appeared to be governed largely by tree size and hydraulic architectural features rather than physiological differences in the responsiveness of stomata. We suggest that reliance on measurements gathered at a single scale or inadequate range of scale may result in misleading conclusions concerning physiological differences in regulation of transpiration.

Key words Hydraulic conductance · Sap flow · Stomata · Transpiration · Tropical forest trees

Introduction

Estimates of whole-tree water use in both tropical (Granier et al. 1992, 1996; Becker 1996; Wullschleger et al. 1998) and temperate (Granier 1987; Kelliher et al. 1992; Köstner et al. 1992; Bréda et al. 1995; Barrett et al. 1996; Wullschleger et al. 1998) species have become more numerous in the last decade with the advent of reliable and inexpensive methods for measuring sap flow in large trees (e.g., Granier 1985). Total daily sap flow is often strongly correlated with tree-size-related characteristics such as basal area and sapwood area, both within species (Köstner et al. 1992; Vertessy et al. 1995; Becker 1996; Haydon et al. 1996) and among similar co-occurring species (Vertessy et al. 1995). These relationships are useful for predicting stand-level water use in forests with relatively few dominant species. However, a similar dependence of water use on tree size among

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diverse species raises questions concerning the scale at which species-specific differences in physiological regulation of water use become apparent.

Few studies have attempted to assess the mechanisms causing similarities in regulation of water use at the tree level to diverge at the leaf level. In larger trees, this would require integrated, concurrent measurements at a minimum of three scales: (1) whole-tree sap flow near the base of the trunk; (2) sap flow in upper branches as a surrogate for transpiration; and (3) measurements of stomatal conductance or resistance in individual representative leaves by a technique such as porometry. Measurements at the two extremes of scale, porometry in single leaves, and sap flow near the base of the stem, will not suffice. For example, the porometer alters the ratio of stomatal to boundary layer conductance resulting in overestimates of transpiration (Jarvis and McNaughton 1986; Meinzer et al. 1993, 1995, 1997), and the relationship between transpiration and sap flow near the base of the trunk may be confounded by withdrawal of water from internal storage above the measurement point (Schulze et al. 1985; Goldstein et al. 1998).

In saplings and small trees, the mass flow rate of water near the base of the stem is essentially equivalent to transpiration. In larger trees, however, exchange of water between the transpiration stream and stem storage compartments may result in a considerable lag period between fluctuations in transpiration and fluctuations in sap flow near the base of the stem thereby precluding use of the daily course of basal sap flow as a surrogate for the daily course of transpiration (Schulze et al. 1985; Loustau et al. 1996; Martin et al. 1997; Saugier et al. 1997; Goldstein et al. 1998). Nevertheless, even in large trees total daily transpiration should be equivalent to total sap flow measured near the base of the trunk provided no substantial net change in whole-tree water content has occurred over a diurnal cycle.

Concurrent measurements of sap flow in upper branches and near the base of the stem can be exploited to characterize both the quantity of water withdrawn daily from internal storage, and the dynamics of exchange of water between the transpiration stream and storage compartments. Estimates of stem water storage obtained in this manner range from about 10% to 25% of total daily transpiration (Goldstein et al. 1998), but relationships between diurnal water storage capacity and tree size, and the potential impact of stem water storage on stomatal regulation of transpiration are not well established.

There is substantial evidence that stomatal conductance and transpiration are positively correlated with the hydraulic conductance of the soil/root/leaf pathway in a wide range of plant species and growth forms (Aston and Lawlor 1979; Küppers 1984; Meinzer et al. 1988; Reich and Hinckley 1989; Meinzer and Grantz 1990; Sperry and Pockman 1993; Meinzer et al. 1995). A close coordination between vapor and liquid phase conductance can restrict variation in daily minimum leaf water potential under a wide range of conditions (Whitehead et al. 1984; Meinzer et al. 1992), thereby limiting the utility of leaf water potential as a predictor of stomatal conductance and transpiration. The influence of plant and soil hydraulic properties on water use and stomatal behavior in large trees has scarcely been examined. It has recently been postulated that growth and maximum tree height may be limited by increasing total axial hydraulic resistance (Ryan and Yoder 1997). Whitehead and Jarvis (1981) have proposed that developmental adjustment of tree architectural features such as the ratio of leaf area to sapwood area serves to balance tree and stand transpiration with tree and stand hydraulic properties, leading to relative homeostasis of leaf water status, but this hypothesis remains to be tested over a wide range of species and conditions.

In this study, we have made concurrent, independent measurements of basal and mid-stem sap flow, transpiration from upper branches, stomatal and total vapor phase conductances, and leaf water status of individual trees of contrasting species from a lowland tropical forest. Our objectives were to determine the relationships between sap flow and sapwood area in trunks and branches of these species, to characterize coordination of vapor phase and liquid phase water transport properties, and to assess the influence of scale on the interpretation of patterns of regulation of water use among species by integrating measurements made at the whole-tree, branch, and leaf levels.

Materials and methods

Field site and plant material

The study was conducted from January through March, 1996 in the Parque Natural Metropolitano (8°58′N, 79°34′W, altitude *c.* 50 m) near Panama City, Panama. The site supports a secondary seasonal tropical forest, with a mean annual rainfall of about 1800 mm and a dry season from mid-December through April, during which about 8% of the annual rainfall occurs. However, total rainfall from January through April 1996 was 377 mm, more than 200% above normal.

A 45-m-tall construction crane with a horizontal jib of 51 m, and equipped with a gondola, was used to access the trunk and branches of the study trees. The gondola, which could reach 8100 m^2 of forest canopy, was raised up above and then lowered into the crowns of the study trees, making the branches and leaves easily approachable. One individual of each of five contrasting tree species were selected for study (Table 1). *Anacardium excelsum* (Bert. & Balb.) Skeels, Anacardiaceae, is an abundant tree that renews all its leaves in the early dry season. *Cecropia longipes* Pitt., Moraceae, is a pioneer tree which has broad leaves, and frequently houses myrmecophilous ants. *Ficus insipida* Willd., Moraceae, is an evergreen tree, abundant in young forests, *Luehea seemannii* Tr. & Planch., Tiliaceae, a pioneer species that is common in both young and mature forests, and *Spondias mombin* L., Anacardiaceae, is normally deciduous during the dry season, but had its full complement of leaves when measurements were carried out during the wetter than normal January of 1996.

Sap flow measurements

Sap flow was measured using the constant heating method described by Granier (1985, 1987). Pairs of 20-mm-long 2-mm

Table 1 Morphological and water use characteristics of the study trees. Sapwood area and maximum sap flow were measured at the base of the tree. Values for maximum g_c and sap flow rates are means ± SE ($n = 6$ to 8) (*DBH* diameter at breast height)

Species	DBH (cm)	Height (m)	Sapwood area (m^2)	Daily total sap flow ($kg\ d^{-1}$)	Maximum Sap flow rate ($kg\ h^{-1}$)	Maximum g_c ($mmol\ m^{-2}\ s^{-1}$)
Anacardium excelsum	101.8	35	0.51	379.0	47.7 ± 2.4	35 ± 2
Ficus insipida	56.7	30	0.21	164.0	21.7 ± 0.4	211 ± 16
Luehea seemannii	38.2	29	0.10	129.0	13.7 ± 0.8	192 ± 24
Spondias mombin	33.1	23	0.06	80.0	8.9 ± 0.2	178 ± 36
Cecropia longipes	19.7	18	0.02	46.5	7.4 ± 0.6	125 ± 6

diameter temperature probes (UP GmbH, Munich, Germany) were installed at various locations on the trees including about 1.5 m height near the base of the trunk, several meters farther up the trunk, in each of three to four exposed branches (averaging 5 cm in diameter) per tree, and in some cases at near the bases of major branches just above their intersection with the trunk. The upper (downstream) probe was continuously heated with a constant current power supply (UP GmbH) while the lower unheated probe measures the reference temperature of the wood. The protruding portions of both 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 datalogger (CR21X, Campbell Scientific Corp., Logan, ut., USA) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and 10-min averages were stored in a solid-state storage module (SM196, Campbell Scientific). Technical constraints associated with availability of instrumentation and maneuvering the crane's gondola precluded concurrent measurements in more than one tree at a time. Sap flow velocity was calculated from the temperature difference between the probes using an empirical relationship developed by Granier (1985). Mass flow of sap was obtained by multiplying flow density by the sapwood cross-sectional area. Sapwood cross-sectional area was determined by dye injections (0.1% indigo carmine) in the main trunk and comparable branches. Cores were extracted after injection and the colored sapwood measured to calculate the cross-sectional area. Leaf area distal to the sap flow probes was determined by multiplying the total number of leaves by the average area per leaf obtained from a subsample from 50–200 leaves removed randomly from each branch (for *C. longipes* ten leaves were removed from the tree). Leaf area was measured using a portable area meter (LI-3000, Li-Cor, Inc., Lincoln, Nel., USA). Transpiration (*E*) was determined as sap flow per unit leaf area through individual upper branches.

Conductances

Stomatal conductance (g_s) was measured with a steady-state porometer (LI-1600, Li-Cor) in five to six leaves representative of the full range of light-exposure on each of the branches fitted with sap flow sensors. Measurements were made between 1000 and 1600 hours during each of the 3–5 days of measurements on a given tree, and three to five complete sets of measurements (45–100) were obtained per day.

Crown conductance (g_c) was calculated as

$$g_c = \frac{EP}{V_a} \tag{1}$$

where P is atmospheric pressure and V_a is the vapor pressure difference between the leaf interior and the bulk air calculated from the saturation vapour pressure at leaf temperature and the ambient vapour pressure. Leaf temperature was measured with fine wire copper-constantan thermocouples attached with porous, paper adhesive tape to the abaxial surface of each of six leaves on each of the branches fitted with sap flow sensors. Temperatures were recorded continuously and 10-min averages stored using the data logging system described above. Ambient vapor pressure was calculated from measurements of relative humidity and temperature made with shielded sensors (HMP35C, Campbell Scientific) at an automated weather station installed in the upper canopy at the crane site. Values of g_c are expressed on a unit leaf area basis.

Total leaf area-specific hydraulic conductance of the soil/leaf pathway (G_t) of the branches fitted with sap flow probes was determined as

$$G_t = \frac{E}{\Delta\Psi} \tag{2}$$

where $\Delta\Psi$ is the difference between soil water potential and leaf water potential at a given time. It was not necessary to apply a height correction to account for variation in the gravitational component of Ψ because differences in Ψ measured at the same height within each tree rather than absolute values were used to calculate G_t. Predawn leaf water potential was used as an approximation of soil water potential. Leaf water potential was measured psychrometrically at 0600 (predawn), 0900, 1200, and 1500 hours. Small leaf discs were rapidly excised with a cork borer and sealed in chamber psychrometers (75 Series, J.R.D. Merrill Specialty Equipment, Logan, Ut., USA). The chambers were transported to the laboratory and placed in a water bath inside an insulated box and allowed to equilibrate for 3–5 h. Measurements were taken with a 12-channel digital microvoltmeter (85 series, JRD Merrill Specialty Equipment) in the psychrometric mode. The psychrometers were calibrated regularly with salt solutions of known water potential.

In addition to G_t, a dimensionless index of potential branch architectural constraints on water supply in relation to transpirational demand was obtained for each branch fitted with sap flow sensors by dividing the total leaf area distal to the sensors by the sapwood area at the point of sensor installation (LA/SA). The ratio LA/SA was used to normalize values of g_c and E. It is roughly equivalent to the so-called Huber value, originally defined as the cross sectional xylem area divided by the fresh weight of the leaves distal to point of xylem area measurement (Zimmermann 1978).

Results

Average total daily sap flow varied about 8-fold from 46.5 kg day^{-1} in *C. longipes*, the smallest tree, to 379.0 kg day^{-1} in *A. excelsum*, the largest tree (Table 1). Both total daily sap flow and maximum sap flow rates at the bases of the five trees were positively correlated with dbh (both with $r = 0.99$, $P < 0.001$; Table 1). Maximum values of crown conductance (g_c) averaged 148 mmol m^{-2} s^{-1} for the five trees and were highest in *Ficus insipida*, which also showed the highest average stomatal conductance (g_s) during the high-light hours (1000–1300 hours), and lowest for *A. excelsum*, which showed the lowest average g_s (Tables 1 and 2).

Average sapwood area (SA) of upper branches in which sap flow was measured ranged from about 11 cm^2 in *Luehea seemannii* and *Spondias mombin* to 15–19 cm^2

Table 2 Morphological and water use characteristics of upper branches of the study trees. Values of stomatal conductance (g_s) are averages of those recorded between 1000 and 1300 hours under high irradiance conditions. Values of maximum transpiration (E) obtained from branch sap flow measurements and g_s are means ± SE ($n = 6$ to 8 daily maximum E values or 6–10 sets of g_s measurements)

Species	Branch	Sapwood area (cm^2)	Leaf area (m^2)	Leaf area / Sapwood area (m^2/cm^2)	Maximum E (mmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})
Anacardium excelsum	1	13.8	18.92	1.37	0.42 ± 0.02	140 ± 14
	2	14.9	17.45	1.17	0.31 ± 0.00	126 ± 13
	3	16.2	20.95	1.29	0.36 ± 0.01	218 ± 90
Ficus insipida	1	16.2	4.11	0.25	3.57 ± 0.26	458 ± 41
	2	23.3	5.04	0.22	4.85 ± 1.56	426 ± 44
	3	16.8	5.35	0.32	2.05 ± 0.11	498 ± 33
	4	19.2	7.05	0.37	3.69 ± 0.61	583 ± 47
Luehea seemannii	1	11.1	4.73	0.42	1.02 ± 0.08	566 ± 30
	2	12.0	4.57	0.38	1.25 ± 0.24	484 ± 41
	3	8.5	2.38	0.28	3.61 ± 0.40	487 ± 44
	4	13.1	3.28	0.25	2.03 ± 0.23	493 ± 45
Spondias mombin	1	12.0	2.82	0.24	3.85 ± 0.15	454 ± 28
	2	8.3	2.30	0.28	2.03 ± 0.03	468 ± 36
	3	11.6	7.56	0.65	1.66 ± 0.08	460 ± 31
	4	11.4	4.29	0.38	1.09 ± 0.03	516 ± 58
Cecropia longipes	1	16.6	5.23	0.31	1.54 ± 0.07	377 ± 48
	2	15.5	3.98	0.26	1.67 ± 0.28	433 ± 23
	3	16.7	7.41	0.44	0.85 ± 0.10	435 ± 15

in *A. excelsum*, *C. longipes* and *F. insipida* (Table 2). The relative variation in leaf area (LA) of these branches was greater than that of SA. Leaf area ranged from about 19 m^2 per branch in *A. excelsum* to 5 m^2 in the remaining species. Consequently, average LA/SA for *A. excelsum* was 3–4 times that of the other four species. There was also substantial variation in upper branch SA, LA, and therefore LA/SA, within individuals. In *S. mombin*, for example, LA/SA of branch 3 was 2.7 times greater than that of branch 1.

Maximum transpiration per unit leaf area (E) on similar sunny days (Table 2) was significantly different among most of the trees ($P < 0.05$) and ranged from 0.36 mmol m^{-2} s^{-1} in *A. excelsum* to 3.54 mmol m^{-2} s^{-1} in *F. insipida*. *L. seemannii* and *S. mombin* showed intermediate, similar values of E, averaging 2.1 mmol m^{-2} s^{-1}. Both maximum E and g_s under high light conditions appeared to be negatively correlated with LA/SA.

Maximum sap velocity initially decreased sharply, then more gradually with increasing branch and trunk sapwood area (Fig. 1). The dependence of sap velocity on SA from the upper branch to the whole-tree scale appeared to be essentially identical in the five trees studied. On a whole-tree basis, basal sapwood area and total daily sap flow both increased exponentially with tree height (Fig. 2).

Large differences in E observed among branches of the same individual were substantially reduced when E was normalized by LA/SA. In *S. mombin*, for example, all four study branches exhibited similar daily courses of E, but average rates were about 2.5 times greater in the branch with the highest rates than in the branch with the lowest rates (Fig. 3A). After normalizing E by the corresponding value of LA/SA for each branch, average E was only about 1.5 times greater in the branches with the highest E (Fig. 3C). Transpiration rates for branches of *L. seemannii* showed a similar convergence after normalizing by their corresponding values of LA/SA (Fig. 3B, D).

A comparison of daily courses of E determined on comparable, clear days indicated that variation in E among trees was even larger than that within trees (Fig. 4A). Average midday E was greatest in *F. insipida* (*c.* 2 mmol m^{-2} s^{-1}) and smallest in *A. excelsum* (*c.* 0.4 mmol m^{-2} s^{-1}). Normalizing E by corresponding branch LA/SA values again caused daily courses of transpiration to converge, except during the early

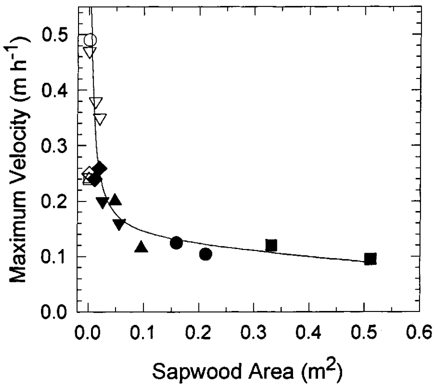

Fig. 1 Maximum sap velocity in relation to sapwood area in trunks (*closed symbols*) and branches (*open symbols*) of the five study species: *Anacardium excelsum* (■ □), *Cecropia longipes* (◆ ◇), *Ficus insipida* (● ○), *Luehea seemannii* (▲ △), and *Spondias mombin* (▼ ▽). *Points* are means of maximum values on 3 representative clear days

morning when E briefly attained maximum values in *S. mombin* and *F. insipida* (Fig. 4B).

Variation in the vapor phase conductances, g_c and g_s, was closely associated with variation in the leaf area-specific total hydraulic conductance of the soil/leaf pathway, G_t (Fig. 5A & B). In each case, a single function appeared to describe the relationship between vapor and liquid phase conductance for all individuals. The results presented in Fig. 5 also reflect diurnal variation in liquid and vapor phase conductance. Concurrent data for determination of both vapor and liquid phase conductance were available at 0900, 1200, and 1500 hours for *F. insipida* and *L. seemannii*, at 0900 and 1200 hours for *C. longipes*, at 1200 and 1500 hours for *A. excelsum*, and only at 1200 hours in *S. mombin*. Hydraulic conductance was highest at 0900 hours and lowest at 1500 hours. In *F. insipida*, for example, G_t was 5.7 mmol m^{-2} s^{-1} at 0900 hours and 2.7 mmol m^{-2} s^{-1} at 1500 hours.

Diurnal variation in G_t was associated with diurnal variation in the difference between sap flow measured in the upper crown and at the base of the trees (Fig. 6). If sap flow in the upper crown is taken to be a surrogate for transpiration, then the difference between crown and basal sap flow reflects the magnitude of water exchange between the transpiration stream and storage in the stem (Goldstein et al. 1998). When this difference is positive, a fraction of transpired water is being derived from internal storage. When the difference is negative, internal storage is partially depleted and being recharged. Thus G_t was high when water was being withdrawn from internal storage and low when internal storage was being recharged.

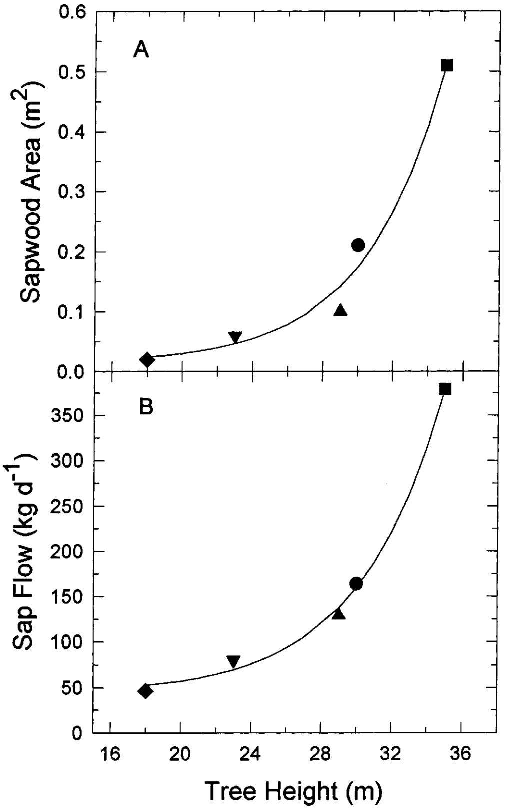

Fig. 2 A Sapwood area and **B** total daily sap flow in relation to tree height for the five study species. Points in **B** are means of daily totals for 3 representative clear days. *Symbols* as in Fig. 1

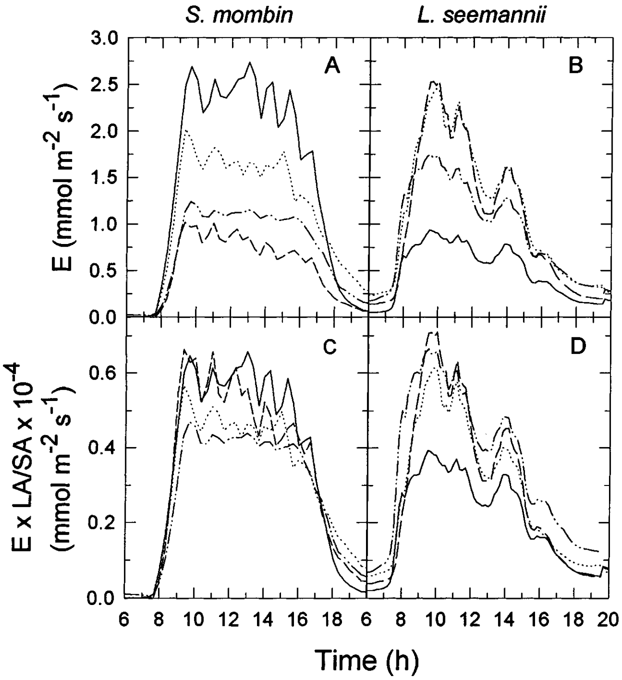

Fig. 3A, B Representative daily courses of transpiration (E) and **C, D** transpiration normalized by the leaf area:sapwood area ratio (LA/SA) for four upper branches of *L. seemannii* and *S. mombin*. Total leaf area, sapwood area, and LA/SA values are given in Table 2

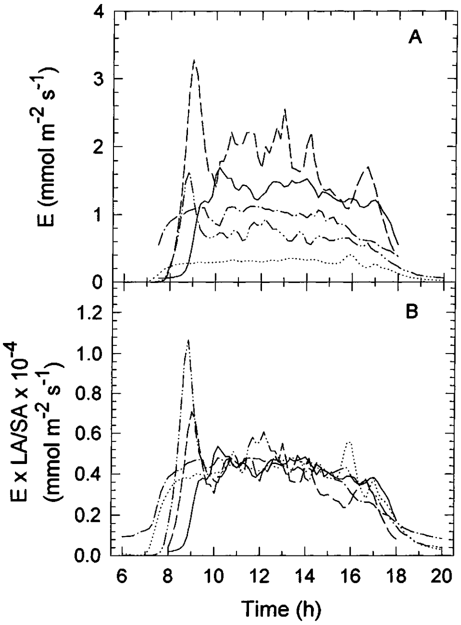

Fig. 4 A Representative daily courses of upper branch transpiration (E), and **B** transpiration normalized by the leaf area:sapwood area ratio (LA/SA) for *A. excelsum* (· · ·), *C. longipes* (——), *F. insipida* (– – –), *L. seemannii* (—·—), and *S. mombin* (—··—). *Lines* are means of three to four branches

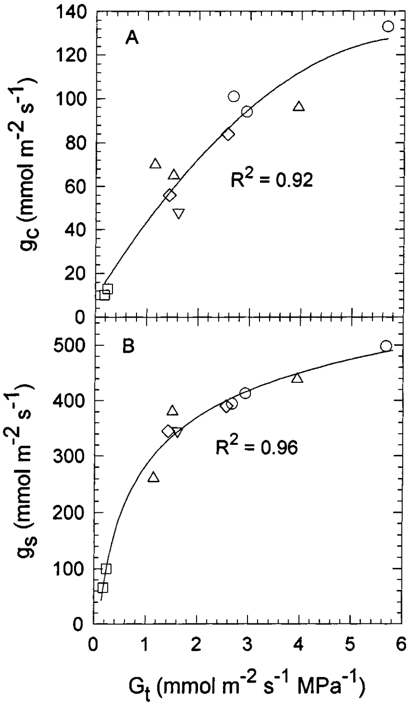

Fig. 5 **A** Crown conductance (g_c) and **B** stomatal conductance (g_s) in relation to leaf area-specific total hydraulic conductance of the soil-root-leaf pathway (G_t) for the five tree species. *Symbols* as in Fig. 1. Multiple points for a given species represent measurements obtained at different times of the day (0900, 1200, or 1500 hours)

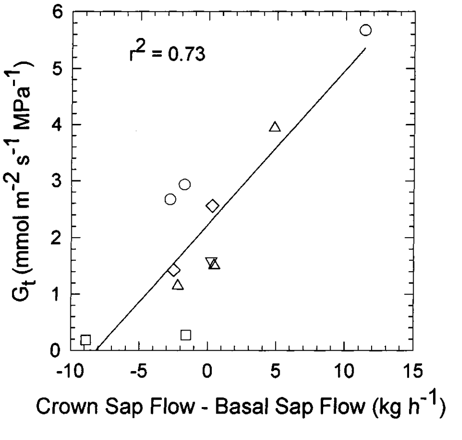

Fig. 6 Leaf area-specific hydraulic conductance (G_t) in relation to the difference between crown sap flow and basal sap flow. *Symbols* as in Fig. 1

Variation in G_t among individuals was negatively correlated with variation in LA/SA (Fig. 7). The exact shape of the relationship between G_t and LA/SA was difficult to discern because data obtained from three of the five individuals studied were clustered around intermediate values of G_t. Nevertheless, G_t appeared to initially decline sharply, then more gradually with increasing LA/SA. Predawn leaf water potential ranged from about −0.35 to −1.2 MPa among the five species studied. No dependence of g_c on leaf water potential was detected over this range. When g_c was normalized by

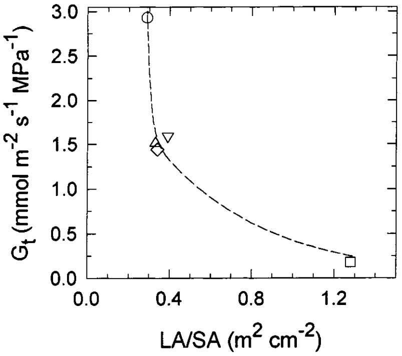

Fig. 7 Leaf area-specific hydraulic conductance (G_t) in relation to mean branch leaf area:sapwood area ratio (LA/SA). *Symbols* as in Fig. 1

LA/SA, its lack of dependence on leaf water potential became even more apparent (data not shown).

Discussion

Our results raise a number of questions concerning the choice of appropriate scales for comparing ecophysiological behavior among individuals of both different and the same species. Reliance on an inappropriate scale or an inadequate range of scale may result in misleading conclusions regarding intrinsic physiological differences in regulation of processes such as transpiration. In the present study, for example, individuals of five contrasting species differing markedly in size, tree architecture, and phylogeny, exhibited a common relationship between sap flow, sapwood area and tree size (Figs. 1 and 2). Thus, at this range of scale, from basal to branch sapwood area, intrinsic physiological differences in the regulation of transpiration were not detected. Only when transpiration was scaled to a unit leaf area basis did apparent differences among species, and even among branches within the same individual, emerge.

Differences in transpiration at the single leaf level were associated with variation in G_t to which stomata of all species responded similarly (Fig. 5). Two major components of variation in G_t, LA/SA (Fig. 7) and exchange of water between internal storage compartments and the transpiration stream (Fig. 6), were consequences of variation in branch architecture and tree size. Furthermore, stomata of these five species responded similarly to variation in evaporative demand when g_s was normalized for variation in LA/SA (Meinzer et al. 1997). Thus, differences in stomatal regulation of transpiration on a leaf area basis among and within trees appeared to be governed largely by tree size and architectural features rather than physiological differences in the responsiveness of stomata to variables affecting their aperture.

Despite the convergence of behavior observed at the whole-tree and branch scales, conclusions derived from measurements on a single individual of each of five species must be regarded as preliminary. The extent to which the observed relationships would persist under conditions beyond those prevailing in our study is not known. The dependence of transpiration on sapwood area and tree height may differ in the same co-occurring species growing in other sites and in additional species with different functional traits such as drought-deciduousness, especially when soil water is more limiting. For example, rainfall was about 250% above normal for the dry season period during which our results were obtained. It is possible that under drier conditions transpiration-sapwood area and transpiration-tree height relationships would be distinct for each species. This would certainly be true for *S. mombin*, which is normally deciduous earlier during the dry season.

The close coordination between vapor and liquid phase water transport properties in individuals of the five tropical forest tree species studied (Fig. 5) suggests that stomata of all five trees responded similarly to changes in water transport efficiency on a leaf area basis. Stomatal adjustments to changing G_t appeared to balance E with water transport efficiency rather than bulk leaf water status. Comparable relationships between vapor and liquid phase conductance have been observed in sugarcane (Saliendra and Meinzer 1989), the riparian tree *Betula occidentalis* (Sperry and Pockman 1993), and five woody tropical forest gap colonizing species (Meinzer et al. 1995).

The mechanisms linking g_s, g_c and therefore transpiration, to variation in G_t are not known. It has been proposed that chemical signals transported from the roots to the leaves may be responsible for coordination of g_s with hydraulic conductance during plant development (Meinzer and Grantz 1990; Meinzer et al. 1991), or during progressive soil drying (Davies and Zhang 1991; Tardieu and Davies 1993). In tall trees, however, transport of chemical signal from the roots to the upper leaves may take several days because maximum sap velocities in the main stem are often less than 0.5 m h^{-1} (Granier 1987; Dye et al. 1996; Zang et al. 1996). Furthermore, the rapidity and reversibility of responses of g_s to perturbation of the hydraulic pathway or to soil drying in some woody species seems inconsistent with regulation of g_s by chemical signals generated in the roots. For example, stomata of *Abies amabilis* seedlings responded within a few minutes to alterations in the hydraulic pathway in the absence of changes in bulk leaf water status (Teskey et al. 1984). In seedlings of other tree species, reductions in g_s arising from soil drying (Fuchs and Livingston 1996) and reduced hydraulic conductance (Saliendra et al. 1995) were rapidly reversed when roots sealed in a chamber were pressurized. Finally, Whitehead et al. (1996) observed a rapid increase in g_s of up to 60% in upper, illuminated needles of *Pinus radiata* trees when the leaf-specific hydraulic conductivity of the illuminated leaves was increased by covering the lower 78% of the foliage. Based on these responses, it has been suggested that rapidly propagated hydraulic perturbations could trigger the release of chemical regulators of g_s directly within the leaves (Whitehead et al. 1996).

Consistent with the above observations, variation in g_s and g_c was also closely associated with short-term variation in G_t (Fig. 5) apparently arising from diurnal depletion and recharge of internal water reserves in the stems (Fig. 6). Exchange of water between the transpiration stream and internal storage compartments was assessed from simultaneous measurements of sap flow in the upper crowns and at the bases of the trees. Using this method with the same group of trees studied in the present work, Goldstein et al. (1998) observed that on clear days, withdrawal of transpirational water from internal stores was maximal by about 0900 hours with recharge of internal stores beginning in the late morning or early afternoon, and that withdrawal of water from and recharge of internal stores was a dynamic process, tightly coupled to variations in environmental conditions. All five trees conformed with a common linear relationship between diurnal water storage capacity and basal sapwood area and a common exponential relationship between diurnal water storage capacity and tree height.

Variation in LA/SA was also likely to have contributed to variation in G_t. When E was normalized by LA/SA, a morphological index of potential transpirational demand relative to water transport capacity, apparent differences among branches on the same individual (e.g., Fig. 2), and even among species (Fig. 3), were substantially reduced. However, E and LA/SA are not independent because E is obtained by multiplying sap velocity by the reciprocal of LA/SA. Normalizing E by LA/SA thus yields the original measurement of sap velocity. Nevertheless, Meinzer et al. (1997) reported that a common relationship between g_s and evaporative demand emerged for *F. insipida*, *C. longipes*, *S. mombin* and *L. seemannii* when independent measurements of g_s were normalized by LA/SA. If intrinsic branch hydraulic properties are similar in all five species, variation in LA/SA may have consequences for stomatal functioning and regulation of transpiration comparable to those of variation in leaf area-specific hydraulic conductivity reported in other studies (e.g., Küppers 1984; Meinzer et al. 1990; 1995; Sperry and Pockman 1993). Indeed, G_t and LA/SA were negatively correlated (Fig. 7), suggesting that variation in LA/SA was an important component of variation in water transport efficiency on a leaf area basis. In this context, data presented by Whitehead et al. (1984) for thinned and unthinned stands of *Pinus sylvestris* show that the ratio of canopy transpiration in the thinned stand to that in the unthinned stand (0.67) was virtually identical to the ratio of the stand-level LA/SA in the unthinned stand to that in the thinned stand (0.68). Stand transpiration rates thus converged when normalized by their corresponding LA/SA values.

It has been suggested that transpiration and photosynthetic gas exchange, and therefore tree growth, are limited by increasing axial hydraulic resistance associated with increasing tree height (Ryan and Yoder 1997). Evidence for this hypothesis comes largely from studies carried out with conifers (e.g., Waring and Sylvester 1994; Yoder et al. 1994; Mencuccini and Grace 1996). For example, Mencuccini and Grace (1996) observed that above-ground leaf area-specific hydraulic conductance decreased with increasing tree size in individuals of *Pinus sylvestris* ranging from 7 to 59 years of age and 1.6 to 24 m in height. However, they also noted that whereas mean path length increased by a factor of 20, leaf area-specific conductance decreased by a factor of 3.5, indicating that substantial compensation had occurred to avoid excessive increase in resistance.

Our results suggest that there were hydraulic connections between the transpiration stream and water stored in the sapwood and that stem water storage may partially compensate for potential increases in axial hydraulic resistance with increasing tree height, thereby limiting the extent of stomatal closure required to maintain leaf water status. Our observations of a close association between diurnal variation in vapor phase conductance and G_t, and between G_t and exchange of water between the transpiration stream and internal storage compartments also raise the possibility that the midday depression in g_s followed by partial recovery in the afternoon often observed in woody species (Tenhunen et al. 1980, 1984) may be a reflection of the hydraulic consequences of diurnal depletion and recharge of internal water reserves.

The exponential increases in sapwood area and daily water use with tree height (Fig. 2) further suggest that whole-tree transpiration may not have become increasingly limited by axial hydraulic resistance as tree height increased. Although sap flow per unit sapwood area decreased with increasing tree height (data not shown), this may have reflected an increasing relative allocation of carbon to sapwood, and therefore water transport capacity, with increasing tree height rather than an increase in axial hydraulic resistance. It is highly unlikely that the pattern shown in Fig. 2B reflected differences between suppressed and emergent trees in this relatively open canopy with numerous gaps. The crown of the shortest study tree, *C. longipes*, was in a large gap and was not overshadowed directly above by the crowns of other trees. The crowns of the remaining study trees were similarly exposed. Furthermore, substantial differences among trees in the prevailing solar radiation regime would have introduced more noticeable variability in the relationship shown in Fig. 5B, and obscured the effects of the normalization procedure applied in Fig. 4B.

We conclude that although the traditional reliance on characterization of ecophysiological behavior at the leaf level may tend to magnify differences among species and individuals, obscure basic similarities, and obscure mechanisms responsible for differences in behavior at the leaf level, these measurements are an essential component of understanding ecophysiological behavior at the whole plant level. We suggest that efforts to characterize and compare regulation of processes such as liquid water transport and transpiration should treat plants, especially large forest trees, as integrated, whole organisms, by incorporating concurrent measurements at multiple scales from the whole-plant to the leaf level. Even when this is done, it is important to recognize that trees representing a substantial range of size classes within each species should be included. Otherwise, interspecific comparisons of behavior among individuals of different size classes may lead to the potentially erroneous conclusion that observed differences are interspecific rather than size-related.

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