

Coordination of leaf and stem water transport properties in tropical forest trees

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Abstract Stomatal regulation of transpiration constrains leaf water potential (Ψ_L) within species-specific ranges that presumably avoid excessive tension and embolism in the stem xylem upstream. However, the hydraulic resistance of leaves can be highly variable over short time scales, uncoupling tension in the xylem of leaves from that in the stems to which they are attached. We evaluated a suite of leaf and stem functional traits governing water relations in individuals of 11 lowland tropical forest tree species to determine the manner in which the traits were coordinated with stem xylem vulnerability to embolism. Stomatal regulation of Ψ_L was associated with minimum values of water potential in branches (Ψ_{br}) whose functional significance was similar across species. Minimum values of Ψ_{br} coincided with the

bulk sapwood tissue osmotic potential at zero turgor derived from pressure–volume curves and with the transition from a linear to exponential increase in xylem embolism with increasing sapwood water deficits. Branch xylem pressure corresponding to 50% loss of hydraulic conductivity (P_{50}) declined linearly with daily minimum Ψ_{br} in a manner that caused the difference between Ψ_{br} and P_{50} to increase from 0.4 MPa in the species with the least negative Ψ_{br} to 1.2 MPa in the species with the most negative Ψ_{br} . Both branch P_{50} and minimum Ψ_{br} increased linearly with sapwood capacitance (C) such that the difference between Ψ_{br} and P_{50} , an estimate of the safety margin for avoiding runaway embolism, decreased with increasing sapwood C . The results implied a trade-off between maximizing water transport and minimizing the risk of xylem embolism, suggesting a prominent role for the buffering effect of C in preserving the integrity of xylem water transport. At the whole-tree level, discharge and recharge of internal C appeared to generate variations in apparent leaf-specific conductance to which stomata respond dynamically.

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Introduction

Maintaining the integrity of the xylem hydraulic continuum running from the roots to the leaves requires that the stomata be highly responsive in coordinating transpiration with dynamic variation in the efficiency of water supply to the leaves. Otherwise, transpiration-induced increases in xylem tension may result in rapid, synergistic propagation of air embolisms leading to critical levels of potentially irreversible hydraulic failure (Tyree and Sperry 1988) and

lethal levels of leaf dehydration. For a given transpiration rate and soil water potential, the magnitude of leaf water potential (Ψ_L) is determined by the whole-plant leaf area-specific hydraulic conductance (K_L), which has led to broad convergence in coordination between leaf gas exchange and various measures of leaf-specific hydraulic capacity among diverse species and growth forms (Meinzer et al. 1995; Brodribb et al. 2002; Mencuccini 2003; Santiago et al. 2004). Although a number of components of plant hydraulic architecture such as xylem specific conductivity (Domec et al. 2007), hydraulic capacitance (C) (Meinzer et al. 2003; Scholz et al. 2007) and leaf hydraulic conductance (Bucci et al. 2003; Brodribb and Holbrook 2004; Woodruff et al. 2007) show substantial variation over the course of a single day, relatively little is known about the suites of functional traits involved in facilitating the dynamic coordination between plant hydraulic capacity and stomatal control of gas exchange and leaf water status.

Stomatal regulation of transpiration constrains leaf water potential within species-specific ranges. In so-called isohydric species, minimum values of Ψ_L remain essentially constant despite variation in soil water availability and atmospheric demand, whereas anisohydric species are generally characterized by increasingly negative values of minimum Ψ_L as soil water availability declines (Turner et al. 1984; Tardieu and Simonneau 1998; Bucci et al. 2005; Fisher et al. 2006). A third type of plant Ψ regulation, isohydrodynamic, in which a constant root-to-shoot $\Delta\Psi$ is maintained seasonally, has recently been described (Franks et al. 2007). Although species may readily be placed in one of the preceding categories, the significance of various Ψ_L set points, thresholds or ranges in the context of stomatal responses to hydraulic perturbations may not be apparent. Recent analyses favor a metabolically mediated response of stomatal guard cells to localized perturbations in epidermal water status (Franks 2004; Buckley 2005). Regardless of the stomatal control mechanisms involved, broader understanding of patterns of stomatal regulation of Ψ_L requires knowledge of the hydraulic architecture of the stems to which the leaves are attached and of the leaves themselves. For example, to determine whether stomata regulate Ψ_L to avoid excessive embolism in terminal branches, both the Ψ and the hydraulic vulnerability of the branches must be assessed. Because the hydraulic resistance of leaves is substantial (Sack and Holbrook 2006), tension in the xylem of transpiring leaves can be poorly coupled to that in the stems to which they are attached (Begg and Turner 1970; Bucci et al. 2004a). Interpretation of Ψ_L alone is further complicated by mounting evidence that leaves normally experience pronounced daily cycles of loss and recovery of their hydraulic conductance, suggesting that reversible embolism

in leaves may constitute part of an essential hydraulic signal that enables stomata to maintain stem and leaf Ψ at set points that insure the integrity of the water transport system upstream (Brodribb and Holbrook 2003; Meinzer et al. 2004; Woodruff et al. 2007).

C is another component of plant hydraulic architecture involved in stomatal regulation of plant water status. Although water derived from internal C typically contributes a relatively small fraction to total daily transpiration (Kobayashi and Tanaka 2001; Phillips et al. 2003; Meinzer et al. 2004), its buffering effect on daily fluctuations in xylem tension and Ψ_L should not be underestimated. Under the transient tension and flow regimes that prevail in intact plants, C has a profound impact on the relationship between Ψ gradients and water flux, especially in large trees (Holbrook and Sinclair 1992; Meinzer et al. 2003; Perämäki et al. 2005). Quasi-steady state measurements of leaf-specific conductivity in excised stem segments do not account for this effect. To the extent that C stabilizes Ψ_L , stomata should respond to its influence as to other components of hydraulic architecture that affect apparent K_L . Intrinsic C of plant tissues varies widely (Scholz et al. 2007), and a number of traits of plant–water relations, including minimum leaf and stem Ψ (Meinzer et al. 2003; Scholz et al. 2007), maximum stomatal conductance (Stratton et al. 2000; Scholz et al. 2007), maximum sap velocity (Meinzer et al. 2006) and stem xylem vulnerability (Pratt et al. 2007) have been shown to scale with sapwood C in a species-independent manner.

Broad global convergence in a variety of plant functional traits (Reich et al. 1997; Meinzer 2003; Wright et al. 2004) implies predictable evolutionary constraints on suites of characteristics governing dynamic coordination between transpiration, plant water status and hydraulic architecture. We examined coordination among a number of traits of leaf and stem water relations, some of which were considered to be dynamic in that they were subject to daily regulation, and others that represented more stable biophysical properties of an organ or tissue. These traits were studied in individuals of 11 lowland tropical forest tree species growing in two sites at opposite ends of a moisture gradient across the Isthmus of Panama. The wetter site contained a mature primary forest and the drier site contained a secondary forest. We were particularly interested in determining the extent to which stomatal regulation of Ψ_L was coordinated with stem Ψ and xylem vulnerability to embolism because the existence of consistent species-independent relationships would imply that suites of functional traits were constrained by selective pressures in a universal manner. Based on our earlier work and that of others, we hypothesized that sapwood C and reliance on stored water would be a strong determinant of the patterns observed.

Materials and methods

Study sites and species

The study was conducted during the dry seasons of 2003 and 2004 from two canopy cranes operated by the Smithsonian Tropical Research Institute in the Republic of Panama. Each crane is equipped with a gondola suspended by cables from a rotating jib that allows access to about 0.8 ha of forest. One crane is located in an old-growth forest in the Parque Nacional San Lorenzo on the Caribbean side of the Isthmus of Panama where the mean annual precipitation is about 3,100 mm. The other crane is located in a seasonally dry secondary forest in the Parque Natural Metropolitano near the edge of Panama City, which receives about 1,800 mm of precipitation annually with a distinct dry season between late December and April. The dry season at Parque San Lorenzo is shorter and less intense than at Parque Metropolitano. There is no overlap among tree species between the two sites. Six individuals were selected for study at the Parque San Lorenzo site and five at the Parque Metropolitano site representing a total of 11 species (Table 1).

Leaf water relations

The pressure–volume technique (Tyree and Hammel 1972) was used to assess bulk leaf osmotic potential at zero turgor in eight of the species. Portions of terminal branches were excised in the upper canopy and their bases immediately recut under water. The cut ends remained under water with the terminal leafy portions enclosed in a plastic bag to allow partial rehydration during transit from the canopy crane to the laboratory. Individual leaves or leafy shoots

were used for pressure–volume analyses depending on petiole length and leaf size. Pressure–volume curves were initiated by first determining the fresh weight of the sample, then measuring its water potential with a pressure chamber (PMS Instrument, Albany, Ore.).

Alternate measurements of fresh weight and Ψ_L were repeated during slow dehydration on the laboratory bench until Ψ_L approached the measuring range of the pressure chamber (-4 MPa). We tested for rehydration-induced artifacts previously reported for some woody species (Bowman and Roberts 1985; Meinzer et al. 1986; Evans et al. 1990) by comparing pressure–volume curves obtained from samples at different levels of initial hydration and found none. The transition point between the non-linear and linear portions of the curve was taken to be the bulk tissue osmotic potential at zero turgor. Values of osmotic potential reported here are means from three to five curves per species. The Ψ of upper canopy leaves was determined with a pressure chamber between 0800 and 1500 hours on five dates between 16 and 24 February 2003 and seven dates between 23 February and 19 March 2004. At each sampling time, measurements were obtained from three to five leaves of each tree.

Stem water relations

Moisture release curves for sapwood of terminal branches of ten species were determined according to the method described in Meinzer et al. (2003). Briefly, small cylinders of sapwood were allowed to hydrate in distilled water overnight, quickly blotted to remove excess water, placed in the caps of thermocouple psychrometer chambers (83 series; JRD Merrill Specialty Equipment, Logan, Utah), weighed, and then sealed inside the rest of the chamber for determination of

Table 1 Trunk diameter, height, percent loss of hydraulic conductivity (PLC) and relative water deficit (RWD) of terminal branches at minimum branch water potentials measured in the field (Ψ_{br}) for the measurement trees at the two study sites

Site/species	Family	Diameter (m)	Height (m)	PLC at Ψ_{br}	RWD at Ψ_{br}
Parque Nacional San Lorenzo					
<i>Manilkara bidentata</i>	Sapotaceae	0.66	30	24	0.40
<i>Protium panamense</i>	Burseraceae	0.28	16	34	0.39
<i>Tachigalia versicolor</i>	Fabaceae	0.31	23	39	0.55
<i>Tapirira guianensis</i>	Anacardiaceae	0.70	34	27	0.41
<i>Trattinnickia aspera</i>	Burseraceae	0.37	24	29	0.32
<i>Vochysia ferruginea</i>	Vochysiaceae	0.42	26	40	0.45
Parque Natural Metropolitano					
<i>Anacardium excelsum</i>	Anacardiaceae	0.98	38	–	0.25
<i>Chrysophyllum cainito</i>	Sapotaceae	0.33	23	34	–
<i>Cordia alliodora</i>	Boraginaceae	0.34	26	–	0.29
<i>Ficus insipida</i>	Moraceae	0.65	28	24	0.41
<i>Schefflera morototoni</i>	Araliaceae	0.47	22	–	0.43

water potential isotherms. Each chamber contained three cylindrical tissue samples. The psychrometer chambers were placed in an insulated water bath and allowed to equilibrate for 2–3 h before measurements were started with a 12-channel digital psychrometer meter (85 series; JRD Merrill Specialty Equipment). Measurements were repeated at 30-min intervals until the water potential values stabilized. The chambers were opened and the samples were allowed to dehydrate for different time intervals, reweighed in the psychrometer caps, resealed inside the psychrometer chambers and allowed to equilibrate for another determination of water potential. Moisture release curves were generated by plotting sapwood water potential (Ψ_{sw}) against relative water deficit (RWD). Data points from three to four replicate curves per species were pooled. Species-specific values of sapwood C ($\text{kg m}^{-3} \text{Mpa}^{-1}$) were taken as the slopes of linear regressions fitted to the initial phase of moisture release curves plotted as the cumulative mass of water released against sapwood water potential (Meinzer et al. 2003). Weight of water per unit tissue volume at saturation (kg m^{-3}) was calculated by multiplying the saturated/dry weight ratio of each tissue by tissue density (kg m^{-3}) and subtracting tissue density. The cumulative weight of water released per unit tissue volume was then calculated by multiplying the tissue RWD at a given value of tissue water potential by the weight of water per unit tissue volume at saturation. Sapwood osmotic potential at zero turgor was estimated by plotting sapwood moisture release curves as pressure–volume curves then determining the transition points between the non-linear and linear portions of the curves.

Hydraulic vulnerability curves for segments of terminal branches of eight species were generated using the air injection method (Sperry and Saliendra 1994). Terminal branches 2–5 cm in diameter and greater than 35 cm in length were excised near the top of the canopy. After excision, the branches were immediately re-cut under water in the crane gondola and transported to the laboratory for measurement. In the laboratory, a 15- to 17-cm-long section of each branch (0.7–1.2 cm in diameter) was cut and both ends were smoothed with clean razor blades. The stem segments were then sealed into a double-ended pressure chamber with both ends protruding and attached via tubing to an apparatus for measuring hydraulic conductivity (k_h). The downstream end of the segment was connected to a 1-ml graduated pipette and the proximal end of the segment was attached to tubing connected to a reservoir of filtered water (0.22 μm) that was pressurized at 0.15 MPa for 40 min to remove emboli and restore the segment to its maximum conductivity ($k_{h \text{ max}}$). The pressure was then lowered to 5.5 kPa to avoid refilling of embolized vessels during the vulnerability curve procedure and the chamber was pressurized to 0.05 MPa to prevent extrusion of water

from leaf scars during measurement of axial flow. When the flow had stabilized, the time required for the meniscus in the pipette to cross five consecutive graduation marks (0.5 ml) was recorded. Maximum conductivity was calculated as the mass flow rate through the segment divided by the pressure gradient across the segment. The chamber pressure was then raised to 0.25 or 0.5 MPa depending on the species and held constant for 3 min after which the pressure was returned to 0.05 MPa and the conductivity re-measured. This process was repeated by raising the pressure in increments of 0.25–1.0 MPa up to a final pressure of 4–5 MPa. Percentage loss of conductivity (PLC) was calculated as $\text{PLC} = 100(1 - k_h/k_{h \text{ max}})$. Values of stem RWD corresponding to the pressures applied were obtained from the sapwood moisture release curves generated as described above. Vulnerability data reported here are means of curves obtained from three stem segments per species.

The water potential of terminal branches (Ψ_{br}) of ten species was estimated with a pressure chamber from balance pressures of covered, non-transpiring leaves. Leaves were enclosed in aluminum foil and plastic bags in the afternoon prior to the day of measurements. At each sampling time between 0800 and 1500 hours, measurements were obtained from three to five leaves of each tree as described above for exposed leaves.

Whole-tree water flux

Sap flow was measured with variable-length heat-dissipation sensors (James et al. 2002) near the base of the trunk and in the crown of four trees at the Parque San Lorenzo site. Mass flow of sap in the trunk and branches was obtained by multiplying sap flux by sapwood cross-sectional area. Basal flow was measured with duplicate sets of probes installed on opposite sides of the trunk at heights of 1–2 m. The probes were installed at three to four depths in the sapwood depending on the trunk diameter. 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 three branches in the upper crown of each tree was taken as a surrogate for transpiration (Goldstein et al. 1998) and expressed on a leaf area basis by dividing sap flow by the total leaf area distal to each set of probes. Crown conductance was estimated by dividing crown transpiration by the vapor pressure deficit measured at half-an-hour intervals at a weather station installed on the crane tower. Daily time courses of utilization of stored water for transpiration were estimated from lags in rates of change in 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. Negative values indicate recharge of C.

Results

Logistical and technical difficulties prevented characterization of all of the functional traits in each of the 11 study species. Nevertheless, a number of significant species-independent relationships were obtained among the traits studied. Bulk leaf osmotic potential and daily minimum Ψ_L were linearly related ($P = 0.003$) across species (Fig. 1). Because the slope of the linear regression was not significantly different from 1, bulk leaf turgor coinciding with minimum Ψ_L was similar across species (~ 0.8 MPa). Branch xylem pressure corresponding to 50% loss of hydraulic conductivity (P_{50}) declined linearly ($P = 0.001$) with daily minimum Ψ_{br} (Fig. 2). However, the slope of the relationship was significantly greater than 1 ($P < 0.05$), indicating that the $\Delta\Psi$ between P_{50} and Ψ_{br} increased as Ψ_{br} became more negative. The margin between Ψ_{br} and P_{50} increased from 0.4 MPa in the species with the least negative Ψ_{br} to 1.2 MPa in the species with the most negative Ψ_{br} . The intercept of the relationship was not significantly different from zero at $\Psi_{br} = 0$.

Representative sapwood water release curves for three co-occurring species having high, intermediate and low values of sapwood C are shown with their respective values of minimum Ψ_{br} in Fig. 3a–c. The slope of linear regressions fitted to the initial portions of the water release curves (dashed lines, Fig. 3a–c) comprising the operating range of

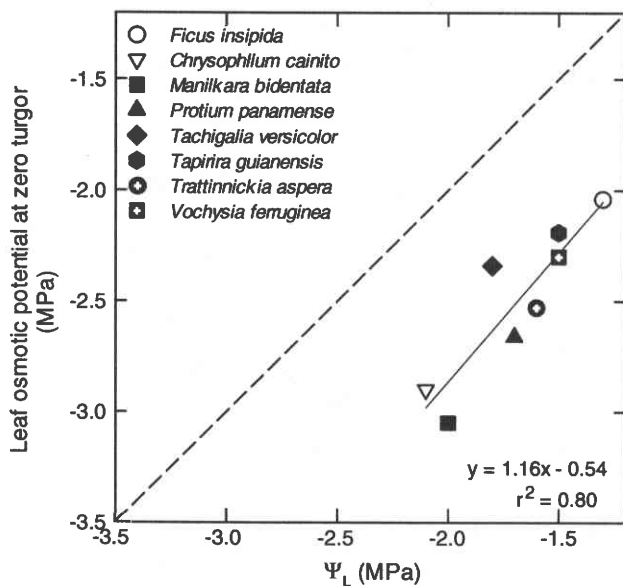


Fig. 1 Relationship between bulk leaf osmotic potential at zero turgor and daily minimum leaf water potential (Ψ_L) for eight tropical tree species. Dashed line indicates a 1:1 relationship

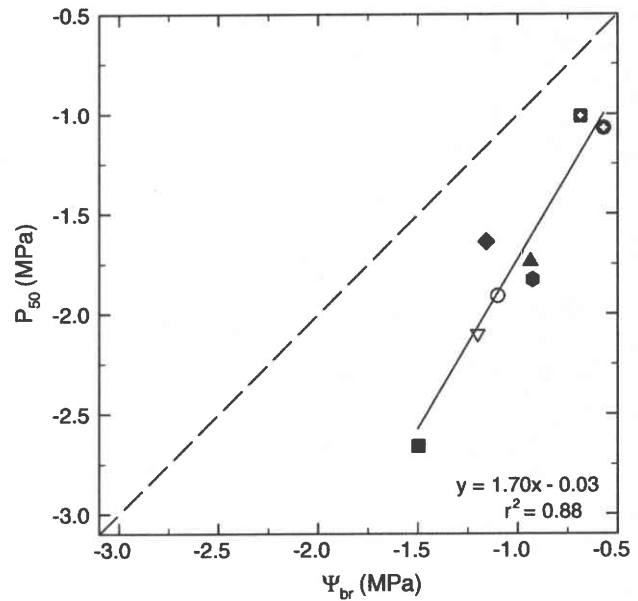


Fig. 2 Relationship between the xylem pressure corresponding to 50% loss of conductivity (P_{50}) in excised branch segments and minimum water potential observed in intact terminal branches (Ψ_{br}) in the field. Symbols are as defined in Fig. 1

Ψ_{sw} in vivo provided a relative measure of sapwood C. Minimum Ψ_{br} was never more negative than the transition region of the water release curve where Ψ_{sw} began to decline more steeply with increasing RWD (intersection of vertical and horizontal dotted lines, Fig. 3a–c). Among the ten species for which data were available, minimum Ψ_{br} ranged from -0.6 to -1.5 MPa, whereas the corresponding values of sapwood RWD ranged from 0.25 to 0.55 (Table 1) with a mean of 0.39 ± 0.03 . The sapwood RWD at the water release curve inflection points also corresponded closely to the transition from the non-linear to linear portions of the sapwood pressure–volume curves (vertical dotted lines, Fig. 3d–f), an estimate of the bulk tissue osmotic potential at zero turgor for sapwood, which contained both non-living xylem elements and living xylem parenchyma. The relationship between sapwood turgor loss points estimated from the pressure–volume curves and minimum values of Ψ_{br} measured in the field was linear ($P < 0.0001$) and not significantly different from 1:1 (Fig. 4). The Ψ_{sw} and RWD thresholds at which Ψ_{sw} began to decline more abruptly with increasing RWD also corresponded to the thresholds at which PLC began to increase more steeply with increasing branch water deficits (cf. dotted lines, Fig. 3g–i, a–c). Despite the 1.7 MPa range of P_{50} among the eight species for which data were available, the range of PLC at minimum Ψ_{br} was relatively small (Fig. 3g–i; Table 1) with a mean PLC of $31 \pm 2\%$.

Branch P_{50} increased linearly ($P < 0.001$) with sapwood C (Fig. 5a) as did minimum Ψ_{br} ($P = 0.001$, Fig. 5b). Variation