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Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees

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Abstract We investigated how water transport capacity, wood density and wood anatomy were related to leaf photosynthetic traits in two lowland forests in Panama. Leaf-specific hydraulic conductivity (k_L) of upper branches was positively correlated with maximum rates of net CO_2 assimilation per unit leaf area (A_{area}) and stomatal conductance (g_s) across 20 species of canopy trees. Maximum k_L showed stronger correlation with A_{area} than initial k_L suggesting that allocation to photosynthetic potential is proportional to maximum water transport capacity. Terminal branch k_L was negatively correlated with A_{area}/g_s and positively correlated with photosynthesis per unit N, indicating a trade-off of efficient use of water against efficient use of N in photosynthesis as water transport efficiency varied. Specific hydraulic conductivity calculated from xylem anatomical characteristics ($k_{theoretical}$) was positively related to A_{area} and k_L, consistent with relationships among physiological measurements. Branch wood density was negatively correlated with wood water storage at saturation, k_L, A_{area}, net CO_2 assimilation per unit leaf mass (A_{mass}), and minimum leaf water potential measured on covered leaves, suggesting that wood density constrains physiological function to specific operating ranges. Kinetic and static indices of branch water transport capacity thus exhibit considerable co-ordination with allocation to potential carbon gain. Our results indicate that understanding tree hydraulic architecture provides added insights to comparisons of leaf level measurements among species, and links photosynthetic allocation patterns with branch hydraulic processes.

Keywords Leaf nitrogen · Leaf specific conductivity · Stomatal conductance · Tropical forest · Xylem anatomy

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Introduction

Plant species often exhibit substantial variation in rates of leaf level carbon gain and resource use. Diversity of physiological function is especially striking in lowland tropical forests, where high tree species richness presents potential difficulty in drawing generalizations about physiological regulation of carbon gain. Nevertheless, results of recent studies point to substantial convergence in plant functioning among species from diverse biomes (Reich et al. 1997). For example, maximum photosynthetic rates, stomatal conductance (g_s), and leaf surface area per unit mass (specific leaf area; SLA) are positively correlated and tend to decrease with increasing leaf life span across a wide array of study sites and angiosperm taxa (Reich et al. 1997; Ackerly and Reich 1999; Reich et al. 1999). However, even within sites, variation in photosynthetic rate and leaf life span is as great or greater than variation in mean differences among biomes (Reich et al. 1999). Since it is well established that plant hydraulic architecture controls maximum g_s (Meinzer and Grantz 1990; Meinzer et al. 1995; Saliendra et al. 1995; Sperry 2000), understanding hydraulic properties at the branch or whole plant scale may explain additional variation in leaf photosynthetic traits among co-occurring individuals and species (Meinzer and Goldstein 1996).

The relationship between hydraulic conductance (k) and g_s is supported by active response of g_s to experimental modification of k. When k per unit leaf area (k_L) is increased as a result of partial defoliation or leaf shading, g_s usually increases (Meinzer and Grantz 1991; Pataki et al. 1998). In addition, when k_L is experimentally reduced through stem notching or root pruning, g_s tends to decrease (Sperry et al. 1993; Hubbard et al. 2001), demonstrating an almost immediate correspondence between these two parameters. Recently Katul et al. (2003) extended the relationship between g_s and k to photosynthetic capacity of foliage through the photosynthesis-g_s-intercellular CO$_2$ equations of Farquhar et al. (1980), thus providing a theoretical basis for hydraulic-photosynthetic co-ordination. There is also mounting empirical evidence for the relationship between photosynthetic carbon assimilation rates and water transport capacity based on correlation between k_L and electron transport capacity among groups of co-occurring species (Brodribb and Feild 2000; Brodribb et al. 2002).

Co-ordination between the plant hydraulic system and regulation of carbon economy at the leaf level may also be related to life history features of a species. High photosynthesis, SLA, and leaf nitrogen concentration are generally associated with rapid growth, high allocation to photosynthetic tissue, early attainment of reproductive age, and regeneration in high resource habitats (Poorter and Remkes 1990; Reich et al. 1992; Cornelissen et al. 1997; Wright and Westoby 1999). In addition, leaf photosynthetic traits are correlated with many of the same whole-organism traits that can be predicted by plant hydraulic conductance. Recent studies have suggested that allometric scaling of plant vascular systems is universal and thus reflects convergence among many species to overcome similar physical limitations of long-distance water transport (Enquist et al. 1998; West et al. 1999; Meinzer 2003). Furthermore, similar relationships in the scaling of plant transpiration and animal metabolism suggest that both share common scaling laws that reflect how resource requirements of organisms affect distribution in ecological communities (Enquist et al. 1998). Since photosynthesis is the sole mechanism of carbon assimilation in most vascular plants, and water is likely to limit photosynthesis at some time scale, even in humid tropical forest, we expect co-ordination between photosynthetic capacity and plant hydraulic properties across an array of tropical forest trees. We also suspect that measurements of plant hydraulic properties may be related to other plant processes such as nutrient use and gross photosynthesis, thus integrating leaf level processes into a more complete understanding of whole-plant function.

This study was designed to examine relationships between branch hydraulic architecture, xylem biophysical and anatomical properties, and suites of leaf photosynthetic traits among 20 species of canopy trees growing in two Panamanian lowland forests. The primary objective was to determine the extent to which variation in leaf area-based hydraulic properties and xylem biophysical properties can explain variation in leaf gas exchange characteristics. Specific questions included: (1) Does allocation to leaf photosynthetic capacity correspond to leaf area-based

Table 1 Area-based maximum photosynthetic rate (A_{area}), maximum leaf specific hydraulic conductivity ($k_{\mathrm{L\ max}}$), wood density, and the number of terminal branches sampled (n) for study species from two lowland tropical forest sites in Panama. Values are means ±1 SE

Species	Family	A_{area} (μmol m^{-2} s^{-1})	$k_{\mathrm{L\ max}}$ (mmol m^{-1} s^{-1} MPa^{-1})	Wood density (g cm^{-3})	n
Fort Sherman					
Aspidosperma cruenta	Apocynaceae	9.7±0.8	15.8±8.3	0.70±0.03	5
Dussia munda	Fabaceae	12.3±0.8	37.4±14.8	0.53±0.01	8
Guatteria dumentorum	Annonaceae	12.2±0.5	38.4±3.9	0.42±0.02	5
Humiriastrum diguense	Hernandiaceae	11.2±0.6	34.1±4.6	0.58±0.04	6
Manilkara bidentata	Sapotaceae	10.3±0.4	31.5±7.4	0.61±0.02	7
Marila laxiflora	Clusiaceae	9.9±0.6	29.9±9.6	0.48±0.01	5
Miconia borealis	Melastomataceae	16.8±0.7	81.0±35.8	0.50±0.02	6
Nectandra purpurascens	Lauraceae	11.1±0.4	58.9±10.1	0.55±0.04	6
Ocotea ira	Lauraceae	12.6±0.6	45.8±10.1	0.58±0.01	6
Poulsenia armata	Moraceae	11.8±0.9	39.5±7.3	0.43±0.06	5
Pourouma bicolor	Moraceae	13.7±0.2	49.9±20.1	0.45±0.02	5
Simarouba amara	Simaroubaceae	17.5±0.9	102.4±13.7	0.41±0.01	5
Tapirira guianensis	Anacardiaceae	12.9±0.8	62.0±27.4	0.43±0.03	5
Trattinickia aspera	Bursuraceae	12.2±0.3	43.0±16.8	0.57±0.02	5
Virola sebifera	Myristicaceae	13.5±1.2	60.8±8.1	0.50±0.06	5
Vochysia ferruginea	Vochysiaceae	18.3±1.1	91.7±69.3	0.35±0.07	5
Parque Metropolitano					
Chrysophyllum cainito	Sapotaceae	9.9±0.8	33.8±7.5	0.61±0.01	5
Cordia alliodora	Boraginaceae	15.4±0.4	61.6±20.4	0.47±0.05	5
Ficus insipida	Moraceae	19.2±1.1	123.1±14.7	0.34±0.03	5
Luehea seemannii	Tiliaceae	17.0±0.6	115.2±7.3	0.33±0.04	5

hydraulic capacity? (2) Are leaf functional traits such as nitrogen concentration and water- and nitrogen-use efficiency correlated with hydraulic efficiency? (3) Are both hydraulic conductivity and leaf gas exchange constrained by wood density? (4) Can photosynthetic traits be predicted from xylem anatomical properties?

Materials and methods

Study site and species

The study was conducted from two canopy cranes operated by the Smithsonian Tropical Research Institute (STRI) in the Republic of Panama. Each crane is equipped with a gondola suspended by cables from a rotating boom that allows coverage of approximately 0.82 ha of forest. One crane is located in Parque Metropolitano, a secondary dry forest on the edge of Panama City that receives approximately 1,800 mm of precipitation annually with a distinct dry season between December and April (ACP 2002). The other crane is located in an old-growth forest at Fort Sherman on the Caribbean side of the Panamanian Isthmus where mean annual precipitation is 3,100 mm and the dry season is shorter and less intense than at Parque Metropolitano. During the dry season of 2002 (February-March), physiological and morphological characteristics in the upper crown of one to four individuals of 20 canopy tree species were measured. Both rare and common species were included in the study (Table 1). We measured at least five sun-exposed terminal branches in all species. In rare species with only one individual at the study site, sample branches were taken from different portions of the crown.

Gas exchange and foliar analyses

Maximum rates of net CO_2 assimilation (A) and stomatal conductance (g_s) were measured with a portable photosynthesis system (6400, Li-Cor, Lincoln, Neb., USA) between 0700 and 1100 hours. Two to four newly formed mature leaves per upper canopy branch (10–20 leaves per species) were measured at 400 μmol mol^{-1} CO_2, and 1,200 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) provided by a red blue light source (6400-02B no. SI-710, Li-Cor, Lincoln).

After measurement of their area, gas exchange leaves were dried for 48 h at 65°C and weighed for the determination of specific leaf area (SLA; cm^2 g^{-1}) so that photosynthesis could be expressed both per unit leaf area (A_{area}) and per unit leaf mass (A_{mass}). The dried leaves were ground in a Wiley mill and one composite sample per branch was analyzed for total leaf nitrogen and carbon isotopic composition (δ^{13}C) on an elemental analyzer connected to a continuous flow mass spectrometer at the University of Idaho. These foliar analyses allowed us to calculate photosynthesis per unit leaf nitrogen (A_{N}), a measure of intrinsic N-use efficiency, and to evaluate intrinsic water use efficiency based on δ^{13}C values (Farquhar and Richards 1984).

Hydraulic measurements

Hydraulic conductivity (k_{H}) was measured on stem segments excised from 1.0 to 1.5-m-long terminal branches that were clear of leaves and wounds. Branches were longer than the measured maximum vessel length determined by the air pressure technique (Ewers and Fisher 1989). Upper crown branches exposed to full sun were cut directly after gas exchange measurements on days with similar environmental conditions and transported to the laboratory. In the laboratory, the first fully developed stem segments supporting the leaves on which gas exchange was measured were excised from the rest of the branch under filtered water (0.2 μm) to prevent xylem embolism. After removing 3–4 mm of bark from each end, the cut ends were shaved with Teflon coated razor blades and connected to the hydraulic conductivity apparatus (Sperry et al. 1988). Pith areas were plugged with plasticine when necessary. The hydraulic conductivity apparatus consisted of a beaker supplying filtered (0.2 μm) water under low (1.4 kPa) gravitational pressure to the stem. A low hydraulic head insured no embolisms were removed and the apparatus was frequently flushed with 10% bleach solution to avoid microbial growth. Flow rates were determined volumetrically 5–15 min after connection when they became steady. Initial k_{H} was estimated as the rate of water flux (J, mmol s^{-1}) in a stem when a pressure gradient (dP/dx, MPa m^{-1}) was applied across the stem

$$k_{\mathrm{H}} = J/(\mathrm{d}P/\mathrm{d}x). \tag{1}$$

Maximum k_{H} was measured after a 20-min high-pressure flush from a captive air tank when flow rates reached steady values.

After hydraulic measurements, stem length, xylem diameter and pith diameter were measured for the calculation of k_{H} and specific conductivity (k_{S}), k_{H} per unit xylem area. Leaf area distal to the stem segment where k_{H} was measured was recorded with a leaf area meter (LI-3100, Li-Cor), and used to calculate leaf specific conductivity (k_{L}), k_{H} per unit leaf area. After hydraulic conductivity measurements, the outer bark, phloem and pith were removed from sample stems, wet mass and volume were determined and stems were dried for 48 h at 65°C and weighed to determine the saturated water content (SWC). Wood density was measured as the ratio of xylem dry mass to xylem wet volume. We measured minimum water potential (Ψ_{min}) of covered leaves on a subset of the study species with a pressure chamber (PMS Instruments, Corvallis, Ore., USA) at 1300 hours. Leaves were covered in the afternoon on the day before measurement with plastic bags and aluminum foil to inhibit transpiration and allow equilibration with stem xylem water potential.

Anatomical measurements

One cross-section from each k_{H} segment from 14 species was used for anatomical analysis. Stem segments adjacent to those used for measuring hydraulic conductivity were stored in a refrigerator and later fixed in 70% ethanol. Stem cross-sections from four branches per species were made with a sliding microtome at 40–90 μm thickness depending on wood properties. Sections were stained with toluidine blue and mounted in glycerin. The xylem at four quadrats near the vascular cambium was photographed at 10× magnification with a digital camera connected to a microscope and computer. All vessels within the image area were measured using image analysis software (Scion Image, Scion, Frederick, Md., USA). Since vessels were not exactly circular, diameter was calculated as the mean of maximum and minimum diameters. Approximately 200 vessels were measured in four images from each stem segment. Diameter (d) of each vessel was elevated to the fourth power then summed to give sampled Σ vessel d^4.

To measure the total xylem area, stem cross sections were drawn using a camera lucida on a dissecting microscope. Regions of tyloses, if present, were included in drawings, which were photographed with a digital camera and measured using Scion Image software. The area of functional xylem was obtained by subtracting area of tyloses from total xylem area. We calculated total Σ vessel d^4 (Σd^4) for the whole stem as sampled Σ vessel d^4 multiplied by total functional xylem area (A_{f}) divided by sampled xylem area (A_{image}; area of images):

$$\sum_{i=1}^{n} d_i^4 = \text{sampled} \sum_{i=1}^{n} d_i^4 \left(\frac{A_{\mathrm{f}}}{A_{\mathrm{image}}}\right) \tag{2}$$

where d_I are the diameters of single vessels summed over the number of vessels, n, per unit cross-sectional area.

Theoretical specific conductivity of branch wood was calculated according to the equation for capillaries (Tyree and Ewers 1991):

$$k_{\text{theoretical}} = \frac{\pi\rho}{128\eta A_{\text{image}}} \sum_{i=1}^{n} d_i^4 \quad (3)$$

where $k_{\text{theoretical}}$ is wood specific conductivity (kg m^{-1} MPa^{-1} s^{-1}), ρ is the density of water at 27°C (kg m^{-3}), η is the dynamic viscosity of water (MPa s), and all other symbols follow Eq. 2.

To ascertain the structure of perforation plates in vessel elements, longitudinal sections of xylem were made by hand with a razor blade, stained with toluidine blue, and mounted in glycerin. Xylem slivers were also macerated by boiling for 2–3 min in 10% aqueous potassium hydroxide, washed in water, and soaked in 20% chromic acid (chromium trioxide) for 15 min. Macerated material was mounted and teased apart in a 1:1 glycerin-water mix after repeated washing in water. The structure of perforation plates in vessel elements was observed after staining with toluidine blue.

Results

There was substantial variation in leaf area-based gas exchange and hydraulic properties among the 20 species studied (Table 1, Fig. 1). Maximum A_{area} varied by a factor of about two, whereas variation in g_s, $k_{\text{L initial}}$ and $k_{\text{L max}}$ was several times greater. Both A_{area} and g_s were positively correlated with $k_{\text{L initial}}$ independent of species (Fig. 1). However, $k_{\text{L max}}$ was a much stronger predictor of A_{area} than $k_{\text{L initial}}$ suggesting that allocation to maximum photosynthetic capacity is proportional to water transport capacity. Leaf nitrogen content per unit leaf area (N_{area}) was independent of $k_{\text{L max}}$, and with the exception of high values for *A. cruenta* and *F. insipida*, remained nearly constant as $k_{\text{L max}}$ varied (Fig. 2a). However, because A_{area} was positively correlated with k_L, photosynthesis per unit N (A_N) increased significantly with increasing $k_{\text{L max}}$ (Fig. 2b). The ratio A_{area}/g_s, an instantaneous measure of intrinsic water-use efficiency, showed a decline with increasing $k_{\text{L max}}$ that was especially sharp at low values of $k_{\text{L max}}$ and leveled off at higher values of $k_{\text{L max}}$ (Fig. 2c). However, foliar δ^{13}C, an integrated measure of

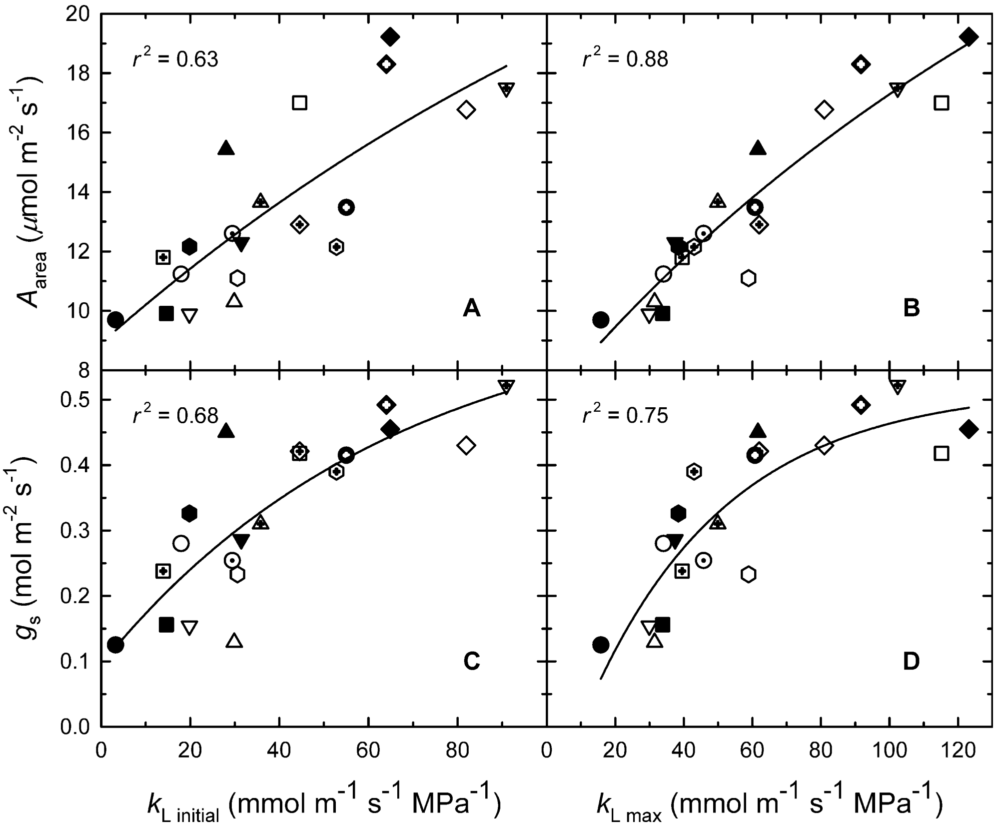

Fig. 1a–d Leaf photosynthetic rate per unit area (A_{area}; **a**, **b**) and stomatal conductance (g_s; **c**, **d**) as a function of initial and maximum leaf specific hydraulic conductivity (k_L) for 20 canopy tree species of lowland tropical forest in Panama. Values are species means. The *solid lines* represent best-fit non-linear regressions. *A. cruenta* (*filled circle*), *C. cainito* (*filled square*), *C. alliodora* (*filled triangle*), *D. munda* (*filled inverted triangle*), *F. insipida* (*filled diamond*), *G. dumentorum* (*filled octagon*), *H. diguense* (*open circle*), *L. seemannii* (*open square*), *M. bidentata* (*open triangle*), *M. laxiflora* (*open inverted triangle*), *M. borealis* (*open diamond*), *N. purpurascens* (*open hexagon*), *O. ira* (*open circle with a dot*), *P. armata* (*open square with a plus*), *P. bicolor* (*open triangle with a plus*), *S. amara* (*open inverted triangle with a plus*), *T. guianensis* (*open diamond with a plus*), *T. aspera* (*open hexagon with a plus*), *V. sebifera* (*filled circle with a plus*), and *V. ferruginea* (*filled diamond with a plus*)

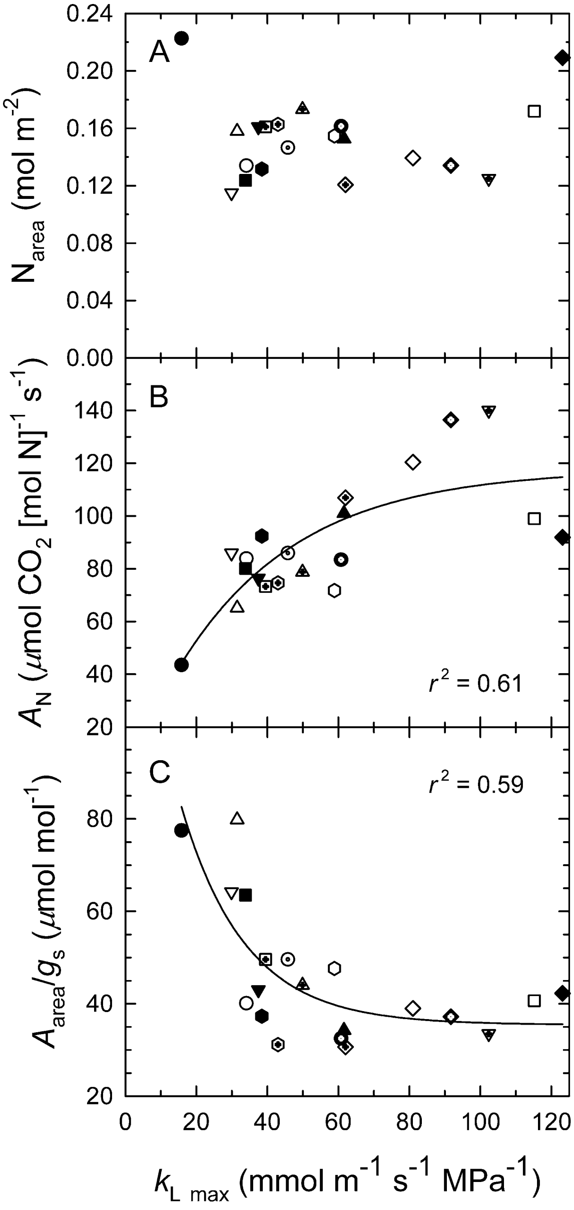

Fig. 2 a Leaf nitrogen per unit leaf area (N_{area}). **b** Leaf photosynthetic rate per unit leaf nitrogen (A_N). **c** Instantaneous water use efficiency (A_{area}/g_s) as a function of maximum leaf specific hydraulic conductivity ($k_{L\ max}$) for 20 canopy tree species in lowland Panama. Values are species means. The *solid lines* represent best-fit non-linear regressions. Symbols as in Fig. 1

intrinsic water use efficiency, was not significantly related to k_L.

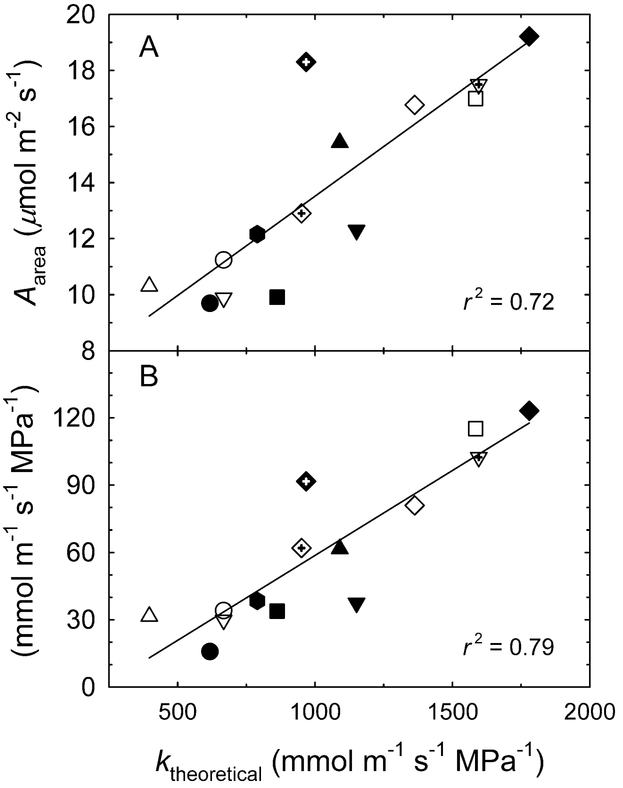

Fig. 3 a Maximum photosynthetic rate per unit area (A_{area}). **b** Maximum hydraulic conductivity per unit leaf area ($k_{L\ max}$) and as a function of hydraulic conductivity per unit stem xylem area based on anatomical calculations ($k_{theoretical}$) for 14 species of lowland forest canopy trees in Panama. Values are species means. The *solid lines* represent best-fit linear regressions. Symbols as in Fig. 1

Leaf gas exchange traits were also correlated with $k_{theoretical}$ (Fig. 3). Both A_{area} (Fig. 3a) and g_s (r^2=0.58; P=0.001) increased with $k_{theoretical}$. In addition, branch k_{Hmax} was positively correlated with $k_{theoretical}$ (r^2=0.57; P=0.002), and branch $k_{L\ max}$ showed a relatively strong positive correlation with $k_{theoretical}$ (Fig. 3b), but branch k_{Smax} was not significantly related to $k_{theoretical}$ (r^2=0.09; P=0.2). Two species (*C. alliodora* and *H. diguense*) had scalariform perforation plates in their wide (≥mean diameter) vessel elements. All other species had simple perforations in their wide vessel elements. Removing the two species with scalariform perforations had essentially no effect on the r^2 values in Fig. 3. Therefore, the results shown in Fig. 3 were not a result of perforation type (and presumably increased resistance of wood vessels) in these two species.

Stem saturated water content and $k_{L\ max}$ both declined with increasing stem wood density, consistent with a tradeoff between mechanical strength and water storage and transport capacity (Fig. 4a, b). An inverse relationship between A_{area} and wood density (Fig. 4c) and between A_{mass} and wood density (r^2=0.50; P<0.001) suggested an additional tradeoff of leaf gas exchange capacity against mechanical strength. In addition, Ψ_{min} also declined with increasing wood density indicating that although higher wood density constrains k_L and water storage (saturated water content), species with higher wood density can withstand lower leaf water potentials to partially compensate (Fig. 4d).

Discussion

Photosynthesis varied proportionally with k_L in a consistent manner among twenty Panamanian forest canopy tree species growing in two sites with distinct rainfall regimes. The results therefore suggest that plant traits

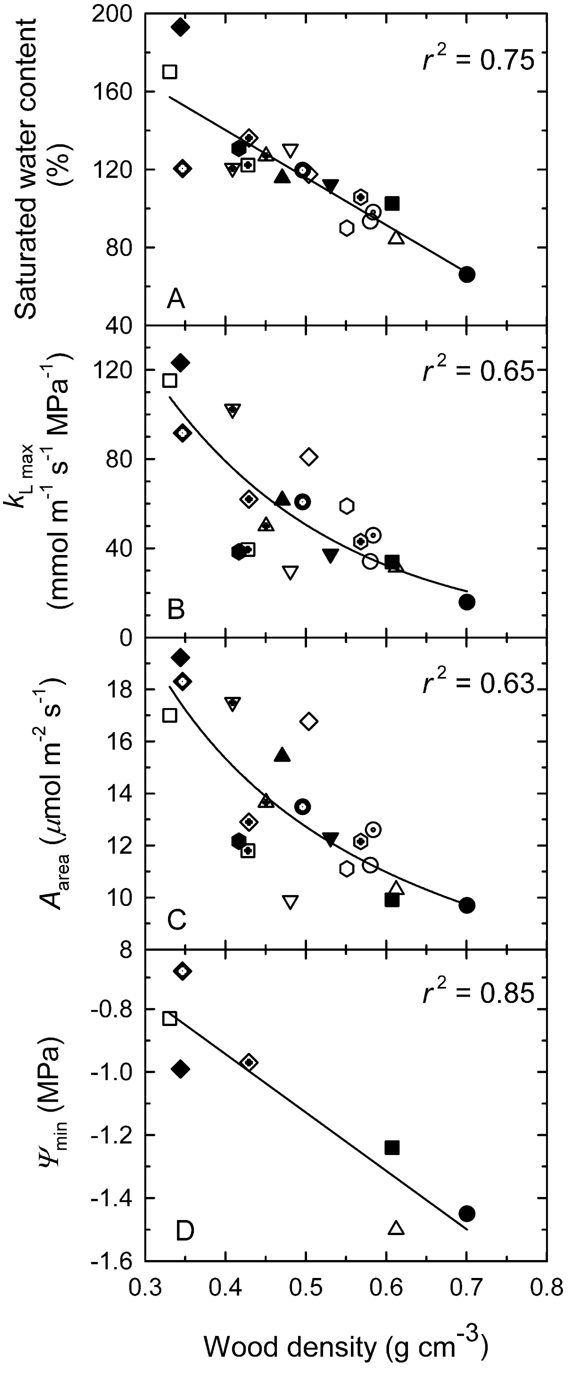

Fig. 4 **a** Stem saturated water content. **b** Maximum leaf specific hydraulic conductivity ($k_{L\ max}$). **c** Photosynthetic rate per unit leaf area (A_{area}). **d** Minimum water potential (Ψ_{min}) measured on covered leaves as a function of stem wood density for lowland forest canopy trees in Panama. Values are species means. The *solid lines* represent best-fit linear and non-linear regressions. Symbols as in Fig. 1

regulating photosynthetic and hydraulic capacity are highly interdependent. Additionally, it appears that trade-offs among functional traits and structural traits such as wood density are associated with the diversity of allocation patterns among coexisting species. For example, species with lower photosynthetic and hydraulic capacity also had denser wood (Fig. 4). Although smaller diameter vessels in dense wood may constrain maximum xylem conductivity, denser wood also provides increased biomechanical support, increased xylem resistance to embolism (Hacke et al. 2001), and appears to allow species to reach lower minimum water potentials. Furthermore, species with lower photosynthetic and hydraulic capacity showed evidence of higher water use efficiency. Solutions to the problem of balancing carbon gain with water loss thus seem to be governed by a series of trade-offs. Our results further indicate that understanding tree hydraulic architecture provides added insights to comparisons of leaf level measurements among species, and links photosynthetic allocation patterns with processes at the branch and whole organism levels of organization.

The relationship between photosynthesis and k_L reflects a balance between carbon gain and water transport capacity, thus the primary feature regulated by k_L is probably g_s and in turn intercellular CO$_2$. This line of reasoning is consistent with theoretical derivations connecting k_L to carboxylation capacity through g_s based on the relationship between g_s and root-to-leaf hydraulic conductance (Sperry et al. 1993), and the relationship between g_s and intercellular CO$_2$ (Farquhar et al. 1980; Katul et al. 2003). The relationship between A and k_L is therefore mediated by stomata to meet the demand for photosynthetic CO$_2$ assimilation while controlling water loss from leaves in a manner that minimizes cavitation in the plant hydraulic system (Katul et al. 2003). Although high rates of photosynthesis in relation to k_L would not contribute to leaf desiccation, the resulting stomatal limitation of photosynthesis (high A_{area}/g_s) would limit efficient utilization of resources allocated to enhance photosynthetic capacity. Therefore, it seems likely that species with high k_L would exhibit correspondingly low A_{area}/g_s resulting in higher photosynthetic rates per unit N, thereby forming a trade-off between photosynthesis per unit N and photosynthesis per unit water lost as observed in the present study.

The proportional decrease in k_L and A_{area} with increasing wood density suggests that biophysical structure of wood may constrain physiological function to specific operating ranges and reflect life-history trade-offs at the whole organism scale. In high-density wood, there is simply less volume available for water transport or storage. Therefore, wood density should capture some of the trade-off between mechanical and hydraulic function (Roderick 2000). Relatively low k_L and saturated water content in species with dense wood may therefore constrain gas exchange to conservative rates, such that bulk leaf water potential is maintained within a safe operating range. Wood density has been linked to support against xylem implosion by negative pressure (Hacke et al. 2001), indicating that species with high density wood may better resist cell wall collapse, and are likely to withstand lower water potential (Fig. 4d). High density wood is also an excellent predictor of mechanical properties; both modulus of rupture (highest tensile strength at rupture) and elasticity are positively correlated with wood density (Niklas 1992). Thus high wood density offers resistance to various environmental forces. The main benefit of low wood density, on the other hand, is high growth rate (Roderick 2000). Therefore, wood density appears central to a suite of plant traits related to patterns of carbon gain, water transport, biomechanics, and growth, at scales ranging from leaf biochemistry to whole organism and community-level processes.

Given the number of technical problems associated with measured and theoretical hydraulic conductivity (Tyree and Ewers 1991), it is encouraging to report statistical correlation between these two approaches. Greater correlation between $k_{\mathrm{theoretical}}$ and k_{L}, as compared to $k_{\mathrm{theoretical}}$ and measured k_{S} is likely due to the relative ease of measuring leaf area as compared to measuring area of conducting xylem. Measurement of xylem vessel diameter in two directions should correct for non-ideal geometry of vessels, although vessels may change dimensions along the length of the stem. Curved or other non-linear vessel orientations may have increased path length without our detection. It can also be difficult to identify non-conducting vessels; it is possible that a significant number of vessels remained non-functional after flushing and this would not be detected in anatomical measurements. Compound scalariform perforations were found in only two species. Thus, we believe that the presumably lower conductance of vessel elements with scalariform versus conductance of simple perforations (Carlquist 2001) contributed little to variation in the relationship. Therefore, although we found statistically significant correlations between measured conductivity and anatomical calculations of conductivity, further refinement in measurement of conductivity and interpretation of anatomical data are likely to increase our understanding of how to rectify these two approaches.

Several studies have highlighted co-ordination between water transport capacity and leaf-level gas exchange or photosynthetic capacity under laboratory (Sperry et al. 1993; Hubbard et al. 2001) or field (Brodribb and Feild 2000; Brodribb et al. 2002) conditions. In addition, Katul et al. (2003) derived a theoretical basis for co-ordination between hydraulic conductance and leaf gas exchange. Our study emphasizes the linkage between hydraulic capacity and a suite of leaf level traits reflecting how a broad array of plant taxa balance carbon gain with water loss along a single functional axis. We found that placing leaf functional traits in the context of hydraulic processes at the branch scale, explained additional variation in the gas exchange behavior of different plant species. We also present evidence that wood density is central to understanding how trade-offs at the leaf-level might be integrated with mechanical resistance and growth, both of which have implications for life-history and persistence of trees in tropical forest plant communities. Further studies on seasonal variation in hydraulic properties (e.g., Brodribb et al. 2002) are likely to increase our understanding of co-ordination with leaf functional traits and how temporal patterns shape trade-offs in plant physiological function.

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