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Hydraulic constraints on photosynthesis in subtropical evergreen broad leaf forest and pine woodland trees of the Florida Everglades

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Abstract The relationship between water transport and photosynthesis represents the trade-off between carbon gain and water loss and was used to evaluate potential differences in water resource utilization among two dominant vegetation types of south Florida: subtropical evergreen broad leaf forests (hardwood hammocks) and pine woodlands (pine rocklands). We found consistent linear positive relationships between the quantum yield of photosystem II (ϕ_{PSII}), an index of photosynthetic capacity, and hydraulic conductivity per sapwood area (k_S) and per leaf area (k_L) across all species. The slope of the ϕ_{PSII}–k_S relationship was steeper for hardwood hammock than for pine rockland species. Mean ϕ_{PSII} was greater in pine rockland species and was greater for a given k_L than in hardwood hammock species. These results are consistent with previous observations demonstrating that pine rocklands tend to have better access to stable water sources than hardwood hammocks. We also found greater photosynthetic carbon isotope discrimination with increasing k_S and k_L in pine rockland species, but not in hardwood hammock species, suggesting increased stomatal conductance with increasing k_S and k_L, consistent with greater water availability in pine rockland habitats. Our study thus utilizes relationships between water transport and photosynthesis to evaluate hydraulic constraints on physiological function between two contrasting vegetation types with contrasting stability of water sources.

Keywords Carbon stable isotope · Chlorophyll fluorescence · South Florida · Hydraulic conductivity · Photosynthetic capacity

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Introduction

Plant hydraulic characteristics have recently been shown to have substantial influence over many aspects of plant form and function (Brodribb and Feild 2000; Edwards 2006; Sack et al. 2005; Santiago et al. 2004; Sperry 2000). Control of plant function may arise from a fundamental tradeoff among woody species between allocation to xylem that resists cavitation, versus a xylem with high-water transport capacity (Tyree and Ewers 1991). Plant species with low water transport capacity may also exhibit reduced gas exchange, because rates of water loss from leaves appear to be limited by stem hydraulic supply and hydraulic architecture (Brodribb

and Feild 2000; Campanello et al. 2008; Katul et al. 2003; Santiago et al. 2004), which determine the structure and water transport properties of the vascular system and govern the balance between water supply and total transpiring leaf area (Zimmermann 1978). If hydraulic capacity limits the supply of water to leaves, we expect coordination between stem and leaf physiological capacity such that allocation to photosynthesis will be reduced. Alternatively, plant species with low capacity to transport water may simply allocate to fewer leaves per unit stem area, thus increasing the supply of water per unit leaf area (Tyree and Ewers 1991; Wright et al. 2006).

We ask whether the potential rate of water supply to leaves is linked to quantum yield of photosystem II, and whether this relationship is influenced by vegetation type in south Florida ecosystems: Subtropical evergreen broad leaf forests (hardwood hammocks) and pine woodlands (pine rocklands) (Snyder et al. 1990). Soil is poorly developed in pine rocklands and tends to accumulate in limestone pockets. Previous studies have indicated that predawn water potentials in pine rockland species, as well as being less negative in the dry season, show less seasonal variation than hardwood hammock species, consistent with a more stable water supply (Ewe et al. 1999). In addition, isotopic studies have confirmed that hardwood hammock species are more dependent on water resources at the surface layers of the soil profile, whereas pine rockland species utilize ground water (Ewe et al. 1999; Ish-Shalom et al. 1992). We hypothesized that because pine rockland species utilize a more stable water supply, hydraulic constraints on photosynthesis would be greater in hardwood hammock species, leading to a stronger relationship between hydraulic conductivity and quantum yield among hardwood hammock species compared to pine rockland species. We do not have a complete understanding of why some species only occur in hammocks, some are found only in pine rocklands, and some are found in both communities. One possible physiological explanation could be species-specific differences in hydraulic architecture and associated traits. This suite of characteristics can be extremely important in determining the tolerance of particular species to drought stress, and is likely to be an important factor in determining the distribution of species in hardwood hammocks and pine rocklands. Hydraulic constraints on physiological performance are also likely to be predictive of species-specific responses to changes in sea level or regional climate. Overall, this study provides information for understanding the contribution of physiological variation in hydraulic and photosynthetic processes in structuring the functional diversity of these two adjacent, but distinct vegetation communities.

Materials and methods

Study sites and species

The study was conducted in two adjacent (<1 km apart) sites in Everglades National Park, Florida, USA, both near the Hidden Lake Education Center (25.4°N, 80.6°W). Mean annual precipitation and temperature at the site are 1,470 mm and 24°C, respectively. South Florida has a subtropical to tropical climate with a wet season (May–October) related to tropical cyclones and thunderstorms in which 75% of annual precipitation is received. Approximately 25% of annual precipitation falls during the dry season (November–April), and is usually caused by cold fronts.

Both sites were located on limestone outcrops in an area that contains a mix of hardwood hammocks and pine rocklands. Hardwood hammocks are evergreen, closed canopy broad-leaved forests with a tree community mostly derived from Caribbean island flora together with an intermixture of temperate genera like *Celtis*, *Morus* and *Quercus*, whereas pine rockland is a fire-maintained open forest community with a diverse understory of tropical and temperate shrubs, palms, and herbs (Snyder et al. 1990). Measurements were performed on eight tree species that ranged from 5 to 15 m in height in hardwood hammock and seven tree species that ranged from 3 to 15 m in height from pine rocklands for a total of 15 of the most dominant species at the sites that also vary widely in overall morphology (Table 1). All measurements were performed between July and August 2002, when leaves were ca. 3–5 months old.

Chlorophyll fluorescence

The quantum yield of photosystem II in the light (ϕ_{PSII}) was measured with a portable photosynthesis yield analyzer (MINI-PAM; Waltz, Effeltrich, Germany) which determined the increase in chlorophyll fluorescence during a single saturating flash of light applied for 0.8 s at an intensity of 3,500 μmol m^{-2} s^{-1} under natural field conditions (Bilger et al. 1995; Brodribb and Feild 2000). We calculated ϕ_{PSII} as $(F'_m - F)/F'_m$, where F is the fluorescence yield of the light adapted leaf and F'_m is the maximum fluorescence yield of the light adapted leaf (Bilger et al. 1995). Leaf temperature during measurements varied naturally from 28 to 33°C. Leaves were induced with an external halogen light source at a photosynthetic photon flux density (PPFD) of 800 μmol m^{-2} s^{-1} for approximately 5 min before application of the saturating pulse. All measurements were made between 1100 hours and 1300 hours on clear days with saturating irradiance (>500 μmol m^{-2} s^{-1} PPFD). Measurements of ϕ_{PSII} were

Table 1 Tree species found in hardwood hammock and pine rockland vegetation types in Everglades National Park, Florida, USA

Species (Family)	k_S	$k_L \times 10^{-4}$	ϕ_{PSII}	$\delta^{13}C$	$A_L:A_S$
Hardwood hammock					
Ardisia elliptica (Myrsinaceae)	1.81 ± 0.37	3.33 ± 0.46	0.11 ± 0.02	-30.92	0.52 ± 0.04
Ardisia escallonoides (Myrsinaceae)	2.79 ± 0.45	6.12 ± 1.12	0.12 ± 0.01	-30.14	0.47 ± 0.04
Bursera simaruba (Burseraceae)	3.86 ± 1.01	4.47 ± 0.90	0.16 ± 0.02	-29.91	0.84 ± 0.07
Coccoloba diversifolia (Polygonaceae)	2.41 ± 0.22	4.64 ± 0.48	0.13 ± 0.03	-33.10	0.54 ± 0.05
Eugenia axillaris (Myrtaceae)	2.39 ± 0.19	4.68 ± 0.45	0.10 ± 0.02	-27.10	0.54 ± 0.05
Lysiloma latisiquum (Fabaceae)	2.53 ± 0.32	12.52 ± 4.83	0.22 ± 0.02	-29.40	0.37 ± 0.07
Quercus virginiana (Fagaceae)	5.36 ± 0.60	16.16 ± 1.75	0.22 ± 0.01	-29.68	0.35 ± 0.04
Tetrazyigia bicolor (Melastomataceae)	2.73 ± 0.19	4.26 ± 0.26	0.12 ± 0.01	-29.90	0.64 ± 0.02
Pine rockland					
Citharexylum fruticosum (Verbenaceae)	4.15 ± 0.38	7.66 ± 0.89	0.17 ± 0.01	-29.12	0.59 ± 0.10
Guettarda scabra (Rubiaceae)	2.69 ± 0.24	7.69 ± 0.90	0.19 ± 0.01	-30.17	0.44 ± 0.03
Ilex krugiana (Aquifoliaceae)	1.97 ± 0.39	4.01 ± 0.64	0.17 ± 0.01	-29.11	0.53 ± 0.10
Myrica cerifera (Myricaceae)	3.50 ± 0.32	8.13 ± 1.81	0.15 ± 0.01	-30.19	0.52 ± 0.07
Pinus elliottii (Pinaceae)	1.81 ± 0.30	3.87 ± 0.91	0.18 ± 0.01	-28.20	0.65 ± 0.07
Rhus copallina (Anacardiaceae)	8.64 ± 1.74	13.30 ± 3.10	0.24 ± 0.02	-29.68	0.61 ± 1.12
Schinus terebinthefolius (Anacardiaceae)	6.65 ± 0.47	13.97 ± 1.47	0.22 ± 0.00	-30.66	0.51 ± 0.09

Values are means (± 1 SE) for sapwood-specific hydraulic conductivity (k_S; kg m^{-1} s^{-1} MPa^{-1}; $n = 3$–6 individuals per species), leaf-specific hydraulic conductivity (k_L; kg m^{-1} s^{-1} MPa^{-1}; $n = 3$–6 individuals per species), quantum yield of photosystem II (ϕ_{PSII}; $n = 3$–8 individuals per species), leaf carbon isotopic composition ($\delta^{13}C$; ‰; $n = 1$ composite sample per species), and leaf area-to-sapwood area ratio ($A_L:A_S$; cm^2 leaf m^{-2} sapwood; $n = 3$–6 individuals per species)

made on 3–5 leaves from 3 to 8 individuals of each species. We accessed canopy branches using a ladder and selected the youngest fully expanded leaves for measurement of ϕ_{PSII}.

The use of fluorescence for evaluating photosynthetic electron transport and CO_2 assimilation has been limited in C_3 plants due to uncertainty in the relationship between electron transport and CO_2 uptake (Bilger et al. 1995; Brodribb and Feild 2000; Genty et al. 1989), because chlorophyll fluorescence measures the reduction state of PSII and therefore cannot distinguish among electrons used for carboxylation versus oxygenation of Ribulose 1,6 bi-phosphate, and other non-assimilatory electron transport pathways (Brodribb and Feild 2000; Edwards and Baker 1993; Fryer et al. 1998). Nonetheless, good agreement between photosynthetic CO_2 assimilation determined with infrared gas analysis and that estimated by ϕ_{PSII} has been shown under a range of temperature, light and humidity, among C_3 species (He and Edwards 1996). In this study, we use ϕ_{PSII} as a relative index of maximum photosynthetic CO_2 assimilation under similar, non-limiting conditions of temperature, light, and water. Under such conditions, which were achieved by measuring only canopy leaves on clear days during the summer thunderstorm season, differences in photorespiration should be small (Brodribb and Feild 2000). Furthermore, a previous investigation of a diverse group of conifers using similar fluorescence measurements has shown very reliable

correlation with maximum CO_2 assimilation rates (Brodribb and Hill 1997).

Hydraulic conductivity

Hydraulic conductivity (k_H) was measured on 5–10 excised stems with leaves on which chlorophyll fluorescence has been previously measured, from 3 to 6 individuals of each species. Early in the morning, upper crown branches 1.5–2 m were detached from the tree and re-cut under filtered water (0.2 µm) to prevent xylem embolism and transported to the laboratory in opaque plastic bags. Vessel lengths were determined by the air pressure technique (Ewers and Fisher 1989), and mean and maximum lengths ranged from 19–130 cm to 21–157 cm, respectively. Thus, excised branches were longer than the measured maximum vessel lengths. While immersed in water the cut ends of un-branched stem segments 6–10 cm in length, 4–8 mm in diameter were shaved with Teflon coated razor blades and subsequently connected to a hydraulic conductivity apparatus. The hydraulic conductivity apparatus consisted of a beaker supplying degassed and filtered water under gravitational pressure to the stem. Flow rates were determined volumetrically. Native k_H was estimated as the rate of water flow (J, kg s^{-1}) in a stem when a small (approx. 0.18 kPa) pressure gradient (dP/dx, MPa m^{-1}) is applied across the stem according to the following equation: $k_H = J/(dP/dx)$. It was assumed that the entire xylem area

was conductive based on low percent loss in conductivity (<20%) after a high-pressure flush, verification with dye in some species, and age of material. Sapwood-specific hydraulic conductivity (k_S) was calculated as k_H per sapwood area of the sample stem. The sapwood area was calculated using measurements of xylem diameter, subtracting pith if present. Leaf-specific conductivity (k_L) was calculated from the ratio of k_H and leaf surface area distal to the stem section used for k_H measurement. Leaf area was measured with a leaf area meter (LI-3100, Li-Cor Biosciences, Lincoln, NE, USA). Leaf area-to-sapwood area ratio (A_L:A_S) was calculated as the quotient of leaf area-to-sapwood area for each sample stem.

Carbon isotope composition

Leaf carbon isotopic composition (δ^{13}C) was measured on one composite sample per species, in which all of the ϕ_{PSII} measurement leaves were combined. Leaves were dried at 50°C to constant mass, ground with a Wiley Mill, and the CO_2 liberated after combustion with a CuO catalyst at 850°C in a sealed glass tube was isolated on vacuum lines and analyzed for ^{13}C/^{12}C ratios in an isotope ratio mass spectrometer (VG Isogas, Middlebury, UK). δ^{13}C was calculated relative to the Pee Dee Belemnite standard using the relationship (Ehleringer and Osmond 1989):

$$\delta^{13}\text{C}(‰) =$$
$$[(^{13}\text{C}/^{12}\text{C in sample})/(^{13}\text{C}/^{12}\text{C in standard}) - 1] \times 1{,}000.$$

Statistical analyses

Comparisons of k_S, k_L, ϕ_{PSII}, A_L:A_S, and δ^{13}C, between hardwood hammock and pine rockland species were performed with t test in SAS version 8.02. Bivariate relationships between measures of hydraulic conductivity and ϕ_{PSII} were analyzed with type II least-squares regression. We first analyzed the relationship among all species in one regression model. We then tested for differences in slope among species from hardwood hammock versus pine rockland vegetation types using likelihood ratios. If no significant difference in slope was detected, tests for differences in elevation (y-intercept) were performed using randomization routines that are analogous to ANCOVA with (S)MATR ver. 1.0 software (Falster et al. 2003). Significance was evaluated at $\alpha = 0.1$.

Results

Mean sapwood-specific hydraulic conductivity (k_S) ranged from 1.8 kg m^{-1} s^{-1} MPa^{-1} in *Ardisia elliptica* and *Pinus elliottii* to 8.64 kg m^{-1} s^{-1} MPa^{-1} in *Rhus copallina*

Table 2 Mean (± 1 SE) for physiological traits of trees in hardwood hammock ($n = 8$) and pine rockland ($n = 7$) vegetation types in Everglades National Park, Florida, USA

Variable	Hardwood hammock	Pine rockland	t Statistic	P value
k_S	2.99 ± 0.42	4.20 ± 0.90	-1.16	0.278
$k_L \times 10^{-4}$	7.02 ± 1.77	8.38 ± 1.41	-0.60	0.561
ϕ_{PSII}	0.148 ± 0.018	0.189 ± 0.011	**-2.06**	**0.062**
A_L:A_S	0.533 ± 0.590	0.550 ± 0.024203	-0.27	0.791
δ^{13}C	-30.02 ± 0.63	-29.74 ± 0.36	-0.39	0.704

Significant differences ($p \leq 0.10$) between means are indicated in bold type. Units as in Table 1

(Table 1). Mean leaf-specific hydraulic conductivity (k_L) ranged from 3.3×10^{-4} kg m^{-1} s^{-1} MPa^{-1} in *A. elliptica* to 16.2×10^{-4} kg m^{-1} s^{-1} MPa^{-1} in *Quercus virginiana*. Mean quantum yield of photosystem II (ϕ_{PSII}) was lowest in *Eugenia axillaris* (0.10) and highest in *R. copallina* (0.24). Leaf carbon isotopic composition (δ^{13}C) ranged from $-33.1‰$ in *Coccoloba diversiflolia* to $-27.1‰$ in *E. axillaris*, and leaf area-to-sapwood area ratio (A_L:A_S) ranged from 0.35 cm^2 m^{-2} in *Q. virginiana* to 0.84 cm^2 m^{-2} in *Bursera simaruba* (Table 1). The only physiological trait that showed variation between vegetation types was ϕ_{PSII}, which was significantly greater in pine rockland species (Table 2).

We measured a significant positive relationship between k_S and ϕ_{PSII} across all species ($r^2 = 0.45$, $P \leq 0.01$), within hardwood hammock species ($r^2 = 0.45$, $P \leq 0.1$), and among pine rockland species ($r^2 = 0.66$, $P \leq 0.05$; Fig. 1). We also measured a significantly greater slope for the ϕ_{PSII}–k_S relationship in hardwood hammock species compared to pine rockland species ($P = 0.005$), but the pine rockland species exhibited an overall greater range and greater values in k_S (Fig. 1).

There was also a significant positive relationship between k_L and ϕ_{PSII} across all species ($r^2 = 0.68$, $P \leq 0.0005$), within hardwood hammock species ($r^2 = 0.85$, $P \leq 0.001$), and within pine rockland species ($r^2 = 0.57$, $P \leq 0.05$; Fig. 2). The slopes of the regression lines were similar between hardwood hammock and pine rockland species for the k_L–ϕ_{PSII} relationship ($P = 0.38$), but there was a significantly greater y-intercept among the pine rockland species compared to the hardwood hammock species ($P = 0.02$), indicating greater ϕ_{PSII} for a given k_L in pine rockland species.

In the relationship between k_L and A_L:A_S, we measured a significant negative relationship across all species ($r^2 = 0.27$, $P \leq 0.05$), and a significant negative relationship among hardwood hammock species ($r^2 = 0.49$, $P \leq 0.05$), but not among pine rockland species ($r^2 = 0.02$,
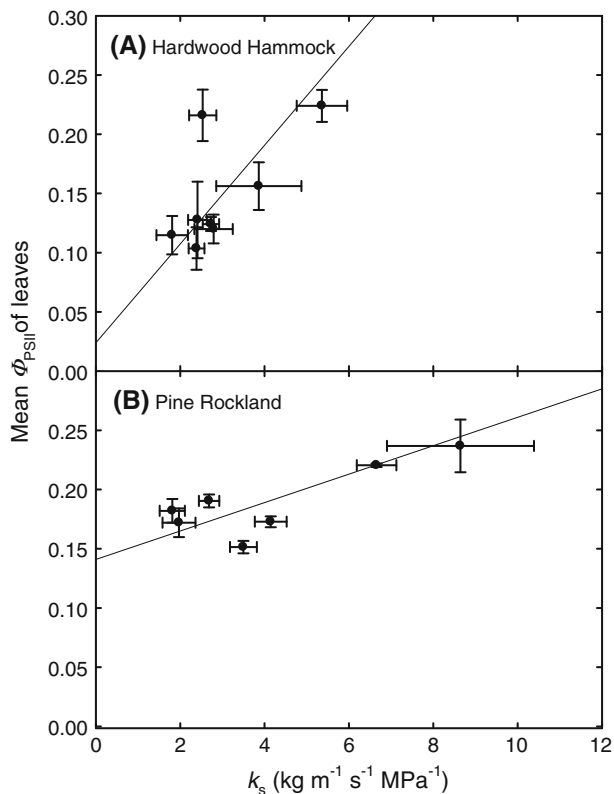
Fig. 1 Relationship between sapwood-specific hydraulic conductivity (k_S) and quantum yield of photosystem II (ϕ_{PSII}) of leaves from south Florida tree species growing in **a** hardwood hammock ($\phi_{PSII} = 0.042k_S + 0.024$; $r^2 = 0.45$, $P \leq 0.1$) and **b** pine rockland ($\phi_{PSII} = 0.012k_S + 0.141$; $r^2 = 0.66$, $P \leq 0.05$) vegetation types in Everglades National Park, Florida, USA. Values are mean $\pm$ SE
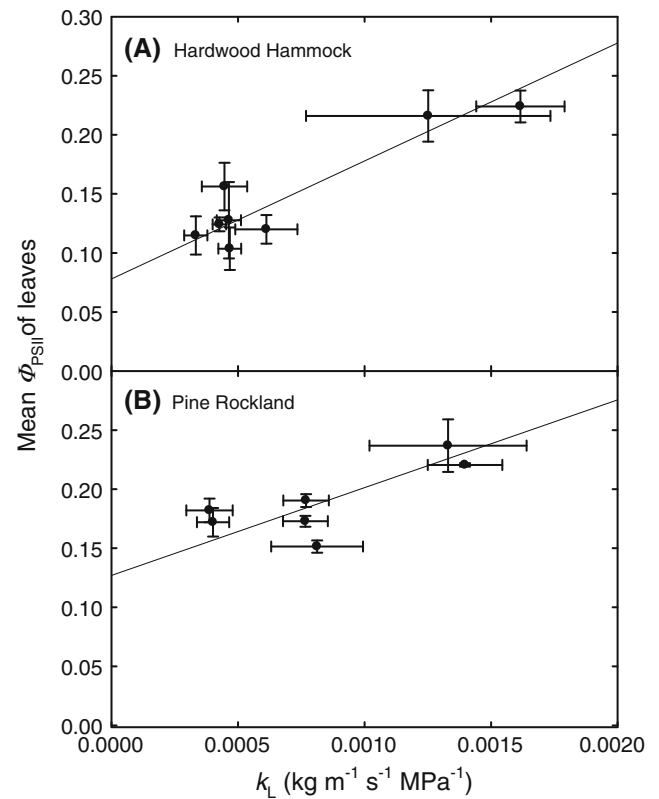
Fig. 2 Relationship between leaf-specific hydraulic conductivity (k_L) and quantum yield of photosystem II (ϕ_{PSII}) of leaves from tree species in **a** hardwood hammock ($\phi_{PSII} = 99.9k_L + 0.078$; $r^2 = 0.85$, $P \leq 0.001$) and **b** pine rockland ($\phi_{PSII} = 74.3k_L + 0.127$; $r^2 = 0.57$, $P \leq 0.05$) vegetation types in Everglades National Park, Florida, USA. Values are mean $\pm$ SE

$P > 0.5$; Fig. 3). The pine rockland species showed a low range of $A_L:A_S$ relative to the hardwood hammock species (Fig. 3). Statistical differences between relationships among hardwood hammock species and pine rockland species were not analyzed in this case due to lack of significance in the relationship among pine rockland species.

Leaf $\delta^{13}C$ was not significantly related to k_S across all species ($r^2 = 0.06$, $P = 0.38$) or within hardwood hammock species ($r^2 = 0.02$, $P = 0.76$), but showed a significant negative relationship as a function of k_S within pine rockland species ($r^2 = 0.58$, $P \leq 0.05$; Fig. 4c). The relationship between $\delta^{13}C$ and k_L was not significant across all species ($r^2 = 0.02$, $P = 0.66$) or within hardwood hammock species ($r^2 = 0.03$, $P = 0.70$), but showed a significant negative relationship as a function of k_L within pine rockland species ($r^2 = 0.75$, $P = 0.01$; Fig 4d). Relationships between $\delta^{13}C$ and $A_L:A_S$, ϕ_{PSII} and $\delta^{13}C$, and ϕ_{PSII} and $A_L:A_S$ were not statistically significant when evaluated across all species or within either vegetation type ($P > 0.1$).

Discussion

The relationship between photosynthetic capacity and hydraulic conductivity represents the physiological coordination between water supply and carbon gain potential. Plants only allocate resources to photosynthesis that can be utilized given the limitations placed on carbon gain through stress and resource availability (Field 1991). Therefore, variation in water source utilization by contrasting vegetation types should be manifested in hydraulic–photosynthesis relationships reflecting the tradeoff between carbon gain and water loss, and constraints imposed on carbon gain by water availability (Cowan 1982; Schulze and Hall 1982; Taylor and Eamus 2008). We detected a general positive relationship between photosynthesis and hydraulic supply to leaves across all species (Brodribb and Feild 2000; Edwards 2006; Santiago et al. 2004), as well as variation in regression parameters between species from hardwood hammock and pine rockland vegetation types. As expected if pine rockland species have better access to
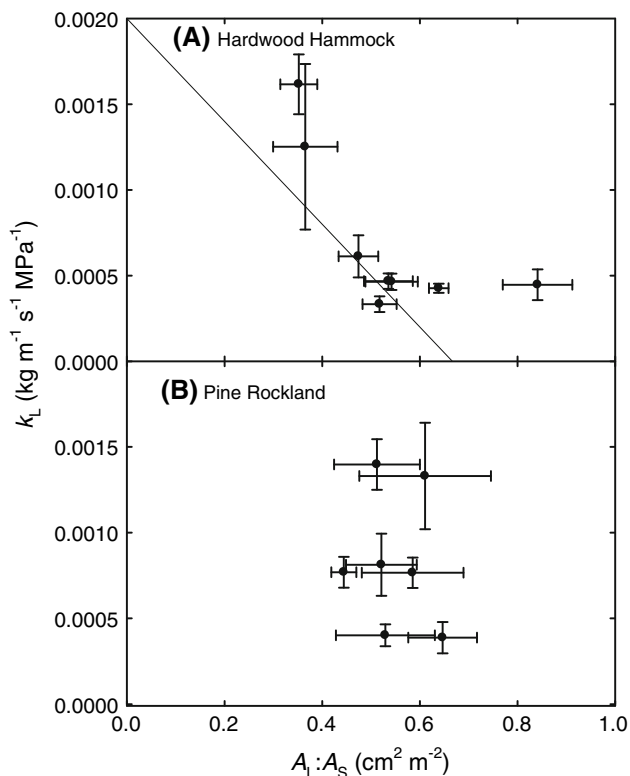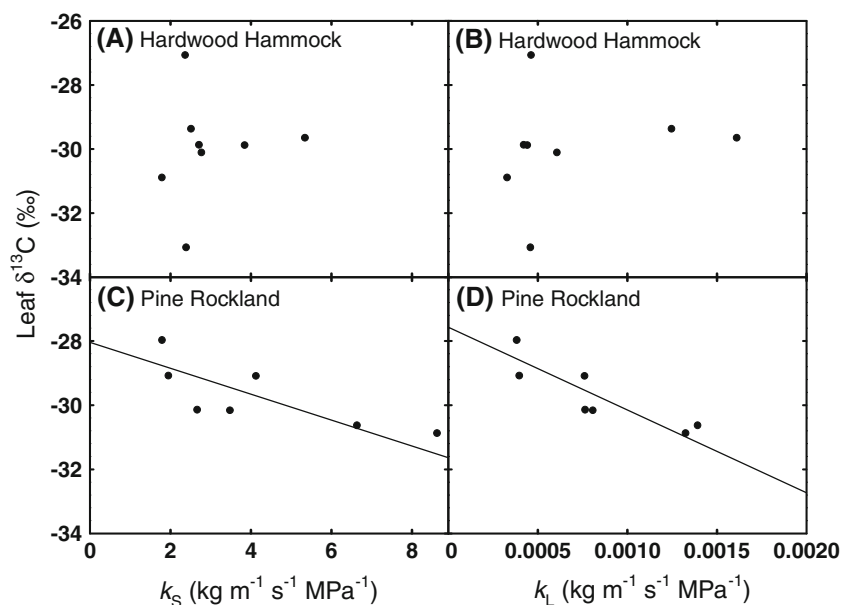
Fig. 3 Leaf-specific hydraulic conductivity (k_L) as a function of leaf area-to-sapwood area ratio (A_L:A_S) for south Florida tree species in **a** hardwood hammock ($k_L = -0.0030A_L$:$A_S + 0.002$; $r^2 = 0.49$, $P \leq 0.05$) and **b** pine rockland ($r^2 = 0.02$, $P > 0.5$) vegetation types in Everglades National Park, Florida, USA. Values are mean ± SE

stable water sources than hardwood hammock species during the dry season (Ewe et al. 1999; Ish-Shalom et al. 1992; Ross et al. 1994), pine rockland species exhibited a greater overall range of values for k_S, greater quantum

yield, and evidence of greater carbon isotope discrimination during photosynthesis with increasing hydraulic supply. Greater quantum yield for a given k_L in pine rockland species is also in line with maximizing allocation to carbon gain potential when a relatively stable water source is available. Overall, the consistency of relationships among leaf and branch traits indicates coordination among branch and leaf function, whereas the variation in relationships between leaf and branch traits among vegetation types demonstrates the potential for site resource availability to mediate the scaling of these relationships.

We used the relationship between photosynthesis and hydraulic supply to compare how trees in two vegetation types with contrasting water supply hydraulically regulate photosynthetic capacity (Meinzer et al. 2008a). This approach is analogous to investigations of leaf trait relationships among sites (Reich et al. 1997; Reich et al. 1999; Santiago and Mulkey 2005; Wright et al. 2005) that can reveal how resources are allocated to maximize carbon gain under a particular resource regime. Evidence is mounting that woody species generally share a positive relationship between hydraulic supply and photosynthetic capacity (Brodribb and Feild 2000; Brodribb et al. 2002; Bucci et al. 2004; Edwards 2006; Meinzer et al. 2008b; Santiago et al. 2004). Yet, species in adjacent vegetation types may not occupy the entire range of bivariate trait relationships and may instead specialize in ranges of the trade-off spectrum where trait values maximize carbon gain potential (Santiago and Wright 2007). The greater slope for hardwood hammock species compared to pine rockland species found in the ϕ_{PSII}–k_S relationship is likely a result of a occupying a lower range of k_S, where there is a greater increase in ϕ_{PSII} for a given increase in k_S (Fig. 1).

Fig. 4 Leaf carbon isotope composition ($\delta^{13}C$) as a function of **a**, **c** sapwood-specific hydraulic conductivity (k_S) and **b**, **d** leaf-specific hydraulic conductivity (k_L) for south Florida tree species from two vegetation types in Everglades National Park, Florida, USA. Regressions: **c** $\delta^{13}C = -0.404k_L - 28.04$; $r^2 = 0.58$; $P \leq 0.05$ and **d** $\delta^{13}C = -2581k_L - 27.57$; $r^2 = 0.75$; $P \leq 0.01$. Values for $\delta^{13}C$ represent composite samples per species and k_S and k_L represent site means per species

The lower slope of the ϕ_{PSII}–k_S relationship in pine rockland species suggests that there may be diminishing returns for ϕ_{PSII} with increasing k_S. To the extent that the lower range in k_S values, as well as lower ϕ_{PSII} for a given k_L in hardwood hammock species (Fig. 2) reduces the risk of cavitation, hardwood hammock species with low rates of k_S would be less vulnerable to drought-induced cavitation and better prepared to rely on less consistent water sources than pine rockland species.

We also employed the ratio of leaf surface area per unit of sapwood area (leaf area/sapwood area; A_L:A_S) as an index of potential transpirational demand relative to water transport capacity (Meinzer 2002; Santiago et al. 2000), because plant species with contrasting photosynthetic and hydraulic strategies can maintain a high k_L through variation in k_S and/or A_L:A_S. There is strong evidence that species share a positive relationship between k_L and maximum photosynthesis per leaf area (Hubbard et al. 2001; Santiago et al. 2004), thus the nature of where species fall on this axis of covariation is determined by the combined effects of variation in k_S and A_L:A_S. Our interspecific negative relationship of k_L as a function of A_L:A_S across all species is consistent with other studies demonstrating a tendency for species with relatively low leaf area per unit sapwood area to be supplied with high-water transport per leaf area (Meinzer et al. 2008a). The negative relationship between k_L and A_L:A_S in hardwood hammocks indicates greater regulation of leaf-specific hydraulic conductivity by hydraulic architecture in hardwood hammock tree species. We did not observe a significant k_L–A_L:A_S relationship within pine rockland species in this study (Fig. 2b). In the case of pine rockland, species with a high A_L:A_S are also able to maintain a relatively high k_L in accordance with greater water availability in pine rocklands.

We also found lower $\delta^{13}C$ with increasing k_S and k_L in pine rockland species, but not in hardwood hammock species (Fig. 4). Discrimination against ^{13}C during photosynthesis reflects the balance between the demand for CO_2 at the site of carboxylation against the diffusive supply through stomata (Farquhar et al. 1989). Our data indicating decreasing leaf $\delta^{13}C$ with increasing k_S and k_L in pine rockland species signifies increasing discrimination against ^{13}C with increasing hydraulic supply. Because pine rockland species with greater k_S and k_L also exhibit greater photosynthesis which would otherwise lower internal CO_2 concentration (c_i) and discrimination against ^{13}C during photosynthesis thus increasing $\delta^{13}C$, it appears that increased stomatal conductance also accompanies greater k_S and k_L in pine rockland species and more than compensates for higher photosynthesis by increasing c_i and thus reducing leaf $\delta^{13}C$ (Fig. 4). The increased stomatal conductance suggested by low $\delta^{13}C$ at high k_S and k_L is consistent with greater water availability in pine rockland

habitats and illustrates the coordinated allocation of leaf and stem hydraulic capacities that reflect variation in water availability in hardwood hammock and pine rockland vegetation types.

Several studies have underscored the coordination between photosynthesis and water transport capacity (Brodribb and Feild 2000; Edwards 2006; Hubbard et al. 2001; Katul et al. 2003; Santiago et al. 2004; Sperry 2000). Several studies have also highlighted that plants with low hydraulic capacity can sometimes increase photosynthetic capacity by increasing allocation to foliar nitrogen (Taylor and Eamus 2008; Wright et al. 2003), thus emphasizing the importance of resource substitution in the coordination of plant hydraulic supply and photosynthetic gas exchange. Studies that incorporate allocation to leaf nitrogen and its role in branch-to-leaf hydraulic relations are likely to increase our understanding of variation in interspecific regulation of carbon gain potential (Meinzer et al. 2008a). Our study draws attention to the use of the relationship between water transport and photosynthesis to ascertain the constraints on physiological function in contrasting vegetation types. We demonstrate that relationships among physiological parameters give us information regarding the efficient utilization of resources to produce the strategies that determine the functional diversity of plant communities.

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