

# Coordination between water-transport efficiency and photosynthetic capacity in canopy tree species at different growth irradiances

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**Summary** Plasticity in hydraulic architecture of five dominant Atlantic forest species differing in light requirements and growth rates was evaluated in saplings grown at different irradiances to determine if hydraulic architecture changes in coordination with photosynthetic capacity. Saplings were grown in shade-houses at 10, 30, 45 and 65% of full solar irradiance for 4 months. In four of the five species, maximum relative growth rates were observed at intermediate irradiances (30 and 40% of full sun). Slow-growing species had lower maximum electron transport rates ( $ETR_{max}$ ) than fast-growing species. A positive correlation between  $ETR_{max}$  and maximum leaf hydraulic conductivity ( $K_L$ ) was found across species, suggesting that species-specific stem hydraulic capacity and photosynthetic capacity were linked. Species with relatively high growth rates, such as *Cedrela fissilis* Vell., *Patagonula americana* L. and *Cordia trichotoma* (Vell.) Arrab. Ex Stend, exhibited increased  $K_L$  and specific hydraulic conductivity ( $K_S$ ) with increased growth irradiance. In contrast,  $K_S$  and  $K_L$  did not vary with irradiance in the slower-growing and more shade-tolerant species *Balfourodendron riedelianum* (Engl.) Engl. and *Lonchocarpus leucanthus* Burkart, despite a relatively large irradiance-induced variation in  $ETR_{max}$ . A correlation between  $K_S$  and  $ETR_{max}$  was observed in fast-growing species in different light regimes, suggesting that they are capable of plastic changes in hydraulic architecture and increased water-transport efficiency in response to changes in light availability resulting from the creation of canopy gaps, which makes them more competitive in gaps and open habitats.

**Keywords:** Atlantic forest, high-light-requiring trees, hydraulic conductivity, shade-tolerant trees, water-use efficiency.

## Introduction

Tropical forest trees are usually classified either as sun (or light-requiring) or shade-tolerant species according to their ecophysiological characteristics and behavior in different light environments (Whitmore 1996). Light-requiring species tend to be pioneers, germinate preferentially in gaps, grow quickly,

have high mortality rates and are usually intolerant of low-light conditions. In contrast, shade-tolerant species germinate, grow and have high survival rates in the understory where solar radiation is low. Consistent with their life history traits, light-requiring species have higher photosynthetic rates and water-transport capacities than shade-tolerant species (Tyree et al. 1998). Sack et al. (2005) reported that leaf hydraulic conductance is higher in tropical species requiring high irradiances for establishment and growth compared with species able to regenerate in low irradiances (Sack et al. 2005).

Water-transport capacity is influenced by intrinsic characteristics of the vascular system, such as conduit size and density, and by the leaf surface area supported by conductive stem tissues. Stomatal conductance, which acts as a variable resistance at the leaf–atmosphere interface, partially regulates water flow through plants during the day (e.g., Meinzer and Grantz 1990, Meinzer et al. 1995, Sperry 2000). Katul et al. (2003) developed a model that provides a theoretical framework linking stomatal conductance, photosynthesis and water-transport capacity to leaves. This model predicts a direct relationship between maximum carboxylation capacity and soil–plant hydraulic properties. Such coordination between water-transport efficiency and photosynthetic capacity has been observed in several species from different ecosystems (Brodribb and Feild 2000, Brodribb et al. 2002, Santiago et al. 2004). More recently, Brodribb et al. (2005) found a strong correlation between hydraulic capacity, measured as leaf hydraulic conductance, and both stomatal conductance and photosynthetic capacity in conifers, ferns and angiosperms.

Resource allocation to adjust water-transport efficiency to the prevailing environmental conditions may be influenced by irradiance. High solar radiation and evaporative demand during growth may trigger increased water-transport efficiency (Bond and Kavanagh 1999). At high irradiances, simple adjustments in plant architecture, such as a reduction in the leaf to sapwood area ratio (LA/SA), enhance water-transport efficiency per unit leaf area. The ratio LA/SA is a morphological index that reflects the relationship between the potential water requirement of foliar tissue and the water-transport capacity of

the plant (Goldstein et al. 2002). Adjustments to the specific conductivity of sapwood in response to irradiance may stabilize water-transport efficiency per unit leaf area (Reid et al. 2003, Renninger et al. 2006, 2007).

The ability of plants to allocate resources among functions in a coordinated manner can determine competitive success in tropical forests, where dramatic and unpredictable changes in environmental conditions occur as a result of the creation and closure of canopy gaps. High water-transport capacity allows maintenance of high leaf water potentials, stomatal conductances and, consequently, high CO<sub>2</sub> assimilation rates in environments with high evaporative demand and solar radiation, as is commonly found in canopy openings. It is unknown whether plants of the same species have the ability to maintain tight coordination between water-transport efficiency and photosynthetic capacity in different light environments, which could be an important acclimation response for trees in forest ecosystems where substantial microclimatic changes occur after gap formation. In this study, we evaluated plasticity of physiological and morphological attributes in response to different irradiances in five tree species that differ in light requirement. Specifically, we evaluated if changes in hydraulic architecture and photosynthetic capacity in five dominant canopy species of the Atlantic Forest in northeastern Argentina changed in a coordinated manner when plants were grown in different solar irradiances, and if so, whether changes in these characteristics were correlated with growth rates and water-use efficiencies.

## Materials and methods

### *Study area and plant material*

Measurements were made in saplings of five canopy species common in the Atlantic Forest of Misiones Province, northeastern Argentina (26°25' S, 54°37' W, elevation 230 m). Mean annual rainfall in the area is about 2000 mm and is evenly distributed throughout the year. Because mean annual temperature is 21 °C, frost seldom occurs in winter, and temperatures are favorable for growth during most of the year. This subtropical semi-deciduous forest has many lianas and bamboo species in the understory that may impede tree regeneration, particularly in gaps and disturbed sites (Oliveira-Filho et al. 1994, Campanello et al. 2007). The five species studied were selected based on their high abundance in forest ecosystems of northern Misiones Province (*Balfourodendron riedelianum* (Engl.) Engl., Rutaceae; and *Lonchocarpus leucanthus* Burkart, Fabaceae) and in gaps or open areas (*Patagonula americana* L., Boraginaceae; *Cedrela fissilis* Vell., Meliaceae; and *Cordia trichotoma* (Vell.) Arrab. Ex Stand, Boraginaceae). Although some ecological data exist for these species (see López et al. 1987, Kageyama and Gandara 2000, Lorenzi 2002), the information is primarily based on survival and growth rates in plantations and observations on secondary succession. According to the literature, in which species are classified as suggested by Swaine and Whitmore (1988), *C. fissilis* can be considered as either an early- or

late-secondary species, and *C. trichotoma*, *P. americana* and *B. riedelianum* as late-secondary species. No information is available for *L. leucanthus*, but the light environment experienced by saplings of this species in Misiones is less than 30% of full sunlight (Campanello 2004). Similar irradiances were found in the field for *B. riedelianum*. The other three species are rarely found in the forest of Misiones, but are common in log landings and logging traffic lanes (author's unpublished observations). Taking into account all the information, we initially assumed that *B. riedelianum* and *L. leucanthus* were more shade tolerant than the other species, and that *C. fissilis* was the most sun-adapted species.

Saplings were collected in July 2001 from four sites covering an area of 20 ha. About eighty 20- to 30-cm-tall individuals of each species were transplanted to 20-l pots filled with inert pine bark substrate and a slow-release N,P,K fertilizer. Plants were transferred to a shade-house and were kept in low light and a high humidity for 3 months until they resumed growth.

### *Growing conditions*

In December 2001, 10 to 20 plants of each species were transferred to each of four light treatments (10, 30, 40 and 65% of full sun) and allowed to grow for four months. The light treatments, which were intended to reproduce a range of light microenvironments encountered in native forests of Misiones Province (Campanello et al. 2007), were obtained using neutral shade filters.

During the experiment, a complete N,P,K plus micronutrients fertilizer was added every 15 days, and fungal and insect attacks were subject to continuous control through the use of fungicides and insecticides as necessary. Rainfall was excluded by clear plastic covers. Irrigation was applied so that substrate water content was always higher than 80%, which is equivalent to water potentials above -0.3 MPa according to moisture release curves for the pine bark substrate used (data not shown).

Photosynthetic photon flux (PPF) was continuously measured in each light treatment in the shade house and under full sun conditions with photodiodes calibrated against a Li-Cor quantum sensor (Li-Cor, Lincoln, NE). Photosynthetic photon flux measurements were made every 10 seconds and data were recorded every 2 min. Air temperature and relative humidity (HMP35C, Vaisala, Helsinki, Finland) were measured hourly from 0900 to 1700 h on four clear days between December and April and air saturation deficit calculated. In addition, HOBO Type T Thermocouples (Onset Computer Corporation, Pocasset, MA) were installed and air temperature recorded at 5-min intervals during 20 days in March.

There were no significant differences among light treatments in air temperature, relative humidity or air saturation deficits (Table 1). Maximum air saturation deficit values were about 4 kPa under all experimental conditions. Microclimatic conditions observed in the light treatments in the shade house were consistent and similar to those of forest sites where the studied species occur naturally.

Table 1. Mean daily photosynthetic photon flux (PPF), maximum air temperature ( $T_{\max}$ ), minimum relative humidity ( $RH_{\min}$ ) and maximum air saturation deficit ( $ASD_{\max}$ ) in different irradiances. Values are means  $\pm$  SE of measurements made on four clear days between December 2001 and April 2002.

Variable	Irradiance (% of full sun)				
	100	65	40	30	10
PPF ( $\text{mol m}^{-2} \text{day}^{-1}$ )	26.0 $\pm$ 3.5	16.4 $\pm$ 2.6	10.9 $\pm$ 1.7	8.1 $\pm$ 1.5	2.6 $\pm$ 0.4
$T_{\max}$ ( $^{\circ}\text{C}$ )	37.5 $\pm$ 1.4	37.6 $\pm$ 1.7	38.2 $\pm$ 1.2	37.5 $\pm$ 1.4	36.9 $\pm$ 1.2
$RH_{\min}$ (%)	38.8 $\pm$ 5.7	39.8 $\pm$ 6.6	34.6 $\pm$ 5.8	36.5 $\pm$ 6.6	37.9 $\pm$ 6.8
$ASD_{\max}$ (kPa)	4.3 $\pm$ 0.8	4.3 $\pm$ 0.8	4.5 $\pm$ 0.6	4.3 $\pm$ 0.7	4.0 $\pm$ 0.6

### Photosynthesis

Three plants of each species per treatment were randomly selected, and chlorophyll fluorescence was measured with a pulse-amplitude modulated yield analyzer (Mini-PAM, Waltz, Effeltrich, Germany). Steady-state light-response curves were generated for a single, young fully expanded leaf per plant using the external halogen light unit of the Mini-PAM. Leaves were allowed to adjust to light conditions for at least 10 minutes at each of the five irradiances used for the light curves before a saturating pulse was applied. Saturation pulses were applied for 0.8 s at  $3500 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Dark-adapted quantum yields ( $F_v/F_m$ ) of PSII were recorded before dawn and corresponded to the initial points of the light curves. As in other studies,  $F_v/F_m$  values below 0.8 were considered indicators of permanent photoinhibition (see Lüttge et al. 1998, Franco et al. 1999, Krause et al. 2001).

Electron transport rates (ETR) through PSII were calculated from light-adapted quantum yield ( $\Delta\phi_F/\Delta\phi_{Fm}$ ) as:

$$\text{ETR} = 0.5\alpha(\Delta\phi_F/\Delta\phi_{Fm})(\text{PPF})$$

where  $\alpha$  is leaf absorbance and the 0.5 factor assumes an even distribution of absorbed quanta between PSII and PSI so that two photons are required for each electron passed through PSII. The ETR correction factor  $\alpha$  takes into account that only a fraction of the incident light is absorbed by the two photosystems. A value of  $\alpha = 0.84$  was used for calculations (Ehleringer 1981, Björkman and Demmig 1987).

Photosynthetic capacity, expressed as the maximum electron transport rate ( $\text{ETR}_{\max}$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), was calculated from the light curves as described by Rascher et al. (2000):

$$y = (\text{ETR}_{\max})(1 - e^{-bx})$$

where  $y$  is photosynthetic rate,  $x$  is irradiance and  $b$  is the instantaneous fractional growth rate of the exponential function. The saturating photosynthetic photon flux ( $\text{PPF}_{\text{sat}}$ ) was calculated as the irradiance at which 90% of maximum electron transport rate was reached.

### Hydraulic conductivity

Predawn hydraulic conductivity was measured on terminal stems or petioles (*C. fessilis*) that had developed under the experimental conditions. Six to 10 branches or petioles per spe-

cies in each of the four light regimes were cut under water before dawn and immediately transferred to an air-conditioned laboratory where they were recut and the cut ends trimmed under water with a razor blade. Leaves were removed from the distal part of the stem and bagged. Branch or petiole segments at least 7 cm in length were perfused with degassed and filtered ( $0.1 \mu\text{m}$ ) water under a hydrostatic pressure head of 3.4 to  $7.4 \times 10^{-3}$  MPa, and allowed to equilibrate for 5 min before the flow rate was measured. Flow rates were recorded at a constant temperature of  $25^{\circ}\text{C}$ . The hydraulic head pressure and segment length were recorded for the calculation of hydraulic conductivity ( $K_H$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ). Stems were then perfused with toluidine blue dye solution and sapwood area determined to calculate specific hydraulic conductivity ( $K_S$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ). Leaves of each sample were scanned and their area measured with Scion Image Analysis software (National Institute of Health). Hydraulic conductivity was expressed as leaf-specific conductivity ( $K_L$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ). Leaf area to sapwood area ratio (LA/SA) was also calculated.

### Leaf carbon stable isotope ratios

All leaves used for fluorescence measurements were dried to constant mass at  $60^{\circ}\text{C}$ . Leaves of the same species were pooled for each treatment, and the carbon isotope composition of the  $\text{CO}_2$  produced by combustion of the foliar tissue was determined by mass spectrometry. Carbon stable isotope composition ( $\delta^{13}\text{C}$ ) was calculated as the  $^{13}\text{C}/^{12}\text{C}$  ratio relative to PeeDee belemnite with a precision of 0.2‰. The  $\delta^{13}\text{C}$  in leaves is proportional to the ratio between internal and ambient  $\text{CO}_2$  partial pressures, and provides an indication of intrinsic water-use efficiency (assimilation/stomatal conductance) when the leaf was being formed (Farquhar and Richards 1984).

### Growth rates

Growth measurements were made at the beginning of December 2001 and at the end of the experiment in April 2002. The height from the base of the stem to the apical bud was recorded. The main stem diameter was measured with a digital caliper. A mark with red paint was made at the base of the stem to assure that subsequent measurements were made in the same place. Total number of leaves per plant was counted and total leaf area estimated based on the mean area per leaf. To calculate the mean leaf area, some leaf outlines were drawn on paper and the areas scanned and measured with image analysis

software. Relative growth rate (RGR) was expressed as the increment in a parameter (stem diameter, height or leaf area) divided by the initial value of the parameter.

#### Data analysis

One of the main problems in comparing morphological and physiological characteristics of plants growing under different conditions is the difficulty of separating plant responses to the environment from ontogenetic differences among individuals (Poorter 2001). Large differences in size can result in commensurate differences in functional characteristics. In this study, no correlation was found between physiological and morphological attributes on the one hand, and plant size measured either as diameter, height or total leaf area, on the other hand. No significant differences in height were observed within species across treatments, but there were differences across species in total height at the end of the experiment as a result of differences in growth rates; however, these differences were small. Significant differences among treatments for the same species were tested by analysis of variance (one-way ANOVA) for hydraulic architecture, specific leaf area (SLA) and RGR (Scheffé Test was used for mean comparisons). Regression functions were fitted between  $K_S$ ,  $K_L$  and  $ETR_{max}$ , between  $K_L$  and  $\delta^{13}C$  leaf, and among these attributes and RGR for each species and for the pooled species and treatments.

## Results

#### Photosynthetic capacity

Electron transport rate increased asymptotically with increasing PPF (Figure 1). Light-response curves differed depending on both species and growth irradiance. Photosynthetic capacity

at light saturation and  $PPF_{sat}$  are indicated in Figure 1. Both  $ETR_{max}$  and  $PPF_{sat}$  increased with increasing irradiance in *Cedrela fissilis* and *Cordia trichotoma*, whereas in the other species,  $ETR_{max}$  was higher in the 30 or 40% of full sun treatments and tended to decrease at 65% of full sun. In all light treatments,  $PPF_{sat}$  values were lower for *Lonchocarpus leucanthus* and *B. riedelianum* than for the other species. At 65% of full sun,  $PPF_{sat}$  was  $303 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *Balfourodendron riedelianum* and  $1091 \mu\text{mol m}^{-2} \text{s}^{-1}$  for *C. fissilis*. Potential quantum yield increased with irradiance and peaked at 65% of full sun, except for *C. trichotoma* and *L. leucanthus*, where  $F_v/F_m$  peaked in 45% of full sunlight and then decreased at higher irradiances. In *C. trichotoma* and *L. leucanthus*,  $F_v/F_m$  values at 65% of full sun were relatively low (0.777 and 0.764, respectively) and plants were permanently photoinhibited (Björkman and Demmig 1987). For this reason, the  $ETR_{max}$  values from these species in 65% of full sunlight were excluded from subsequent analysis involving photosynthetic capacity.

#### Hydraulic conductivity

A saturating exponential function described the relationship between  $K_S$  and  $K_L$  across all species and light treatments ( $K_L = 4.08(1 - \exp(-0.20K_S))$ ;  $r^2 = 0.89$ ,  $P < 0.0001$ , data not shown). Specific hydraulic conductivity of *C. fissilis* increased significantly ( $F_{3,25} = 3.75$ ,  $P < 0.05$ ) with increasing irradiance from  $2.89 \pm 0.39$  to  $6.65 \pm 1.48 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$  between 10 and 65% of full sun (Table 2). The  $K_S$  of *Patagonula americana* increased between the 10 and 65% of full sun treatments, but was higher at 30% of full sun ( $F_{3,28} = 3.71$ ,  $P < 0.05$ ). The other species exhibited no significant differences in  $K_S$  with growth irradiance. Consistent with adjustments in  $K_S$ ,  $K_L$  increased significantly at higher irradiances in *C. fissilis* ( $F_{3,34} =$

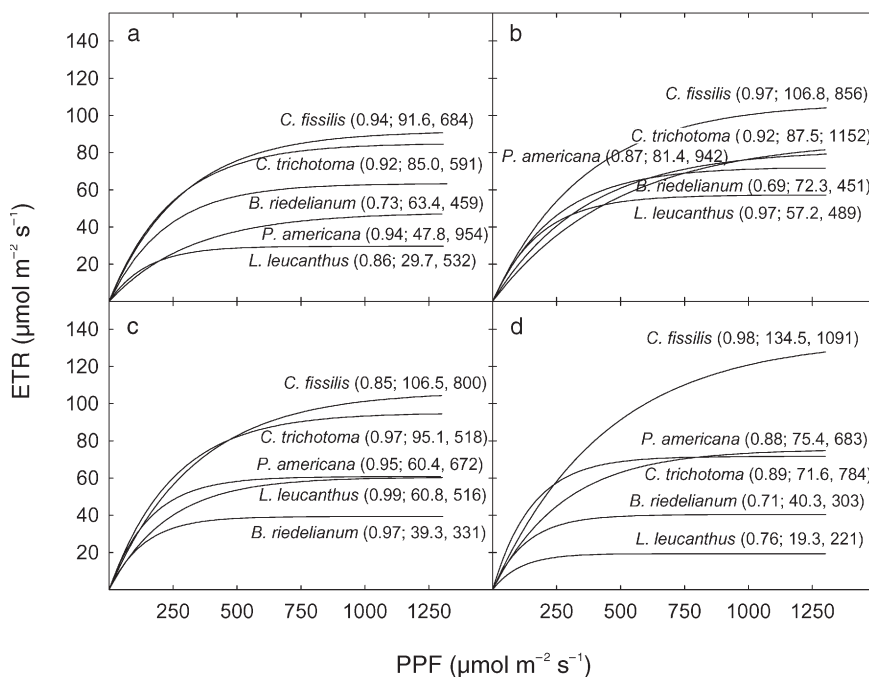


Figure 1. Electron transport rate (ETR) as a function of photosynthetic photon flux (PPF) for *Cedrela fissilis*, *Cordia trichotoma*, *Balfourodendron riedelianum*, *Patagonula americana* and *Lonchocarpus leucanthus* saplings grown in (a) 10, (b) 30, (c) 40 and (d) 65% of full sun. An exponential function for each species was fitted to the ETR-PPF relationships obtained for three individuals grown at the same irradiance ( $n = 3$  for each species  $\times$  irradiance combination). The  $r^2$  values of the regression fitted  $ETR_{max}$  ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ ) and PPF at 90% of maximum ETR ( $PPF_{sat}$ ,  $\text{mmol s}^{-1} \text{m}^{-2}$ ) are indicated in parentheses ( $r^2$ ;  $ETR_{max}$ ;  $PPF_{sat}$ ) next to each light response curve.



Table 2. Specific hydraulic conductivity ( $K_S$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), leaf specific conductivity ( $K_L$ ;  $10^{-4} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) and leaf to sapwood area ratio (LA/SA,  $10^8 \text{m}^2 \text{m}^{-2}$ ) in five species growing in different irradiances. Values are means  $\pm$  SE (one-way analysis of variance,  $n = 6$  to 10). Different letters indicate significant differences among treatments per species ( $P < 0.05$ , Scheffé test).

Light treatment (% of full sun)	<i>Cedrela fissilis</i>	<i>Patagonula americana</i>	<i>Cordia trichotoma</i>	<i>Lonchocarpus leucanthus</i>	<i>Balfourodendron riedelianum</i>
$K_S$					
10	2.89 $\pm$ 0.39 a	0.72 $\pm$ 0.11 a	2.67 $\pm$ 0.45 a	1.05 $\pm$ 0.30 a	1.31 $\pm$ 0.41 a
30	3.34 $\pm$ 0.68 ab	1.24 $\pm$ 0.15 b	2.92 $\pm$ 0.59 a	1.05 $\pm$ 0.27 a	0.90 $\pm$ 0.08 a
40	5.01 $\pm$ 0.89 ab	0.96 $\pm$ 0.07 ab	3.41 $\pm$ 0.65 a	0.91 $\pm$ 0.17 a	1.09 $\pm$ 0.34 a
65	6.65 $\pm$ 1.48 b	1.20 $\pm$ 0.15 b	1.77 $\pm$ 0.37 a	0.94 $\pm$ 0.22 a	0.85 $\pm$ 0.22 a
$K_L$					
10	1.61 $\pm$ 0.17 a	0.53 $\pm$ 0.06 a	1.62 $\pm$ 0.15 a	0.51 $\pm$ 0.09 a	0.38 $\pm$ 0.14 a
30	2.66 $\pm$ 0.30 ab	1.13 $\pm$ 0.11 b	1.76 $\pm$ 0.18 a	0.80 $\pm$ 0.18 a	0.34 $\pm$ 0.08 a
40	3.33 $\pm$ 0.33 b	1.03 $\pm$ 0.16 ab	2.14 $\pm$ 0.16 a	0.81 $\pm$ 0.23 a	0.42 $\pm$ 0.15 a
65	3.12 $\pm$ 0.41 b	1.23 $\pm$ 0.16 b	1.75 $\pm$ 0.18 a	0.86 $\pm$ 0.12 a	0.31 $\pm$ 0.08 a
LA/SA					
10	1.86 $\pm$ 0.21 a	1.28 $\pm$ 0.14 a	1.42 $\pm$ 0.15 a	2.32 $\pm$ 0.34 a	3.64 $\pm$ 0.47 a
30	1.69 $\pm$ 0.16 a	1.10 $\pm$ 0.08 a	1.51 $\pm$ 0.16 a	1.41 $\pm$ 0.22 ab	3.30 $\pm$ 0.78 a
40	1.66 $\pm$ 0.20 a	1.04 $\pm$ 0.13 a	1.64 $\pm$ 0.30 a	1.26 $\pm$ 0.22 b	3.41 $\pm$ 0.98 a
65	1.69 $\pm$ 0.25 a	1.03 $\pm$ 0.13 a	1.09 $\pm$ 0.13 a	1.05 $\pm$ 0.18 b	2.78 $\pm$ 0.05 a

6.56,  $P < 0.005$ ) and *P. americana* ( $F_{3,26} = 5.58$ ,  $P < 0.005$ ) (Table 2). Among species, *C. fissilis* and *C. trichotoma* exhibited the highest  $K_L$  values, varying between 1.61 and 3.33  $\times 10^{-4} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ , and 1.62 and 2.14  $\times 10^{-4} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ , respectively. Leaf-to-sapwood area ratios decreased with increasing irradiance for all species, and were statistically different for *L. leucanthus* ( $F_{3,22} = 4.86$ ,  $P < 0.01$ ).

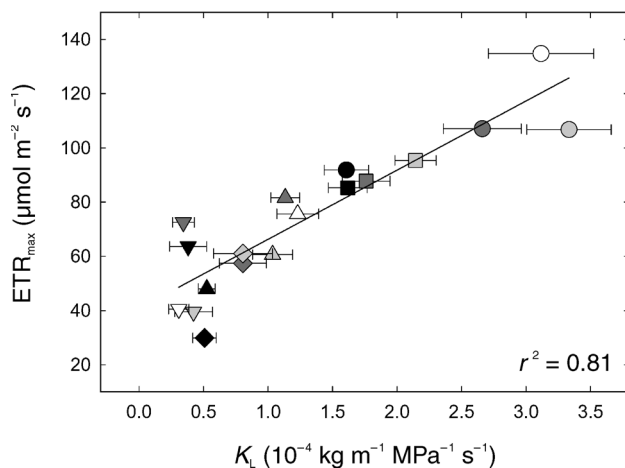


Figure 2. Maximum electron transport rate of PSII ( $\text{ETR}_{\text{max}}$ ) versus leaf specific hydraulic conductivity ( $K_L$ ). A linear regression was fitted to the data ( $\text{ETR}_{\text{max}} = 25.51K_L + 40.53$ ,  $P < 0.0001$ ). Symbols represent mean values  $\pm$  SE for  $K_L$  ( $n = 6$  to 10) and maximum electron transport rates obtained from light response curves for each species and treatment. Irradiances of 10, 30, 40 and 65% of full sun are indicated by black, dark gray, light gray and open symbols, respectively. Species are *Balfourodendron riedelianum* ( $\blacktriangledown$ ), *Cedrela fissilis* ( $\bullet$ ), *Cordia trichotoma* ( $\blacksquare$ ), *Lonchocarpus leucanthus* ( $\blacklozenge$ ) and *Patagonula americana* ( $\blacktriangle$ ).

#### Relationship between photosynthetic capacity and water-transport efficiency

A positive linear correlation between  $\text{ETR}_{\text{max}}$  and  $K_L$  across species and light treatments was observed (Figure 2). Species with higher  $K_S$  or  $K_L$  values (*C. fissilis* and *C. trichotoma*) also had higher photosynthetic capacities. The relationship between  $\text{ETR}_{\text{max}}$  and  $K_S$  was well described by a hyperbolic function ( $\text{ETR}_{\text{max}} = 149.44K_S/(1.75 + K_S)$ ;  $r^2 = 0.81$ ;  $P < 0.0001$ ). Within a species, the relationships between  $K_S$  and  $K_L$  with  $\text{ETR}_{\text{max}}$  were significant across light treatments for *C. fissilis*, *C. trichotoma* and *P. americana* saplings (Table 3).

#### Leaf carbon stable isotope ratios

Stable carbon isotope ratios in leaves varied among species and light treatments, and ranged between  $-27.5$  and  $-33.0\text{‰}$ . Across species, plants with high  $K_L$  were enriched in  $^{13}\text{C}$  and

Table 3. The  $r^2$  values of positive linear regressions ( $P < 0.05$ ) obtained between specific conductivity ( $K_S$ ;  $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), leaf specific conductivity ( $K_L$ ;  $10^{-4} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ) and maximum electron transport rate ( $\text{ETR}_{\text{max}}$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in five canopy tree species growing in 10, 30, 40 or 65% of full sun. For each species, the number of individuals is indicated in parenthesis.

Species	$K_S$	$K_L$	
	$K_L$	$\text{ETR}_{\text{max}}$	$\text{ETR}_{\text{max}}$
<i>Cedrela fissilis</i>	0.84 (23)	0.52 (12)	0.44 (12)
<i>Patagonula americana</i>	0.46 (28)	0.54 (12)	0.39 (12)
<i>Cordia trichotoma</i>	0.27 (24)	0.40 (12)	0.56 (12)
<i>Lonchocarpus leucanthus</i>	0.29 (27)	–	–
<i>Balfourodendron riedelianum</i>	0.77 (20)	–	–

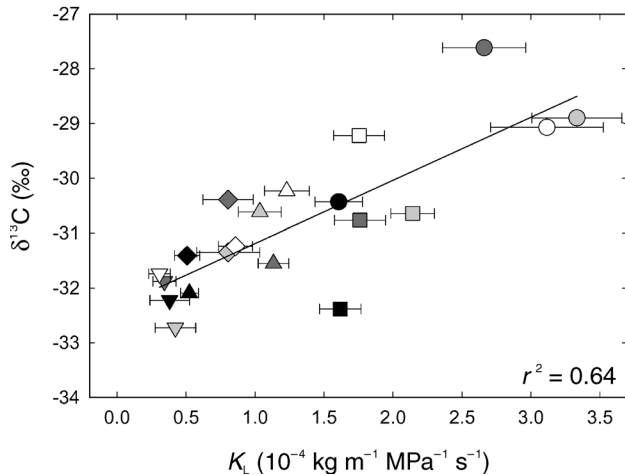


Figure 3. Leaf stable carbon isotope composition ( $\delta^{13}\text{C}$ ) versus leaf specific hydraulic conductivity ( $K_L$ ). A linear regression was fitted to data for saplings of five canopy tree species grown in four irradiances ( $\delta^{13}\text{C} = 1.1K_L - 32.36$ ,  $P < 0.001$ ). Irradiances of 10, 30, 40 and 65% of full sun are indicated by black, dark gray, light gray and open symbols, respectively. Species are *Balfourodendron riedelianum* ( $\blacktriangledown$ ), *Cedrela fissilis* ( $\bullet$ ), *Cordia trichotoma* ( $\blacksquare$ ), *Lonchocarpus leucanthus* ( $\blacklozenge$ ) and *Patagonula americana* ( $\blacktriangle$ ). For  $K_L$ , symbols represent mean values  $\pm$  SE ( $n = 6$  to  $10$ ). Isotope composition values were obtained from a composite sample of foliar tissue; thus, there is only one value per treatment and species.

had less negative  $\delta^{13}\text{C}$  values. A positive linear regression between  $\delta^{13}\text{C}$  and  $K_L$  was fitted to all species and light treatments (Figure 3). Maximum electron transport rate was positively correlated with  $\delta^{13}\text{C}$  across species and light treatments ( $\delta^{13}\text{C} = -33.04 + 0.03\text{ETR}_{\text{max}}$ ;  $r^2 = 0.44$ ,  $P < 0.01$ , data not shown).

#### Growth rates

Growth responses to the light treatments, expressed as stem diameter increments, were similar for four of the five species, reaching maximum values at intermediate irradiances (30 and 40% of full sun) (Table 4). Differences in RGR across all light treatments were not significant for *B. riedelianum*. Relative

growth rates expressed as diameter increments at 65% of full sun ranged from 0.62 in *C. fissilis* to 0.18 in *B. riedelianum*. Relative increments in total leaf surface area per individual were largest in *B. riedelianum* and *L. leucanthus* (Table 4).

Growth rates measured as height increments were not statistically different within species at different irradiances (data not shown). There was a positive linear relationship between RGR and  $K_L$  or  $\text{ETR}_{\text{max}}$  across all species and treatments (Figure 4). Within each species, the relationships between hydraulic conductivity or photosynthetic capacity and RGR were not maintained across light treatments except in *P. americana*, where the correlations were significant (e.g.,  $r^2$  values of the linear regressions were 0.99, 0.94 and 0.89 for  $K_S$ ,  $K_L$  and  $\text{ETR}_{\text{max}}$  versus RGR, respectively).

## Discussion

### Irradiance and hydraulic architecture

Differences in leaf-specific water-transport capacity for the five species grown in different light treatments were observed, but the responses were species-specific. The hydraulic architecture of *Cedrela fissilis* and *Patagonula americana*, the species with the highest growth rates, acclimated to the light regime through changes in  $K_L$  and  $K_S$ . The term acclimation, as used here, is based on the assumption that genetic differences among plants of the same species were relatively small, and that the responses to light environment were substantially larger than intraspecific genotypic differences. *Lonchocarpus leucanthus* had intermediate RGR and exhibited a small increase in  $K_L$  between 10 and 65% of full sun. In addition, this species acclimated to high irradiances by lowering its LA/SA ratio, similar to the findings of Maherali et al. (1997) for two *Acer* species. Acclimation of hydraulic architecture to the light treatments was apparently the result of changes in the water-transport capacity of the conducting pathway or in the pattern of carbon allocation to photosynthetic versus xylem tissues. Changes in hydraulic architecture traits in response to the light regimes were greater in the fast-growing Atlantic Forest species than in the slow-growing species, reflecting the adaptive

Table 4. Growth rate measured as the relative increment in plant stem diameter and total leaf area in saplings of five canopy tree species growing in 10, 30, 40 or 65% of full sun (December 2001 to April 2002). Values are means  $\pm$  SE (one-way analysis of variance,  $n = 9$  to  $17$ ). Different letters indicate significant differences among treatments per species ( $P < 0.05$ ; Scheffé test).

Light treatment (% of full sun)	<i>Cedrela fissilis</i>	<i>Patagonula americana</i>	<i>Cordia trichotoma</i>	<i>Lonchocarpus leucanthus</i>	<i>Balfourodendron riedelianum</i>
<i>Diameter</i>					
10	0.43 $\pm$ 0.03 a	0.20 $\pm$ 0.05 a	0.20 $\pm$ 0.04 a	0.12 $\pm$ 0.02 a	0.18 $\pm$ 0.02 a
30	0.68 $\pm$ 0.05 ab	0.58 $\pm$ 0.04 b	0.36 $\pm$ 0.06 ab	0.20 $\pm$ 0.05 ab	0.24 $\pm$ 0.04 a
40	0.76 $\pm$ 0.10 b	0.41 $\pm$ 0.05 b	0.46 $\pm$ 0.05 a	0.24 $\pm$ 0.04 ab	0.20 $\pm$ 0.04 a
65	0.62 $\pm$ 0.06 ab	0.59 $\pm$ 0.04 b	0.38 $\pm$ 0.07 ab	0.27 $\pm$ 0.04 b	0.18 $\pm$ 0.03 a
<i>Leaf area</i>					
10	3.393 $\pm$ 0.51 a	1.12 $\pm$ 0.21 a	4.14 $\pm$ 0.91 a	2.14 $\pm$ 0.22 ac	10.53 $\pm$ 6.20 a
30	3.563 $\pm$ 0.46 a	3.63 $\pm$ 0.84 a	3.10 $\pm$ 1.5 a	7.88 $\pm$ 1.16 b	8.08 $\pm$ 2.95 a
40	6.864 $\pm$ 1.86 a	3.32 $\pm$ 0.71 a	1.84 $\pm$ 0.79 a	5.73 $\pm$ 1.31 abc	12.50 $\pm$ 7.75 a
65	5.540 $\pm$ 2.31 a	6.45 $\pm$ 1.10 b	2.90 $\pm$ 1.5 a	3.80 $\pm$ 1.15 ac	8.67 $\pm$ 4.60 a

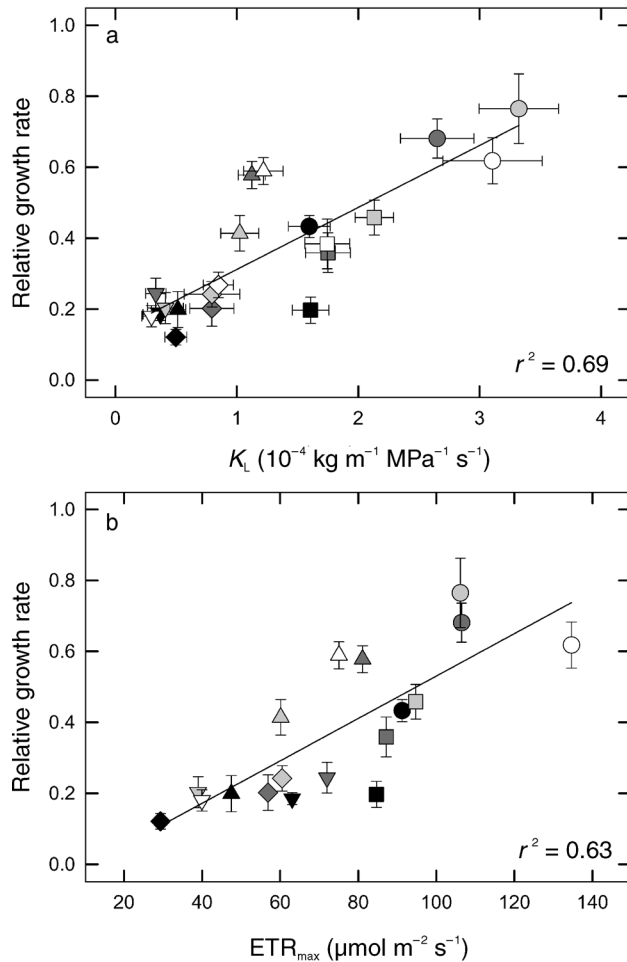


Figure 4. Relative growth rate (RGR) measured as relative increment in stem diameter versus (a) leaf specific hydraulic conductivity ( $K_L$ ) ( $RGR = 0.174K_L + 0.137$ ,  $P < 0.001$ ) and (b) maximum electron transport rate ( $ETR_{max}$ ) of PSII ( $RGR = 0.006ETR_{max} - 0.066$ ,  $P < 0.001$ ). Irradiances of 10, 30, 40 and 65% of full sun are indicated by black, dark gray, light gray and open symbols, respectively. Species are *Balfouriodendron riedelianum* ( $\nabla$ ), *Cedrela fissilis* ( $\bullet$ ), *Cordia trichotoma* ( $\blacksquare$ ), *Lonchocarpus leucanthus* ( $\blacklozenge$ ) and *Patagonula americana* ( $\blacktriangle$ ). Symbols represent mean values  $\pm$  SE for  $K_L$  ( $n = 6$  to 10) and  $ETR_{max}$  obtained from light response curves for each species and irradiance.

value for fast-growing species of maintaining high photosynthetic rates in gaps and open canopy sites.

#### Photosynthetic capacity and growth responses to solar radiation

Growth responses to solar irradiance, expressed as differences in stem diameter increment, were similar for four of the five species, reaching maximum values at intermediate irradiances (30 to 40% of full sun). This pattern is consistent with results for other tropical tree species (e.g., Poorter 1999). Within a species, larger differences would have been obtained among treatments if the plants had been grown in a shade house for longer. However, growth rates of *C. fissilis* were high, so it would have been necessary to use pots larger than 20 l to avoid

root limitations. Despite similar growth responses to differences in irradiance, the study species exhibited a wide range of maximum relative growth rates (expressed as diameter increments), ranging from 0.76 in *C. fissilis* to 0.25 in *Balfouriodendron riedelianum*. Relative diameter increments measured in the field for *B. riedelianum* and *L. leucanthus* were similar to values observed in a shade house, being  $0.25 \pm 0.04$  and  $0.24 \pm 0.03$ , respectively, in the low-light treatment (i.e., less than 10% of total radiation reaching the upper canopy), and  $0.39 \pm 0.06$  and  $0.50 \pm 0.07$  in 16 and 25% of full sunlight, respectively (Campanello 2004).

The slow-growing species had lower photosynthetic capacities than the fast-growing species, as reported previously (e.g., Kitajima 1994, Poorter 1999). For example, *B. riedelianum*, with an RGR of 0.22 at 45% of full sun, had an  $ETR_{max}$  of  $39.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas *C. fissilis*, with an RGR of 0.65 at the same irradiance, had an  $ETR_{max}$  of  $106.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Maximum electron transport rates were within the range reported in the literature (e.g., Lüttge et al. 1998, Myers et al. 1999, De Lucia and Thomas 2000). The highest values of  $ETR_{max}$  for the slow-growing species, *B. riedelianum* and *L. leucanthus*, were achieved at 30% of full sun in the shade-house, implying that these species may be able to adjust their photosynthetic capacity to the low irradiances encountered in the field. Mean irradiance in the field for *B. riedelianum* and *L. leucanthus* is less than 30% of full sun (Campanello 2004). Maximum ETRs were relatively low for these species when growing at higher irradiances, consistent with their limited ability to colonize high-light environments compared with the fast-growing and more light-requiring species, such as *C. fissilis*, which exhibited the highest photosynthetic capacity at 65% of full sun.

A study in Panama with seedlings acclimated to artificial forest gaps differing in size showed differences in photo-inhibitory responses, with potential quantum yield being permanently reduced in shade-tolerant species when exposed to high irradiances (Krause et al. 2001). In our study, a permanent photoinhibitory decline in predawn  $F_v/F_m$  was observed in *L. leucanthus* and *Cordia trichotoma* in 65% of full sunlight. A similar photoinhibitory response was observed in rooted stem cuttings of *Cordia alliodora* (Rulz & Pavon) Oken in Costa Rica, a high-light-requiring species closely related to *C. trichotoma* (Gibbs and Taroda 1983, Mesén et al. 1997).

#### Carbon stable isotope ratios

The well-ventilated shade-houses had similar  $\text{CO}_2$  isotopic composition, air temperature and air saturation difference; consequently, tissue-specific differences in stable carbon isotope ratios should have reflected physiological differences related to both physical and chemical discrimination against  $^{13}\text{C}$ . Water-transport capacity to leaves was positively correlated with  $^{13}\text{C}$  abundance in leaf tissues across the studied species, implying that species with greater water-transport efficiencies also had higher photosynthetic water-use efficiencies. Santiago et al. (2004) observed no relationship between leaf  $\delta^{13}\text{C}$  and  $K_L$  among 20 trees of tropical lowland forests in Panama. Panek (1996), working with *Pseudotsuga menziesii*

(Mirb.) Franco across a climate gradient, observed an inverse relationship between  $\delta^{13}\text{C}$  and  $K_L$ . In this case, variations in  $K_L$  explained changes in the  $\delta^{13}\text{C}$  of foliage through changes in stomatal conductance. Positive, negative and no relationships between leaf  $\delta^{13}\text{C}$  and  $K_L$  across species, or across individuals of one species growing in different habitats, exist which may reflect different species-specific responses to different selective pressures.

Leaf  $\delta^{13}\text{C}$  was more negative at lower solar irradiances in every species studied. Fast-growing species (*C. fissilis*, *P. americana* and *C. trichotoma*) had the highest water-use efficiencies (higher  $\delta^{13}\text{C}$ ) in 40 and 65% of full sunlight. Slower-growing shade-tolerant species (*B. riedelianum* and *L. leucanthus*), in contrast, exhibited little variation in stable isotope composition, and consequently, in water-use efficiency, despite differences in irradiance. The differences between fast- and slow-growing species can be explained by the higher photosynthetic rates of fast-growing species at high irradiances compared with slow-growing species.

#### *Coordination between photosynthetic capacity and hydraulic conductivity across and within species*

Similar to patterns observed in other studies (e.g., Brodribb and Feild 2000, Santiago et al. 2004), photosynthetic capacity across species increased with increasing leaf specific hydraulic conductivity of upper branches. Maximum hydraulic conductivity was not determined during measurements but branches were collected before dawn, and consequently, the values of hydraulic conductivity reported in this study are assumed to be the highest attained under the various light conditions. The results suggest that plant traits regulating photosynthetic and hydraulic capacity are interdependent. The relationship between photosynthesis and  $K_L$  reflects a balance between carbon gain and water-transport capacity. The relationship between photosynthetic capacity and  $K_L$  may be mediated by stomata in such a way as to meet the demand for  $\text{CO}_2$  uptake while minimizing cavitation of the plant hydraulic system (Katul et al. 2003).

Coordination between photosynthetic capacity and hydraulic conductivity has been evaluated previously for different groups of species (Brodribb and Feild 2000, Brodribb et al. 2002, 2005, Santiago et al. 2004); however, this is the first study in which individuals of the same species growing in different light irradiances were compared. Species requiring high irradiances are exposed to selective pressures that promote rapid growth and high photosynthetic rates, which are usually achieved when solar irradiance and evaporative demand are high. If rapid influx of  $\text{CO}_2$  is constrained by the balance between transpirational water loss and the supply of soil water, then sun-adapted species should exhibit coordination between water transport and photosynthetic capacity. Our study showed that the coordination between water-transport efficiency and photosynthetic capacity observed across species was maintained within fast-growing species across irradiance treatments (greater photosynthetic up-regulation within species was associated with greater capacity for hydraulic up-reg-

ulation). Such coordination was achieved by increasing  $K_L$  as irradiance increased. In contrast, the slow-growing and more shade-tolerant *B. riedelianum* and *L. leucanthus* showed no variation in  $K_S$  or  $K_L$ , despite showing considerable variation in  $\text{ETR}_{\text{max}}$  with variation in solar irradiance. Shade tolerant species are adapted to survive and grow under relatively low light and consequently high photosynthetic capacity and an efficient system of water supply to the leaves may not be of adaptive value. Shade-adapted species, in general, grow slower than sun-adapted species and have relatively lower photosynthetic rates, but comparatively longer leaf life spans and higher survival rates in shaded conditions, compared with high-light-requiring plants (Williams et al. 1989, Kitajima 1994, Walters and Reich 1999, Poorter 2001).

#### *Coordination of ecophysiological attributes in light-requiring and shade-adapted species*

Shade-tolerant and light-requiring species could be viewed as the endpoints of a continuum of ecological and physiological behavior rather than as two distinct functional groups. Convergence between physiological and morphological traits as observed previously (Brodribb and Feild 2000, Bucci et al. 2004, 2005, Meinzer et al. 2004, Santiago et al. 2004, Brodribb et al. 2005) and in our study, would better describe relative differences among species than an arbitrary division into clusters of species, each one having distinct physiological attributes. In particular, the coordination we observed between photosynthetic capacity and water-transport efficiency across species and treatments helps explain the performance of different canopy species in different light environments. Our study also demonstrates coordination between photosynthetic capacity and water-transport efficiency across light regimes within fast-growing species.

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