Allometric relationships predicting foliar biomass and leaf area:sapwood area ratio from tree height in five Costa Rican rain forest species

J. C. CALVO-ALVARADO,[1,2] N. G. McDOWELL[3] and R. H. WARING[4]

[1] *Escuela de Ingeniería Forestal, Instituto Tecnológico de Costa Rica (ITCR), Cartago, Costa Rica*

[2] *Corresponding author (jucalvo@itcr.ac.cr)*

[3] *Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA*

[4] *College of Forestry, Oregon State University, Corvallis, OR 97331-5704, USA*

Summary We developed allometric equations to predict whole-tree leaf area (A_l), leaf biomass (M_l) and leaf area to sapwood area ratio (A_l:A_s) in five rain forest tree species of Costa Rica: *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae/Mim)*, Carapa guianensis* Aubl. (Meliaceae)*, Vochysia ferruginea* Mart. (Vochysiaceae), *Virola koshnii* Warb. (Myristicaceae) and *Tetragastris panamensis* (Engl.) Kuntze (Burseraceae). By destructive analyses ($n = 11$–14 trees per species), we observed strong nonlinear allometric relationships ($r^2 \geq 0.9$) for predicting A_l or M_l from stem diameters or A_s measured at breast height. Linear relationships were less accurate. In general, A_l:A_s at breast height increased linearly with tree height except for *Pentaclethra*, which showed a negative trend. All species, however, showed increased total A_l with height. The observation that four of the five species increased in A_l:A_s with height is consistent with hypotheses about trade-offs between morphological and anatomical adaptations that favor efficient water flow through variation in the amount of leaf area supported by sapwood and those imposed by the need to respond quickly to light gaps in the canopy.

Keywords: Carapa guianensis, hydraulic model, leaf area, leaf biomass, Pentaclethra macroloba, pipe-model theory, sapwood area, specific leaf area, Tetragastris panamensis, Virola koshnii, Vochysia ferruginea.

Introduction

Physiologists and ecologists have long recognized the importance of canopy leaf surface area (A_l) and mass (M_l) as structural properties that affect important physiological processes such as photosynthesis, respiration and transpiration. Silviculturists have incorporated estimates of leaf area and mass into stand responses to various manipulations (e.g., Turner et al. 1999, Meadows and Hodges 2002, Cohen et al. 2003, Fernandes et al. 2003, Fournier et al. 2003, Landsberg et al. 2005, Arias et al. 2007). Because direct measurement of leaf area is impractical, allometric relationships have been de-

veloped to predict A_l and M_l from tree diameter at breast height (DBH), stem basal area (A_b) or sapwood area (A_s).

The first use of sapwood cross-sectional area to estimate leaf area, which was by Shinozaki et al. (1964a, 1964b), assumed that a given quantity of leaves was serviced by a pipe system of conducting vascular tissue (sapwood). Consequently, Shinozaki's pipe model predicted a correlation between A_s at breast height and A_l or M_l (Grier and Waring 1974, Meadows and Hodges 2002). The original pipe model, which assumed that the ratio of leaf area to sapwood area (A_l:A_s) remained constant throughout plant development (Shinozaki et al. 1964a, Waring et al. 1982), has been applied to various temperate coniferous and hardwoods tree species (e.g., Grier and Waring 1974, Waring et al. 1977, 1982, Kendall and Brown 1978, Rogers and Hinckley 1979, Kaufmann and Troendle 1981, Oren et al. 1986, Vertessy et al. 1995), but it has rarely been evaluated for tropical species (but see Whitehead et al. 1981, Morataya et al. 1999).

Tests of the pipe model in temperate species have revealed that A_l:A_s is not constant within species: A_l:A_s often declines with increasing evaporative demand (Waring et al. 1982, Mencuccini and Grace 1995, White et al. 1998), tree height (McDowell et al. 2002a) and stocking density (Brix and Mitchell 1983, McDowell et al. 2006). This range in variation can usually be explained by a simple model based on Darcy's Law, first applied by Whitehead and Jarvis (1981) and Whitehead et al. (1984):

$$\frac{A_l}{A_s} \approx \frac{k_s(\Psi_s - \Psi_l)}{h \, \eta \, g_s D} \tag{1}$$

where k_s is sapwood permeability of the hydraulic pathway, $(\Psi_s - \Psi_l)$ is the soil-to-leaf water potential difference including the effect of gravity, h is tree height, η is the temperature dependent viscosity of water, g_s is canopy conductance to water vapor, and D is the atmospheric vapor pressure deficit. With this model, the parameters are constrained so that if all other

variables remain constant, the A_l:A_s ratio must decrease as trees become taller to minimize reductions in leaf-specific hydraulic conductivity and canopy stomatal conductance. The other parameters may, however, change in concert with A_l:A_s as height increases (Mencuccini and Magnani 2000, McDowell et al. 2002*b*).

Numerous studies support the premise that increasing tree height results in decreasing A_l:A_s (Equation 1) (Mencuccini and Grace 1996*a*, 1996*b*, Grace 1997, Mencuccini and Magnani 2000, Schäfer et al. 2000, McDowell et al. 2002*a*, Delzon et al. 2004, Gilmore and Seymour 2004). There are far fewer observations that A_l:A_s increases with tree height (Dean and Long 1986, Oren et al. 1986, Long and Smith 1988, Gerrish 1990, Vertessy et al. 1995, Watson et al. 1999, Barnard and Ryan 2003, Mokany et al. 2003, Phillips et al. 2003). One reason why A_l:A_s might increase with tree height is that light or nutrient limitation negates the requirement for a constant soil-to-leaf sapflow resistance (McDowell et al. 2002*a*). Consistent with this interpretation, increases in A_l:A_s with height co-occur with adjustments to parameters in Equation 1, including reductions in g_s (McDowell et al. 2002*a*, Ryan et al. 2006), k_s (Pothier et al. 1989, McDowell et al. 2002*b*, Mokany et al. 2003), and $\Psi_s - \Psi_l$ (McDowell et al. 2002*b*, Barnard et al. 2003).

Our objectives were to: (1) compare allometric relationships between A_l and M_l with DBH and A_s for five representative tropical tree species that grow in the wet tropical rain forest of Costa Rica; and (2) interpret these relationships within the framework of the hydraulic model (Equation 1). Our working hypotheses were that (1) relationships between DBH or A_s and A_l or M_l are a function of tree height, and (2) based on observations in other non-water-limited environments, the relationship between A_l:A_s and height is positive.

Materials and methods

Site description

The field research was completed during 1986 in an experimental forest, about 8 km southeast of La Selva Biological Station (OTS) in Puerto Viejo, in the north Caribbean lowlands of Costa Rica (10°14′18″ N, 83°01′13″ W, 60 m a.s.l.). Soils are predominantly acidic and infertile Typic Tropohumults (Pérez et al. 1978, Sollins et al. 1994). Mean annual temperature is 25 °C and mean annual precipitation is 3960 mm with all months receiving at least 150 mm (Sanford et al. 1994). According to Holdridge's (1947) vegetation classification, the Life Zone is Tropical Wet, which is the second most extensive in Costa Rica (Hartshorn and Hammel 1994). This Life Zone supports a tall, multistoried evergreen forest, with dominant trees reaching 45–55 m. Tree crowns are round to umbrella-shaped, with DBHs up to 200 cm, and boles are clear of branches up to 30 m above ground. Understory trees, which reach heights between 10 and 25 m, exhibit narrow conical crowns supported on slender boles. Dwarf palms and tree seedlings are abundant in the sub-canopy. Total flora in these forests include 1458 native species and 220 exotic species of

which 20% are trees, 6% lianas, 23% epiphytes, 17% shrubs and 35% herbs (Harstshorn and Hammel 1994). More information about this region is available in McDade et al. (1994).

Species descriptions

Species selection was based on the fraction of basal area contributed to the total recorded per hectare. Five species were studied: *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae/ Mim), *Carapa guianensis* Aubl. (Meliaceae), *Vochysia ferruginea* Mart. (Vochysiaceae), *Virola koshnii* Warb. (Myristicaceae) and *Tetragastris panamensis* (Engl.) Kuntze (Burseraceae).

Pentaclethra macroloba is a large, shade-tolerant evergreen that may reach 45 m in height and 1.8 m in diameter. It has alternate bipinnate leaves up to 30 cm long, without glands (atypical of Mimosaceae) and small leaflets (about 1–2 × 6–9 mm). The tree usually has a spreading, irregular fluted base with minimal buttress development. The species can account for as much as half the canopy on relatively infertile soils. It is capable of fixing atmospheric nitrogen and is widely distributed from Nicaragua to Amazonia (McHargue and Hartshorn 1983, Oberbauer and Strain 1986, Flores and Obando 2003).

Carapa guianensis is an evergreen, sometimes deciduous, shade-tolerant species that may reach 60 m in height and 2 m in diameter. Its trunk is straight and cylindrical, with buttresses to a height of 1 to 2.5 m. Mature trees lack branches in the lower one-half to two-thirds of the bole and have wide and dense crowns with thick, curved ascendant branches. Leaves are alternately pinnate and reach lengths between 30 and 120 cm. They are displayed in a helical arrangement, crowded toward the ends of branches. The species can be found in pure stands in the lowlands, usually near marsh edges, swamps, riverbanks and areas that are periodically flooded. In range, the species extends from Belize to the Amazonia with some representation in the Antilles (McHargue and Hartshorn 1983, Flores y Obando 2003).

Vochysia ferruginea is a fast-growing species that reaches 20 to 34 m in height and 40 to 90 cm in diameter. Mature individuals have a clear trunk up to one-half of total tree height and a dense, wide crown of ascendant branches. Leaves are simple, opposite, elliptical and up to 6–13 cm in length. *Vochysia ferruginea* establishes itself beneath the forest canopy but requires a gap for successful emergence. It grows on upper slope soils and on well-drained ridges and colonizes abandoned pastures and other disturbed sites. The species is distributed from Belize to the Amazonia (Flores y Obando 2003).

Virola koschnyi is a shade-tolerant species that reaches 30 to 45 m in height and 1.0 to 1.5 m in diameter. The uppermost portion of the bole is straight and cylindrical, whereas the basal third is heavily buttressed to a height of 1.0 to 3.0 m. The branch system extends horizontally and forms an extended flat crown over the strong monopodial axis. Leaves are simple, alternate, obovate or laceolate and up to 7–29 cm in length. It is common in both primary and secondary wet forests across the Atlantic and Pacific lowlands of Costa Rica and extends throughout much of Central America (Flores y Obando 2003).

Tetragastris panamensis is a shade-tolerant species reaching heights of 10–35 m and diameters up to 1.0 m. The bole is straight and usually quadrangularly shaped without buttresses. The leaves are spirally arranged and imparipinnate with 7–9 leaflets, each leaflet is elliptic or ovate, 5–21 cm long and 4–7.2 cm wide. This species is common in both primary and secondary wet forests across the Atlantic and Pacific lowlands of Costa Rica and extends from Belize to Brazil and Bolivia (Flores y Obando 2003).

Field measurements

Twenty well-formed, healthy randomly selected trees per species, representing a wide range in diameter classes, were felled during the rainy season when trees were in full leaf. Trees damaged during felling or on which the foliage was saturated by heavy rain after falling were excluded, reducing the sample size to between 11 and 14 trees per species (Table 1).

Tree heights and diameters were measured after felling. Felled trees were divided into stems, large, medium and small branches and foliage. The total fresh mass of each component was measured in the field with a spring balance. Several subsamples of the stems and branches components were oven-dried to constant mass at 70 °C to determine fresh mass:dry mass ratios.

Sapwood area and leaf area and mass measurements

A 10-cm-thick cross section was cut at breast height from each sampled tree. In all species the sapwood–heartwood boundary was clearly visible and was marked before transporting the stem cross section to the laboratory in a plastic bag. In the laboratory, the cross sections were photocopied. The cross-sectional area of the sapwood was determined from the photocopies with a Li-Cor 3100c area meter.

To obtain the fresh mass–dry mass relationship for the whole tree and to account for variations in leaf morphology, mass and area associated with different positions within the crown, a composite subsample of 1 to 3 kg fresh mass of leaves was taken at random from all the large branches of each sampled tree. Three subsamples of 30 leaves each were collected at random from the entire tree crown and taken to the laboratory to determine specific leaf area (SLA, $m^2 kg^{-1}$). To prevent shrinkage before measurement, leaves were stored between sheets of moist paper and refrigerated until measured. Mea-sured leaves were oven dried at 70 °C for 48 h and weighed. The projected leaf area for each sample tree (A_l, m^2) was calculated by multiplying total foliage biomass (M_l, kg) by mean SLA of the three subsamples. For the large composite leaves of *Carapa guianensis,* the long petiole was removed before the area was measured but was included in the foliage fresh mass and dry mass measurements. We calculated A_l:A_s ($m^2 cm^{-2}$) for each sampled tree from the estimated total leaf area and measured sapwood area.

Statistical analysis

Linear regression analysis was used to evaluate the appropriateness of each of the two independent variables (x), DBH (cm) and A_s (cm^2), as estimators of total tree A_l and M_l (dependent variables = y) for each species. Initially, the data were fitted to the model $y = a + bx$. Both the regression coefficient and intercept were tested to determine if they were statistically different from zero ($P < 0.05$). For those regressions yielding nonsignificant intercepts, the regression was forced through the origin. When linear regression analysis resulted in significant negative intercepts ($P < 0.05$), the linear model was rejected as biologically invalid. We then analyzed the data by nonlinear regression of the model $y = ax^b$. For both models, the root mean square error of the estimate (RMSE) and the coefficient of determination (r^2) were used to evaluate goodness of fit. To examine our main hypothesis of Equation 1, we evaluated if A_l:A_s decreases with tree height by testing the significance ($P < 0.05$) of the regression coefficient of a linear model with A_l:A_s as the dependent variable and height as the independent variable.

Results

Specific leaf area

Specific leaf area of sampled trees ranged between 15.89 m^2 kg^{-1} for *Pentaclethra macroloba* and 6.38 $m^2 kg^{-1}$ for *Carapa guianensis,* and tree heights ranged from 7 to 42 m. Field and laboratory measurements are summarized in Table 1.

Sapwood area and stem diameter as estimators of leaf mass and area

Table 2 summarizes the linear and nonlinear regression equations derived to predict A_l or M_l with DBH or A_s as the inde-

Table 1. General characteristics and sample size of the study species. Abbreviations: DBH, diameter at breast height; and SLA, specific leaf area (standard deviation in parenthesis).

Species	Common name	n	Tree height (m)	DBH (cm)	SLA ($m^2 kg^{-1}$)	DBH increment (mm year^{-1})
Tetragastris panamensis	Canfín	14	7–25	4–32	13.23 (1.4)	4.5[1]
Virola koshnii	Sangrillo	11	13–40	12–50	13.06 (2.8)	11[2]
Carapa guianensis	Cedro Macho	14	19–42	20–81	6.38 (1.37)	4[2]
Vochysia ferruginea	Botarrama	12	19–40	25–94	9.73 (1.87)	17[2]
Pentaclethra macroloba	Gavilán	12	18–37	17–115	15.89 (2.31)	11[2]

[1] Estimate from School of Forestry (ITCR) permanent plots databases.
[2] Estimate from Finnegan et al. 1999.

pendent variable. Diameter at breast height was the best predictor for A_l and M_l in both models for *Capara guianensis, Vochysia ferruginea* and *Virola koschnii*; whereas A_s was the best predictor for *Pentaclethra macroloba* and *Tetragastris panamensis*. For all species, nonlinear models provided the best estimates of A_l and M_l with either A_s or DBH as the independent variable. The linear models estimating A_l from DBH in *Pentaclethra macroloba* and estimating A_l and M_l in *Carapa guianensis* and *Virola koshnii*, were rejected because the intercepts were significantly negative ($P < 0.05$).

Leaf area:sapwood area ratio with tree height

Except for *Pentaclethra macroloba,* the A_l:A_s ratio increased with tree height (Figure 1). The regression coefficients for the slope of A_l:A_s versus height were significant for all species except *Virola koshnii.* Thus, the results for three of the five study species were consistent with our working hypothesis. The results for *Virola* were ambiguous, and the results for *Pentaclethra* did not support the hypothesis. All species showed consistent exponential increases in whole-tree leaf area with height (Figure 2).

Discussion

Allometric equations

The best nonlinear allometric equations for all but one sampled species, *Vochysia ferruginea*, accounted for 90% or more of the observed variations in A_l and M_l (Table 2), providing a sound, nondestructive means to predict these canopy properties in similar lowland rain forests of Central America. Given the paucity of allometric equations for tropical regions, we expect these relationships to prove valuable in future research that requires estimates of leaf area or biomass of these species.

All least squares equations and regression coefficients reported in Table 2 were significant ($P < 0.05$). We recommend using the equations that have the highest r^2 for estimating A_l or M_l. The nonlinear models explained more of the variation and fit the data better as A_s approached zero than the linear models. Although A_s was the best predictor for two species (*Pentaclethra macroloba* and *Tetragastris panamensis*), DBH-based allometric equations gave results that were nearly as accurate.

Tree height and leaf area:sapwood area ratios

In contrast to most temperate species (Mencuccini and Grace 1996*a*, 1996*b*, Grace 1997, Mencuccini and Magnani 2000, Schäfer et al. 2000, McDowell et al. 2002*a*, Delzon et al. 2004, Gilmore and Seymour 2004), four of the five species we sampled exhibited positive relationships between tree height and A_l:A_s (Figure 1). All five species studied showed increased A_l with height (Figure 2). In a tropical forest where monthly rainfall exceeds 150 mm and the humidity is often near saturation (Sanford et al. 1994), the hydraulic model (Equation 1) may be inadequate to account for differences in aboveground growth partitioning between A_l and A_s. Low irradiances, for example, could favor height growth over diameter growth, and limit the amount of foliage that can be supported. In our study,

Table 2. Linear regression analysis of tree foliar mass (M_l, kg) and tree leaf area (A_l, m²) with diameter at breast height (DBH, cm) and sapwood area (A_s, cm²) for five tree species using the linear model $y = a + bx$ (L) and the nonlinear model $y = ax^b$ (NL).

Model	x	a	b	RMSE	F	$F > F_b$	r^2
Tetragastris panamensis							
L M_l	DBH	–	–	–	–	–	–
	A_s	–	0.108	1.7	186.0	< 0.001	0.93
NL M_l	DBH	0.040	1.737	1.9	143.9	< 0.001	0.96
	A_s	0.048	1.168	1.7	200.1	< 0.001	0.97
L A_l	DBH	–	–	–	–	–	–
	A_s	–	1.445	24.4	166.8	< 0.001	0.93
NL A_l	DBH	0.506	1.756	27.7	126.9	< 0.001	0.95
	A_s	0.587	1.187	23.4	180.2	< 0.001	0.97
Virola koschnii							
L M_l	DBH	–	0.436	21.3	14.8	0.003	0.60
	A_s	–	0.055	8.3	7.2	0.025	0.45
NL M_l	DBH	0.002	2.468	5.0	54.7	< 0.001	0.89
	A_s	0.068	0.963	8.3	17.0	< 0.001	0.67
L A_l	DBH	–	5.929	101.6	12.1	0.006	0.55
	A_s	–	0.745	116.1	7.0	0.025	0.41
NL A_l	DBH	0.010	2.700	78.1	42.4	< 0.001	0.87
	A_s	0.865	0.974	122.3	14.6	< 0.001	0.64
Carapa guianensis							
L M_l	DBH	–	–	–	–	–	–
	A_s	–	0.085	27.3	17.5	< 0.001	0.57
NL M_l	DBH	0.012	2.089	19.1	80.7	< 0.001	0.89
	A_s	0.007	1.364	27.5	35.6	< 0.001	0.77
L A_l	DBH	–	–	–	–	–	–
	A_s	–	0.547	174.6	17.9	< 0.001	0.58
NL A_l	DBH	0.079	2.094	125.1	77.9	< 0.001	0.89
	A_s	0.036	1.403	175.0	36.9	< 0.001	0.78
Vochysia ferruginea							
L M_l	DBH	–	0.863	18.5	11.9	0.005	0.52
	A_s	–	0.078	21.1	6.5	0.027	0.37
NL M_l	DBH	0.673	1.058	19.4	47.6	< 0.001	0.72
	A_s	0.100	0.962	22.2	35.3	< 0.001	0.61
L A_l	DBH	–	7.959	184.3	8.6	0.014	0.44
	A_s	–	0.731	186.3	8.2	0.015	0.43
NL A_l	DBH	10.717	0.930	193.0	40.9	< 0.001	0.66
	A_s	0.537	1.047	195.3	39.8	< 0.001	0.65
Pentaclethra macroloba							
L M_l	DBH	–	0.325	4.2	39.9	< 0.001	0.78
	A_s	5.348	0.030	2.1	196.2	< 0.001	0.95
NL M_l	DBH	0.958	0.757	3.7	256.7	< 0.001	0.91
	A_s	0.199	0.748	1.8	1143.0	< 0.001	0.98
L A_l	DBH	–	5.118	46.6	91.3	< 0.001	0.89
	A_s	74.361	0.482	23.8	382.5	< 0.001	0.97
NL A_l	DBH	9.985	0.850	44.4	448.8	< 0.001	0.95
	A_s	2.326	0.792	24.8	1451.6	< 0.001	0.98

leaf area increased with tree size regardless of the relationship of A_l:A_s with height (Figure 2) and foliage was restricted to the upper half of the stem (J.C. Calvo-Alvarado, personal observation). Other studies that documented increases in whole-tree A_l:A_s with height have also been from relatively wet environments where competition for light is intense (e.g., *Picea* and
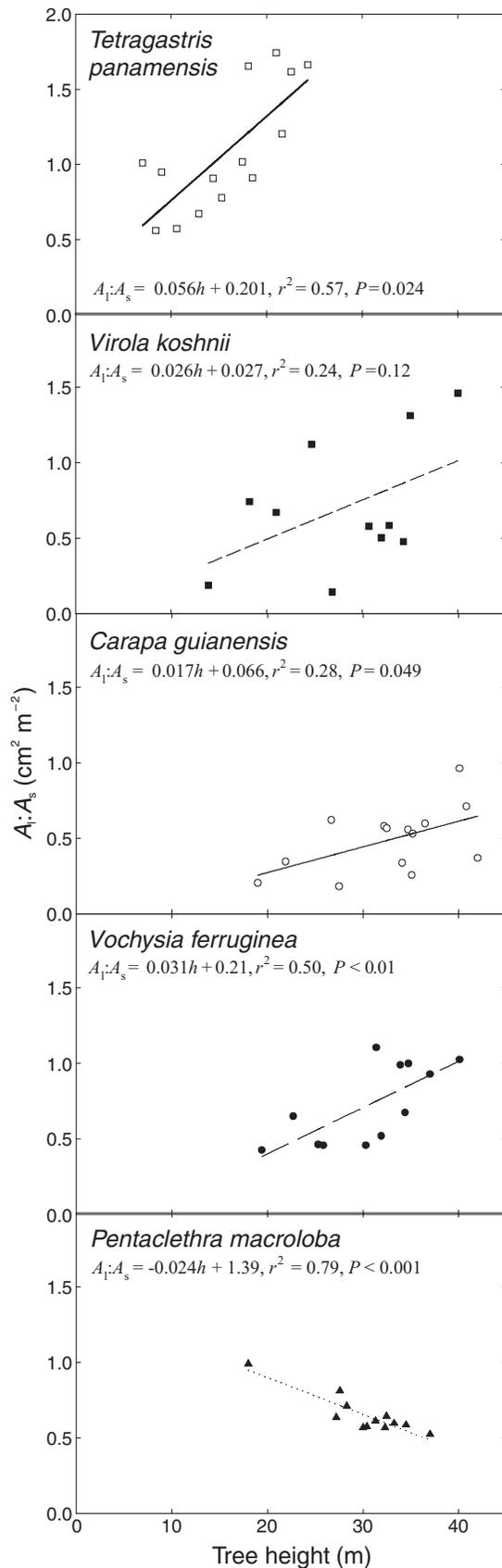
Figure 1. Relationship between leaf area to sapwood area ratio (A_l:A_s) and tree height (h) in five tropical tree species.

Abies, McDowell et al. 2002*a*; *Eucalyptus*, Barnard and Ryan 2003; but for an exception see Phillips et al. 2003). Consistent with expectations from the hydraulic model, mean A_l:A_s is substantially higher in tropical rain forests than in drought-prone regions (e.g., McDowell et al. 2002*a*).

If increasing A_l:A_s with height is advantageous for light capture in wet lowland tropical rain forests, what might explain *Pentaclethra's* decrease in A_l:A_s with height (Figure 1)? *Pentaclethra* is not notably different in canopy position or successional status from other species, (Oberbauer and Strain 1986, Finegan et al. 1999), and has similar vessel diameters (Table 3). The only obvious difference between *Pentaclethra* and the other species we studied is in leaf morphology. *Pentaclethra* averages over 2600 leaflets on pinnately compound leaves, whereas the other species have 1–7 leaflets per leaf (Table 3). With such a highly divided water pathway through the compound leaves of *Pentaclethra*, leaf specific hydraulic conductivity may decrease, depending on compensations at the branch (i.e., xylem structure, McCulloh et al. 2003) or whole-tree level (e.g., A_l:A_s). Direct measurements of leaf specific conductivity are needed to test this hypothesis.

The consequences of growing taller and increasing in leaf area (Figure 2) may be common among all the species studied, despite differences in leaf morphology and height–A_l:A_s relationships. With Equation 1, we modeled g_s as a function of tree height and A_l:A_s observations, assuming that viscosity, k_s, D and $\Psi_s - \Psi_l$ remained constant among species, regardless of size. These are common simplifying assumptions (Mokany et al. 2003, Phillips et al. 2003, Domec et al. 2007, McDowell et al. 2008) and provide a starting point from which to examine the consequences of different leaf area–tree height responses. Regardless of the different relationships between A_l:A_s and tree height, all study species exhibited decreased g_s with increased tree height (Figure 3), and they converged to similarly low g_s values at half maximum height. Low g_s values at the upper end of the sampled height range are consistent with both modeled and empirical observations from around the world (Ryan et al. 2006). Our analysis suggests that trees trade off
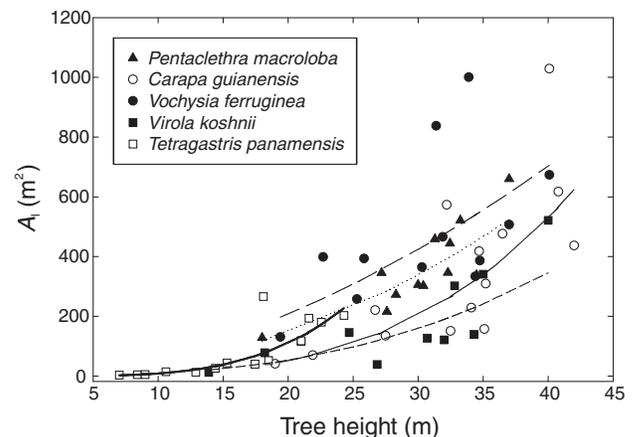

Figure 2. Relationship between whole-tree leaf area (A_l) and tree height in five tropical tree species.

Table 3. Mean (SD in parenthesis) individual leaf and wood vessel characteristics for selected tree species and regression coefficient (*b*) for the relationship of A_l:A_s with tree height.

Species	Leaf area (cm^2)	Leaf biomass (g)	Leaflets (leaf^{-1})	Leaflet area (cm^2)	Wood vessel diameter[1] (μm)	Maximum tree height (m)	*b*
Tetragastris panamensis	691 (225)	4.5 (1.5)	7	98.7	125 (90–160)	35	0.056
Vochysia ferruginea	22 (7.2)	0.2 (0.04)	1	22.1	270 (160–430)	40	0.031
Virola koshnii	112 (33)	0.9 (0.5)	1	111.0	151 (110–220)	40	0.026
Carapa guianensis	1050 (486)	12.3 (3.5)	14	75.0	190 (130–250)	42	0.017
Pentaclethra macroloba	255 (45)	1.4 (0.2)	2600	0.098	210 (80–355)	37	−0.024

[1] Mean (range in parenthesis) values from Richter 1972, except for *Pentaclethra macroloba*, which is from Kribs (1968).

high leaf conductances for high leaf areas as they grow in height and diameter. Where light (or nutrient availability) is limiting and water is readily available, as in wet tropical forests, maximizing leaf area will maximize photosynthesis (McDowell et al. 2002*a*). Measurement of g_s across the height range of these species is required to confirm this prediction.

Our study provides the first allometric equations to predict A_l and M_l from DBH and A_s for these five tropical species, and it provides support for the conclusion that A_l:A_s is positively related to height in wet environments (McDowell et al. 2002*a*). Consistent with the findings of McDowell et al. (2002*a*) and Phillips et al. (2003), increasing A_l:A_s with height may benefit trees through increased photosynthetic leaf area, but at the cost of reduced g_s per unit leaf area (Figure 3). This may not be a negative consequence in a wet, cloudy environment where photosynthesis is constrained more by electron transport than by g_s. The slope of the relationship between A_l:A_s and tree height (*b* from Table 3) was consistent with the findings of McDowell et al. (2002*a*). For the four species that had increased A_l:A_S with height, the maximum height was negatively correlated with the slope, such that the ratio A_l:A_s decreases the taller a species may grow (Table 3). For *Pentaclethra,* the relationship of *b* to maximum height almost

exactly matched that of temperate species (Figure 4 in McDowell et al. 2002*a*).

Acknowledgments

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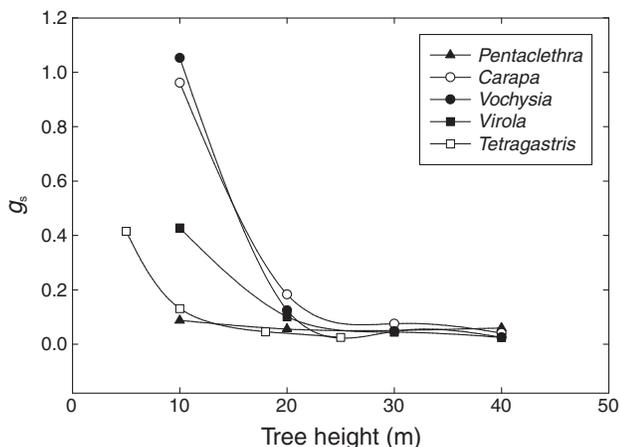
Figure 3. Relationship between mean canopy conductance (g_s, in relative units) and tree height in five tropical tree species. The g_s values were calculated from A_l:A_s and height data with Equation 1. *Pentaclethra* maintains a constant g_s once trees exceed a height of 10 m.

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