

# Leaf functional traits of tropical forest plants in relation to growth form

L. S. SANTIAGO\*† and S. J. WRIGHT‡

\*Department of Botany and Plant Sciences, University of California, Riverside, CA 92521 USA, and †Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Ancón, Republic of Panamá

## Summary

1. We tested the generality of global leaf trait relationships among 44 tropical plant species from a broad array of growth forms (trees, lianas and understorey plants) in lowland Panamá to determine how leaf trait relationships vary with whole-plant morphology within one site.
2. We observed significant variation among growth forms for seven out of 10 leaf traits. Variation in leaf traits among growth forms was more pronounced per area than per mass. Thirteen bivariate leaf trait relationships that describe how plants allocate resources to photosynthesis were significant across all species. Growth forms showed distinct slopes, intercepts or shifts in the common slope for 12 of the 13 relationships.
3. Trait relationships within trees and lianas showed good agreement with a global leaf trait data set. However, for understorey plants, trait relationships that included specific leaf area (SLA) deviated from the global data set, suggesting that understorey leaf-allocation patterns optimize SLA, and hence growth.
4. Lianas showed lower values and rates of gas exchange than trees, and longer leaf life span for a given SLA, illustrating variation in leaf traits associated with growth form and canopy geometry.
5. Functional variation in allocation to photosynthetic capacity among tropical forest species is related to microhabitat variations in light availability and whole-plant morphology among growth forms.

*Key-words:* canopy crane, leaf life span, liana, palm, photosynthesis, tropical forest physiology

*Functional Ecology* (2007) **21**, 19–27

doi: 10.1111/j.1365-2435.2006.01218.x

## Introduction

At the global scale, maximum photosynthetic CO<sub>2</sub> assimilation per mass ( $A_{\text{mass}}$ ), leaf nitrogen per mass ( $N_{\text{mass}}$ ), leaf phosphorus per mass ( $P_{\text{mass}}$ ), specific leaf area (SLA) and leaf life span (LL) are correlated, and variation among these traits is captured by a single axis in multidimensional space (Reich, Walters & Ellsworth 1997; Westoby *et al.* 2002; Wright *et al.* 2004). However, the presence of relationships at the global scale does not necessarily mean the same relationships will be detected in regional or site-specific data sets. Within-site variation in plant traits is generally equal to, or greater than, mean differences across sites (Reich *et al.* 1999). Within-site leaf trait relationships may reflect constraints on how resources are allocated to maximize carbon gain at a given site. Even if species at a specific site have trait relationships similar to those observed at the global scale, different growth forms may not occupy

the entire range of the relationship, and may instead specialize in one end of the trade-off spectrum. Alternatively, each growth form may occupy a large range of the site-specific trait relationship if the distribution of traits increases resource partitioning spatially or temporally (Cody 1986).

We ask whether microsite variation and growth form (trees, lianas and understorey plants) influence leaf traits and bivariate relationships among leaf traits. We hypothesized that whole-plant morphology constrains photosynthetic carbon gain. For example, emergent tree species are exposed to high irradiance, whereas understorey species depend on light flecks for the majority of their carbon gain. As a second example, relative to trees lianas tend to have deep roots and larger xylem vessels with high water-transport capacity (Tyree & Ewers 1996; Andrade *et al.* 2005), potentially increasing the supply of water for leaf gas exchange. Therefore whole-plant morphology may constrain leaf-level characteristics related to plant carbon economy.

We also explore the role of leaf potassium (K) in the leaf economics spectrum. Potassium has been found to

be only loosely related to the suite of leaf traits that form the global leaf economics spectrum (Wright, I.J. *et al.* 2005). Potassium is largely related to osmotic potential and stomatal control: depending on seasonality and water availability, this trait could be important for leaf carbon economy at a single site. However, the importance of  $K_{\text{mass}}$  for leaf function may be obscured by the complex interplay between plant adaptations to nutrient stress and differences in nutrient availability, which can introduce variations in cross-site comparisons.

The purpose of this study is to test constraints of growth form on leaf functional traits. Specific questions included: (1) Do mean leaf physiological traits vary among growth forms? (2) Do relationships among leaf traits vary among growth forms? (3) Do growth forms occupy the entire range of site-specific leaf trait relationships, or a limited portion of the range? (4) Do leaf trait relationships for particular growth forms differ from the global relationship in predictable ways?

## Methods

### STUDY SITE AND GROWTH FORM CLASSIFICATION

The study was conducted in lowland tropical forest in the Parque Nacional San Lorenzo on the Caribbean coast of Central Panama (9°17' N, 79°58' W). Mean annual precipitation is 3100 mm with a moderate dry season from January to March in which ≈10% of annual precipitation is received (Paton & Wright 2003). Mean annual temperature is 26 °C with little variation among months, and mean relative humidity is ≈95% (Paton & Wright 2003). The vegetation is old-growth lowland tropical forest located on a plateau 140 m above sea level and ≈5 km from the Caribbean coast. The site contains a canopy crane maintained by the Smithsonian Tropical Research Institute, and a 6-ha forest dynamics plot established by the Center for Tropical Forest Science (CTFS) in which all stems ≥1 cm diameter at breast height have been measured, mapped and identified to species. We conducted this study in the canopy crane plot, a 1-ha subplot containing 169 species of plants with a stem diameter ≥1 cm (S. Lao CTFS, personal communication). Forty-four plant species were selected for study, representing a broad selection of growth forms including canopy and pioneer trees, lianas and understorey herbs, palms and shrubs (Table 1). Nomenclature follows Correa, Galdames & de Stapf (2004).

Only three growth forms were distinguished: canopy trees; canopy lianas; and understorey plants, including herbs and shrubs. Prior work indicates that regeneration requirements vary continuously among canopy tree species in central Panama, with most species occupying intermediate positions along a continuum of light requirements for regeneration (Wright *et al.* 2003). We constructed an independent index of light demand during early regeneration for 25 of our study

species based on long-term seedling data sets from the Parque Nacional San Lorenzo and Barro Colorado Island, Panama (Wright, S.J. *et al.* 2005; Gilbert *et al.* 2006; unpublished data). The index is based on the well known trade-off between survival and relative growth rate (Gilbert *et al.* 2006). The index consists of factor scores for the first principal component calculated for relative height growth rate and the proportion of first-year seedlings surviving ( $r = -0.56$ ,  $n = 172$  species). Larger values indicate greater shade tolerance (Table 1). Factor scores were calculated using SYSTAT version 11.0.

Measurements for all species were restricted to individuals of the maximum height that each species commonly attains, and gas-exchange measurements and leaf collections were made on the most exposed leaves of each individual to minimize within-plant variations in leaf morphology (Westoby 1998). Trees and lianas were always measured in fully sun-exposed conditions, and understorey plants were always measured in heavily shaded conditions.

### LEAF GAS EXCHANGE, STRUCTURE AND CHEMISTRY

In the wet seasons of 2000 and 2001 (June–November), maximum rates of net CO<sub>2</sub> assimilation ( $A$ ) and stomatal conductance ( $g_s$ ) were measured with an infrared gas analyser (6400, Li-Cor, Lincoln, NE, USA) between 07:00 and 11:00 h. Five newly formed mature leaves from three to five individuals of each species were measured at 370 μmol mol<sup>-1</sup> CO<sub>2</sub> (slightly higher than ambient CO<sub>2</sub> concentration), and 1500 μmol m<sup>-2</sup> s<sup>-1</sup> photosynthetic photon flux density (PPFD) provided by a red blue light source (6400-02B #SI-710, Li-Cor). Leaves of understorey species were induced in a step-wise fashion at PPFD levels of 500, 700 and 1000 μmol m<sup>-2</sup> s<sup>-1</sup> before maximum photosynthesis was measured at 1500 μmol m<sup>-2</sup> s<sup>-1</sup>. Temperature was allowed to vary naturally unless it rose above 33 °C, in which case it was maintained at 33 °C because photosynthetic rates decline above this temperature (Santiago 2003). Gas-exchange measurements were made the day after rain and at low (<1.5 kPa) leaf-to-air vapour pressure deficits to minimize variation due to possible stomatal closure. Therefore gas-exchange measurements represent the maximum values that each species achieves, given the light level and CO<sub>2</sub> concentration in the cuvette. For trees and lianas, terminal leaves were accessed using the canopy crane. For understorey plants, measurements were made from the forest floor.

Following photosynthetic measurements, leaf area was measured with a portable area meter (3000A, Li-Cor) and leaves were dried for 48 h at 65 °C, weighed for determination of SLA, and ground to a fine powder. All leaves from the same individual were pooled for chemical analysis. Leaf N was measured using an elemental analyser (NCS 2500, Carlo Erba Instruments, Milan, Italy). Leaf P and K were determined using

**Table 1.** Plant species and growth forms encountered in lowland wet forest in the Parque Nacional San Lorenzo, Panama. Light habitat is characterized by the trade-off between survival and relative height growth for first-year seedlings from San Lorenzo and Barro Colorado Island (Gilbert *et al.* 2006). Light habitat scores are factor scores for the first principal component calculated for relative height growth and the proportion of individuals surviving, where a larger number indicates greater shade tolerance. Photosynthesis per mass ( $A_{\text{mass}}$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ), stomatal conductance ( $g_s$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ), leaf nitrogen per mass ( $N_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), leaf phosphorus per mass ( $P_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), leaf potassium per mass ( $K_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), specific leaf area (SLA,  $\text{g cm}^{-2}$ ), and median leaf life span (LL, days).

Species	Family	Growth form	Light habitat	$g_s$	SLA	$A_{\text{mass}}$	$N_{\text{mass}}$	$P_{\text{mass}}$	$K_{\text{mass}}$	LL
<i>Apeiba membranacea</i> Spruce ex. Benth.	Tiliaceae	Tree	-1.89	0.468	89.4	133.3	25.8	1.12	12.91	220
<i>Aspidosperma cruentum</i> Woodson	Apocynaceae	Tree	0.71	0.231	64.5	65.9	20.4	0.84	8.89	337
<i>Brosimum utile</i> (Kunth) Pittier	Moraceae	Tree	0.41	0.323	68.4	77.6	18.2	1.04	7.67	324
<i>Calophyllum longifolium</i> Willd.	Clusiaceae	Tree	1.05	0.311	38.7	43.3	12.1	0.72	6.60	502
<i>Carapa guianensis</i> Aubl.	Meliaceae	Tree		0.207	48.7	49.3	13.7	0.86	5.02	690
<i>Cecropia insignis</i> Liebm.	Cecropiaceae	Tree	-2.89	0.48	90.9	143.1	17.1	1.24	11.43	231
<i>Cecropia obtusifolia</i> Bertol.	Cecropiaceae	Tree	-2.39	0.556	266.8	350.8	41.6	3.04	23.80	
<i>Dussia munda</i> C.H. Stirt.	Fabaceae	Tree	0.55	0.479	89.2	105.8	21.1	1.14	11.37	340
<i>Jacaranda copaia</i> (Aubl.) D. Don	Bignoniaceae	Tree	-2.03	0.538	96.6	157.8	25.5	1.21	11.82	
<i>Lonchocarpus latifolius</i> Kunth	Fabaceae	Tree	-0.19	0.439	69.4	102.9	18.4	1.06	10.93	285
<i>Manilkara bidentata</i> (A. DC.) A. Chev.	Sapotaceae	Tree	-0.04	0.223	58.1	78.0	16.5	0.83	8.54	427
<i>Miconia borealis</i> Gleason	Melastomataceae	Tree		0.602	103.8	158.3	22.0	1.30	15.29	175
<i>Nectandra purpurea</i> (Ruiz & Pav.) Mez.	Lauraceae	Tree	2.13	0.338	67.7	73.6	17.8	0.77	6.94	462
<i>Ochroma pyramidale</i> (Cav. Ex Lam.) Urb.	Bombacaceae	Tree		0.577	154.6	224.7	21.4	1.49	15.74	
<i>Oenocarpus mapora</i> H. Karst.	Arecaceae	Tree		0.186	89.1	67.9	20.5	1.27	7.13	
<i>Pourouma bicolor</i> Mart.	Cecropiaceae	Tree	0.66	0.508	70.1	110.5	20.0	1.24	11.11	254
<i>Simarouba amara</i> Aubl. var. typical Cronq.	Simaroubaceae	Tree	0.18	0.406	56.8	78.6	17.4	0.65	6.62	253
<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	Arecaceae	Tree	1.43	0.344	68.4	76.7	19.9	1.24	6.53	547
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	Tree	0.29	0.406	70.8	92.2	15.4	0.88	5.83	322
<i>Trema micrantha</i> (L.) Blume	Ulmaceae	Tree		0.539	126.7	169.7	20.9	0.87	9.34	
<i>Vochysia ferruginea</i> Mart.	Vochysiaceae	Tree	-0.75	0.647	87.5	138.7	17.3	1.00	7.58	214
<i>Abuta panamensis</i> (Standl.) Krukoff & Barneby	Menispermaceae	Liana	0.78	0.238	142.3	143.8	27.7	1.70	29.06	35
<i>Anomospermum reticulatum</i> (Mart.) Eichler	Menispermaceae	Liana		0.23	110.8	80.6	15.9	0.62	7.62	268
<i>Arrabidaea verrucosa</i> (Standl.) A.H. Gentry	Bignoniaceae	Liana	-1.48	0.379	95.9	91.8	22.1	1.68	21.02	361
<i>Cayaponia granatensis</i> Cogn.	Cucurbitaceae	Liana		0.386	97.0	89.5	33.8	2.24	12.48	525
<i>Doliodocarpus dentatus</i> (Aubl.) Standl.	Dilleniaceae	Liana	-1.06	0.298	90.1	97.1	14.7	0.79	5.79	299
<i>Heisteria scandens</i> Ducke	Oleaceae	Liana		0.138	108.7	90.2	17.6	0.86	5.57	335
<i>Maripa panamensis</i> Hemsl.	Convolvulaceae	Liana	0.73	0.319	91.4	112.1	18.9	1.21	14.45	
<i>Paullinia fibrigera</i> Radlk.	Sapindaceae	Liana	0.55	0.229	115.1	131.2	21.2	1.08	18.08	
<i>Phryganocydia corymbosa</i> (Vent.) Bureau ex K. Schum	Bignoniaceae	Liana	0.46	0.229	87.4	70.8	17.5	1.00	13.48	302
<i>Pleotoma variabilis</i> (Jacq.) Miers	Bignoniaceae	Liana	-0.34	0.265	78.5	80.1	16.7	0.80	7.65	179
<i>Tontelea richardii</i> (Peyr.) A.C. Sm.	Hypocrateaceae	Liana		0.161	68.9	50.2	18.3	0.90	6.90	541
<i>Calyptrogyne costatifrons</i> (L.H. Bailey) Nevers	Arecaceae	Understorey		0.071	169.9	53.5	22.4	1.53	18.88	
<i>Carludovica palmata</i> Ruiz & Pav.	Cyclanthaceae	Understorey		0.189	206.9	131.5	19.6	1.41	14.47	
<i>Clidemia</i> spp.	Melastomataceae	Understorey		0.192	298.3	165.8	17.8	1.08	18.08	
<i>Costus pulverulentus</i> C. Presl.	Costaceae	Understorey		0.236	199.4	122.1	18.4	1.41	22.82	
<i>Dieffenbachia pittieri</i> Engl. & Krause	Araceae	Understorey		0.117	186.8	55.4	18.7	2.42	40.66	
<i>Geonoma cuneata</i> H. Wendl. Ex Spruce	Arecaceae	Understorey		0.061	166.2	27.9	16.2	1.02	15.97	
<i>Heliconia pogonantha</i> Cufod.	Heliconiaceae	Understorey		0.266	179.6	129.0	23.2	1.58	18.13	
<i>Lozania pittieri</i> (S.F. Blake) L.B. Sm.	Flacourtiaceae	Understorey	-1.26	0.111	285.7	92.7	19.2	1.07	11.12	
<i>Mollinedia darienensis</i> Standl.	Monimiaceae	Understorey		0.076	259.9	87.8	18.9	1.06	10.02	
<i>Psychotria suerrensii</i> Donn. Sm.	Rubiaceae	Understorey	0.16	0.071	228.9	59.2	20.4	0.80	11.75	
<i>Stromanthe jacquinii</i> (R. & S) H. Kenn. & Nicholson	Maranthaceae	Understorey		0.186	272.6	138.0	20.0	1.17	24.44	
<i>Zingiber officinale</i> Roscoe	Zingiberaceae	Understorey		0.175	221.9	125.5	23.2	1.29	19.30	

inductively coupled plasma emission spectroscopy at the University of Florida Institute of Food and Agricultural Sciences. Leaf life span was determined for marked leaves on upper canopy shoots that were censused every 4–6 weeks for 3–6 years as part of a larger study on canopy leaf dynamics (S.J.W., unpublished data). The leaf life span data set includes most of our tree and liana species.

#### DATA ANALYSIS

Data were averaged for each species, and the average values for each species were analysed for differences among growth forms. Data were tested for normality and homogeneity of variance and, when necessary, were log<sub>e</sub>-transformed before analysis. Comparisons of leaf functional traits among growth forms were

performed with one-way ANOVA in SAS ver. 8.02. Differences among growth forms were evaluated with a *post hoc* Duncan's multiple range test. In addition, we evaluated 13 bivariate relationships among leaf traits that are believed to describe how plants allocate resources to photosynthesis. Bivariate relationships were assessed using standardized major axis estimation (model II regression) with (s)MATR ver. 1.0 software (Falster, Warton & Wright 2003). The program first tested for differences in slope among growth forms using likelihood ratios. If no significant difference in slope was detected, tests for differences in elevation ( $\gamma$ -intercept) and whether growth forms were separated along the standardized major axis with a common slope were performed using randomization routines that are analogous to ANCOVA. Model II regression was chosen over linear regression (ordinary least-squares regression, model I regression) because all leaf traits were measured with error and our objective was to describe the relationships between traits, not to predict values of one trait from another trait (Falster *et al.* 2003).

We used leaf trait relationships from the Global Plant Trait Network (GLOPNET; Wright *et al.* 2004) to evaluate whether bivariate relationships at our site were similar to global relationships. When there was a significant global relationship to compare with our data, we plotted the non-transformed model II regression line with our data.

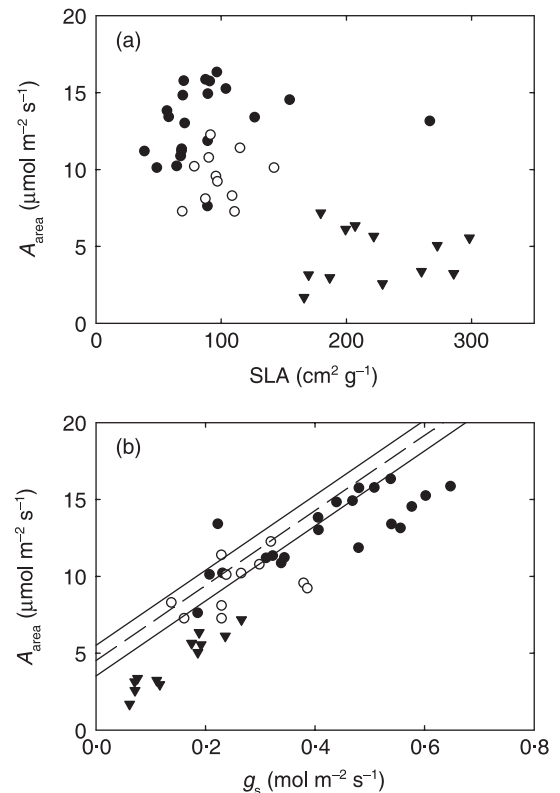
## Results

### AREA-BASED TRAIT RELATIONSHIPS

Across all 44 species, we observed 9.7-fold variation in photosynthetic CO<sub>2</sub> assimilation rate per area ( $A_{\text{area}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), 5.8-fold variation in leaf N per area ( $N_{\text{area}}$ ,  $\text{mg cm}^{-2}$ ), 6.6-fold variation in leaf P per area ( $P_{\text{area}}$ ,  $\text{mg cm}^{-2}$ ), 6.2-fold variation in leaf K per area ( $K_{\text{area}}$ ,  $\text{mg cm}^{-2}$ ), and 10-fold variation in stomatal conductance ( $g_s$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ).

We observed significant variation among growth forms in all five area-based leaf functional traits.  $A_{\text{area}}$  was highest in trees, moderate in lianas and lowest in understorey plants ( $F_{2,41} = 68.66$ ,  $P < 0.0001$ ); and  $g_s$  ( $F_{2,41} = 24.61$ ,  $P < 0.0001$ ),  $N_{\text{area}}$  ( $F_{2,41} = 39.38$ ,  $P < 0.0001$ ),  $P_{\text{area}}$  ( $F_{2,41} = 16.53$ ,  $P < 0.0001$ ) and  $K_{\text{area}}$  ( $F_{2,41} = 2.61$ ,  $P < 0.10$ ) showed patterns similar to  $A_{\text{area}}$ , with trees and lianas consistently showing greater values than understorey plants.

The relationship between  $A_{\text{area}}$  and SLA was significant and negative across all species (Fig. 1a;  $r^2 = 0.39$ ,  $P < 0.0001$ ,  $n = 44$ ), but was insignificant within each growth form. The significant relationship across all species arises largely because understorey species have low  $A_{\text{area}}$  and high SLA. The relationship between  $A_{\text{area}}$  and  $g_s$  was significant and positive across all species (Fig. 1b;  $r^2 = 0.79$ ,  $P < 0.0001$ ,  $n = 44$ ) and within trees ( $r^2 = 0.64$ ,  $P < 0.0001$ ,  $n = 21$ ) and understorey



**Fig. 1.** Relationship between CO<sub>2</sub> assimilation rate per area ( $A_{\text{area}}$ ) and (a) specific leaf area (SLA); (b) stomatal conductance ( $g_s$ ) for 44 plant species from three growth forms in lowland Panamanian wet forest. Canopy trees (●); lianas (○); understorey (▼). Results of regression analyses are presented in Table 2. Dashed line represents model II regression with 95% confidence intervals for the global data set (GLOPNET; Wright *et al.* 2004).

plants ( $r^2 = 0.90$ ,  $P < 0.0001$ ,  $n = 12$ ), but not within lianas ( $r^2 = 0.21$ ,  $P = 0.16$ ,  $n = 11$ ). The relationship between  $A_{\text{area}}$  and  $N_{\text{area}}$  was significant and positive across all species ( $r^2 = 0.42$ ,  $P < 0.0001$ ,  $n = 44$ ). However,  $A_{\text{area}}$  and  $N_{\text{area}}$  were not significantly related within any growth form.  $A_{\text{area}}$  showed weak positive relationships with  $P_{\text{area}}$  ( $r^2 = 0.29$ ,  $P < 0.0005$ ,  $n = 44$ ) and  $K_{\text{area}}$  ( $r^2 = 0.10$ ,  $P < 0.05$ ,  $n = 44$ ), but these relationships were insignificant within growth forms. The relationship between  $N_{\text{area}}$  and SLA was significant and negative across all species ( $r^2 = 0.75$ ,  $P < 0.0001$ ,  $n = 44$ ), and for canopy trees ( $r^2 = 0.56$ ,  $P < 0.0001$ ,  $n = 21$ ) and understorey plants ( $r^2 = 0.76$ ,  $P < 0.0005$ ,  $n = 12$ ).

We also observed significant differences among growth forms in the slopes, intercepts or positions along a common slope for bivariate area-based leaf trait relationships. For the  $A_{\text{area}}-g_s$  relationship, slopes were indistinguishable among growth forms, but the intercept was significantly greater for trees than for lianas and understorey plants (Table 2). For the  $A_{\text{area}}-SLA$ ,  $A_{\text{area}}-N_{\text{area}}$  and  $A_{\text{area}}-P_{\text{area}}$  relationships, slopes were indistinguishable among growth forms, but the intercept differed significantly among growth forms and was largest for trees, intermediate for lianas, and smallest

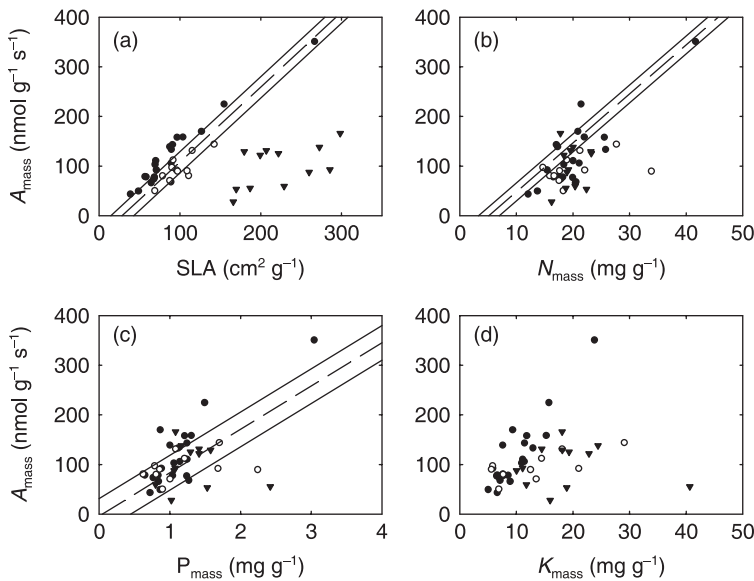
**Table 2.** Tests for heterogeneity of slope, shifts in intercept, and whether growth forms are separated along a standardized major axis with a common slope and intercept for relationships among leaf traits

		Slope			Heterogeneity of slope	Intercept Heterogeneity			Shift in intercept	Common slope
y	x	Trees	Lianas	Understorey		Trees	Lianas	Understorey		
Area-based relationships										
$A_{\text{area}}$	$g_s$	16.9	20.7	25.3	$P = 0.08$	<b>6.0<sup>a</sup></b>	<b>4.1<sup>b</sup></b>	<b>0.7<sup>b</sup></b>	$P < 0.0001$	$P < 0.0001$
$A_{\text{area}}$	SLA	0.05	0.08	0.04	$P = 0.26$	<b>8.7<sup>a</sup></b>	<b>1.3<sup>b</sup></b>	<b>-4.1<sup>c</sup></b>	$P < 0.0001$	$P < 0.05$
$A_{\text{area}}$	$N_{\text{area}}$	-44.0	-28.8	78.6	$P = 0.12$	<b>23.9<sup>a</sup></b>	<b>15.5<sup>b</sup></b>	<b>-2.9<sup>c</sup></b>	$P < 0.0001$	$P = 0.22$
$A_{\text{area}}$	$P_{\text{area}}$	-799	339	622	$P = 0.16$	<b>23.8<sup>a</sup></b>	<b>5.4<sup>b</sup></b>	<b>0.5<sup>c</sup></b>	$P < 0.0001$	$P < 0.001$
$A_{\text{area}}$	$K_{\text{area}}$	<b>81.2<sup>a</sup></b>	<b>29.2<sup>b</sup></b>	<b>-36.8<sup>b</sup></b>	$P < 0.05$	3.5	5.8	7.7		
$N_{\text{area}}$	SLA	<b>-0.001<sup>a</sup></b>	<b>-0.003<sup>b</sup></b>	<b>-0.0005<sup>c</sup></b>	$P < 0.001$	0.3	0.5	0.2		
Mass-based relationships										
$A_{\text{mass}}$	SLA	1.4	1.3	0.9	$P = 0.28$	<b>-10.3<sup>a</sup></b>	<b>-37.4<sup>b</sup></b>	<b>-106.3<sup>c</sup></b>	$P < 0.0001$	$P < 0.0001$
$A_{\text{mass}}$	$N_{\text{mass}}$	<b>11.7<sup>a</sup></b>	<b>4.7<sup>b</sup></b>	<b>19.7<sup>a</sup></b>	$P < 0.05$	-117.6	-0.5	-291.1		
$A_{\text{mass}}$	$P_{\text{mass}}$	<b>142.5<sup>a</sup></b>	<b>54.9<sup>a</sup></b>	<b>-103.4<sup>b</sup></b>	$P < 0.05$	-42.7	31.9	234.1		
$A_{\text{mass}}$	$K_{\text{mass}}$	<b>16.1<sup>a</sup></b>	<b>3.6<sup>b</sup></b>	<b>-5.2<sup>b</sup></b>	$P < 0.001$	-42.5	48.1	196.7		
$N_{\text{mass}}$	SLA	<b>0.1<sup>a</sup></b>	<b>0.3<sup>b</sup></b>	<b>-0.04<sup>c</sup></b>	$P < 0.005$	9.1	-7.9	30.3		
$A_{\text{mass}}$	LL	-0.2	-0.1		$P = 0.15$	179	123		$P = 0.17$	$P = 0.54$
SLA	LL	-0.1	-0.1		$P = 0.91$	<b>114<sup>a</sup></b>	<b>132<sup>b</sup></b>		$P < 0.005$	$P = 0.11$

Significant ( $P < 0.05$ ) variation among growth forms indicated in bold; superscript letters distinguish growth forms that differ significantly in *post hoc* tests.

for understorey plants, with all pairwise comparisons differing significantly (Table 2). There were also significant shifts in the common slopes of the  $A_{\text{area}}$ -SLA and  $A_{\text{area}}$ - $P_{\text{area}}$  relationships, indicating that understorey plants occupy the region of the  $A_{\text{area}}$ -SLA relationship with the smallest  $A_{\text{area}}$  and largest SLA (Fig. 1a;

Table 2), and the region of the  $A_{\text{area}}$ - $P_{\text{area}}$  relationship with the smallest  $A_{\text{area}}$  and smallest  $P_{\text{area}}$  (Table 2). Understorey plants and lianas had significantly smaller slopes than trees in the relationship between  $A_{\text{area}}$  and  $K_{\text{area}}$  (Table 2). Slopes of the relationship between  $N_{\text{area}}$  and SLA differed significantly for all pairwise comparisons (Table 2).



**Fig. 2.** Relationship between photosynthetic rate per mass ( $A_{\text{mass}}$ ) and (a) specific leaf area (SLA); (b) leaf nitrogen per mass ( $N_{\text{mass}}$ ); (c) leaf phosphorus per mass ( $P_{\text{mass}}$ ); and (d) leaf potassium per mass ( $K_{\text{mass}}$ ) for 44 plant species of three growth forms from lowland Panamanian wet forest. Canopy trees (●); lianas (○); understorey (▼). Results of regression analyses are presented in Table 2. Dashed lines represent model II regressions with 95% confidence intervals for the global data set (GLOPNET; Wright *et al.* 2004).

#### MASS-BASED TRAIT RELATIONSHIPS

Among the 44 species studied, we observed 12.5-fold variation in photosynthetic  $\text{CO}_2$  assimilation rate per mass ( $A_{\text{mass}}$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ), 3.5-fold variation in leaf N per mass ( $N_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), 4.7-fold variation in leaf P per mass ( $P_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), 8.1-fold variation in leaf K per mass ( $K_{\text{mass}}$ ,  $\text{mg g}^{-1}$ ), and 7.7-fold variation in SLA. The only mass-based traits that showed significant differences among growth forms were SLA ( $F_{2,41} = 37.19$ ,  $P < 0.0001$ ) and  $K_{\text{mass}}$  ( $F_{2,41} = 8.13$ ,  $P < 0.005$ ), both of which were greatest in understorey plants.

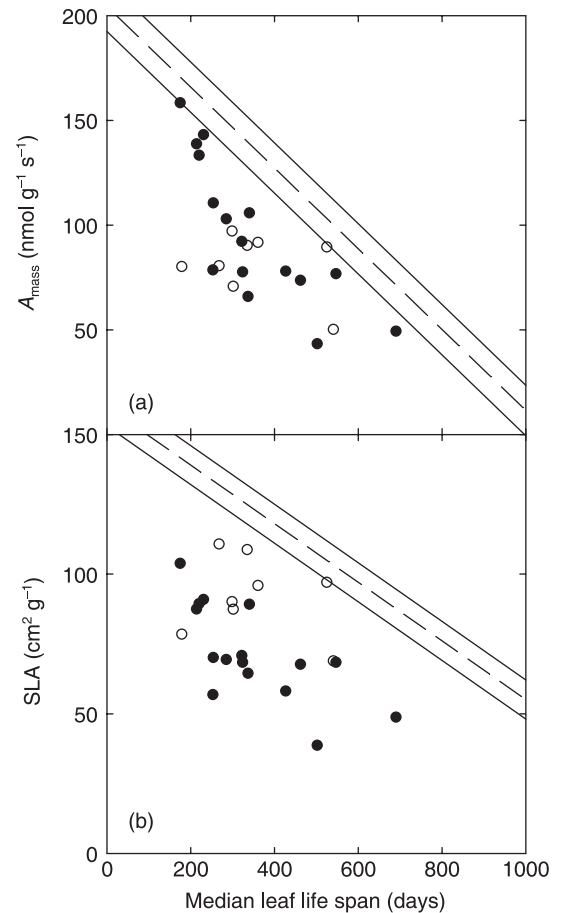
There was a relatively weak positive relationship between  $A_{\text{mass}}$  and SLA across all species (Fig. 2a;  $r^2 = 0.15$ ,  $P < 0.01$ ,  $n = 44$ ). However, SLA explained a significant amount of variation in  $A_{\text{mass}}$  within growth forms from the upper strata of the canopy (trees,  $r^2 = 0.93$ ,  $P < 0.0001$ ,  $n = 21$ ; lianas,  $r^2 = 0.65$ ,  $P < 0.005$ ,  $n = 11$ ). The  $A_{\text{mass}}$ -SLA relationship for trees and lianas was similar to the global relationship, but understorey species fell well below the global relationship (Fig. 2a).  $A_{\text{mass}}$  increased significantly with  $N_{\text{mass}}$  across all species ( $r^2 = 0.42$ ,  $P < 0.0001$ ,  $n = 44$ ) and within trees ( $r^2 = 0.71$ ,  $P < 0.0001$ ,  $n = 21$ ), but not within lianas ( $r^2 = 0.14$ ,  $P = 0.26$ ,  $n = 11$ ) or understorey species ( $r^2 = 0.04$ ,  $P = 0.53$ ,  $n = 12$ ).  $A_{\text{mass}}$

also increased significantly with  $P_{\text{mass}}$  across all species ( $r^2 = 0.28$ ,  $P < 0.0005$ ,  $n = 44$ ), and within trees ( $r^2 = 0.74$ ,  $P < 0.0001$ ,  $n = 21$ ), but not within other growth forms. Both the  $A_{\text{mass}}-N_{\text{mass}}$  and the  $A_{\text{mass}}-P_{\text{mass}}$  relationships showed good agreement with global relationships (Fig. 2b,c).  $A_{\text{mass}}$  increased significantly with  $K_{\text{mass}}$  across all species ( $r^2 = 0.10$ ,  $P < 0.05$ ,  $n = 44$ ), but the relationship was weaker than for  $N_{\text{mass}}$  or  $P_{\text{mass}}$  (Fig. 2d). Nonetheless,  $A_{\text{mass}}$  was strongly related to  $K_{\text{mass}}$  in trees ( $r^2 = 0.83$ ,  $P < 0.0001$ ,  $n = 21$ ). There was a weak positive relationship between  $N_{\text{mass}}$  and SLA across all species ( $r^2 = 0.10$ ,  $P < 0.05$ ,  $n = 44$ ). This relationship was much stronger in trees ( $r^2 = 0.78$ ,  $P < 0.0001$ ,  $n = 21$ ), but not significant in the other growth forms. Overall, mass-based relationships tended to be stronger within growth forms than across all species, whereas area-based relationships tended to be stronger across all species than within growth forms.

We also observed differences among growth forms for mass-based leaf trait relationships. For the  $A_{\text{mass}}-SLA$  relationship, slopes could not be distinguished among growth forms; however there was a significant shift in intercept, with values being largest for trees, intermediate for lianas, and smallest for understorey plants (Table 2). This pattern is similar to the  $A_{\text{area}}-SLA$  relationship. There was also a significant shift along the common slope of the  $A_{\text{mass}}-SLA$  relationship, indicating that understorey plants have significantly larger values of SLA than trees or lianas. For the  $A_{\text{mass}}-N_{\text{mass}}$  relationship, slopes differed significantly, the slope for lianas being lower than those for trees or understorey plants (Table 2). Trees and lianas showed significantly steeper slopes than understorey plants in the  $A_{\text{mass}}-P_{\text{mass}}$  relationship, and trees showed steeper slopes than understorey plants and lianas in the  $A_{\text{mass}}-K_{\text{mass}}$  relationship. For the  $N_{\text{mass}}-SLA$  relationship, slopes were heterogeneous, with significant differences for all pairwise comparisons among the three growth forms.

#### LEAF LONGEVITY

Median leaf life span (LL, days) was negatively related to  $A_{\text{mass}}$  and SLA among trees and lianas (Fig. 3), indicating that species with shorter-lived leaves tend to exhibit relatively thin leaves with high rates of  $\text{CO}_2$  assimilation. Within growth forms,  $A_{\text{mass}}-LL$  and  $SLA-LL$  relationships were significant in trees ( $A_{\text{mass}}-LL$ ,  $r^2 = 0.64$ ,  $P < 0.0005$ ,  $n = 16$ ;  $SLA-LL$ ,  $r^2 = 0.50$ ,  $P < 0.005$ ,  $n = 16$ ) but not in lianas ( $A_{\text{mass}}-LL$ ,  $r^2 = 0.12$ ,  $P = 0.40$ ,  $n = 9$ ;  $SLA-LL$ ,  $r^2 = 0.05$ ,  $P = 0.61$ ,  $n = 9$ ). For the  $A_{\text{mass}}-LL$  relationship, slopes were indistinguishable, and we found no evidence for a difference in intercept or a shift along the common slope (Table 2). For the  $SLA-LL$  relationship, slopes were also indistinguishable and there was no shift along the common slope, but there was a shift in intercept, indicating that liana leaves live significantly



**Fig. 3.** Relationship between median leaf life span (LL) and (a) photosynthetic  $\text{CO}_2$  assimilation rate per mass ( $A_{\text{mass}}$ ); (b) specific leaf area (SLA) for 25 plant species of trees (●) and lianas (○) in a lowland wet forest in Panama. Results of regression analyses are presented in Table 2. Dashed lines represent model II regressions with 95% confidence intervals for the global data set (GLOPNET; Wright *et al.* 2004).

longer than tree leaves for a given SLA (Table 2). In both the  $A_{\text{mass}}-LL$  and  $SLA-LL$  relationships, lianas and trees fell just below the global relationship (Fig. 3).

#### Discussion

Variation in leaf functional traits among growth forms from a lowland wet forest in Panama was driven by microhabitat variation related to plant stature, reflecting the vertical continuum of environmental conditions through the canopy (Chazdon & Fetcher 1984). We found substantial variation between sun leaf traits of trees and lianas compared with the shade leaves of understorey species. However, we also observed differences in leaf trait relationships between sun leaves of lianas and trees indicating that, even in the same light habitat, species of contrasting growth forms can exhibit differences in how photosynthetic resources are deployed. Trees and lianas, which were measured from the top of the canopy, showed good agreement in leaf trait relationships when compared with a global

leaf trait data set. In contrast, understorey plants, which were measured in the deeply shaded understorey, fell off of the global relationship in some instances, perhaps reflecting abundance of sun leaves in the global data set. Overall, variation among growth forms in seven out of 10 leaf traits, and in 12 out of 13 leaf trait relationships, indicates that microsite variation and whole-plant morphology have substantial bearing on how resources are allocated to photosynthesis.

One of the most striking patterns to emerge from our data is that sun leaves of lianas exhibit a lower range of  $A_{\text{area}}$  than trees, despite having similar ranges of SLA values (Fig. 1a). We expected high gas-exchange rates in lianas because of larger vessel diameters and greater sapwood-specific hydraulic conductivity (Patiño, Tyree & Herre 1995; Tibbetts & Ewers 2000). Instead, trees tended to have greater  $A_{\text{area}}$  and  $g_s$  than lianas (Fig. 1; Table 2). One possible explanation for this pattern is that, although lianas have greater sapwood-specific hydraulic conductivity, leaf area per stem area may also be high, and water transported through the xylem may be shared by more leaves, leading to low supply to individual leaves and relatively low gas-exchange rates (low leaf specific hydraulic conductivity). Lianas have been shown to have proportionally larger increases in leaf area per stem cross-section than trees (Putz 1983; Gerwing & Farias 2000). Lianas have also been shown to contribute 9–12% of forest transpiration even though they represent only 5.5% of forest basal area in eastern Amazonia (Restom & Nepstad 2001), consistent with greater transpiring surface area per basal area in lianas. Therefore the evidence demonstrating high leaf area per stem area in Neotropical lianas is in line with our data showing low gas-exchange rates in lianas relative to trees. Greater path length for water transport in lianas may also contribute to this pattern, although further studies are needed to evaluate this possibility.

Two alternative explanations for the strong difference in gas-exchange rates between canopy trees and lianas can be discounted. The first alternative is that tree and liana species tend to differ in shade tolerance and successional status, with trees tending to be characterized by the high gas-exchange rates typical of species that recruit early in secondary forest succession and in recent treefall gaps. In fact, seedling light habitat scores have similar mean values and broad ranges among species for the liana ( $-0.05 \pm 0.37$ , mean  $\pm$  1 SE) and tree ( $-0.17 \pm 0.36$ ) species that we studied, indicating that the two growth forms have broadly similar regeneration requirements (Table 1; Gilbert *et al.* 2006). The second alternative explanation is that lianas might occupy less-exposed canopy positions than trees. However, all our measurements on lianas were in exposed canopy positions, and liana crowns almost always overtop and shade tree crowns at our site. With the leading alternatives discounted, we hypothesize that hydraulic limitation causes the relatively low gas-exchange rates observed for canopy lianas. This

hypothesis could be tested by direct measurements of leaf specific hydraulic conductivity for trees and lianas.

We also observed longer LL for a given SLA in lianas than in trees (Table 2). One possible explanation for this trend is that liana leaves suffer less self-shading as a result of their growth pattern. Carbon-assimilation rates have been found to decline as a function of canopy geometry and leaf position rather than age (Ackerly 1999). Longer LL for a given SLA is consistent with less self-shading and leaf production to maximize growth and reduce light availability for co-occurring species (Givnish & Vermeij 1976). Therefore our data suggest that, although lianas occupy a moderate range of gas-exchange values, they produce leaves that live longer and that might contribute to shading competitors. Further work is needed on water transport and the spatial arrangement of lianas to evaluate the possible mechanisms for relatively low gas exchange in lianas, and to assess the generality of these patterns.

In contrast to trees and lianas, understorey plants exhibited low  $A_{\text{area}}$ , consistent with low understorey light availability, but similar  $A_{\text{mass}}$  (Figs 1 and 2). Understorey plants did not show greater  $A_{\text{mass}}$  with greater SLA at a given  $N_{\text{mass}}$ , as expected from global analyses of leaf traits (Reich *et al.* 1999), presumably because of N allocation to optimize light capture at the expense of maximum carboxylation rates (Osmond 1983; Evans 1989). High SLA for a given  $A_{\text{mass}}$  in understorey plants also suggests that understorey leaf-allocation patterns are related to growth. Within the narrow  $A_{\text{mass}}$  range for understorey plants, variation in SLA has greater potential for optimizing growth rate (Givnish 1988; Sims, Gebauer & Pearcy 1994). Therefore it appears that understorey plants specialize in one end of the trade-off spectrum, but further studies are needed to determine how flexible these traits are in response to changing conditions, in order to better understand photosynthetic strategies in understorey plants (Grubb 1998).

The most noteworthy difference observed between canopy and understorey plants was the high values for  $K_{\text{mass}}$  in the understorey. Shade leaves tend to have higher  $K_{\text{mass}}$  than conspecific sun leaves (Grubb 1977). However, our study is the first that we are aware of to document this pattern among species and relate it to growth form. For example, the five monocot herbs (*Costus*, *Diffenbachia*, *Heleconia*, *Stromanthe* and *Zingiber*), which had the highest values of  $K_{\text{area}}$  and  $K_{\text{mass}}$ , have leaves with many colourless mesophyll and epidermis layers (Roth 1990; Tomlinson 1969), where K concentration is often higher (Fricke *et al.* 1994). Potassium is also an osmoregulator (Morgan 1984), so high  $K_{\text{mass}}$  in light-limited understorey plants may reflect use of K for osmotic control in place of hexose, which is more costly in terms of carbon (Sharp, Hsiao & Silk 1990). The osmoregulatory effects of K are likely to be important in controlling stomatal aperture as light flecks move through the forest understorey (Pearcy 1988). Potassium limitation has been shown to



have a negative effect on the ability of plants to control stomata, often leading to a reduction in water-use efficiency and photosynthetic rate, and an increase in respiration (Marschner 1986). However, for purposes of stomatal control, K would be concentrated only near the guard cells and it is therefore unlikely that use of K in stomatal regulation has such profound effects on  $K_{\text{mass}}$ . Rather, it is more likely that high  $K_{\text{mass}}$  in understorey species is related to osmoregulation at the whole-leaf or whole-plant scale, and K involved in stomatal responses is only part of this pattern. We suggest that K is an important resource for tropical understorey species, and that further studies of K physiology are likely to deepen our understanding of constraints on carbon gain in low light. In addition, little is known about the extent of K limitation in natural ecosystems. It is likely that the importance of  $K_{\text{mass}}$  in the leaf economic spectrum is not generally observed in global data sets because of large site-to-site variation in nutrient availability.

Current thinking suggests that plant growth forms are a convenient way of simplifying the diversity of plant physiological function into discrete, manageable groups that can be modelled more easily (Gitay, Noble & Connell 1999). Our data showing variation in leaf traits and leaf trait relationships among growth forms support this view. However, we also found substantial variation in trait values within growth forms, indicating that understanding continuous variation in leaf functional traits within growth forms can potentially refine model predictions. Variation in trait values within growth forms is consistent with recent modelling efforts demonstrating that different trait combinations can lead to alternative functional designs with approximately equivalent fitness, thus promoting species diversity in relatively uniform habitats (Marks & Lechowicz 2006). Therefore we suggest that understanding leaf functional strategies among co-occurring species will be enhanced by identifying major axes of plant strategy variation that link leaf function to whole-plant function and fitness (Westoby *et al.* 2002; Ackerly 2004; Santiago *et al.* 2004). Groups such as understorey plants, which appear to diverge from global leaf trait relationships because of whole-plant processes, also illustrate opportunities to integrate the leaf economics spectrum with other functional dimensions of plant strategy variation. Overall, our study shows that examining microhabitat differences across global data sets may increase the explanatory power of global studies.

### Acknowledgements

We thank Elizabeth Osorio, Steve Davis, Mirna Samaniego and Katia Silvera for field assistance; David Ackerly, Radika Bhaskar, Will Cornwell, Todd Dawson, Kaoru Kitajima, Tim Martin, Stephen Mulkey, Dave Noletti, Jack Putz, Kevin Simonin and Amy Zanne for comments and discussions on earlier

drafts; Edwin Andrade, José Herrera and Osgard Saldaña for their dexterity and expertise in operating the canopy crane; Ian Wright and Peter Reich for use of the GLOPNET data; and Vibeke Horlyck for administrative support. Funding was provided by the United Nations Environmental Programme and the Mellon Foundation (to S.J.W.) and the Florida–Georgia Alliance, an STRI short-term fellowship and EPA STAR Graduate Fellowships (to L.S.S.).

### References

- Ackerly, D. (1999) Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* **119**, 300–310.
- Ackerly, D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* **74**, 25–44.
- Andrade, J.L., Meinzer, F.C., Goldstein, G. & Schnitzer, S.A. (2005) Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* **19**, 282–289.
- Chazdon, R.L. & Fetcher, N. (1984) Light environments of tropical forests. *Physiological Ecology of Plants of the Wet Tropics* (eds E. Medina, H.A. Mooney & C. Vázquez-Yanes), pp. 553–564. Dr W. Junk, The Hague.
- Cody, M.L. (1986) Structural niches in plant communities. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 381–405. Harper & Row, New York.
- Correa, M.D., Galdames, C. & de Stapf, M.S. (2004) *Catálogo de Las Plantas Vasculares de Panamá*. Quebecor World Bogotá, Bogotá.
- Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of  $C_3$  plants. *Oecologia* **78**, 9–19.
- Falster, D.S., Warton, D.I. & Wright, I.J. (2003) *User's Guide to (s)matr: Standardised Major Axis Tests and Routines, Version 1.0*. Macquarie University, Sydney.
- Fricke, W., Pritchard, E., Leigh, R.A. & Tomes, A.D. (1994) Cells of the upper and lower epidermis of barley (*Hordeum vulgare* L.) leaves exhibit distinct patterns of vacuolar solutes. *Plant Physiology* **104**, 1201–1208.
- Gerwing, J.J. & Farias, D.L. (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* **16**, 327–335.
- Gilbert, B., Wright, S.J., Muller-Landau, H.C., Kitajima, K. & Hernández, A. (2006) Life history trade-offs in tropical trees and lianas. *Ecology* **87**, 1281–1288.
- Gitay, H., Noble, I.R. & Connell, J.H. (1999) Deriving functional types for rain-forest trees. *Journal of Vegetation Science* **10**, 641–650.
- Givnish, T.J. (1988) Adaptation to sun and shade – a whole-plant perspective. *Australian Journal of Plant Physiology* **15**, 63–92.
- Givnish, T.J. & Vermeij, G.J. (1976) Sizes and shapes of liane leaves. *American Naturalist* **110**, 743–778.
- Grubb, P.J. (1977) Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* **8**, 83–107.
- Grubb, P.J. (1998) A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics* **1**, 3–31.
- Marks, C.O. & Lechowicz, M.J. (2006) Alternative designs and the evolution of functional diversity. *American Naturalist* **167**, 55–66.
- Marschner, H. (1986) *Mineral Nutrition in Higher Plants*. Academic Press, London.
- Morgan, J.M. (1984) Osmoregulation and water-stress in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **35**, 299–319.



- Osmond, C.B. (1983) Interactions between irradiance, nitrogen nutrition, and water-stress in the sun–shade responses of *Solanum dulcamara*. *Oecologia* **57**, 316–321.
- Patiño, S., Tyree, M.T. & Herre, E.A. (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic *Ficus* species from Panama. *New Phytologist* **129**, 125–134.
- Paton, S. & Wright, S.J. (2003) *Terrestrial Environmental Science Program*. Balboa, Republic of Panama. <http://striweb.si.edu/esp/>.
- Pearcy, R.W. (1988) Photosynthetic utilization of lightflecks by understory plants. *Australian Journal of Plant Physiology* **15**, 223–238.
- Putz, F.E. (1983) Liana biomass and leaf-area of a tierra firme forest in the Rio-Negro Basin, Venezuela. *Biotropica* **15**, 185–189.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Science, USA* **94**, 13730–13734.
- Reich, P.B., Ellsworth, D.S., Walters, M.B. *et al.* (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**, 1955–1969.
- Restom, T.G. & Nepstad, D.C. (2001) Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant and Soil* **236**, 155–163.
- Roth, I. (1990) *Leaf Structure of a Venezuelan Cloud Forest in Relation to Microclimate*. Gebrüder Borntraeger, Stuttgart.
- Santiago, L.S. (2003) Leaf traits of canopy trees on a precipitation gradient in Panama: integrating plant physiological ecology and ecosystem science. PhD thesis, University of Florida, Gainesville, FL, USA.
- Santiago, L.S., Goldstein, G., Meinzer, F.C. *et al.* (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* **140**, 543–550.
- Sharp, R.E., Hsiao, T.C. & Silk, W.K. (1990) Growth of the maize primary root at low water potentials. 2. Role of growth and deposition of hexose and potassium in osmotic adjustment. *Plant Physiology* **93**, 1337–1346.
- Sims, D.A., Gebauer, R.L.E. & Pearcy, R.W. (1994) Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance. 2. Simulation of carbon balance and growth at different photon flux densities. *Plant, Cell & Environment* **17**, 889–900.
- Tibbetts, T.J. & Ewers, F.W. (2000) Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae). *American Journal of Botany* **87**, 1272–1278.
- Tomlinson, P.B. (1969) *Anatomy of the Monocotyledons. III. Commelinales – Zingiberales*. Clarendon Press, Oxford.
- Tyree, M.T. & Ewers, F.W. (1996) Hydraulic architecture of woody tropical plants. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 217–243. Chapman & Hall, New York.
- Westoby, M. (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**, 125–159.
- Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004) The worldwide leaf economics spectrum. *Nature* **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C. *et al.* (2005) Assessing the generality of global leaf trait relationships. *New Phytologist* **166**, 485–496.
- Wright, S.J., Muller-Landau, H.C., Condit, R. & Hubbell, S.P. (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* **84**, 3174–3185.
- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology* **86**, 848–860.

Received 22 February 2006; revised 15 August 2006; accepted 21 September 2006

Editor: Lawren Sack