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

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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 Panama 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

Introduction

At the global scale, maximum photosynthetic CO₂ 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 $K_{\text{max}}$ 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 $\approx 10\%$ of annual precipitation is received (Paton & Wright 2003). Mean annual temperature is 26 °C with little variation among months, and mean relative humidity is $\approx 95\%$ (Paton & Wright 2003). The vegetation is old-growth lowland tropical forest located on a plateau 140 m above sea level and $\approx 5$ 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 $\geq 1$ 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 $\geq 1$ 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$_2$ 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$^{-1}$ CO$_2$ (slightly higher than ambient CO$_2$ concentration), and 1500 µmol m$^{-2}$ s$^{-1}$ photosynthetic photon flux density (PFD) provided by a red blue light source (6400-02B #SI-710, Li-Cor). Leaves of understorey species were induced in a stepwise fashion at PFD levels of 500, 700 and 1000 µmol m$^{-2}$ s$^{-1}$ before maximum photosynthesis was measured at 1500 µmol m$^{-2}$ s$^{-1}$. 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$_2$ concentration in the cuvette. For trees and lianas, terminal leaves were accessed using the canopy crane. For understory 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...
indirectly coupled plasma emission spectroscopy and data analysis.

### Data Analysis

Data were averaged for each species, and the average 6 values for each species were analyzed for differences among growth forms. Data were tested for normality and homogeneity of variance and, when necessary, log-transformed before analysis. Comparisons of leaf functional traits among growth forms were made using 2-way ANOVA followed by Bonferroni’s test. All statistical analyses were performed using R software (R Core Team, 2016).

## Table 1: Leaf life span in lowland wet forest

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Growth Form</th>
<th>Light</th>
<th>SLA (m²/g)</th>
<th>N (mg/g)</th>
<th>K (mg/g)</th>
<th>P (mg/g)</th>
<th>LL (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arecaceae</td>
<td>Malpighia lucida</td>
<td>Tree</td>
<td>0.69</td>
<td>89.4</td>
<td>12.0</td>
<td>17.5</td>
<td>0.76</td>
<td>258</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Mucuna pruriens</td>
<td>Tree</td>
<td>1.30</td>
<td>112.6</td>
<td>12.5</td>
<td>25.5</td>
<td>1.09</td>
<td>341</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Helicteres australis</td>
<td>Tree</td>
<td>0.89</td>
<td>91.3</td>
<td>13.2</td>
<td>24.6</td>
<td>0.96</td>
<td>318</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td>Averrhoa bilimbi</td>
<td>Tree</td>
<td>0.65</td>
<td>96.4</td>
<td>13.4</td>
<td>24.1</td>
<td>1.01</td>
<td>328</td>
</tr>
</tbody>
</table>

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*Note: This text is a partial excerpt from a longer document and is meant to be read as a snippet of a larger study on canopy leaf dynamics.*
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 (smatr 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 (y-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 CO2 assimilation rate per area ($A_{area}$, $\mu$mol m$^{-2}$ s$^{-1}$), 5.8-fold variation in leaf N per area ($N_{area}$, mg cm$^{-2}$), 6.6-fold variation in leaf P per area ($P_{area}$, mg cm$^{-2}$), 6.2-fold variation in leaf K per area ($K_{area}$, mg cm$^{-2}$), and 10-fold variation in stomatal conductance ($g_s$, mol m$^{-2}$ s$^{-1}$).

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

The relationship between $A_{area}$ 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 understory species have low $A_{area}$ and high SLA. The relationship between $A_{area}$ 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 understory 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 $A_{area}$ and $N_{area}$ was significant and positive across all species ($r^2 = 0.42, P < 0.0001, n = 44$). However, $A_{area}$ and $N_{area}$ were not significantly related within any growth form. $A_{area}$ showed weak positive relationships with $P_{area}$ ($r^2 = 0.29, P < 0.0005, n = 44$) and $K_{area}$ ($r^2 = 0.10, P < 0.05, n = 44$), but these relationships were insignificant within growth forms. The relationship between $N_{area}$ 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 understory 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 $A_{area}$–$g_s$ relationship, slopes were indistinguishable among growth forms, but the intercept was significantly greater for trees than for lianas and understory plants (Table 2). For the $A_{area}$–SLA, $A_{area}$–$N_{area}$ and $A_{area}$–$P_{area}$ 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
Fig. 2. Relationship between photosynthetic rate per mass (A$_{mass}$) and (a) specific leaf area (SLA); (b) leaf nitrogen per mass (N$_{mass}$); (c) leaf phosphorus per mass (P$_{mass}$); and (d) leaf potassium per mass (K$_{mass}$) 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).

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

<table>
<thead>
<tr>
<th></th>
<th>Slope</th>
<th>Intercept</th>
<th>Heterogeneity</th>
<th>Shift in Intercept</th>
<th>Common slope</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>y</td>
<td>x</td>
<td>Trees</td>
<td>Lianas</td>
<td>Understorey</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area-based relationships</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{area}$ g$_c$</td>
<td>16·9</td>
<td>20·7</td>
<td>25·3</td>
<td>P = 0·08</td>
<td></td>
</tr>
<tr>
<td>$A_{area}$ SLA</td>
<td>0·05</td>
<td>0·08</td>
<td>0·04</td>
<td>P = 0·26</td>
<td></td>
</tr>
<tr>
<td>$A_{area}$ N$_{area}$</td>
<td>−44·0</td>
<td>−28·8</td>
<td>7·8</td>
<td>P = 0·12</td>
<td></td>
</tr>
<tr>
<td>$A_{area}$ P$_{area}$</td>
<td>−799</td>
<td>339</td>
<td>622</td>
<td>P = 0·16</td>
<td></td>
</tr>
<tr>
<td>$A_{area}$ K$_{area}$</td>
<td>81·2$^a$</td>
<td>29·2$^b$</td>
<td>−36·8$^b$</td>
<td>P &lt; 0·05</td>
<td></td>
</tr>
<tr>
<td>N$_{area}$ SLA</td>
<td>−0·001$^a$</td>
<td>−0·003$^b$</td>
<td>−0·0005$^c$</td>
<td>P &lt; 0·001</td>
<td></td>
</tr>
<tr>
<td>Mass-based relationships</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{mass}$ SLA</td>
<td>1·4</td>
<td>1·3</td>
<td>0·9</td>
<td>P = 0·28</td>
<td></td>
</tr>
<tr>
<td>$A_{mass}$ N$_{mass}$</td>
<td>11·7$^a$</td>
<td>4·7$^b$</td>
<td>19·7$^b$</td>
<td>P &lt; 0·05</td>
<td></td>
</tr>
<tr>
<td>$A_{mass}$ P$_{mass}$</td>
<td>142·5$^a$</td>
<td>54·9$^b$</td>
<td>−103·4$^b$</td>
<td>P &lt; 0·05</td>
<td></td>
</tr>
<tr>
<td>$A_{mass}$ K$_{mass}$</td>
<td>16·1$^a$</td>
<td>3·6$^b$</td>
<td>−5·2$^b$</td>
<td>P &lt; 0·001</td>
<td></td>
</tr>
<tr>
<td>N$_{mass}$ SLA</td>
<td>0·1$^a$</td>
<td>0·3$^b$</td>
<td>−0·04$^b$</td>
<td>P &lt; 0·005</td>
<td></td>
</tr>
<tr>
<td>N$_{mass}$ LL</td>
<td>−0·2</td>
<td>−0·1</td>
<td>−0·1</td>
<td>P = 0·15</td>
<td></td>
</tr>
<tr>
<td>SLA LL</td>
<td>−0·1</td>
<td>−0·1</td>
<td>−0·1</td>
<td>P = 0·91</td>
<td></td>
</tr>
</tbody>
</table>

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 $A_{area}$–SLA and $A_{area}$–P$_{area}$ relationships, indicating that understorey plants occupy the region of the $A_{area}$–SLA relationship with the smallest $A_{area}$ and largest SLA (Fig. 1a; Table 2), and the region of the $A_{area}$–P$_{area}$ relationship with the smallest $A_{area}$ and smallest $P_{area}$ (Table 2). Understorey plants and lianas had significantly smaller slopes than trees in the relationship between $A_{area}$ and K$_{area}$ (Table 2). Slopes of the relationship between N$_{area}$ and SLA differed significantly for all pairwise comparisons (Table 2).

**MASS-BASED TRAIT RELATIONSHIPS**

Among the 44 species studied, we observed 12·5-fold variation in photosynthetic CO$_2$ assimilation rate per mass (A$_{mass}$, nmol g$^{-1}$ s$^{-1}$), 3·5-fold variation in leaf N per mass (N$_{mass}$, mg g$^{-1}$), 4·7-fold variation in leaf P per mass (P$_{mass}$, mg g$^{-1}$), 8·1-fold variation in leaf K per mass (K$_{mass}$, 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$_{mass}$ ($F_{2,41} = 8·13$, P < 0·005), both of which were greatest in understorey plants.

There was a relatively weak positive relationship between A$_{mass}$ 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$_{mass}$ 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$_{mass}$–SLA relationship for trees and lianas was similar to the global relationship, but understorey species fell well below the global relationship (Fig. 2a). A$_{mass}$ increased significantly with N$_{mass}$ 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$_{mass}$
also increased significantly with \( P_{\text{max}} \) 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 \( A_{\text{mass}}-\text{SLA} \) 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 understory plants (Table 2). This pattern is similar to the \( A_{\text{area}}-\text{SLA} \) relationship. There was also a significant shift along the common slope of the \( A_{\text{mass}}-\text{SLA} \) relationship, indicating that understory 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 understory plants (Table 2). Trees and lianas showed significantly steeper slopes than understory plants in the \( A_{\text{mass}}-P_{\text{mass}} \) relationship, and trees showed steeper slopes than understory plants and lianas in the \( A_{\text{mass}}-K_{\text{mass}} \) relationship. For the \( N_{\text{mass}}-\text{SLA} \) 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 CO\(_2\) assimilation. Within growth forms, \( A_{\text{mass}}-\text{LL} \) and SLA–LL relationships were significant in trees \((A_{\text{mass}}-\text{LL}, \; r^2 = 0.64, \; P < 0.0005, \; n = 16); \text{SLA–LL}, \; r^2 = 0.50, \; P < 0.005, \; n = 16)\) but not in lianas \((A_{\text{mass}}-\text{LL}, \; r^2 = 0.12, \; P = 0.40, \; n = 9); \text{SLA–LL}, \; r^2 = 0.05, \; P = 0.61, \; n = 9)\). For the \( A_{\text{mass}}-\text{LL} \) 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 longer than tree leaves for a given SLA (Table 2). In both the \( A_{\text{mass}}-\text{LL} \) 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 understory 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, understory plants, which were measured in the deeply shaded understory, 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 $A_{\text{max}}$ 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, understory plants exhibited low $A_{\text{area}}$, consistent with low understory light availability, but similar $A_{\text{max}}$ (Figs 1 and 2). Understorey plants did not show greater $A_{\text{max}}$ with greater SLA at a given $N_{\text{area}}$, 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 $A_{\text{max}}$ in understorey plants also suggests that understory leaf-allocation patterns are related to growth. Within the narrow $A_{\text{area}}$ 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 understory plants was the high values for $K_{\text{area}}$ in the understory. Shade leaves tend to have higher $K_{\text{area}}$ 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 $K_{\text{max}}$, 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 $K_{\text{max}}$ 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 $K_{\text{max}}$. Rather, it is more likely that high $K_{\text{max}}$ in understory 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 understory 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 understorey species, and that further studies of K suggest that K is an important resource for tropical whole-leaf or whole-plant scale, and K involved in respiration (Marschner 1986). However, for purposes

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 understory 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.

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