*Ecological Applications*, 21(1), 2011, pp. 85–98


# Taxonomy and remote sensing of leaf mass per area (LMA) in humid tropical forests

Gregory P. Asner,[1,5] Roberta E. Martin,[1] Raul Tupayachi,[1] Ruth Emerson,[1] Paola Martinez,[1] Felipe Sinca,[1] George V. N. Powell,[2] S. Joseph Wright,[3] and Ariel E. Lugo[4]

[1]*Department of Global Ecology, Carnegie Institution for Science, 260 Panama Street, Stanford, California 94305 USA*
[2]*World Wildlife Fund, 1250 24th St. NW, Washington, D.C. 20037 USA*
[3]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama*
[4]*International Institute of Tropical Forestry, Jardin Botanico Sur, 1201 Calle Ceiba, San Juan, Puerto Rico 00926-1119*

*Abstract*. Leaf mass per area (LMA) is a trait of central importance to plant physiology and ecosystem function, but LMA patterns in the upper canopies of humid tropical forests have proved elusive due to tall species and high diversity. We collected top-of-canopy leaf samples from 2873 individuals in 57 sites spread across the Neotropics, Australasia, and Caribbean and Pacific Islands to quantify environmental and taxonomic drivers of LMA variation, and to advance remote-sensing measures of LMA. We uncovered strong taxonomic organization of LMA, with species accounting for 70% of the global variance and up to 62% of the variation within a forest stand. Climate, growth habit, and site conditions are secondary contributors (1–23%) to the observed LMA patterns. Intraspecific variation in LMA averages 16%, which is a fraction of the variation observed between species. We then used spectroscopic remote sensing (400–2500 nm) to estimate LMA with an absolute uncertainty of 14–15 g/m$^2$ ($r^2 = 0.85$), or ~10% of the global mean. With radiative transfer modeling, we demonstrated the scalability of spectroscopic remote sensing of LMA to the canopy level. Our study indicates that remotely sensed patterns of LMA will be driven by taxonomic variation against a backdrop of environmental controls expressed at site and regional levels.

*Key words: canopy chemistry; imaging spectroscopy; leaf mass per area, LMA; leaf traits; phylogenetics; rain forest; remote sensing; specific leaf area, SLA; taxonomy.*

## Introduction

Leaf mass per area (LMA) is the ratio of the dry mass of a leaf to its surface area (grams dry mass per square meter); its well-known reciprocal is specific leaf area ($SLA = LMA^{-1}$). As simple as it appears, LMA is a trait indicative of plant physiological processes ranging from light capture to growth rates as well as the life strategies of plants (Niinemets et al. 1999, Westoby et al. 2002). LMA is also linked to investments in chemical compounds distributed throughout the leaf mesophyll, which strongly affects leaf thickness and mass. LMA is broadly correlated with leaf nitrogen concentrations across biomes (Reich et al. 1997, Wright et al. 2004). These and other factors have made LMA a measurement of central interest in plant biology and ecology.

A number of potential environmental controls over LMA have been investigated, and studies agree that photosynthetic radiation is a key factor (Niinemets and Kull 1998, Cunningham et al. 1999). To maximize light capture per unit nitrogen invested, shade leaves usually have much lower LMA than do sun leaves (Evans 1989). A new comprehensive review by Poorter et al. (2009) also shows that variation in temperature and water availability cause substantial variation in LMA among terrestrial plants. These and other environmental factors create LMA variation at scales ranging from the vertical profile within a single tree (the "light gradient") to regional variation associated with differing climate regimes.

Compared to most biomes, the canopy chemistry and physiology of humid tropical forests are poorly understood (Townsend et al. 2008). Tall, inaccessible trees of hundreds to thousands of species challenge our ability to quantify and understand the properties of canopies in these regions. LMA has been measured in a few studies of tropical forests, but usually with small sample sizes relative to the high species diversity within and among these ecosystems (Poorter et al. 1995, Paoli 2006, Sanchez-Azofeifa et al. 2009). With relatively small sample sizes, neither the environmental nor taxonomic (or phylogenetic) controls over LMA can be assessed. For example, in a recent study by Asner et al. (2009), 162 canopy species from the Australian Wet Tropics were collected and measured, but even this substantial data set was too small, lacked species-level replication, and was spread across too wide an array of conditions to quantify and compare environmental and taxonomic patterns. Although the Asner et al. (2009) study controlled for canopy position (and thus sunlight

Manuscript received 29 October 2009; revised 18 March 2010; accepted 24 March 2010. Corresponding Editor: V. C. Radeloff.

[5] E-mail: gpa@stanford.edu

conditions) to yield a comparative data set across taxa, combining data from that study with previous literature does not produce a data set suitable for inter-site and taxonomic study. Even more problematic, when leaves are collected from a range of light-gradient positions in the forest, as has been done in and among past studies, most environmental and taxonomic sources of LMA variation are trumped by lighting conditions (Poorter et al. 2009). As a result, there are not enough data available to develop a broad understanding of environmental or taxonomic controls over LMA in tropical forests.

The labor required to study humid tropical forest canopies not only limits our measurements and knowledge, but also makes repeated analysis or monitoring of forests intractable from the ground. Remote sensing thus continues to grow in importance as a means to measure canopies from above. Tropical forest remote sensing has mainly focused on forest structure and deforestation, but new capabilities in remote sensing of leaf traits are evolving (see reviews by Kokaly et al. 2009, Ustin et al. 2009). In a study by Asner and Martin (2008), spectroscopic remote-sensing signatures of SLA were examined in the same 162 species from Australia presented by Asner et al. (2009). This worked yielded insight into the use of imaging spectroscopy for SLA mapping in tropical forests with varying structural properties. However, that study did not incorporate enough data to test the generality of the approach or to determine whether remote sensing would be sensitive to taxonomic composition in the canopy.

The challenge in remote sensing of canopy properties rests not only in the technologies and algorithms for detection, but also in the ecological patterns and sources of variation that may be present within and across forests. We do not know what to expect in terms of local and regional diversity of leaf traits, so we do not know how sensitive the remote-sensing methods will need to be in order to detect variation in space and time. LMA is an important case in point: the measurement remains relatively rare in humid tropical forests, and thus we do not know the variance in LMA at stand or regional levels. As a result, we do not know the relative importance of environmental, taxonomic, or random variation determining patterns in remotely sensed LMA, which would be highly indicative of other chemical and physiological processes.

Here we report on a study to determine sources of variation in LMA among a very large number of canopy species found in humid tropical forests. Although LMA and SLA are simple reciprocals of one another, we adopt LMA in this paper to facilitate easy comparison to the recent global synthesis provided by Poorter et al. (2009). We then refine and test a method for remote sensing of LMA using high-fidelity spectroscopy, an improved form of hyperspectral remote sensing, that has become possible from aircraft in recent years (Asner and Martin 2009). Our specific questions are: (1) What is the relative importance of environmental control and taxonomic organization in LMA among humid tropical forest canopies? (2) How well can LMA be remotely sensed at leaf and canopy levels? (3) If remote sensing of LMA is universally possible, will the patterns be driven by environmental conditions, taxonomic composition, or random variability?

## Materials and Methods

### *Leaf samples*

We analyzed top-of-canopy leaf samples from 2873 individuals in 57 sites spread across the Neotropics, Australasia, and Caribbean and Pacific Islands (Appendix A). Of these 2873 individuals, we had 2279 identified to the genus level and 2013 definite taxonomic identifications to the species level. A small portion of the Pacific Island collection includes species originating in the Paleotropics ($n = 38$). The data set is composed of several common growth habits found in tropical forest canopies, including tree ($n = 2400$), liana (316), palm (54), hemi-epiphyte (55), and vine (45) (Appendix B). We are only interested in humid tropical forest species, so we controlled for minimum mean annual precipitation (MAP). The MAP range across sites is 1165–7340 mm/yr based on long-term climate records. Concomitant variation in total annual incident solar radiation ($R_s$) is 4.6–6.0 $kWh \cdot m^{-2} \cdot yr^{-1}$, as estimated from the NASA Surface meteorology and Solar Energy (SSE) Release 6.0 data set (January 2008) of regional annual averages, July 1983–June 2005 (*available online*).[6] We did not control for mean annual temperature (MAT), which ranges from 13.2° to 27.2°C. Combined, our sites include subtropical and tropical moist, wet, and rain forests in the Holdridge Life Zone classification system (Holdridge 1967; Appendix A). In addition, we only include specimens collected within the global humid tropical forest biome as delineated by Hansen et al. (2008). Detailed information and maps for the species and sites can be viewed through Carnegie Institution Spectranomics (*available online*).[7]

### *Field methods*

*Leaf collections.*—At each site, species were carefully selected to control for full-sunlight canopies. This process requires that two or more trained workers agree that at least 50% of a selected canopy maintains an unobstructed exposure to the sky (see Plate 1). Individuals meeting this criterion were then marked, and a voucher specimen was collected. Vouchers were matched by local expert taxonomists to type specimens kept at the CSIRO Tropical Research Centre in Atherton, Australia, the National Agrarian University La Molina Herbarium in Peru, and the Missouri Botanical Garden. We also matched genus names to

[6] ⟨http://eosweb.larc.nasa.gov/sse/⟩
[7] ⟨http://spectranomics.ciw.edu⟩

information provided by Kew Botanic Gardens. Family-level taxonomy followed the Angiosperm Phylogeny Group III (*available online*).[8] All project reference vouchers are kept at the CSIRO, La Molina, or Carnegie Institution facilities, and all specimens can be viewed through Carnegie Spectranomics (see footnote 7).

Leaf collections were conducted using a combination of tree climbing, crane, shooting, and pole-clipping techniques. Only fully sunlit branches of mature leaves were taken and processed within 20 min in the field for leaf spectroscopy. The branches were sealed in large polyethylene bags to maintain moisture, stored on ice in coolers, and transported to a local site for LMA processing within 4 h.

*Leaf spectroscopy*.—Hemispherical reflectance and transmittance from 400 to 2500 nm was measured on 12 randomly selected leaf surfaces immediately after acquiring each branch at the field site. The spectral measurements were taken at or close to the midpoint between the main vein and the leaf edge, and approximately halfway from petiole to leaf tip. Care was taken to avoid large primary or secondary veins, while allowing for smaller veins to be incorporated into the measurement.

The spectra were collected with a field spectrometer using 1.4-nm sampling (FS-3 with custom detectors and a custom-built exit slit configuration to maximize signal-to-noise performance; Analytical Spectra Devices, Boulder, Colorado, USA), an integrating sphere designed for high-resolution spectroscopic assays, and a custom illumination collimator. Measurements were collected with 136-ms (millisecond) integration time per spectrum. The spectra were then calibrated for dark current and stray light, and referenced to a calibration block (Spectralon, Labsphere, Durham, New Hampshire, USA) within the integrating sphere. The high-fidelity measurement capability of our system resulted in calibrated spectra that did not require smoothing or other filters commonly used in leaf optical studies.

### *LMA measurements*

A subset of leaves was selected from the branches for scanning and weighing. Leaf area was determined on a 600 dots-per-inch (dpi) flatbed optical scanner using enough leaves to fill two scan areas each of $21 \times 25$ cm (up to about 75 leaves per sample depending upon leaf size). Petioles were removed from each leaf before scanning, and mid-veins were cut out of the leaves when they reached or exceeded 2 mm in diameter. Leaves exceeding the surface area of the scanner were cut into sections (without petiole or mid-vein if $>2$ mm diameter) until two full scan areas were completed. The scanned leaves were then dried at 70°C for a minimum of 72 h before dry mass was measured. LMA was then calculated as grams of dry mass per square meter.

### *Canopy modeling*

Using the leaf spectra collected in the field, we simulated canopy reflectance signatures for each specimen based on growth habit. The canopy model has been presented by Asner (2000) and updated by Asner and Martin (2008). It simulates top-of-canopy spectral reflectance based on the following scale-dependent factors:

$$R = f(r_{\text{tiss}}, t_{\text{tiss}}, \text{LAI}, \text{LAD}, \text{SSAI}, \text{SAD}, \text{GO-params}, \text{Geometry}) \quad (1)$$

where $r_{\text{tiss}}$ and $t_{\text{tiss}}$ are the hemispherical reflectance and transmittance properties of plant tissues, LAI is the canopy leaf area index, LAD is the canopy leaf angle distribution, SSAI is the stem silhouette area index, and SAD is the stem angle distribution. The tissues can include both live green foliage and senescent foliage or wood surfaces. GO-params are three crown geometric-optical properties that include the areal density of tree stems, the ratio of crown vertical to horizontal radius (BR), and the ratio of tree height (ground to crown center) and crown depth (HB). Geometry includes four parameters of solar zenith and solar azimuth angles (SZA, SAZ), and sensor-viewing zenith and azimuth angles (VZA, VAZ).

For our purposes, we are implicitly modeling high-spatial-resolution, high-fidelity airborne data, as would be acquired from sensors such as the Carnegie Airborne Observatory (Asner et al. 2007) and AVIRIS (Green et al. 1998; with referenced 2005 sensor revisions *available online*).[9] This is important here because, in the context of mapping humid tropical forests, the spectra would be collected at a spatial resolution finer than that of most tree crowns and vegetation clusters, thus simplifying the modeling problem, especially in terms of the geometric-optical parameters. Specifically, we do not address tree density, intra-crown gaps, and shadows in this study. Although the modeling covers the 400–2500 nm spectra range, we did not simulate portions of the spectrum between 1350–1450 nm and 1850–1975 nm because they cannot be measured from aircraft due to atmospheric water absorption at these wavelengths.

For each specimen, a randomly selected combination of the field-measured leaf spectra and canopy structural properties based on growth habit (Table 1) was used to generate a canopy reflectance signature. This was repeated 250 times per specimen, and the mean reflectance signatures were recorded for subsequent analyses. The canopy structural properties permitted to vary included LAI, LAD, SSAI, and SAD. The viewing and solar zenith angles were also varied within the range

[8] ⟨http://www.mobot.org/mobot/research/apweb/welcome.html⟩

[9] ⟨http://aviris.jpl.nasa.gov⟩

TABLE 1. Parameter ranges used for canopy reflectance simulations of 2875 tropical forest canopy specimens.

| Growth habit | LAI ($m^2/m^2$) | SSAI ($m^2/m^2$) | LAD (°) | SAD (°) |
|---|---|---|---|---|
| Tree | 3.0–7.0 | 0.2–0.5 | 20–60 | 70–90 |
| Hemi-epiphyte | 1.0–3.0 | 0.1–0.3 | 20–60 | 70–90 |
| Liana | 1.0–3.0 | 0.2–0.4 | 0–30 | 70–90 |
| Palm | 3.0–5.0 | 0.2–0.4 | 20–70 | 70–90 |
| Vine | 0.5–2.0 | 0.01–0.1 | 0–30 | 70–90 |

*Notes:* LAI is leaf area index. Typical LAI range information is derived from the global synthesis of Asner et al. (2003). SSAI is the stem silhouette area index; data are from Asner (1998). LAD and SAD are, respectively, the leaf and stem angle distributions in degrees; the values shown indicate the mean tendency of foliar angle based on the two-parameter beta distribution (Verhoef and Bach 2003).

typical for airborne flight operations (VZA = 0–30°, SZA = 0–30°). Given that airborne studies will not generally incorporate such large SZA variation in a single mapping flight, our approach is conservative. A more detailed explanation of the technique is reported in a study of canopy structural variation and its quantitative impact on the chemical analysis of tropical forests by Asner and Martin (2008).

### *Statistical and taxonomic analysis*

Taxonomic patterns in LMA were examined with respect to family, genus, species, and growth habit classification. Environmental factors examined were mean annual temperature (MAT), mean annual precipitation (MAP), total annual solar radiation ($R_s$), and collection site location. For all models, we used the maximum number of samples for which we had accurate identifications. For the environmental factors of MAT, MAP, radiation, and site, this amounted to the complete 2873 sample data set. Sample numbers were further constrained by positive taxonomic identifications, permitting the use of 2279 samples for family- and genus-level analyses and 2013 samples for species-level analyses.

We employed single-variable linear models to analyze the variation in LMA explained by individual predictors and multiple linear regression models to analyze the variation explained by logical combinations of predictors, including the interaction among predictors. For these analyses, we only considered one taxonomic level of aggregation at a time (e.g., family, genus, or species). AIC (Akaike's information criterion) values were used to determine the best predictive models through stepwise regression. We performed a site-level regression using the continuous environmental variables of MAT, MAP, and $R_s$ as predictors of site median LMA values. We used ANOVA with Tukey's post hoc tests to examine the multiple pairwise comparison of growth habit classification.

To more thoroughly investigate the relationship between taxonomic grouping and LMA, we modeled the nested nature of the taxonomic levels (e.g., a given genus is only found in a single family). We modeled family, genus nested within family, and species nested within genus all as random effects in a linear mixed-effects model using restricted maximum likelihood estimation (Faraway 2005, Bates and Maechler 2009). These analyses were performed using R, version 2.9.2 (R Development Core Team 2009) and Sigmaplot, version 11.0 (2008, Systat Software, SPSS, Chicago, Illinois, USA).

We used partial least-squares (PLS) regression analysis (Haaland and Thomas 1988) to determine whether LMA can be remotely sensed at the leaf and/or canopy level using high-fidelity spectroscopy. Leaf spectral measurements and canopy simulations used 210 spectral bands with 10-nm band width (FWHM; full width at half maximum) spanning the 400–2500 nm wavelength range, again with the 1350–1450 nm and 1850–1975 nm atmospheric water vapor regions removed. This configuration simulated measurements acquired by airborne instruments such as the AVIRIS sensor. The full-range leaf spectral data were convolved to 10-nm resolution using 2008 AVIRIS spectral response functions provided by the Jet Propulsion Laboratory, Pasadena, California, USA.

Beginning at the leaf level, we used PLS analysis to determine the contribution of LMA to the 220-band leaf reflectance and transmittance spectra of all samples ($n = 2873$). The PLS approach is beneficial because it utilizes the continuous spectrum as a single measurement rather than as a band-by-band analysis. To avoid overfitting, the number of factors used in the PLS analysis was determined by minimizing the prediction residual error sum of squares (PRESS) statistic (Chen et al. 2004). The PRESS statistic was calculated through a cross-validation prediction for each model. This cross-validation procedure iteratively generates regression models while reserving one sample from the input data set until the root mean-square error (RMSE) for the PRESS statistic is minimized. The PLS models were then used to estimate LMA from the original leaf spectral data.

To quantify our ability to predict LMA of unknown species in a forest, we ran PLS analyses on the simulated canopy spectra using a random selection of about half of the total specimen data set. The resulting PLS model was then used to estimate LMA values of the other half of the samples. This entire procedure was then repeated on a nonrandom basis, with the PLS model built on the first half of the families (from Acanthaceae to Lauraceae; Appendix B), and then predicting the LMA of the second half (Lecythidaceae to Winteraceae). Finally, we used PLS analysis to predict the LMA of samples at each site using models built with data from remaining sites. This allowed us to explore the potential to remotely quantify LMA at any given site, given a model developed from other sites containing mostly different species. PLS analyses were carried out using the

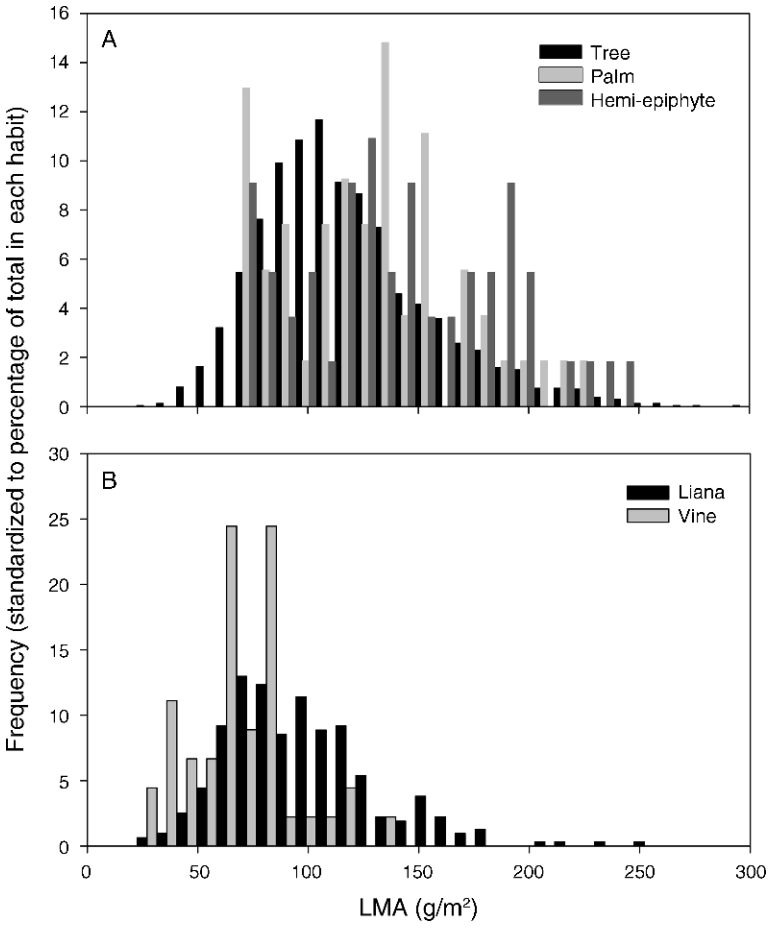


FIG. 1. Frequency histograms of leaf mass per area (LMA; the ratio of the dry mass of a leaf to its surface area) for all samples, calculated separately for each growth habit.

SAS JMP 7.0 statistical software package (2008, SAS Institute, Cary, North Carolina, USA).

## RESULTS

### *Basic statistics*

The total LMA range is 22.2–307.6 g/m$^2$. Median LMA values by growth habit are 61.7 g/m$^2$ for vines, 88.9 for lianas, 107.2 for trees, 121.2 for palms, and 134.3 for hemi-epiphytes (Fig. 1). The LMA range is greatest for trees (25.6–307.6 g/m$^2$) and smallest for vines (22.2–134.6 g/m$^2$). A one-way ANOVA indicates a significant difference ($P < 0.05$) in mean LMA by growth habit. A variety of post hoc tests (Tukey's, Bonferroni's $t$ test, Holm-Sidak method, and Fisher's LSD method) indicate that most pairwise comparisons are significant, with only two exceptions; palms are indistinguishable from both trees and hemi-epiphytes. Treating growth habit as a factor variable, a single-variable linear regression analysis shows that 6% of the variation in the LMA data set is explained by habit alone ($P < 0.001$; Table 2). Here we report adjusted-$r^2$, rather than multiple-$r^2$ values, to reduce the impact of overfitting.

### *Intraspecific variation*

Our data set includes 249 species for which there are two or more replicates spread among 44 of 57 sites, permitting their use in an analysis comparing inter- to intraspecific variation. The coefficients of variation (CV) within these species vary from less than 0.01 to a maximum of 0.55 (Fig. 2). The mean intraspecific CV is 0.16, and most species (80%) have CV values less than 0.25. Only a small portion of species (3%) have CV values exceeding 0.50. Families with lowest and highest median intraspecific variation in LMA are Cyrllicaeae (2%) and Convolvulaceae (41%), respectively. A one-way analysis of variance of LMA by species produces a highly significant $F$ statistic ($P < 2.2 \times 10^{-16}$), demonstrating that the interspecific variation in LMA in fully sunlit leaves is much greater than the intraspecific variation in LMA in fully sunlit leaves.

TABLE 2. General linear regression modeling results for environmental and phylogenetic factors determining leaf mean area (LMA; the ratio of the dry mass of a leaf to its surface area) in humid tropical forests.

| Model and factor types | LMA prediction (adjusted $r^2$) | $n$ |
|---|---|---|
| Phylogenetic factors | | |
| Family | 0.27 | 2279 |
| Genus | 0.41 | 2279 |
| Species | 0.70 | 2013 |
| Habit | 0.06 | 2279 |
| Environmental factors | | |
| MAT | 0.04 | 2873 |
| MAP | 0.01 | 2873 |
| Radiation | 0.04 | 2873 |
| Site | 0.19 | 2873 |
| Site + Habit | 0.23 | 2870 |
| MAT + Habit | 0.08 | 2870 |
| Family + | | |
| MAT | 0.29 | 2279 |
| MAP | 0.27 | 2279 |
| Site | 0.39 | 2279 |
| Radiation | 0.29 | 2279 |
| MAT + MAT × Family | 0.31 | 2279 |
| Genus + | | |
| MAT | 0.44 | 2279 |
| MAP | 0.42 | 2279 |
| Site | 0.53 | 2279 |
| Radiation | 0.43 | 2279 |
| MAT + MAT × Genus | 0.46 | 2279 |
| Species + | | |
| MAT | 0.70 | 2013 |
| MAP | 0.70 | 2013 |
| Site | 0.73 | 2013 |
| Radiation | 0.70 | 2013 |
| MAT + MAT × Species | 0.76 | 2013 |

*Notes:* Multiplication symbols (×) indicate an interaction term between two factors. The plus symbols (+) in the first column indicate that the regressions utilized two factors together. Sample size $n$ is the number of tropical forest canopy specimens.

### *Site and climate effects*

Among all samples, there is no significant effect of precipitation on LMA patterns (Fig. 3). This is not surprising, given that we controlled for minimum MAP for moist, wet, and rain forest sites. Mean MAT and $R_s$ each explain 4% of the variance in LMA among all samples, and although the signal is small, both effects are highly significant ($P < 0.001$; Fig. 3). Using the median LMA value for each site, MAP and $R_s$ remain minor determinants of LMA (and in the case of MAP, insignificant); however, MAT increases in importance to account for 29% of LMA variation among sites ($P < 0.001$).

We did not attempt to analyze the LMA data using soils as an independent variable because the quality and type of soil information varies greatly from region to region. Instead, we tested the effect of site, which incorporates factors ranging from climate to substrate age and soil chemistry. Site explains 19% of the variance in LMA ($P < 0.001$), and site combined with habit accounts for 23% of the measured variation ($P < 0.001$; Table 2). Given that MAT + Habit account for only 8% of LMA variation, by difference, we infer that soils may explain up to 15% of the variability in LMA among all samples.

### *Taxonomic controls*

In comparison to environmental properties, we observe strong taxonomic organization over LMA within and across sites. Using linear regression models with single taxonomic levels as predictor variables, family, genus, and species account for 27%, 41%, and 70% of the overall LMA variation, respectively (Table 2). Adding site to the regression explains a maximum of 39% and 53% of the overall variation in LMA at the family and genus levels, respectively. At the species level, adding site as a covariate increases the strength of the prediction from 70% to 73%, whereas a combination of species, MAT, and their interaction term yields the maximum predictive power of 76% (Table 2). Explicit accounting of taxonomic nesting with the linear mixed-effects model shows that 32% of LMA variation is explained at the family level, 14% is explained by genera-within-families, and 25% is explained by species-within-genera. This sums to 71%, which is on par with the maximum levels of explained variance from Table 2. The remaining 29% is undetermined.

We also examined taxonomic grouping of LMA at the site level using linear regression models (Table 3). We selected three sites that contributed a relatively large number of species to the study (Appendix A), including Barro Colorado Island (BCI, Panama), Monteverde (Costa Rica), and Tambopata Forest Reserve (Peru). At family and genus levels, the strongest phylogenetic controls over LMA are observed at BCI (32%) and Monteverde (40%), respectively. Sufficient replication of individuals at Tambopata allowed for an analysis among species, which indicated that 62% of the LMA variation is driven at this taxonomic level.

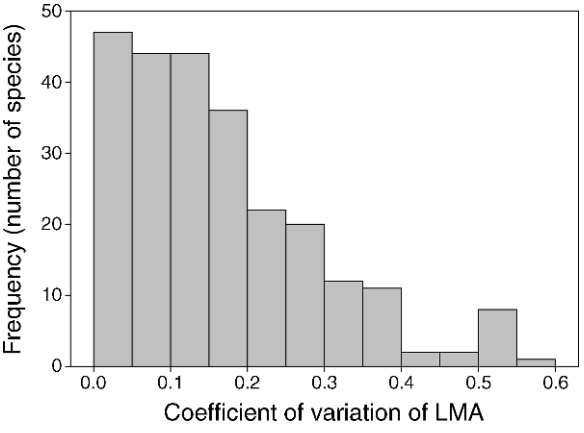


FIG. 2. Frequency histogram of the coefficients of variation (CV) for within-species leaf mass per area (LMA; $n = 249$ species).

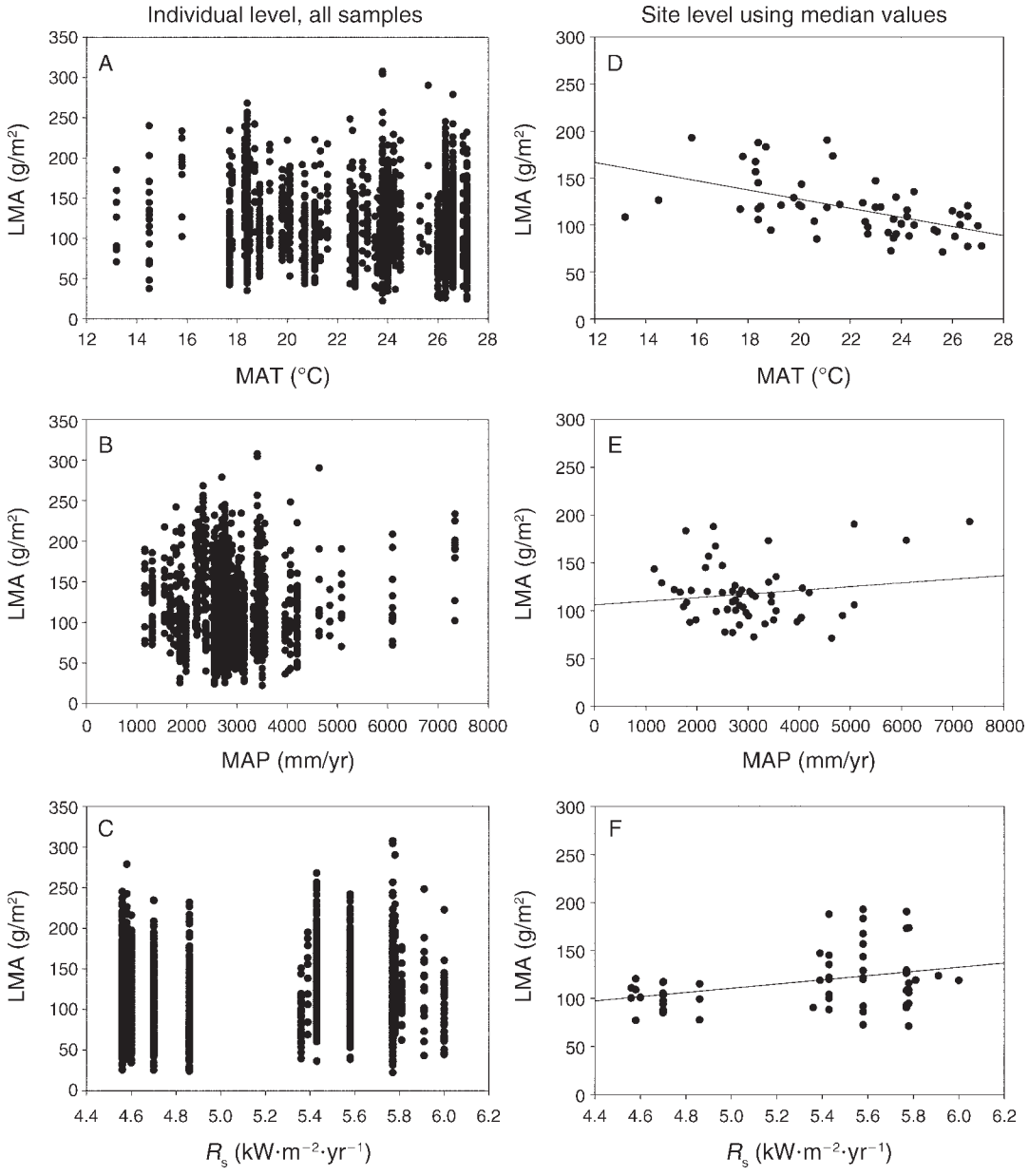


FIG. 3. (A–C) Effects of mean annual temperature (MAT), mean annual precipitation (MAP), and total solar radiation ($R_s$) on leaf mass per area (LMA) at the individual level. (D–F) Effects of MAT, MAP, and $R_s$ on median values of LMA at the site level.

*Remote sensing*

The reflectance regions of greatest variance (calculated as CVs), and thus potentially the most information related to variation in LMA, are the shortwave-infrared (SWIR) between 1900 and 2500 nm (22–32%), the shortwave-infrared from 1300 to 1700 nm (up to 21%), and the visible region from 400 to 800 nm (up to 19%) (Fig. 4). The near-infrared (800–1300 nm) shows relatively low variation (8%) among samples. Leaf transmittance variation follows a similar pattern to that of reflectance, but shows even higher CV values in the SWIR and visible ranges (reaching 55–60%).

PLS regression indicates strong statistical relationships between the spectral signatures of the specimens and LMA (Fig. 5). Leaf reflectance and transmittance spectra each account for 85% of the variation in LMA, with a root mean-square error (RMSE) of ~15 g/m$^2$ or ~10% of the global mean LMA value for the data set. The few outliers in Fig. 5 showed no taxonomic pattern and thus may be related to random noise or measurement error, neither of which was assessed. Standardized PLS spectral weightings and prediction equation vectors are used to understand which regions of the spectrum are most important to the LMA analysis (Fig. 6). With

TABLE 3. Phylogenetic controls over LMA at three sites; *n* is the number of samples per site.

| Site | *n* | Taxonomic level | LMA (adjusted $r^2$) |
|---|---|---|---|
| Barro Colorado Island, Panama | 146 | family | 0.32 |
| | | genus | 0.32 |
| Monteverde, Costa Rica | 400 | family | 0.29 |
| | | genus | 0.40 |
| Tambopata, Peru | 436 | family | 0.24 |
| | | genus | 0.36 |
| | | species | 0.62 |

standardized spectral weightings, departures from the zero line indicate regions of the spectrum most important to the PLS regression (Fig. 6A). The near- and shortwave-infrared contribute the most to reflectance-based estimates of LMA, with relatively little contribution from the visible portion of the spectrum. Transmittance-based PLS analysis shows a much different result, with a steady increase in the importance (more negative spectral weighting) as wavelength increases. Prediction vectors (Fig. 6B) highlight the important spectral features relative to the PLS spectral weightings from Fig. 6A. It is clear that features in the near- and

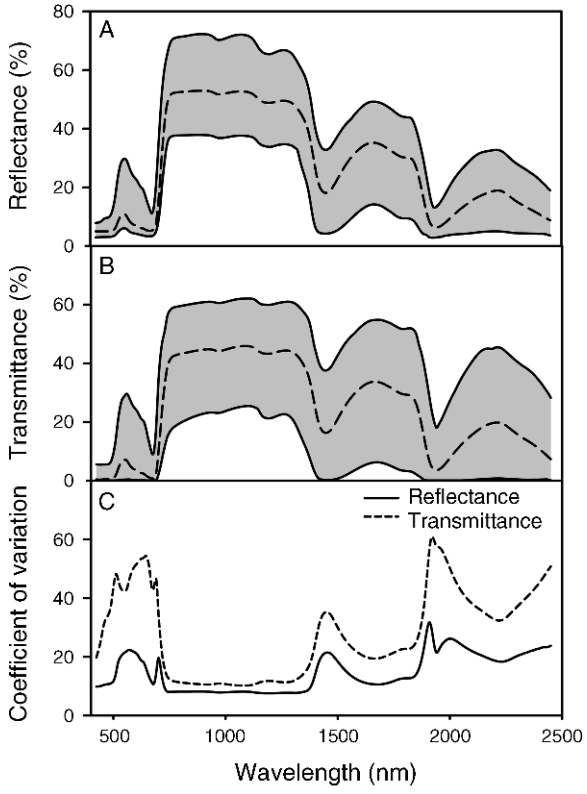


FIG. 4. Minimum, mean, and maximum leaf (A) reflectance and (B) transmittance for 2871 samples collected in tropical rain forests. (C) Spectral coefficients of variation for leaf reflectance and transmittance.

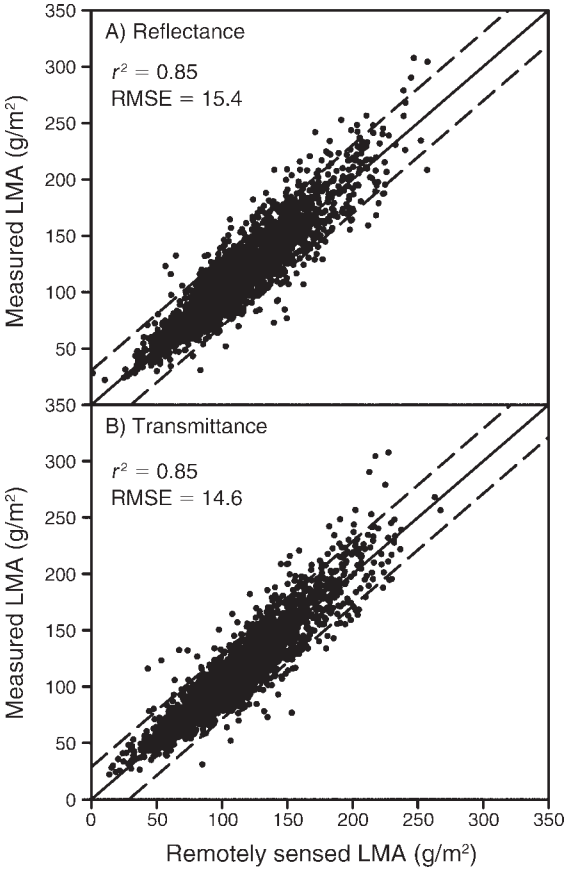


FIG. 5. Partial least-squares (PLS) regression results for leaf mass per area (LMA), measured vs. remotely sensed, based on leaf (A) reflectance and (B) transmittance. RMSE is root mean-square error.

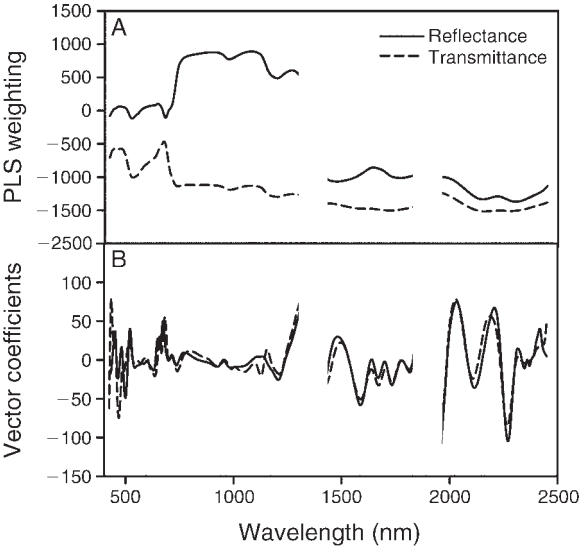


FIG. 6. (A) Standardized PLS spectral weightings for leaf reflectance- and transmittance-based analysis of leaf mass per area (LMA). (B) PLS prediction vector coefficients. Departures from the zero line indicate regions of the spectrum most important to the PLS regression.

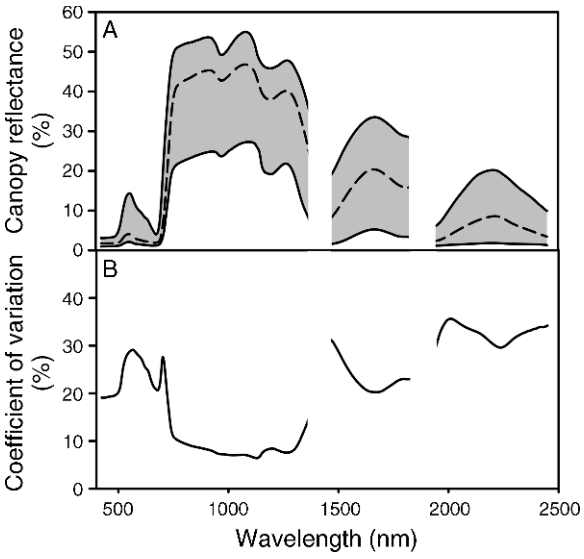


FIG. 7. (A) Minimum, mean, and maximum canopy reflectance for 2875 samples simulated using the radiative transfer model with field-measured leaf optical properties and varying canopy and illumination conditions (see Table 1). (B) Spectral coefficient of variation of canopy reflectance.

shortwave-infrared, especially between 1300 and 2400 nm, are critical to the LMA results.

Canopy radiative transfer models incorporate the measured leaf reflectance and transmittance values for each sample, the modeled canopy structural variation typical of each major vegetation habit found in tropical canopies, and the simulated variation in illumination and viewing geometry (Fig. 7, Table 1). At the canopy scale, reflectance CV values are highest in the shortwave-infrared (1400–2500 nm), peaking at 36%, and are also high in the visible (up to 29%) (Fig. 7B). PLS analyses indicate a strong correlation between spectral signatures of specimens and their LMA values (Fig. 8). The spectra account for 81% of the variance among all samples, with a RMSE value of 17 g/m$^2$. Again, the few outliers apparent in the regression are not phylogenetically distinct. PLS weightings indicate that the shortwave-infrared (1300–2500 nm) is critical to the prediction of LMA at the canopy level (Fig. 9). The visible and near-infrared regions play a relatively small role in determining LMA, as evidenced in the smaller weightings and vector coefficients.

We tested the predictive capability of the canopy spectra by splitting the data set, using over half ($n$ = 1488) for model development and the remaining samples ($n$ = 1383) to test predictions. With randomly selected training and test data, we found that canopy reflectance spectroscopy predicts LMA with an $r^2$ value of 0.82 and a RMSE of 17 g/m$^2$ (data not shown). We then sorted the data taxonomically, and developed the regression using all specimens from families Acanthanceae through Lauraceae ($n$ = 1478) to predict the LMA of remaining families Lecythidaceae to Winteraceae ($n$ = 1393). This

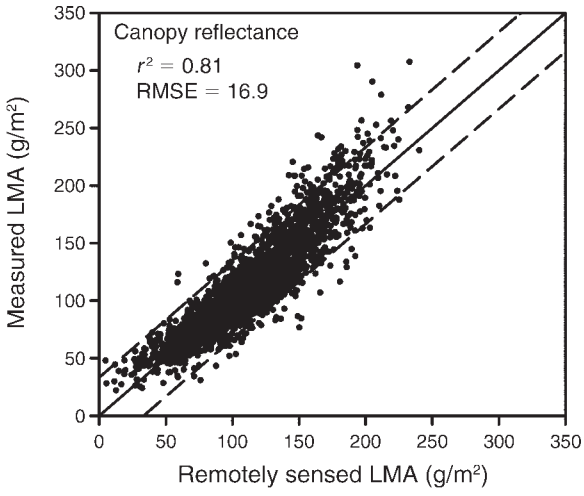


FIG. 8. Partial least-squares (PLS) regression results for measured vs. remotely sensed leaf mass per area (LMA) based on mean canopy reflectance signatures of each sample.

yielded an $r^2$ value of 0.81 and RMSE of 18 g/m$^2$ (Fig. 10).

We tested our ability to predict the LMA from canopy spectra collected at the site level (Table 4), thereby simulating data collection at a new site with the analysis driven by a general tropical spectral-LMA library. Our predictive ability varies slightly from site to site, with a low and high $r^2$ of 0.77 and 0.84 in two lowland Peruvian Amazon sites of Tambopata and Jenaro Herrera, respectively. The RMSE values of the predictions ranged from 14 to 21 g/m$^2$. Finally, we predicted the LMA values of individuals within each family as

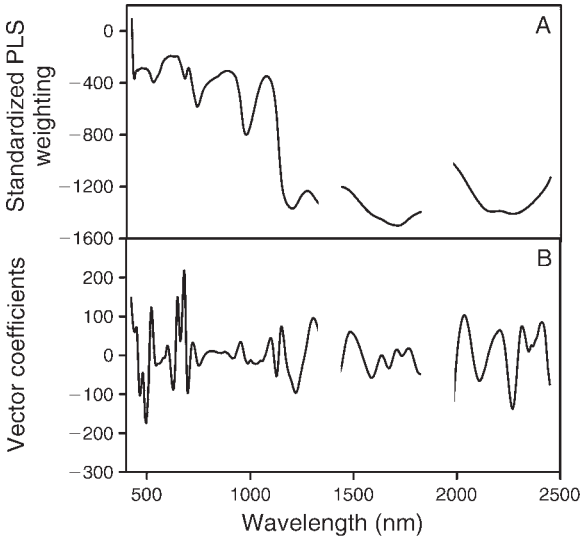


FIG. 9. (A) Standardized PLS spectral weightings for canopy reflectance analysis of leaf mass per area (LMA). (B) PLS prediction vector coefficients. Departures from the zero line indicate regions of the spectrum most important to the PLS regression.

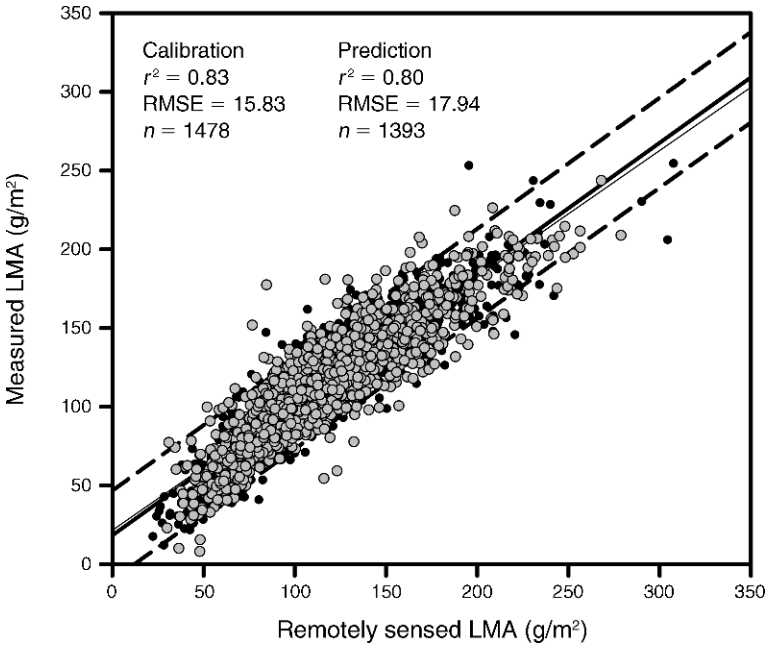


FIG. 10. Results of calibrating the PLS model using families Acanthaceae through Lauraceae (black circles) to predict leaf mass per area (LMA) for families Lecythidaceae through Winteraceae (gray circles). See Appendix B for a complete list of families. The heavy solid line is the regression of the prediction step, and the two dashed lines show the 95% confidence interval on the prediction. The thin solid line is the regression of the calibration step.

shown in Appendix C. The results indicate significant $r^2$ values for predicting all families, yet the strength of the regressions varies from a low $r^2$ of 0.48 for Phyllanthaceae to a high of 0.95 for Convolvulaceae.

## DISCUSSION

### *Environment vs. taxonomic controls*

We found enormous variation in LMA values within all growth habits found in humid tropical forest canopies (Fig. 1). In total, our LMA range was a remarkable 22.2–307.6 g/m$^2$, yet the LMA range for humid tropical forests was thought to be on the order of about 30–150 g/m$^2$ (Poorter et al. 2009). In fact, our reported variation in LMA encompasses nearly the global range of values found within and across most plant functional types and ecosystems including aquatic marine, grassland, tundra, woodland, and all major forest types (Poorter et al. 2009). The only groups to exceed the minimum or maximum limits of our data set are aquatic freshwater and desert succulent groups, respectively.

Why do we see such variation at the top of humid tropical forest canopies? If it is random sample variation, we would expect high intraspecific variation in LMA, but our results indicate an average CV of only 16% for LMA within species (Fig. 2). If the observed pattern is environmentally driven, then we would have uncovered more than the 19% contribution of site conditions to the LMA variation (Table 2). Despite annual precipitation and temperature ranges of 1800–7340 mm and 13.2–27.2°C, respectively, only temperature has a modest 4% contribution to the

TABLE 4. Estimation of LMA by research site, using LMA and high-fidelity spectra collected at other sites in the data set; *n* is the number of samples per site.

| Campaign and country | $r^2$ | RMSE | Slope | Intercept | *n* |
|---|---|---|---|---|---|
| Jenaro Herrera, Peru | 0.84 | 14.26 | 0.95 | 5.76 | 461 |
| Wet Tropics, Australia | 0.83 | 20.51 | 0.99 | 1.83 | 162 |
| Limahuli Valley, Hawaii, USA | 0.82 | 16.87 | 1.03 | −1.61 | 40 |
| BCI and region, Panama | 0.82 | 14.47 | 1.02 | −2.91 | 284 |
| Monteverde, Costa Rica | 0.81 | 16.07 | 0.90 | 7.18 | 400 |
| Allpahuayo, Peru | 0.81 | 15.43 | 1.01 | 0.41 | 599 |
| Puerto Rico, USA | 0.81 | 20.97 | 1.11 | −9.51 | 106 |
| Cape York, Australia | 0.80 | 17.69 | 1.01 | −2.96 | 196 |
| Hawaiian Islands, USA | 0.79 | 24.22 | 1.08 | −11.05 | 175 |
| Tambopata, Peru | 0.77 | 14.99 | 0.98 | 2.57 | 448 |

*Note:* All linear regression *P* values are <0.0001.

PLATE 1. Carnegie botanists climb high into the tropical forest canopy in the Amazon basin in the search for full-sunlight leaves destined for chemical and spectral analysis. (Left) Felipe Sinca hoists long pole clippers from high in the canopy, and (right) Nestor Jamillo works his way up a palm for leaf collection. More photos are available on the Carnegie Spectranomics website at ⟨http://spectranomics.ciw.edu⟩. Photo credits: G. P. Asner.

measured LMA variation among samples. Site conditions are clearly important overall, especially when the median LMA values of a site are tested against temperature (Fig. 3), but environment still does not account for the observed diversity of LMA.

The most likely explanation for the wide range of observed LMA variation rests in the high biological diversity of humid tropical forest canopies. The size and taxonomic structure of our data set, combined with a careful treatment of average lighting conditions, reveal strong species-level control over LMA variation. This pattern begins to emerge at the level of growth habits, albeit weakly with only 6% of the variation in LMA explained by habit. From there, plant families, genera, and finally species show increasing control over LMA patterns. Fully 70% of LMA variation is attributable to variation among species, with small additions from site and/or temperature that maximize our predictive capability to 76%. Finally, within our nested linear mixed-effects model, we can partition the total variance to family (32%), genera-within-families (14%), species-within-genera (25%), and unexplained (29%). This approach provides a quantitative understanding of how well taxonomic groupings reflect LMA. The fact that family and species-within-genera are dominant levels of control over LMA indicates that leaf structure correlates more strongly with taxonomic partitioning at these levels. The lower percentage of variance explained by genera-within-families suggests that families must organize genera relatively well in terms of LMA. The unexplained variance could be due to some combination of site conditions (e.g., soils, elevation, climate), tree selection, measurement error, and random variation.

The dominant role that taxa play in creating patterns of LMA in humid tropical forest canopies is an expression of the processes that create high biodiversity in these regions. The causes of such high levels of diversity remain heavily debated, with neutral processes, niche differentiation, and environmental filtering being the top contenders (Givnish 1999, Wright 2002). LMA is biophysically and biochemically linked to these processes via its role in plant growth (Wright et al. 2004), defense (Coley and Barone 1996), and life strategy (Hikosaka 2004). Because our study indicates strong taxonomic organization of LMA, it suggests that whichever forces control taxonomic diversity also control functional diversity among species. Such functional diversity is unlikely to be driven by purely stochastic processes, but rather by community-scale differentiation based largely on niche availability (Kraft et al. 2009).

Environmental filtering is probably an important additional determinant of LMA in humid tropical forests, although our study directly considers only cross-site environmental controls that proved relatively weak compared to taxonomic signals within and across a wide range of forest conditions. Nonetheless, at the site level we did observe variation in the strength of species-level control (Table 3), implying that there is variation in the strength of environmental filtering on LMA and/or on the species present and their leaf traits. A detailed (and laborious) analysis of micro-site vs. inter-site environmental controls is needed to more fully quantify these effects.

The notion that canopy diversity begets a diversity of leaf traits has also been demonstrated recently in terms of nutrient concentrations and biologically mediated processes. Townsend et al. (2007) showed that taxonomically driven variation in leaf nutrient concentrations, and particularly nitrogen : phosphorus ratios, in just a few humid tropical forest sites in Costa Rica and Brazil exceeds the range found throughout forests globally. At the site level, Epps et al. (2007) have shown that foliar litter quality and decomposition rates, which are driven directly by leaf chemistry, follow phylogenetic patterns. LMA is closely linked to these leaf traits, so in one sense our observations of high diversity in tropical forest LMA are not surprising, but the strong taxonomic structure to the patterns is new. It suggests that remotely sensed patterns of LMA will be dominated by the taxonomic composition of the canopy.

### *Remote sensing of LMA*

Remote sensing of leaf properties is not new; many have demonstrated how leaf pigments, nutrients, and carbon fractions can be estimated at both leaf and canopy levels (reviewed by Kokaly et al. 2009, Ustin et al. 2009). Moreover, modeling studies demonstrate the importance of leaf structure in defining the spectral properties of foliage (Jacquemoud and Baret 1990, Feret et al. 2008). In tropical forests, leaf and canopy spectroscopic analyses have provided estimates of water, nutrient, pigment, and even SLA (the reciprocal of LMA; Asner et al. 2009), but a comprehensive remote-sensing analysis of a single leaf property has not been made among a wide range of tropical forest sites.

Using 2873 samples representing the growth habits that dominate canopy leaf biomass distributed across 149 plant families found in upper-canopy positions of humid tropical forests, we found that high-fidelity leaf spectra predict LMA with an $r^2$ value of 0.85 and RMSE $<15$ g/m$^2$ (Fig. 5). However, reflectance and transmittance regressions make differential use of the spectrum to achieve these high accuracies (Fig. 6). This is caused by differences in how mesophyll structure and chemical composition are expressed in absorption and scattering of light on a leaf (reflectance) vs. through a leaf (transmittance) (Govaerts et al. 1996, Jacquemoud et al. 1996, Vogelmann et al. 1996).

Despite the strong leaf-level results, the true test rests in the retrieval of leaf properties from canopy spectra, which incorporates the myriad canopy structural contributions and angular "artifacts" inherent to HiFIS (high-fidelity imaging spectroscopy) measurements taken from aircraft. Canopy radiative transfer models are not perfect surrogates for actual aircraft measurements, but they are physically based and have proven useful for leaf analyses from the air (Jacquemoud et al. 2000, Zarco-Tejada et al. 2001, Ustin et al. 2004, Asner and Vitousek 2005). They can be used conservatively, such as we have done, to understand the sensitivity of canopy reflectance to various leaf and canopy properties (e.g., Baret et al. 1994). If the method does not work well using simulated canopy data, then it is unlikely to work with actual data collected from aircraft.

Our results indicate that LMA can be retrieved from canopy spectra with $r^2$ values exceeding 0.80 and RMSE values in the 14–20 g/m$^2$ range (Figs. 8 and 10, Table 4; Appendix C). Importantly, the spectroscopy of LMA appears to be unaffected by growth habit. We also showed that the strength of the predictions holds well for randomly or taxonomically selected subsamples. However, observed variation in our ability to predict LMA within plant families (Appendix C) suggests that particular leaf characteristics associated with phylogeny may still play a role in determining the relationship between spectroscopy, LMA, and other leaf properties.

The site-specific strength of the relationship between spectra and LMA does vary ($r^2 = 0.77$–$0.84$; RMSE = 14–21 g/m$^2$), which could be due to undetermined site-level factors affecting our data compilations. There were no obvious contributors (e.g., epiphylls, drought stress, phenology) to variation in the LMA predictions (data not shown). One unknown factor might be soil fertility, which could impart a nutrient effect on the spectra–LMA relationship. However, the spectra are differentially sensitive to nitrogen concentrations (e.g., spectral features for nitrogen are somewhat different from those relating to LMA) (Asner and Martin 2008), and nitrogen shows relatively weak correlations with LMA among tropical forest species (Wright et al. 2004, Poorter and Bongers 2006).

This study emphasizes that the most important portion of the spectrum required for accurate LMA determination is the shortwave-infrared (1300–2500 nm), a region that has proven extremely difficult to measure well at leaf or aircraft levels. This wavelength region is currently intractable to measure with high fidelity from space due to low signal-to-noise performance of orbital sensors (Ungar et al. 2003). Even at the leaf level, these measurements are rare, and thus we have dedicated much time to developing systems that provide high-fidelity measurements under tropical-forest field conditions. At the aircraft level, the only system to demonstrate high-fidelity shortwave-infrared measurements at high spectral resolution is the latest version of

AVIRIS (post-2005). The results we presented here—that a major leaf trait, LMA, is both taxonomically organized and measureable with high-fidelity reflectance spectroscopy—highlight the potential role that new shortwave-infrared sensors can play in breaking long-standing barriers to biodiversity sensing, even in speciose humid tropical forests.

Acknowledgments

We thank Carnegie, our collaborating organizations, and our volunteers for assistance with field, laboratory, and logistical steps to develop the data sets. Special thanks go to C. Anderson, L. Carranza, J. Ccoycosi, J. A. Escudero, A. Ford, M. Houcheime, N. Jaramillo, C. Lamprecht, K. Ledesma, M. Papes, and P. Weiss. We thank three anonymous reviewers for a helpful critique of the manuscript. The Spectranomics Project ⟨http://spectranomics.ciw.edu⟩ and this study are supported by the John D. and Catherine T. MacArthur Foundation.

Literature Cited

Asner, G. P. 1998. Biophysical and biochemical sources of variability in canopy reflectance. Remote Sensing of Environment 64:134–153.

Asner, G. P. 2000. A hyperspectral photon transport system for simulating imaging spectrometer observations of terrestrial ecosystems. Pages 126–138 *in* R. O. Green, editor. Ninth Annual Airborne Earth Science Workshop. Jet Propulsion Laboratory, Pasadena, California, USA.

Asner, G. P., D. E. Knapp, T. Kennedy-Bowdoin, M. O. Jones, R. E. Martin, J. Boardman, and C. B. Field. 2007. Carnegie Airborne Observatory: In-flight fusion of hyperspectral imaging and waveform light detection and ranging (LiDAR) for three-dimensional studies of ecosystems. Journal of Applied Remote Sensing 1:013536. [doi: 10.1117/1.2794018]

Asner, G. P., and M. E. Martin. 2008. Spectral and chemical analysis of tropical forests: scaling from leaf to canopy levels. Remote Sensing of Environment 112:3958–3970.

Asner, G. P., and R. E. Martin. 2009. Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. Frontiers in Ecology and the Environment 7:269–276.

Asner, G. P., R. E. Martin, A. J. Ford, D. J. Metcalfe, and M. J. Liddell. 2009. Leaf chemical and spectral diversity of Australian tropical forests. Ecological Applications 19:236–253.

Asner, G. P., J. M. O. Scurlock, and J. A. Hicke. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Global Ecology and Biogeography 12:191–205.

Asner, G. P., and P. M. Vitousek. 2005. Remote analysis of biological invasion and biogeochemical change. Proceedings of the National Academy of Sciences USA 102:4383–4386.

Baret, F., V. C. Vanderbilt, M. D. Steven, and S. Jacquemoud. 1994. Use of spectral analogy to evaluate canopy reflectance sensitivity to leaf optical properties. Remote Sensing of Environment 48:253–260.

Bates, D., and M. Maechler. 2009. LME4: Linear mixed-effects models using S4 classes. ⟨http://cran.r-project.org/web/packages/lme4/index.html⟩

Chen, S., X. Hong, C. J. Harris, and P. M. Sharkey. 2004. Spare modeling using orthogonal forest regression with PRESS statistic and regularization. IEEE Transaction on Systems, Man and Cybernetics 34:898–911.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305–335.

Cunningham, S. A., B. Summerhayes, and M. Westoby. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69:569–588.

Epps, K. Y., N. B. Comerford, J. B. Reeves, W. P. Cropper, and Q. R. Araujo. 2007. Chemical diversity: highlighting a species richness and ecosystem function disconnect. Oikos 116:1831–1840.

Evans, J. R. 1989. Partitioning of nitrogen between and within leaves grown under different irradiances. Australian Journal of Plant Physiology 16:533–548.

Faraway, J. J. 2005. Extending the linear model with R: generalized linear, mixed effects, and nonparametric regression models. Chapman and Hall/CRC Press, New York, New York, USA.

Feret, J.-B., C. Francois, G. P. Asner, A. A. Gitelson, R. E. Martin, L. P. R. Bidel, S. L. Ustin, G. le Maire, and S. Jacquemoud. 2008. PROSPECT-4 and 5: Advances in the leaf optical properties model separating photosynthetic pigments. Remote Sensing of Environment 112:3030–3043.

Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology 87:193–210.

Govaerts, Y. M., S. Jacquemoud, M. M. Verstraete, and S. L. Ustin. 1996. Three-dimensional radiation transfer modeling in a dicotyledon leaf. Applied Optics 35:6585–6598.

Green, R. O., M. L. Eastwood, C. M. Sarture, T. G. Chrien, M. Aronsson, B. J. Chippendale, J. A. Faust, B. E. Pavri, C. J. Chovit, M. S. Solis, M. R. Olah, and O. Williams. 1998. Imaging spectroscopy and the Airborne Visible Infrared Imaging Spectrometer (AVIRIS). Remote Sensing of Environment 65:227–248.

Haaland, D. M., and E. V. Thomas. 1988. Partial least-squares methods for spectral Analyses. 1. Relation to other quantitative calibration methods and the extraction of qualitative information. Analytical Chemistry 60:1193–1202.

Hansen, M. C., S. V. Stehman, P. V. Potapov, T. R. Loveland, J. R. G. Townshend, R. S. DeFries, K. W. Pittman, B. Arunarwati, F. Stolle, M. K. Steininger, M. Carroll, and C. DiMiceli. 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. Proceedings of the National Academy of Sciences USA 105:9439–9444.

Hikosaka, K. 2004. Interspecific difference in the photosynthesis–nitrogen relationship: patterns, physiological causes, and ecological importance. Journal of Plant Research 117:481–494.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Jacquemoud, S., C. Bacour, H. Poilve, and J. P. Frangi. 2000. Comparison of four radiative transfer models to simulate plant canopies reflectance: direct and inverse mode. Remote Sensing of Environment 74:471–481.

Jacquemoud, S., and F. Baret. 1990. PROSPECT: a model of leaf optical properties spectra. Remote Sensing of Environment 34:75–91.

Jacquemoud, S., S. L. Ustin, J. Verdebout, G. Schmuck, G. Andreoli, and B. Hosgood. 1996. Estimating leaf biochemistry using the PROSPECT leaf optical properties model. Remote Sensing of Environment 56:194–202.

Kokaly, R. F., G. P. Asner, S. V. Ollinger, M. E. Martin, and C. A. Wessman. 2009. Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. Remote Sensing of Environment 113:S78–S91.

Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2009. Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582.

Niinemets, U., and O. Kull. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiology 18:467–479.

Niinemets, U., O. Kull, and J. D. Tenhunen. 1999. Variability in leaf morphology and chemical composition as a function

of canopy light environment in coexisting deciduous trees. International Journal of Plant Sciences 160:837–848.
Paoli, G. D. 2006. Divergent leaf traits among congeneric tropical trees with contrasting habitat associations in Borneo. Journal of Tropical Ecology 22:397–408.
Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182:565–588.
Poorter, L., and F. Bongers. 2006. Leaf traits are a good predictor of plant performance across 53 rain forest species. Ecology 87:1733–1743.
Poorter, L., S. F. Oberbauer, and D. B. Clark. 1995. Leaf optical propeties along a vertical gradient in a tropical rain forest canopy in Costa Rica. American Journal of Botany 82: 1257–1263.
R Development Core Team. 2009. R, version 2.9.2. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.R-project.org⟩
Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences USA 94: 13730–13734.
Sanchez-Azofeifa, G. A., K. Castro, S. J. Wright, J. Gamon, M. Kalacska, B. Rivard, S. A. Schnitzer, and J. L. Feng. 2009. Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: implications for remote sensing in tropical environments. Remote Sensing of Environment 113(Supplement 1):2076–2088.
Townsend, A. R., G. P. Asner, and C. C. Cleveland. 2008. The biogeochemical heterogeneity of tropical forests. Trends in Ecology and the Environment 23:424–431.
Townsend, A. R., C. C. Cleveland, G. P. Asner, and M. M. C. Bustamante. 2007. Controls over foliar N:P ratios in tropical rain forests. Ecology 88:107–118.
Ungar, S. G., J. S. Pearlman, J. A. Mendenhall, and D. Reuter. 2003. Overview of the Earth Observing-1 (EO-1) mission. IEEE Transactions on Geoscience and Remote Sensing 41: 1149–1160.
Ustin, S. L., A. A. Gitelson, S. Jacquemoud, M. Schaepman, G. P. Asner, J. A. Gamon, and P. Zarco-Tejada. 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. Remote Sensing of Environment 113(Supplement 1):567–577.
Ustin, S. L., D. A. Roberts, J. A. Gamon, G. P. Asner, and R. O. Green. 2004. Using imaging spectroscopy to study ecosystem processes and properties. BioScience 54:523–534.
Verhoef, W., and H. Bach. 2003. Simulation of hyperspectral and directional radiance images using coupled biophysical and atmospheric radiative transfer models. Remote Sensing of Environment 87:23–41.
Vogelmann, T. C., J. N. Nishio, and W. K. Smith. 1996. Leaves and light capture: light propagation and gradients of carbon fixation within leaves. Trends in Plant Science 1:65–70.
Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159.
Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.
Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14.
Zarco-Tejada, P. J., J. R. Miller, T. L. Noland, G. H. Mohammed, and P. H. Sampson. 2001. Scaling-up and model inversion methods with narrowband optical indices for chlorophyll content estimation in closed forest canopies with hyperspectral data. IEEE Transactions on Geoscience and Remote Sensing 39:1491–1507.

## APPENDIX A

List of site names and countries, climate information, and number of samples used for environmental and taxonomic analysis (*Ecological Archives* A021-005-A1).

## APPENDIX B

Taxonomic list of species included in the study (*Ecological Archives* A021-005-A2).

## APPENDIX C

Estimation of leaf mass per area (LMA) by family using data for half of the families in the data set (*Ecological Archives* A021-005-A3).