

Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches

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Summary

1. One way to simplify the high taxonomic diversity of plant species in vegetation models is to place species into groups based on shared, dominant traits. Many studies have suggested that morphological and physiological traits of tropical dry forest tree species vary with leaf habit (i.e. leaves from evergreen, deciduous or semi-deciduous species) and thus this characteristic may serve as a useful way to distinguish ecologically meaningful functional types.

2. In this study we examine whether 10 plant traits vary with leaf habit in replicated leaves and individual trees of 87 species from a tropical dry forest in Costa Rica. We also looked for evidence of phylogenetic conservatism, i.e. closely related species sharing similar trait values compared to more distantly related taxa.

3. While some of the traits varied within and among individual trees of the same species, inter-specific variation accounted for 57–83% of the variance among samples. Four traits in addition to leaf habit showed evidence of phylogenetic conservatism, but these results were strongly dependent on the inclusion of the 18 species of legumes (Fabaceae) in our dataset. Contrary to our predictions, none of the traits we measured differed among leaf habits. However, five traits (wood density, leaf C, leaf N, N/P and C/N) varied significantly between legumes and other functional types. Furthermore, when all high-nitrogen non-legume taxa were compared to the high-nitrogen legumes, six traits excluding leaf N differed significantly, indicating that legumes are functionally different from other tree species beyond high N concentrations. Similarly, the 18 legume taxa (which all have compound leaves) also differed from other compound-leaved species for six traits, thus leaf type does not explain these patterns.

4. Our main conclusions are that (i) a plant functional type classification based on leaf habit alone has little utility in the tropical dry forest we studied, and (ii) legumes have a different suite of traits including high leaf carbon and wood density in addition to high leaf nitrogen. Whether this result generalizes to other tropical forests is unknown, but merits future research due to the consequences of these traits for carbon storage and ecosystem processes.

Key-words: Fabaceae, nitrogen, phosphorus, phylogeny, plant functional type, stable isotopes, stoichiometry

Introduction

Understanding the ecology, physiology and potential responses to global environmental change of the > 250 000 species of vascular plants is an overwhelming challenge. One approach for simplifying this challenge is to identify groups of species with shared characteristics. These groups, or functional types, can then be used to simplify biological diversity in dynamic global vegetation models (DGVMs)

(Purves & Pacala 2008; Ostle *et al.* 2009) and make predictions about community and ecosystem processes (Duckworth, Kent & Ramsay 2000). Identifying effective classification schemes can, however, be challenging. Classification schemes can be continuous (through identification of correlations among quantitative traits that reflect life history trade-offs) or discrete (through assignment of species to plant functional groups based on dominant traits such as life form, leaf habit, or ability to fix nitrogen) (Smith, Shugart & Woodward 1997; Duckworth, Kent & Ramsay 2000; Wright *et al.* 2004; Reich, Wright & Lusk 2007).

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For example, leaf area per unit mass (SLA), photosynthetic capacity and leaf nitrogen concentrations are correlated and can be arrayed along a 'leaf economic spectrum', reflecting investment in short-lived leaves with high photosynthetic capacity on one end of the spectrum, to long-lived, thick leaves with lower photosynthetic capacity at the other end (Wright *et al.* 2004). These multi-trait distributions have been interpreted as reflective of evolutionary constraints (Ackerly *et al.* 2000), and trade-off axes have also been proposed as a way to simplify DGVMs by obviating the need for species-specific parameters (Purves & Pacala 2008). Combinations of quantitative plant traits also have been shown to explain variation in litter decomposition (Santiago 2007), community assembly (Cavender-Bares, Kitajima & Bazzaz 2004), co-existence of tree species in diverse Amazonian forests (Kraft, Valencia & Ackerly 2008), demographic rates (Poorter *et al.* 2008), invasion resistance (Funk *et al.* 2008), net primary productivity (Vile, Shipley & Garnier 2006), and are useful in assessing ecosystem services (Diaz *et al.* 2007).

On the other hand, assigning species to plant functional type on the basis of discrete traits such as leaf habit (i.e. evergreen, deciduous, etc) may be sufficient for placing species into distinct groups and most DGVMs employ such an approach (Ostle *et al.* 2009). Trees with deciduous leaf habit avoid environmental stresses during unfavourable seasons (e.g. cold temperatures during winter in temperate forests or low water availability during the dry season in tropical dry forest), but must maximize carbon gain during favourable conditions. By contrast, evergreen trees must tolerate these unfavourable conditions (Aerts 1995). In general, plants with different leaf habits have different sets of traits (Mooney & Dunn 1970; Eamus 1999) and thus leaf habit alone may be effective for identifying ecologically meaningful functional groups, i.e. groups with different effects on or responses to environmental variation. For example, in tropical dry forests, broad-leaved deciduous trees are reported to have greater nutrient resorption efficiencies, higher nitrogen contents, nutrient use efficiencies, specific leaf area and rates of photosynthesis but lower water use efficiencies, compared to broad-leaved evergreen trees (Sobrado 1991; Eamus 1999; Eamus & Prior 2001; Lal *et al.* 2001; Prior, Eamus & Bowman 2003; Ishida *et al.* 2006). One caveat to these generalizations, however, is that they are typically based on very small sample sizes (e.g. 4–8 species per leaf habit). Moreover, data supporting leaf-habit based groupings have sometimes been made using species that are closely related to one another. As a result, the apparent value of leaf habit in defining functional type may reflect biased sampling or close phylogenetic relatedness. The potential for identifying plant functional types on the basis of leaf habit is particularly attractive because data on leaf habit are relatively easy to collect by remote sensing – potentially making it possible to extrapolate ecophysiology from leaf to regional scales and for representing plant function in DGVMs.

In this study we examine the extent to which plant traits vary with leaf habit in a tropical dry forest in Costa Rica. Dry forests comprise ~40% of tropical forests and are of consid-

erable conservation interest (Murphy & Lugo 1986; Miles *et al.* 2006). The strong seasonal drought that is characteristic of dry forests (often lasting for 6 months or longer) imposes harsh environmental conditions, and plants have diverse adaptations to cope with limited water availability (Borchert 1994; Eamus & Prior 2001). Although tropical dry forests typically harbor fewer tree species than tropical rain forests (Murphy & Lugo 1986), these ecosystems have high phenological and functional diversity (Eamus 1999; Sandquist & Cordell 2007). Most rain forests are dominated by broad-leaved, evergreen canopies; in contrast, leaf habits of dry forest tree species range from evergreen to deciduous, with intermediate strategies such as semi-deciduousness (trees that lose a fraction of their canopy during the dry season) and brevi-deciduousness (trees that shed leaves at the start of the dry season followed by immediate flushing) (Eamus 1999).

We measured eight traits in multiple individuals of 87 species of dry forest trees. The traits were specific leaf area (SLA), leaf water content (LWC), wood density, leaf carbon (C), leaf nitrogen (N), leaf phosphorus (P) concentrations, leaf $\delta^{13}\text{C}$ as a potential indicator of water use efficiency (WUE) (Farquhar & Richards 1984) and $\delta^{15}\text{N}$ as a potential indicator of nitrogen fixation in legumes (Delwiche *et al.* 1979). We chose these traits because they are indicators of plant physiological status and life history strategy and are important for ecosystem processes such as decomposition and carbon storage. Leaf water content, while perhaps not typically considered a plant trait, is important for processes such as flammability (Alessio *et al.* 2008) and can be quantified through remote sensing (Ceccato *et al.* 2001). We also examined the stoichiometric ratios of C/N and N/P. Stoichiometry is increasingly recognized as a property that integrates variation in life history (Elser & Hamilton 2007) as well as environmental effects (Reich & Oleksyn 2004).

Our overall goal was to evaluate the potential utility of leaf habit as a trait for defining ecologically meaningful groups of tropical dry forest species. To accomplish this, we had three specific objectives. First, we estimated the relative magnitude of variance among leaves within a tree, among trees of a single species and among species. For traits to be useful for categorizing species into functional groups, it is necessary for intraspecific variation to be less than interspecific variation (Mcgill *et al.* 2006). Second, we tested whether traits differed among species with different leaf habits or other functional classifications and estimated the strengths of correlations among traits. Finally, we tested for evidence of phylogenetic signal i.e. closely related taxa being phenotypically more similar to one another than they are to distantly related taxa (Chave *et al.* 2006; Kerkoff *et al.* 2006) to evaluate the potential value of incorporating phylogenetic relatedness when designing functional classifications. We predicted that deciduous species would have traits that maximize carbon gain during the growing season, i.e. higher leaf N, SLA, P, and lower wood density, and that evergreen species would have traits consistent with nutrient conservation strategies, i.e. lower N, P, SLA, but higher wood density and WUE.

Materials and methods

We sampled 284 trees representing 87 species from species-rich tropical dry forests in two conservation areas in Northwest Costa Rica; the Area de Conservación Guanacaste (Sector Santa Rosa, 215 trees) and the Area de Conservación Tempisque (Parque Nacional Palo Verde, 69 trees). Both conservation areas have similar climates and forests in various stages of succession that are regenerating following grazing and agriculture (Gillespie, Grijalva & Farris 2000; Powers *et al.* 2009). Annual precipitation over the past 26 years has ranged from 880 to 3030 mm per year (mean = 1575) in Santa Rosa, and from 714 to 2130 mm per year (mean ~1700) at Palo Verde (Gillespie, Grijalva & Farris 2000; Powers *et al.* 2009). Approximately 85–95% of the precipitation falls between May and November. To minimize seasonal variation in leaf traits (S. G. Gotsch, unpublished data), nearly all samples were collected during the later part of the wet season in 2007 (from late August to December, with a few evergreen taxa sampled in January).

SAMPLING AND DATA COLLECTION

Our criteria for including trees in the sample were that the species was reasonably abundant and that we could find trees that could be sampled from the ground with a ladder and/or pole pruner. Because we sampled trees from the ground, most trees were sampled in young secondary forest (10–35 years old), which is abundant in both Conservation Areas. Importantly, however, the species we sampled are not restricted to early successional habitats (Powers *et al.* 2009). For each of the 87 species that met these criteria we sampled three leaves from each of 1 to 7 individuals (three or more trees were sampled from 64 species with trees of the same species separated by > 30 m). We acknowledge that our within-species sampling is limited, but our goals were to sample the largest number of species possible given limited resources, and our results seem robust to this limitation. The 87 species represent 71 genera and 37 families (Table S1) with 18 species from the Fabaceae (i.e. legumes), which are particularly common in the tropics in general and dry tropics in particular (Gentry 1988; Pennington, Lavin & Oliveira-Filho 2009); other families were represented by 1–5 species. The 37 families span much of the angiosperm phylogenetic diversity found in these forests and include members of the magnoliids, rosids and asterids. Species were assigned to one of three leaf habits based on the knowledge of three experts of the local flora (Daniel Janzen, Daniel Pérez-Aviles and Jeff Klemens). Sampled species include deciduous species that remain leafless for at least several months during the dry season, semi-deciduous and brevi-deciduous species that drop their entire canopy of leaves synchronously and then flush a new canopy and/or remain partially leafless during the dry season (which we lumped together and refer to as 'semi-deciduous'), and evergreen species that retained a full canopy throughout the year.

All sampled leaves were from trees with crowns exposed to sunlight. The diameters at breast height (1.3 m, DBH) of sampled trees ranged from 10 to 190 cm, with an average DBH of 25 cm and a median DBH of 17 cm. At each tree, three sunlit branches were collected with clippers or a pole pruner, and one fully expanded, damage-free leaf was collected from each branch and placed in a plastic bag in a cooler (note that we did not analyse shade leaves). All leaves were collected 2–4 m from the ground, as $\delta^{13}\text{C}$ can vary with height above the ground (Martinelli *et al.* 1998).

On the same day leaves were sampled, fresh leaves were weighed then scanned, and leaf areas were measured for the images with ImageJ (Abramoff, Magelhaes & Ram 2004). Leaves were then dried

at ~60 °C for > 48 h and re-weighed. SLA ($\text{cm}^2 \text{g}^{-1}$) and percent leaf water content (LWC) were calculated as leaf area/Wd and $((\text{Wf} - \text{Wd})/\text{Wf}) \times 100$, respectively (with Wf referring to fresh leaf weight and Wd referring to leaf dry weight). Dried leaves were ground in a coffee grinder, and transported to the United States for further analyses. Because we are especially interested in how leaf traits may scale to ecosystem carbon and nutrient dynamics via decomposition, we included petioles in our leaf trait measurements following standard protocols (Cornelissen *et al.* 2003) and compound leaves were not subdivided into leaflets.

Ground leaf tissue was dried at 65 °C prior to weighing. Leaf carbon (C) and nitrogen (N) concentrations and their stable isotopes, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured from subsamples of ground leaves at the University of California – Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Leaf P concentrations on all 284 trees were measured in Kjeldahl digests on composite leaf samples obtained by bulking dried, ground samples from the three sampled leaves per tree (samples were pooled by tree due to financial constraints). P analyses were performed on an Astoria 305D Flow Solution at the Central Analytical Lab at Oregon State University. All leaf element data are reported on a mass basis. SLA, LWC, leaf C, leaf N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed for three leaves per tree from each of 190 trees of 62 species (3–4 individuals per species) allowing us to evaluate the magnitude of variation among leaves sampled from an individual tree, among trees of the same species, and among species.

We estimated wood density for each of the 87 species using the water displacement method (Chave *et al.* 2006). In brief, trees were cored with an increment borer at breast height and cores were immediately returned to the field lab. Cores were soaked in water to rehydrate them, bark was removed, cores were sectioned into 6–13 cm long pieces, and green volume was estimated as the weight of water needed to displace the core. Cores were then dried at ~60 °C for > 48 h and re-weighed. Wood density (also referred to as wood specific gravity) was estimated as the ratio of dry weight to green volume (g cm^{-3}). Due to time constraints, the trees we sampled for wood density were not the same from which we sampled leaves, but they were sampled from the same area and were of similar sizes (DBH ranged from 10.2 to 88.3 cm, with an average DBH of 28.8 cm and a median of 24.5 cm). All species were sampled in duplicate, and variation between duplicates was low (the mean coefficient of variation was < 7.0%).

STATISTICAL ANALYSES

For traits measured on multiple leaves from ≥ 3 individuals per species (SLA, leaf water content, leaf N%, leaf C%, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, C/N), we first asked whether the largest source of variation was among leaves, trees of the same species, or species using nested analyses of variance (ANOVA) for each trait separately (Splus 8.0; Insightful Corp., Palo Alto, CA, USA). Next we tested for relationships between traits and leaf habit using species mean values of each trait and assuming each species was independent, i.e. ignoring phylogenetic relatedness. Preliminary analyses indicated that the legumes (family Fabaceae) were responsible for strong phylogenetic signal in several traits and that they had a large effect on relationships between leaf habit and other traits. Therefore, we treated the legumes as a separate plant functional type (PFT) resulting in 4 PFTs for subsequent analyses; deciduous (39 species), semi-deciduous (13 species), evergreen (17 species) and legumes (18 species). After conducting a multivariate ANOVA (MANOVA) with all 10 traits as responses, PFT as the main effect and Pillai's trace

as the test of significance, we tested for significant variation among PFTs using separate ANOVAS for each trait. When *F*-values revealed significant variation among PFTs, we used Tukey's means separation tests to determine how PFTs differed from one another. Data were transformed (log10) when appropriate to normalize variances. We tested for linear relationships between traits using Pearson correlation coefficients, which were conducted on the entire data set, as well as a reduced dataset in which legumes were excluded (see below). We also performed a principal components analysis on the trait correlation matrix to test whether the PFTs explained variation in multivariate phenotypes that are not represented by the individual traits (Splus 8.0; Insightful Corp.).

We tested whether any traits showed evidence of phylogenetic signal using the analytical approaches implemented in the AOT (Analysis of Traits) module for trait analyses found in the Phylocom computer package (Webb, Ackerly & Kembel 2008). In brief, AOT tests for evidence of greater resemblance among closely related lineages, i.e. phylogenetic signal, by comparing the variance of standardized contrasts across the phylogenetic tree calculated from the actual trait values to a distribution generated from 999 random assignments of the trait values across the tips of the given phylogeny. Because preliminary analyses revealed that the legumes were responsible for significant phylogenetic signal in several traits, these analyses were run with the entire data set, only the legumes, and the entire data set minus the legumes. Leaf habit is a categorical variable, but AOT accepts only bivariate or continuous variables, therefore we treated leaf habit as a pseudo-continuous variable by assigning deciduous, semi-deciduous, and evergreen species values of 0, 1, and 2 respectively. The phylogenetic relationships used to conduct these analyses were taken from the on-line version of Phylomatic (February 2009 version, <http://www.phylodiversity.net/phyloomatic/>) (Webb, Ackerly & Kembel 2008) based on a maximally resolved angiosperm tree of Peter Stevens (Stevens 2001) with branch lengths obtained by running phylocom bladj (branch length adjuster) on Phylocom's maximally resolved tree with angiosperm node ages from Wikstrom, Savolainen & Chase (2001), which are based on the estimated MRCA of the two most distant taxa in a clade (<http://www.phylodiversity.net/bladj/#wikstrom01>).

Results

SOURCES OF VARIATION

For four of the seven traits measured on replicate leaves and individuals, nested ANOVAS revealed no evidence that leaves

Table 1. *F*-values from nested ANOVAS investigating leaf (d.f. = 190), tree (d.f. = 128) and interspecific (d.f. = 61) variation among traits

Trait	Species	Tree	Leaf
Leaf N (%)	128.3 (0.83)	9.1 (0.12)	1.2 (0.02)
Leaf C (%)	78.0 (0.82)	5.1 (0.11)	1.1 (0.03)
C/N	98.0 (0.80)	9.1 (0.15)	1.2 (0.03)
$\delta^{15}\text{N}$ (‰)	54.3 (0.57)	17.3 (0.38)	0.5 (0.02)
$\delta^{13}\text{C}$ (‰)	41.7 (0.60)	9.6 (0.29)	1.5 (0.07)
Leaf water content (%)	77.8 (0.79)	6.5 (0.14)	1.3 (0.04)
SLA ($\text{cm}^2 \text{g}^{-1}$)	73.7 (0.80)	5.6 (0.13)	1.5 (0.05)

The numbers in parentheses are the proportion of total variance explained by that factor. *F*-values in bold are significant at $P < 0.0001$, in italics $P < 0.05$, otherwise not significant.

varied significantly within trees (Table 1). By contrast, $\delta^{13}\text{C}$, LWC and SLA varied significantly among leaves. Nevertheless, the variation in these traits among leaves from an individual tree comprised 4–7% of the total variance, whereas variation among species accounted for 57–82% of the total variance (Table 1). Similarly, although we detected significant variation among trees of the same species for all seven traits (Table 1), interspecific variation was far greater than the variance found among trees of the same species, which accounted for 11–38% of the total variance (Table 1). Because the among-species variance was much greater than other sources we conducted all subsequent analyses using species means. The magnitude of among-species variation, relative to the means, ranged widely among traits with coefficients of variation (CVs) ranging from < 12% for $\delta^{13}\text{C}$ leaf C%, and LWC, to > 300% for leaf $\delta^{15}\text{N}$ (Table 2).

TRAITS IN RELATION TO PLANT FUNCTIONAL TYPES

A MANOVA revealed strong evidence that traits differed significantly among the four PFTs ($F = 3.34$, $P < 0.0001$). Individual ANOVAS revealed significant variation among PFTs for six of 10 traits (Fig. 1). The stoichiometric ratios of elements (C/N, N/P) varied significantly among PFTs although these were tightly correlated with either leaf C and leaf N (for C/N) or leaf N (for N/P) suggesting that the ratios provide little information that is not contained in the total element concentrations. For most traits, the significant ANOVAS were due to differences between legumes and other PFTs; on average, legumes had wood that was ~15% more dense than deciduous species, and had ~5.5% greater leaf C and 23% more leaf N than other PFTs. By contrast, means separation tests revealed no evidence for differences among functional types defined by leaf habit (i.e. all non-legume taxa). Results from analyses of PCA were consistent with conclusions from the analyses of individual traits; there was little separation of the PFTs along PC 1 (35% of total variation) and an ANOVA of PC1 scores by PFT was not significant ($F_{3,83} = 1.7$; $P = 0.17$), whereas legumes differed significantly from the other PFTs along PC2 (20% of variation; $F_{3,83} = 16.2$; $P < 0.0001$). No other clustering of PFTs or species was evident along these two axes.

Table 2. Means, ranges and coefficients of variation (CV) of 10 traits for Costa Rican dry forest tree species ($N = 87$)

Trait	Mean	Minimum	Maximum	CV (%)
SLA ($\text{cm}^2 \text{g}^{-1}$)	101.8	54.8	229.5	33.0
Leaf water content (%)	58.8	40.2	73.9	11.8
Wood density (g cm^{-3})	0.62	0.18	0.90	25.1
Leaf $\delta^{13}\text{C}$ (‰)	-29.2	-32.7	-26.4	4.0
Leaf $\delta^{15}\text{N}$ (‰)	0.61	-3.29	6.80	331.1
Leaf C (%)	45.9	37.6	52.3	6.3
Leaf N (%)	2.33	1.17	3.63	26.7
Leaf P (%)	0.11	0.06	0.20	31.0
C/N	21.6	12.3	37.7	29.2
N/P	22.5	12.6	43.5	27.4

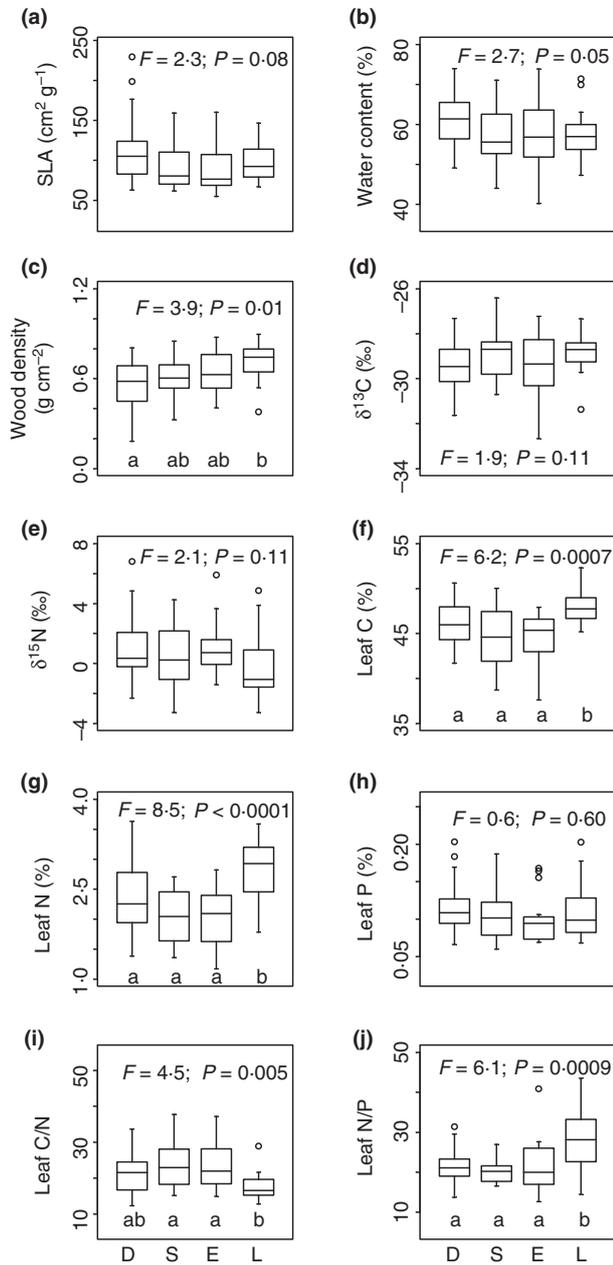


Fig. 1. Distributions of trait values for tropical dry forest tree species grouped by leaf habit including (a) specific leaf area ($\text{cm}^2 \text{g}^{-1}$), (b) leaf water content (%), (c) wood density (g cm^{-3}), (d) leaf $\delta^{13}\text{C}$ (‰), (e) leaf $\delta^{15}\text{N}$ (‰), (f) leaf C (%), (g) leaf N (%), (h) leaf P (%), (i) leaf C/N and (j) leaf N/P. The center line indicates the median, and upper and lower box heights indicate interquartile range. Uppercase letters correspond to functional groups as follows: D = deciduous, S = semi-deciduous, E = evergreen and L = legume. *F*-statistics (d.f. = 3,83) and *P*-values from ANOVAs are presented. Functional groups that do not share a lowercase letter are statistically different from one another as determined by *post-hoc* Tukey's mean separation tests.

PHYLOGENETIC PATTERNS

Evidence for trait conservatism was strongly dependent on the taxa included in the analyses. When all species were included, leaf habit, N, C and $\delta^{13}\text{C}$ were non-randomly distributed with respect to phylogeny (Table 3). These results

Table 3. The number of randomizations (999 conducted) which resulted in stronger phylogenetic signal than our data

Trait	All species (N = 87)	Fabaceae (N = 18)	All species excluding Fabaceae (N = 69)
Leaf habit	27	63	284
SLA ($\text{cm}^2 \text{g}^{-1}$)	82	322	136
LWC (%)	241	185	547
Wood density (g cm^{-3})	682	174	970
$\delta^{15}\text{N}$ (‰)	85	58	350
$\delta^{13}\text{C}$ (‰)	34	634	14
Leaf N (%)	14	288	168
Leaf C (%)	11	656	127
Leaf P (%)	569	368	565
N/P	244	349	239
C/N	36	335	347

Randomizations were conducted on three partitions of the data (all species, legumes only, and all species excluding legumes). Significant ($P < 0.05$) results are in bold.

were, however, largely dependent on the inclusion of the legumes (Fabaceae); when members of this family were removed from the analyses, only $\delta^{13}\text{C}$ showed significant phylogenetic signal (Table 3). The lack of strong phylogenetic signal in our data (after excluding Fabaceae) indicates that relationships between leaf habit and other functional traits are not confounded by evolutionary relationships among taxa and suggests the evolution of these traits is not strongly constrained by genetic covariances or lack of genetic variation – at least not over the evolutionary time scales captured by our sampling. This conclusion should, however, be viewed with caution given that with the exception of the Fabaceae, the plant families were represented by five or fewer species.

TRAIT CORRELATIONS

For the entire 87 species dataset, 26 of 45 pairwise correlations were statistically significant ($P < 0.05$, Fig. 2). Omitting legumes resulted in two fewer significant correlations, but in general the correlation coefficients were higher (results not shown). Many of the expected correlations between traits were statistically significant, including positive correlations between SLA, leaf N and leaf P (Fig. 2). There was a strong, negative correlation between SLA and $\delta^{13}\text{C}$ (Fig. 2; $r = -0.64$; $P < 0.001$). Wood density was positively correlated to leaf C and negatively correlated with LWC. Not surprisingly, many of the total element concentrations were well correlated with their stoichiometric ratios (results not shown).

ARE LEGUMES REALLY DIFFERENT?

We explored two potential explanations for the differences between legumes and non-legumes; the high leaf N and 'high-N lifestyle' of legumes (Mckey 1994) and compound leaves, which are found in all the legumes we studied but only 20 of the non-legume taxa. To test the importance of leaf N we used

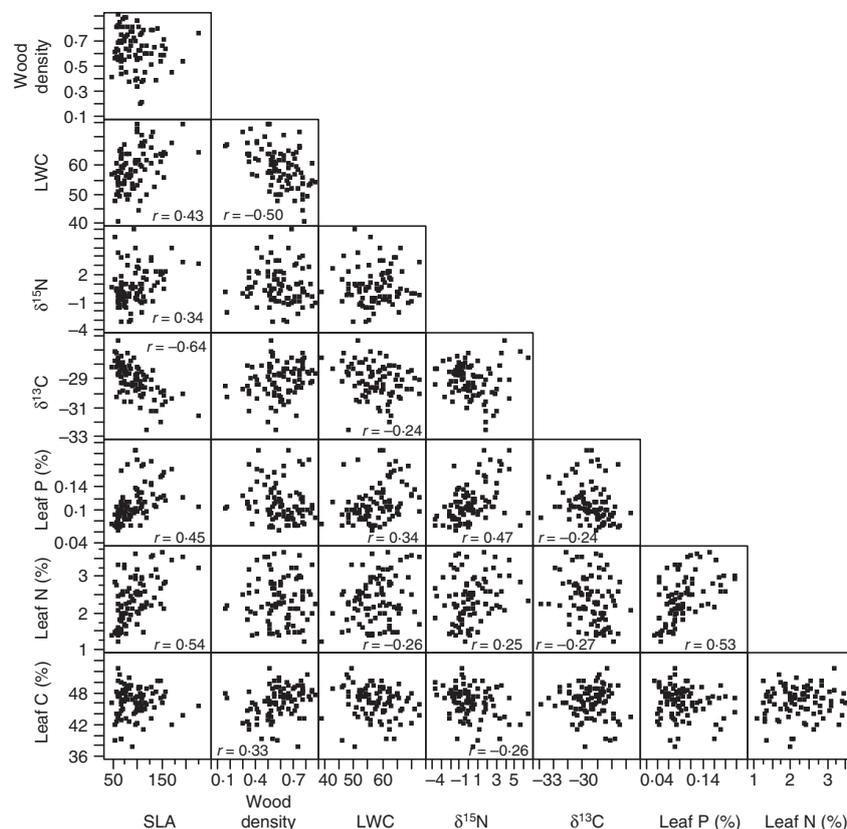


Fig. 2. Scatterplots showing bivariate relationships between specific leaf area, wood density, leaf water content (LWC), $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, leaf N and leaf P. Each point represents the mean value for each of 87 species of tropical dry forest tree. Statistically significant Pearson's correlation coefficients (r) are indicated as follows: bold type $P < 0.05$ and italics $P < 0.001$.

T -tests to compare traits of the 11 legume species with leaf N $> 2.8\%$ (the mean value for all legumes) with the 10 non-legume species (representing the Annonaceae, Apocynaceae, Boraginaceae, Capparaceae, Meliaceae, Moraceae, Nyctaginaceae and Rubiaceae) that also had leaf N $> 2.8\%$ (Table S1). All but one of the non-legume taxa are deciduous, and the legumes include eight deciduous and three semi-deciduous species. T -tests revealed no differences between high-N legumes and high-N non-legumes in leaf N, P, N/P or $\delta^{13}\text{C}$ (Table 4). However, leaf C was significantly higher ($P < 0.05$), $\delta^{15}\text{N}$ was $\sim 2.6\%$ lower ($P < 0.01$) and SLA was $\sim 25\%$ lower ($P < 0.05$) in high-N legumes compared to high-N non-legumes. There was also marginally significant evidence ($P < 0.10$) for lower LWC, and higher wood density and C/N in high-N legumes (Table 4). T -tests comparing traits of the 18 legumes to the 20 compound leaf non-legumes revealed no significant differences in SLA, leaf water content, $\delta^{13}\text{C}$, or leaf P between the two groups (Table 4). However, legumes had significantly higher wood density, leaf C, leaf N, and N/P compared to non-legume taxa with compound leaves, while $\delta^{15}\text{N}$, and C/N were significantly lower ($P < 0.0001$, Table 4).

Discussion

Tropical forests harbor immense diversity of tree species, complicating our ability to incorporate species-level effects

into our understanding of the ecosystem ecology and biogeochemistry of tropical forests. It would therefore be valuable to identify functional groups that could be used to simplify the categorization of biodiversity in these forests. In this study, we found large variation in morphological variables such as SLA and wood density, leaf nutrients, stable isotopic composition, and stoichiometry among 87 dry forest tree species growing in tropical dry forest habitat in north-west Costa Rica. These data are consistent with the emerging view that trait differences among tropical species are large (Guehl *et al.* 1998; Roggy *et al.* 1999; Bonal *et al.* 2000; Townsend *et al.* 2007) and previous studies finding that interspecific diversity is much greater than that found among leaves or trees of the same species (Markesteijn, Poorter & Bongers 2007; Hättenschwiler *et al.* 2008; Hulshof & Swenson 2010). The mean values of traits grouped by leaf habit were consistent with many of our initial hypotheses [e.g. higher SLA, N% and P% in deciduous trees compared to evergreens (Fig. 1)] but the range of values among leaf habits overlapped substantially, and none of the traits differed significantly among leaf habits. Although leaf habit was not a good predictor of functional trait values, legumes differed significantly from non-legumes for several traits. This suggests that for our study site, and perhaps tropical dry forests more generally, the distinction between legumes and non-legumes may be a better criterion than leaf habit for placing dry forest tree species into functional types.

PLANT FUNCTIONAL TYPE AND TRAITS

In temperate ecosystems, trees with deciduous and evergreen leaves differ in many functional traits, and leaf habit defines useful functional types for understanding some of the variation in ecosystem processes such as aboveground net primary productivity and nitrogen mineralization (Reich *et al.* 1997). Because of the ease of collecting information on leaf habit using remote sensing, it would be highly desirable if these generalizations hold for other ecosystems such as tropical dry forests, which also contain both evergreen and deciduous trees. Somewhat surprisingly, leaf habit explained only a small and not statistically significant proportion of the differences in functional traits among dry forest trees in this study.

There are likely many reasons that leaf habit appears to be a good predictor of plant traits in temperate and boreal forest species, but not tropical dry forest species. One potentially important reason is differences in the relationships between leaf morphology, leaf life span, and leaf habit in these different habitats. Many evergreen species in temperate and boreal forests have long-lived needle-like leaves and many of the generalizations about leaf habit derived from literature syntheses compare needle-leaved evergreen species with broad-leaved deciduous species (Killingbeck 1996; Wright *et al.* 2005). By contrast, many if not most species found in tropical dry forests are broad-leaved, regardless of their leaf habit. Moreover, in tropical dry forests, evergreen leaf habit does not necessarily correspond directly with longer leaf lifespans (LLS) and true evergreen species with short leaf lifespans (< 35 weeks) co-exist with drought-deciduous species with longer leaf lifespans (Brodribb & Holbrook 2005). Other studies in the forest we studied have found that LLS of evergreen species varies by a factor of two (S. G. Gotsch, unpublished data), suggesting that LLS may be a promising trait that may be better than leaf habit at grouping species into functional types.

The lack of evidence for leaf habit predicting plant functional traits appears to differ from some previous work in tropical dry forests that found significant differences among species of different leaf habits (Sobrado 1991; Prior, Eamus & Bowman 2003), but is consistent with another study also in Costa Rican dry forest that found no differences in leaf $\delta^{13}\text{C}$ between evergreen and deciduous trees in a sample of 23 species (Leffler & Enquist 2002). A possible reason for our contrasting results is that many previous studies have sampled only a small number of taxa to represent each of the putative functional groups, and in many cases these taxa are not phylogenetically independent (discussed in Eamus & Prior 2001). In contrast, our sample of 87 tree species is taxonomically diverse, and represents a significant portion of the community diversity (Powers *et al.* 2009). If we had selected a smaller number of species from the tail ends of the trait distributions, our conclusions may have been similar (or opposite!) to results from studies that compare only a few taxa. Nevertheless, even a small number of species may be quite diverse from a functional standpoint. For example, the physiology, morphology and growth of six evergreen dry forest species in

Hawaii revealed substantial functional diversity and unusual combinations of traits (Sandquist & Cordell 2007). The potential for high intra-group variation underscores the importance of conducting random and robust sampling when trying to identify useful functional types.

Regardless of the exact reasons or mechanisms, our analyses clearly indicate that leaf habit alone is not sufficient for placing species into ecologically meaningful groups in the forests we studied. It is, of course, possible that more complicated classification schemes may be useful. For example, Borchert (1994) found that a combination of leaf habit and wood density was necessary to divide 37 species sampled in Costa Rica into five functional groups that differed in patterns of leaf flushing and shedding, which were related to stem water storage capacity and distribution on sites with different microhabitats. Such *post-hoc* approaches for classifying functional types are presumably more effective at identifying functional types given that *a priori* classifications of species into functional groups often fail to account for effects on ecosystem processes (Wright *et al.* 2006). However, the predictive power and utility of such *post-hoc* classifications for forecasting ecological processes may be limited. Regardless, for our data neither the individual traits or multivariate traits identified by PCA revealed evidence for clear species groups (with the exception of the legumes), suggesting that it would be difficult to assign *a posteriori* the species we measured into groups based upon the quantitative traits we measured.

WHY ARE LEGUMES DIFFERENT?

One clear pattern in our data is that legumes form a distinct plant functional type with respect to leaf N, C, wood density and leaf stoichiometry. It is likely that both sampling and biology contributed to the Fabaceae being identified as distinct. Reflecting their occurrence in the sampled forests, the Fabaceae were represented by 18 species, while we had data for only five species from the next best represented families. Of the five traits that showed significant phylogenetic conservatism only $\delta^{13}\text{C}$ and %C, showed significant phylogenetic conservatism when only 5 of the 18 legume species were analysed (based on 20 datasets in which the five legumes were randomly selected for inclusion). These results are consistent with suggestions that the power to detect phylogenetic conservatism is affected by sampling (Swenson & Enquist 2009), but does not detract from legumes being a distinct grouping in the sampled forests.

Neither the reasons for the legumes being different nor the consequences of these differences are apparent from this study. Nevertheless, one obvious question is whether the differences between legumes and non-legumes are related to N content, given that it has been known for over a century that they have high N requirements that are partially obtained through symbiotic associations with N-fixing bacteria (Quispel 1988). The large differences in leaf $\delta^{15}\text{N}$ for high-N legumes and legumes compared other compound-leaved species (Table 4) provides strong, albeit indirect, evidence

Trait	High-N legumes (N = 11)	High-N non-legumes (N = 10)	All legumes (N = 18)	All non-legumes with compound leaves (N = 20)
SLA (cm ² g ⁻¹)	107.6**	146.0	98.3	99.8
Leaf water content (%)	60.1*	64.6	57.0	59.2
Wood density (g cm ⁻³)	0.68*	0.58	0.71**	0.56
Leaf δ ¹³ C (‰)	-29.1	-29.8	-28.9	-29.2
Leaf δ ¹⁵ N (‰)	0.03**	2.64	-0.37*	1.16
Leaf C (%)	47.7***	44.3	48.0**	46.3
Leaf N (%)	3.15	3.19	2.84***	2.12
Leaf P (%)	0.12	0.14	0.11	0.12
C/N	15.3*	14.1	17.6***	23.4
N/P	28.5	24.8	28.0***	18.7

Significant differences between high-N legumes and non-legumes, and all legumes and compound-leaved species were assessed by *T*-tests. Significance levels are as follows: **P* < 0.10; ***P* < 0.05; ****P* < 0.001.

that the individual legume trees we sampled (all with crowns exposed to sunlight) are relying on nitrogen fixation to meet some of their N demand (Roggy *et al.* 1999). In fact, high leaf N accounts for much of differences between legumes and other taxa in stoichiometric ratios (C/N, N/P). Leaf N, does not, however, directly explain other differences we observed including higher leaf C in legumes compared to other PFTs (Fig. 1f) and higher wood density in legumes compared to deciduous species (Fig. 1c). Moreover, when we restricted our comparisons to legumes and non-legumes with leaf N > 2.8% to determine whether all 'high-N' species share similar traits, we found that legumes had significantly higher C% and lower SLA, and marginally significant differences in wood density and LWC (Table 4), suggesting legumes are indeed functionally different from other species. Together these data imply that legumes may differ, on average, from the other taxa in physiological processes (e.g. photosynthetic rates), effects on ecosystem processes (e.g. carbon storage and coarse woody debris decomposition rates), and leaf defensive chemistry and palatability to herbivores (Reich & Walters 1994; Coley & Barone 1996; Poorter *et al.* 2008).

A second possible reason for legumes differing from non-legumes is related to all the legumes we sampled having compound leaves whereas fewer of the other taxa did. In our data, this may mean a greater proportion of the leaf mass was due to petioles, possibly explaining the lower SLA and higher leaf C (Niinemets *et al.* 2007) in legumes. This almost certainly explains why the 11 high-N legumes had >25% lower SLA than the 10 high-N non-legume species, nine of which have simple leaves (Table 4). However, our analyses comparing all legumes with other species that have compound leaves suggest that legumes also are distinct from this group, having 27% higher wood density and 4% higher leaf C, in addition to predictably higher leaf N and lower δ¹⁵N (Table 4). Thus, the distinction between simple and compound leaves alone is insufficient to explain the patterns in our data.

A third, unexplored possibility is that the leaflets of legumes' compound leaves, may be effectively functioning as many small leaves, constraining water relations, investment

Table 4. Mean trait values for legumes with high leaf N (N% > 2.8) compared to non-legume species with high leaf N, and all legumes compared to all non-legume, compound leaved species

in structural support and other associated traits. Under this hypothesis, legumes might differ from other compound-leaved species in having smaller leaflets. For example, in a study of ecophysiology and morphological traits of chaparral vegetation, minimum leaf water potential was negatively correlated with wood density and positively correlated to leaf size for 13 evergreen species (Ackerly 2004).

TRAIT CORRELATIONS AND ECOLOGICAL STRATEGIES

Whereas our data do not support the utility of using leaf habit as an indicator of plant functional type, we did find strong correlations among traits that may reflect physiological and/or evolutionary trade-offs in plant form and function (Wright *et al.* 2007). In our data, some of the strongest correlations involved SLA, which was positively correlated to leaf N, leaf P, δ¹⁵N, and leaf water content, and negatively correlated to δ¹³C (Fig. 2). These correlations are consistent with the classic 'leaf economics' trade-off between investment in leaves with high SLA and leaf nutrients that maximize resource capture (i.e. photosynthesis) and investment in thicker leaves that maximize resource conservation and efficient use, including water as reflected by the negative correlation between SLA and δ¹³C (which suggests higher water use efficiency in leaves with lower SLA). Even after correcting for phylogenetic relatedness, leaf N and δ¹³C were negatively correlated (results not shown) – possibly reflecting a tradeoff between carbon gain (assuming leaf N is a robust proxy for photosynthetic rates) and water use efficiency, a tradeoff that has been also detected among six evergreen tree species in a dry forest in Hawaii (Sandquist & Cordell 2007).

Conclusions

Two main conclusions emerged from our study. First, a plant functional type classification based on leaf habit alone has little utility in the tropical dry forests we studied. Although the ranges of interspecific variation for the 10 traits we measured were comparable to other tropical forests, little to none of this variation was explained by leaf habit. Second,

most of the phylogenetic conservatism for the traits we measured was due to one plant family, Fabaceae. Our data suggest that legume trees, which account for a substantial fraction of the family diversity in tropical dry forests as well as elsewhere, have a different suite of traits including high leaf carbon and wood density in addition to high leaf nitrogen. Whether this result generalizes to other tropical forests is not known, but merits future research due to the consequences of these traits for carbon storage and ecosystem processes.

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Supporting information

Additional Supporting information may be found in the online version of this article.

Table S1. Mean trait values for 87 species of tropical dry forest trees.

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