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Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest

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ABSTRACT

Aim To assess the hypotheses that compound leaves of trees in the Amazon forest are an adaptation to drought and/or rapid growth.

Location Amazon rain forest, South America.

Methods Genera from 137 permanent forest plots spread across Amazonia were classified into those with compound leaves and those with simple leaves. Metrics of compound leaf prevalence were then calculated for each plot and regression models that accounted for spatial autocorrelation were used to identify associations between climate variables and compound leaf structure. We also tested for associations between compound leaf structure and a variety of ecological variables related to life history and growth strategies, including wood density, annual increase in diameter and maximum height.

Results One plant family, Fabaceae, accounts for 53% of compound-leaved individuals in the dataset, and has a geographical distribution strongly centred on north-east Amazonia. On exclusion of Fabaceae from the analysis we found no significant support for the seasonal drought hypothesis. However, we found evidence supporting the rapid growth hypothesis, with possession of compound leaves being associated with faster diameter growth rates and lower wood densities.

Main conclusion This study provides evidence that possession of compound leaves constitutes one of a suite of traits and life-history strategies that promote rapid growth in rain forest trees. Our findings highlight the importance of carefully considering the geographical distribution of dominant taxa and spatial clustering of data points when inferring ecological causation from environment–trait associations.

Keywords

Adaptation, Amazonia, Fabaceae, functional traits, geographical ecology, Neotropical forests, permanent plots, phylogeny, RAINFOR, spatial autocorrelation.

INTRODUCTION

A leaf can be considered as an optimal solution to the complex multi-dimensional environmental problem of capturing enough light for photosynthesis (carbon fixation) while main-

taining a healthy water balance and minimizing herbivory (Westoby *et al.*, 2002). The proximate factors that determine leaf characteristics are the result of a combination of genetic control (Niinemets, 1998; Franks & Britton, 2000) and the influence of environmental conditions during leaf development (Bongers &

Popma, 1990; Martínez-Garza & Howe, 2005). One consequence of the influence of evolution and development on leaves is that they should vary in predictable and quantifiable ways with important environmental variables such as elevation, climate and soil characteristics (Fonseca *et al.*, 2000; Reich *et al.*, 2004; Wright *et al.*, 2004; Traiser *et al.*, 2005).

One fundamental division in leaf architecture is whether the leaf is simple (a single lamina and single rachis) or compound (subdivided into leaflets that occur in various arrangements along the rachis) in structure. Compound leaves are relatively abundant (around 30% of both species and individual trees) in many tropical rain forests (Cain *et al.*, 1956; Rollet, 1990; Turner, 2001). Rollet (1990) reported that in tropical South American rain forests the frequency of compound leaf-bearing trees and species varied between 20% and 45% with increasing frequencies in montane, lowland evergreen and semi-deciduous rain forests, respectively.

Therefore it is perhaps surprising that despite our clear understanding of the genetics and development of compound leaves, their functional significance is still being debated. Two main hypotheses and non-mutually exclusive explanations for the adaptive function of compound leaves have been suggested: (1) they are an adaptation allowing rapid growth during favourable light conditions (Givnish, 1978, 1984; Niinemets, 1998) and/or (2) they are an adaptation to seasonal drought (Givnish, 1978; Gates, 1980; Stowe & Brown, 1981).

The rapid growth hypothesis was inferred from observations that trees with compound leaves are often associated with early successional environments and pioneer species autoecology (Givnish, 1978), although this hypothesis has not been subject to rigorous empirical testing (Niinemets, 1998). The advantage of compound leaf structure is thought to derive from the rachis functioning as a cheap 'throwaway' twig, thereby decreasing the need for permanent branching and investment in woody structures and so promoting rapid vertical growth of a leader shoot. Branching (in trees) may be an ecologically expensive strategy not only because it slows down the rate of vertical growth, but also because it incurs the additional physiological (carbon/biomass investment) costs of investing in the lateral branches in addition to any growth required to support the crown (Niinemets, 1998). Moreover, it is important to recognize that, compared with a simple leaf of the same area, compound leaves have a relatively greater investment in (within-leaf) leaf tissue support (Niinemets *et al.*, 2006).

The seasonal drought hypothesis for compound leaves rests on a set of linked assumptions. Compound leaves (or lobed leaves) are more efficient at losing heat through convective processes, and this leads to lower leaf temperatures and less transpiratory water loss than from simple leaves of a similar surface area (Gates, 1980). Furthermore, Givnish (1978) has hypothesized that the ability of trees with compound leaves to shed their leaf units (leaves and accompanying twig) during drought conditions could provide further important reductions in the rate of transpiration by a simple and instant reduction in the number of leaves and amount of woody tissue transpiring. In a rare macrogeographical test of the seasonal drought hypothesis,

Stowe & Brown (1981) compared the proportion of tree species with compound leaves from 37 areas of the United States using data from published floras. They found that tree species with compound leaves tend to occur in areas of high spring and summer temperatures and low rainfall, and that this pattern was not strongly influenced by phylogeny.

Despite Stowe & Brown's (1981) groundbreaking study there have been no attempts (to our knowledge) to repeat this work in tropical forests, despite the considerable abundance of tree species with compound leaves in these ecosystems. This is partly due to the lack of knowledge concerning the geographical distribution of species. Indeed, only a tiny fraction of tropical Amazonia, the largest tropical rain forest on Earth, is covered by any sort of flora or inventory (e.g. Bush & Lovejoy, 2007; Hopkins, 2007). However, with the advent of long-term international projects such as the Large Scale Biosphere–Atmosphere experiment in Amazonia (LBA) and, more recently, the development of the RAINFOR project that networks permanent botanical and forest structure plots across Amazonia (Peacock *et al.*, 2007; <http://www.rainfor.org>) and the ATDN (Amazon Tree Diversity Network) project (ter Steege *et al.*, 2003), analysis of macrogeographical patterns of tree functional traits in Amazonia has now started.

In this paper we use the RAINFOR database of permanent plots (Peacock *et al.*, 2007) to: (1) describe the geographical distribution of compound leaf structure in plots from across Amazonia; and (2) investigate the two main hypotheses (above) for the function of compound leaves in tropical forests. Specifically, we use taxonomic and individual-based metrics of the incidence of compound leaf structure to test the various assumptions and predictions of the two alternative (but not necessarily mutually exclusive) hypotheses.

The most direct predictions of these hypotheses are: (1) if compound leaves are an adaptation to seasonal drought then the contribution of individual trees and genera of trees with compound leaves to Amazonian tree communities will increase with increasing length and severity of the dry season (Givnish, 1978; Stowe & Brown, 1981); and (2) if compound leaves are an adaptation for rapid growth then the diameter growth rate of the trees with compound leaves will be higher than for trees with simple leaves (Givnish, 1978, 1979, 1984, 1987), having controlled for tree size. Here we assume that diameter growth is a reasonable proxy for vertical growth.

We also test several subsidiary predictions that can be derived from the rapid growth hypothesis. Specifically, it has been suggested that trees with compound leaves are more likely to be pioneer species (Givnish, 1978). However, here it should be noted that rain forest pioneer species are often divided into two classes, consisting of 'long-lived' and 'tall' (> 30 m) species and 'short-lived' or 'short' (< 30 m) taxa (Ackerly, 1996). In the current study we test whether the proportion of trees with compound leaves is greater among taller or shorter height classes. We also test the related prediction that trees with compound leaves have lower wood densities – a prediction derived from the observation that early successional species typically grow fast and build low-density stems – while

slow-growing late successional species have higher wood densities (Köhler *et al.*, 2000).

MATERIALS AND METHODS

Database construction

For exploring spatial variation in compound leaf structure across the Amazon we used 137 permanent plots distributed across eight South American countries (see Appendix S1 in Supporting Information; remaining data are available on request). Some ecological and environmental data are unavailable for particular plots and, consequently, plots with missing environmental data were removed prior to some analyses. The complete database used in this study (date of extraction August 2006) contained a total of 105,262 individual trees ≥ 100 mm diameter at breast height (d.b.h.) from 727 genera. The RAINFOR database includes multiple censuses for many plots, allowing derivation of diameter growth rates.

To this existing database, information was added on the leaf organization (compound or simple) for each genus. Tree genera were classified as compound or simple leaved (hereafter denoted as CL and SL, respectively) if all species in the genus showed this trait or if there were only single exceptions (670 genera). The following types of genera were excluded from the analysis: (1) genera containing a mixture of SL and CL species ($n = 24$), (2) palms ($n = 17$), and (3) genera for which data on leaf organization were not available ($n = 16$). We used data at the taxonomic level of genus to: (1) decrease the influence of species showing similarities in leaf structure simply because they share a recent common ancestor, and (2) because data on genera are more complete (ter Steege *et al.*, 2006) and using species-level data would introduce errors due to uncertain identities at that taxonomic level.

All information on leaf organization was derived, where possible, from a single source to reduce variation caused by conflicting interpretations of CL form. In our study Gentry (1996) was used as the primary reference to determine the leaf organization of genera and species. A Brazilian guide for the Ducke Reserve (Ribeiro *et al.*, 1999) and a Peruvian guide for the Biological Reserves of Iquitos (Vásquez-Martínez, 1997) were used as supplementary sources of information where required.

The plots used in this study span local and regional environmental gradients that naturally occur in Amazonia. All sites consisted of an apparently mature forest with natural gap-phase dynamics and a canopy dominated by non-pioneer species and, furthermore, none of the plots is believed to have experienced any recent human-caused disturbance. The individual plots range in size from 0.25 to 9 ha (mean \pm SD = 1.1 ± 0.98 ha, total sampled area = 156.5 ha). The number of stems per plot (after removing the undetermined stems) ranged from 209 to 838 ha⁻¹ (mean \pm SD = 508 ± 92 ha⁻¹).

Leaf structure metrics

The spatial patterns of variation in leaf organization (SL or CL) were assessed through the use of several simple metrics, which

acted as descriptor variables for our geographical analysis and dependent variables within ordinary least squares (OLS) regressions that accounted for spatial autocorrelation (see below). Our four main variables are: (1) 'individual % CL' = the proportion of individual trees in each plot that displayed the functional trait of CL; (2) 'generic % CL' = the proportion of genera in each plot with CL structure; (3) 'basal area % CL' = the contribution of trees with CL to the summed basal area for each plot; and (4) 'size class % CL' = the distribution of trees with different leaf organization across six ordinal size classes of d.b.h. (100–199, 200–299, 300–399, 400–499, 500–599, > 600 mm). For mapping purposes, each plot was assigned to one of six ordinal categories (< 15, 15–30, 31–45, 46–60, 61–75, > 75%) based on the proportion of trees (or genera) with CL.

Geographical patterns in leaf structural arrangements and environment–trait correlations might also be found if a particular leaf type (e.g. compound) is associated with a large dominant taxon (Stowe & Brown, 1981). In the current study, for instance, the observed geographical distribution of CL could be due to environmental or historical factors driving or accounting for the spatial distribution of the dominant taxon, rather than the trait *per se*. To assess the potential influence of taxonomic dominance, we also performed all analyses of simple versus compound leaves on both the full dataset (hereafter called CL-ALL) and the following sub-sets: (1) CL trees excluding the largest family of CL trees (Fabaceae) (hereafter called CL-OTHERS) (cf. Stowe & Brown, 1981); (2) the Fabaceae only, i.e. with all other CL genera removed (hereafter called CL-FABACEAE). Although a crude filter, due to the numerical abundance of the Fabaceae in Amazonia, this analysis provides a simple control for the potential impact of phylogeny on the dataset – more sophisticated factoring in of phylogenetic effects also being unfeasible with the type of regression models used in the study (see below). Another potential confounding factor in this sort of analysis is that ecological and physical variables may be more similar (or dissimilar) because of their spatial proximity, and it was therefore appropriate to account statistically for spatial autocorrelation (Legendre, 1993; see below).

Geographical distribution of compound leaves

Recent studies (e.g. Baker *et al.*, 2004; Malhi *et al.*, 2004; ter Steege *et al.*, 2006; Malhado *et al.*, 2009) have demonstrated consistent ecological differences in tree characteristics among different regions of the Amazon. Here, to aid direct comparisons with these studies, we follow the practice of splitting the Amazon into four main regions: Region 1, north Amazonia, containing plots from Guyana, Suriname and Venezuela; Region 2, north-west Amazonia, containing plots from Ecuador, Colombia and north Peru; Region 3, central and east Amazonia, all Brazilian plots (states of Amazonas and Pará only); Region 4, south-west Amazonia, containing plots from Bolivia and south Peru.

The seasonal drought hypothesis

The seasonal drought hypothesis was assessed by searching for spatially corrected correlations between plot-based metrics of

CL structure and a range of precipitation variables. Potential predictor variables were chosen to reflect the main factors that have been observed, or predicted, to influence the distribution of CL structure in forests. We used a time series (1998–2005) of cumulative monthly rainfall derived from the Tropical Rainfall Measuring Mission (TRMM 3B43-V6) at 0.25° spatial resolution. This product combines multiple data sources, including satellite information on rainfall, with ground precipitation gauge adjustment (Huffman *et al.*, 2007). These data have been shown to represent the rainfall patterns over the Amazonian region with acceptable accuracy (Aragão *et al.*, 2007). The following variables were estimated: (1) the cumulative annual rainfall (mm year⁻¹); (2) the standard deviation (SD) of rainfall within the year, as a measure of seasonality; (3) the maximum climatological water deficit (MWD; mm), calculated by assuming that the actual evapotranspiration rate is approximately 100 mm month⁻¹ in tropical forests (Heuvelink & Neumann, 1983); and (4) the length of the dry season, as the number of months with rainfall < 100 mm month⁻¹ (see Malhado *et al.*, 2009, for figure). Although crude, the MWD is thought to be a useful indicator of meteorologically induced water stress without taking into account local soil conditions and plant adaptations, which are poorly understood in Amazonia (Aragão *et al.*, 2007).

It should be recognized that a 7-year climate time series represents a small sample of current climate, and that this may not necessarily represent the historical environment within which the tree species evolved. Here, we make the assumption that current climate provides a sufficient approximation of historical climate to pick up any strong environment–trait associations. However, due to this assumption we would still advise a cautious approach to interpreting these results.

The rapid growth hypothesis

The rapid growth hypothesis was assessed by comparing the diameter growth rate of SL trees with that of CL trees. We calculated the annual diameter growth rate as the change in d.b.h. year⁻¹ and we controlled for the relationship between absolute growth and tree size by adding initial d.b.h. as a co-variable within a generalized linear model (GLM). It should be noted that we were not able to control for competition and assumed that spatial differences in this parameter were independent of, or weakly related to, trait variation. Data were extracted from the RAINFOR database for 51,809 trees for which data exist from more than one census (the census interval ranged from 4 to 20 years). For the purposes of harmonization, following Baker *et al.* (2004), we removed ‘extreme’ diameter growth rates (≤ -2 mm year⁻¹ or ≥ 40 mm year⁻¹). Furthermore, we also controlled for the influence of plot-level effects and the possibility of spatial pseudoreplication (e.g. competition among trees) through the comparison of diameter growth rates of CL trees and SL trees within a plot. Specifically, we calculated the mean (logged) diameter growth rate for CL and SL trees within a plot and calculated a relative growth index by subtracting the value for CL trees from that of SL trees. To assess if CL trees have a higher (or lower) diameter growth rate than SL trees across the

entire dataset we tested whether the mean relative growth index for all the plots combined was significantly different from zero. The same procedure was repeated on the subsets and using two different d.b.h. size categories (100–200 mm and >400 mm) to account for the possible influence of initial tree size on diameter growth rates.

We also tested whether SL and CL genera differ in mean wood density, mean maximum height and whether they predominantly comprise pioneer species. Here, mean wood density and mean maximum height of genera were calculated using information available in the RAINFOR database and derived from published sources (Baker *et al.*, 2004; Peacock *et al.*, 2007). We define the growth strategy of each genus through a simple index (henceforth referred to as the pioneer index) based on expert judgement. This index reflects the degree of consensus among botanists familiar with the taxa, in this case Oliver Phillips, Rodolfo Vásquez-Martínez and Abel Monteagudo, and was cross-referenced with information from herbarium material collection labels. For the purposes of developing the pioneer index, the pioneer concept was defined for the experts as ‘plants that are specialists in forest gaps and other disturbed areas’. To calculate the index, each taxon was judged independently by each botanist and given a value between 0 (‘non-pioneer’) and 1 (‘pioneer’). The pioneer index was then calculated as the average score for each taxon.

Statistical analysis

Although the permanent plots in the RAINFOR database are distributed across Amazonia, they do show some spatial pattern of clustering that must be accounted for in the statistical analysis (see latitude and longitude in Appendix S1). There are several techniques available that describe and control for spatial structure in ecological datasets (e.g. Rangel *et al.*, 2006; Dormann *et al.*, 2007). Herein, we used spatial filters based on principal coordinates of neighbouring matrices (PCNM) to partition the effects of spatial and environmental components on the response variable. In PCNM, statistically significant eigenvectors describing the relationship between permanent plots can be entered into a partial regression model as predictor variables along with the environmental variables of interest (Diniz-Filho & Bini, 2005). Here, we first tested for the presence of spatial autocorrelation in the residuals through the use of Moran’s *I* index and Moran’s *I* correlograms. Second, because of evidence of spatial autocorrelation, we used PCNM to generate spatial eigenvectors that were then tested for significance against the response variable (following Diniz-Filho & Bini, 2005). Finally, statistically significant eigenvectors and climate metrics were entered as explanatory variables into standard OLS regression models. All spatial analyses were performed using the software Spatial Analysis in Macroecology (SAM v. 2) (Rangel *et al.*, 2006).

We used a generalized linear model (GLM) and *t*-test to test the rapid growth hypothesis. To account for potential interactions between the mean maximum published height, wood density and pioneer index of a genus, a GLM was used to identify significant differences between simple-leaved and

compound-leaved tree categories. Unless otherwise noted above, all analyses were performed using SPSS 14.0.

In the following we use 'CL-Trees' to refer to the (percentage) frequency of trees in a plot assigned to CL genera and we use 'CL-Genera' to refer to the (percentage) frequency of genera in a plot that are deemed to be CL genera.

RESULTS

Geographical distribution of compound leaves

The CL-Genera values varied from 7% up to 50% (Fig. 1). Values for CL-Trees varied in a broader range from 2% to 83%. There is a clear clustering of plots with high CL-Genera and CL-Trees in Venezuela and Guyana and plots with low frequencies in southern Amazonia (Fig. 1). However, there is also considerable variation within each region. For example, we also found plots with very low CL-Trees values in the Guiana Shield region.

The average CL-Trees across the 137 plots was $27.9 \pm 13.5\%$ (mean \pm SD). CL-Trees make up an average of $29.0 \pm 13.3\%$ (mean \pm SD) of the total basal area for all trees in all plots with

available data ($n = 101$). The average CL-Genera across the 137 plots was $27.55 \pm 7.55\%$ (mean \pm SD). There was no significant difference between the CL-Trees (individuals with CL) and CL-Genera (genera with CL) within a plot ($t = -0.236$, d.f. = 136, $P = 0.814$). The most abundant CL genera were: *Protium* (Bursaceae; representing 13.9% of individuals with CL), *Inga* (Fabaceae; 9.5%), *Eperua* (Fabaceae; 7.7%), *Guarea* (Meliaceae; 5.5%) and *Trichilia* (Meliaceae; 4.4%). Fabaceae trees with CL constitute 53.4% of all CL trees.

When the plots (CL-ALL) were divided into four Amazonian regions, we found significant differences among the regions in the frequency of CL trees ($F = 16.29$, d.f. = 3, $P < 0.001$; Table 1) and the distribution of CL trees in different d.b.h. size categories (Fig. 2). Tukey's post hoc test revealed that the statistically significant differences are between the high values for CL-Trees in the north Amazonia region and the lower values in all others regions. Furthermore, the central and east Amazonia region has significantly higher CL-Trees values than the south-west Amazonia region. However, when we removed genera belonging to the largest family of CL-Trees (CL-OTHERS, i.e. all data excluding the Fabaceae) we found no statistically significant differences in the average CL-Trees across the four regions ($F = 0.83$,

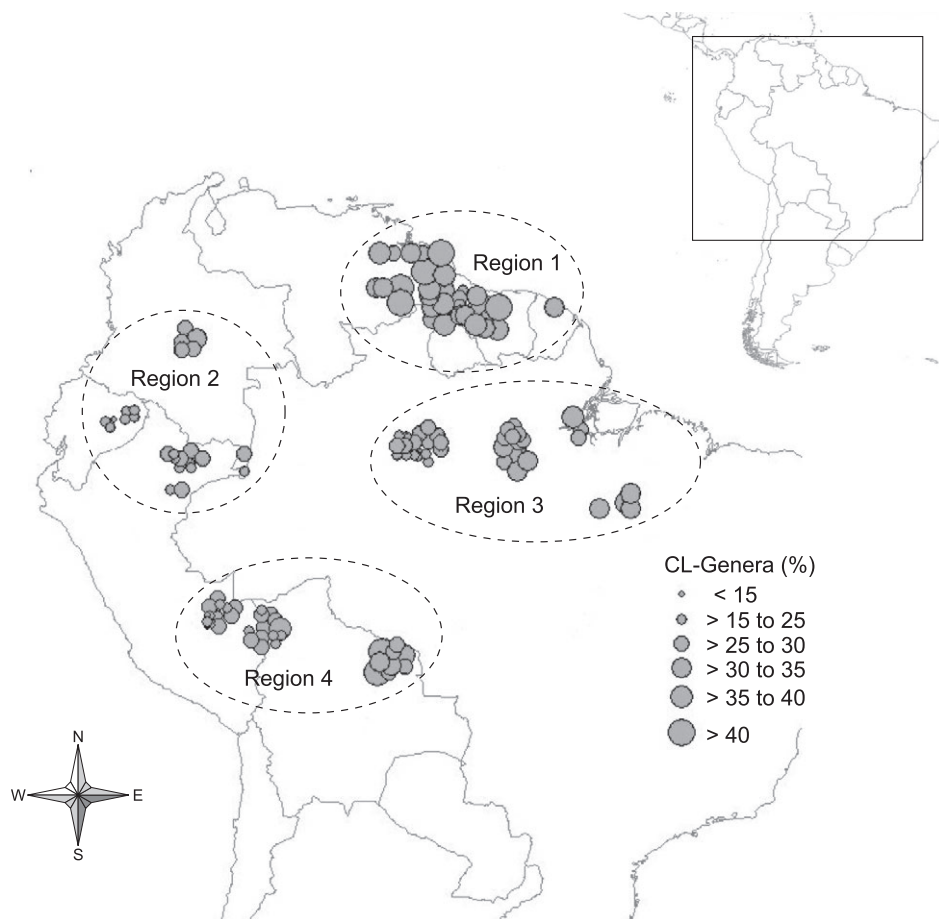
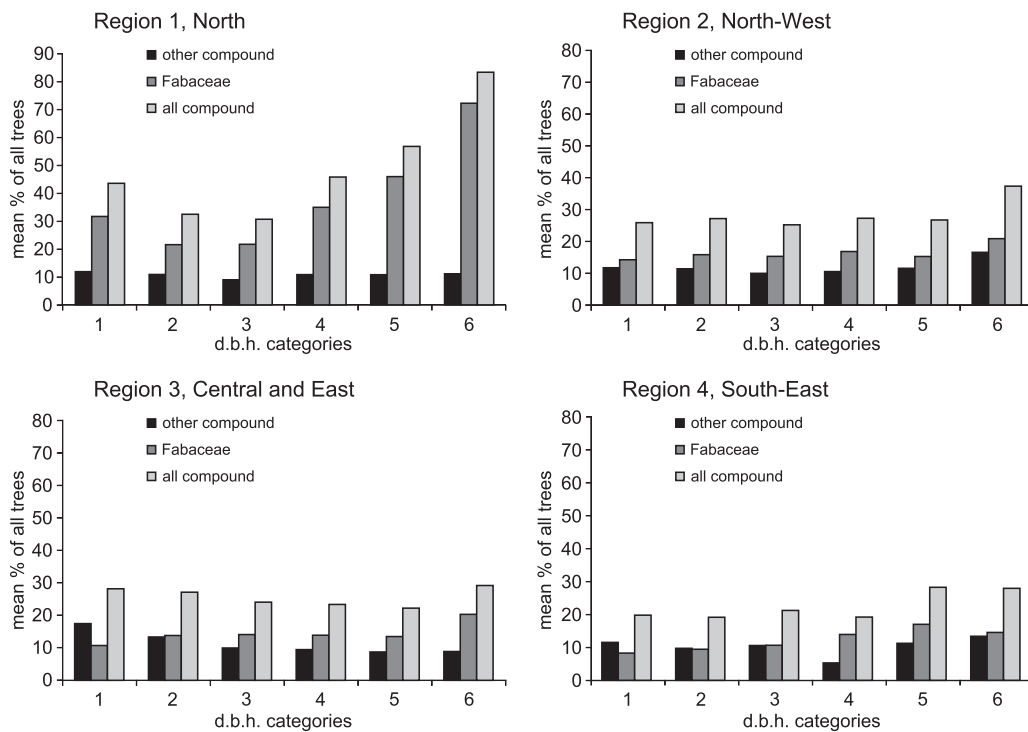


Figure 1 Map of the incidence of genera with compound leaves (CL) in each plot organized by frequency categories and regions. For the purposes of clear visualization the positions of some plots within clusters have been adjusted, and may not correspond to exact geographical location. The inset shows the geographical context.

Table 1 Proportion of trees with compound leaves (%CL), proportion of trees with compound leaves when Fabaceae are excluded from analysis, and density of Fabaceae (trees ha⁻¹) in plots in the four Amazonian regions and all regions combined.

Regions	Mean	No. of plots	Std deviation	Std error	Lower bound*	Upper bound*
% of CL in the whole database						
Region 1: north Amazonia	38.69	34	19.52	3.35	31.88	45.50
Region 2: north-west Amazonia	26.54	27	6.36	1.23	24.02	29.06
Region 3: central-east Amazonia	27.48	37	7.07	1.16	25.13	29.84
Region 4: south-west Amazonia	19.64	39	8.46	1.35	16.90	22.39
All regions = total	27.85	137	13.51	1.15	25.57	30.13
% of CL when Fabaceae are removed						
Region 1: north Amazonia	21.39	34	5.31	0.91	19.54	23.25
Region 2: north-west Amazonia	19.88	27	3.80	0.73	18.38	21.39
Region 3: central-east Amazonia	20.46	37	4.08	0.67	19.11	21.82
Region 4: south-west Amazonia	19.96	39	4.26	0.68	18.58	21.34
All regions = total	20.44	137	4.41	0.38	19.69	21.18
Density of Fabaceae						
Region 1: north Amazonia	137.29	34	86.61	14.85	107.08	167.51
Region 2: north-west Amazonia	80.40	27	45.45	8.75	62.42	98.38
Region 3: central-east Amazonia	67.62	37	23.29	3.83	59.85	75.39
Region 4: south-west Amazonia	36.44	39	30.46	4.88	26.56	46.31
All regions = total	78.56	137	63.42	5.42	67.84	89.27

*95% confidence interval of mean.

**Figure 2** Mean proportion of trees per plot with compound leaves (% of CL) in different d.b.h. size categories in relation to the total number of trees in each category for plots in the four Amazonian regions (size class: 1 = 100–199 mm, 2 = 200–299 mm, 3 = 300–399 mm, 4 = 400–499 mm, 5 = 500–599 mm, 6 = > 600 mm). ‘all compound’ = all trees with compound leaves; ‘Fabaceae’ = trees in the Fabaceae (all of which have compound leaves); ‘other compound’ = non-Fabaceae trees possessing compound leaves.

Dependent variable	Independent variables	<i>B</i>	<i>t</i>	<i>P</i>
% CL-Trees (CL-ALL)	Total rainfall	0.18	0.81	0.42
	Maximum water deficit	-0.15	-0.72	0.47
	Length of dry season	0.04	0.13	0.90
	Variation of rainfall	0.09	0.47	0.64
% CL-Genera*	Total rainfall	-0.06	-0.29	0.78
	Maximum water deficit*	-0.38	-2.02	0.05
	Length of dry season	-0.44	-1.64	0.10
	Variation of rainfall*	0.43	2.75	0.01
% Contribution to basal area	Total rainfall	0.52	1.72	0.09
	Maximum water deficit	0.08	0.30	0.77
	Length of dry season	0.44	1.19	0.23
	Variation of rainfall	0.24	1.07	0.29
Density of Fabaceae trees in each plot (CL-FABACEAE)	Total rainfall	0.40	1.84	0.07
	Maximum water deficit	0.20	0.97	0.33
	Length of dry season	0.52	1.78	0.08
	Variation of rainfall	-0.02	-0.09	0.93
% of CL when Fabaceae family is removed (CL-OTHERS)	Total rainfall	-0.29	-1.20	0.23
	Maximum water deficit	-0.08	-0.36	0.72
	Length of dry season	-0.22	-0.65	0.52
	Variation of rainfall	0.12	0.64	0.52

Spatial structure was accounted for in the regressions by adding eigenvector filters produced with the principal coordinates of neighbouring matrices (PCNM) – these eigenvector filters are omitted from the table. Only plots with measurements for all variables were used in the regressions. All dependent variables were transformed prior to analysis. CL = compound leaves, CL-Trees = individual trees with compound leaves. CL-Genera = genera of trees with compound leaves. *Statistically significant result at $P < 0.05$.

d.f. = 3, $P = 0.481$; Table 1). As anticipated, we also found significant regional differences in the prevalence of Fabaceae (CL-FABACEAE) ($F = 23.78$, d.f. = 3, $P < 0.001$; Table 1).

The seasonal drought hypothesis

The result of OLS regressions using the entire dataset (all taxa) indicates that CL-Trees and the contribution of compound leaves to the total summed basal area of each plot are not significantly associated with water availability metrics (Table 2). However, CL-Genera values are correlated with MWD, and standard deviation of total rainfall (Table 2). In the analyses of the data subsets, no statistically significant relationships were found with water deficit for either (1) the density of Fabaceae in each plot or (2) the frequency of CL-OTHERS (Table 2).

The rapid growth hypothesis

Trees with CL showed significantly higher annual diameter growth rates than trees with SL ($F = 307$, d.f. = 1, $P < 0.001$; mean diameter growth rate 1.3 times that of SL). This difference in diameter growth rates is more apparent when analysing the data subset CL-FABACEAE. In this case the CL Fabaceae have a mean diameter growth rate 1.5 times that of SL genera ($F = 557.9$, d.f. = 1, $P < 0.001$). However, this difference in growth rates is still significant in the CL-OTHERS analysis ($F = 9.609$, d.f. = 1, $P = 0.002$; mean diameter growth rate 1.03 times that of SL). The

Table 2 Partial regression coefficients of the ordinary least squares (OLS) regression (*B*), *t* statistics and associated *P*-values for metrics of compound leaf (CL) structure, indicating the contribution of climatic variables (taking into account spatial autocorrelation) to explaining the frequency of trees with compound leaves in plots.

plot-level analyses (controlling for spatial pseudoreplication and plot-level effects) of relative diameter change of CL versus SL trees confirms a higher diameter growth rate of CL-Trees in the full dataset ($t = 8.4$, d.f. = 100, $P < 0.001$; Fig. 3), the Fabaceae-only dataset ($t = 13.6$, d.f. = 100, $P < 0.001$; Fig. 3) and the CL-OTHERS dataset ($t = 4.8$, d.f. = 100, $P < 0.001$; Fig. 3). Plot-level analysis of trees in the small diameter class (100–200 mm) also showed higher diameter growth rates for CL trees ($t = 4.6$, d.f. = 98, $P < 0.001$) and the same pattern is seen in the larger diameter category subset (> 400 mm) ($t = 4.9$, d.f. = 99, $P < 0.001$).

No significant differences were found between SL and CL genera for wood density ($F = 0.2$, d.f. = 1, $P = 0.652$). However, in the CL-OTHERS, SL genera showed a higher wood density than their CL counterparts ($F = 8.8$, d.f. = 1, $P = 0.003$). In contrast, the Fabaceae have higher wood density than SL genera ($F = 5.2$, d.f. = 1, $P = 0.023$), which explains the non-significant result for the complete dataset (Fig. 4).

Genera with CL have significantly greater maximum heights than SL counterparts ($F = 7.2$, d.f. = 1, $P = 0.008$). This pattern is entirely attributable to the Fabaceae; when they are excluded (CL-OTHERS) there is no significant difference between the maximum published heights of trees for the two categories of leaf organization ($F = 1.3$, d.f. = 1, $P = 0.261$).

No significant associations were found between SL and CL genera and the pioneer index ($F = 0.025$, d.f. = 1, $P = 0.876$). Likewise, no associations were found between the pioneer index

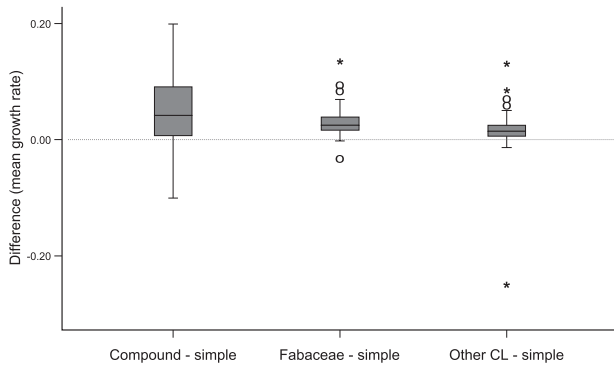


Figure 3 Relative annual diameter (d.b.h.) increment of compound-leaved trees versus simple-leaved trees for each plot calculated as the difference between: (left) the mean d.b.h. increment of all compound-leaved trees minus the mean d.b.h. increment of simple-leaved trees; (centre) the mean d.b.h. increment of compound-leaved trees in the Fabaceae minus mean d.b.h. increment of simple-leaved trees, and (right) the mean d.b.h. increment of non-Fabaceae compound-leaved trees (other-CL) minus mean d.b.h. increment of simple-leaved trees. The top of each box represents the 75th percentile, the bottom represents the 25th percentile, and the line in the middle represents the 50th percentile (median). The whiskers represent the highest and lowest values that are not outliers or extreme values. Circles represent outliers and asterisks represent extreme values.

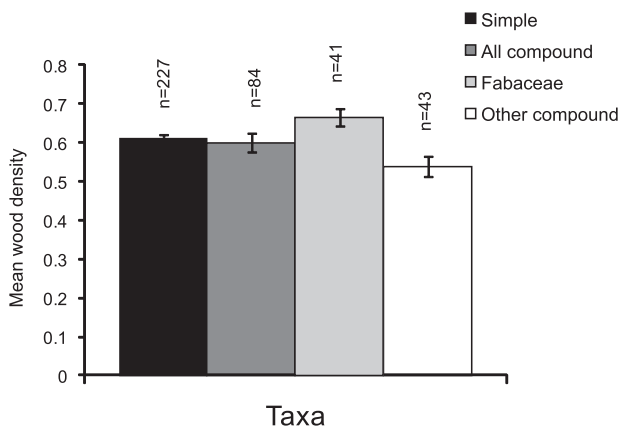


Figure 4 Mean wood density of genera with compound and simple leaves using the three datasets. Error bars represent one standard deviation of the mean.

and CL-FABACEAE ($F = 0.001$, d.f. = 1, $P = 0.975$) or CL-OTHERS ($F = 0.206$, d.f. = 1, $P = 0.615$).

DISCUSSION

Geographical distribution of the compound leaf trait

The average incidence of individual CL trees and genera was approximately 28%, which is similar to values reported by

several other studies in tropical forests (Cain *et al.*, 1956; Rollet, 1990; Turner, 2001). However, there were large variations between plots and among the four Amazonian regions. Specifically, the north has a greater proportion of CL trees, a pattern largely attributable to the high frequency of Fabaceae in this region.

The geographical distribution of compound leaves in Amazonia does not therefore fit simply into any of the observed ecological gradients in this region, such as those uncovered by ter Steege *et al.* (2006) using a dataset largely based on forest inventories of trees > 30 cm diameter. Their study found two dominant gradients in tree composition across the Amazon. The first gradient (north-east to south-west) corresponded to a major gradient in soil fertility and the second (north west to south east) was related to length of the dry season. In the current study, no similar general geographical patterns were found.

Members of the CL family Fabaceae are numerically abundant in the Amazon and show clear spatial patterns in and across the four geographical regions. The ecological driver of the observed distribution of Fabaceae may be related to the fact that tree species within this family are able to produce larger seeds under low nutrient conditions than many other tree species, and may therefore be favoured in the low-nutrient and low-dynamics environments of Guyana and north-eastern Amazonia (ter Steege *et al.*, 2006). Hence, it is possible that a trait shared by the Fabaceae other than their leaf type may account for the patterns in their distribution and abundance.

The seasonal drought hypothesis

The OLS analyses performed on the complete dataset suggest that the proportion of CL genera (Table 2) is associated with two water availability metrics – in this case MWD and standard deviation of total rainfall. These results may indicate that seasonality plays a role in favouring CL structure. This result has some similarity with that of Stowe & Brown (1981) who found that CL trees in North America were associated with regions of low rainfall (and high spring and summer temperatures).

It is notable that this result was only evident after accounting for the spatial structure of the data. However, no further explanatory variables were significant when the Fabaceae were included or removed from the dataset (Table 3). Moreover, analyses based on CL-Trees showed no relationship with water variables. Only one metric of CL structure (CL-Genera) gave significant results. This was correlated with two out of four climate metrics, possibly indicating that the environment–trait association is relatively weak in this case. This result is perhaps not surprising given that a key assumption herein is that contemporary climatic variables are a good proxy for the historical climates and, by extension, climate-related selection filters experienced by the Amazonian tree flora. The weakness of the relationship might thus be evidence of the ‘ghost of selection past’ – which is likely to be related, but not identical, to conditions currently experienced.

Table 3 Table of level of significance (significant: $0.05 > P > 0.01$; highly significant: $P < 0.01$) for hypotheses and predictions using the full dataset, the dataset without the Fabaceae, and the dataset considering only the Fabaceae.

Hypotheses/predictions	Whole dataset	Fabaceae removed	Just Fabaceae
Frequency of CL shows regional patterns	Highly significant	Not significant	Highly significant
Frequency of CL increases with length and intensity of dry period	Significant	Not significant	Not significant
Trees with CL have higher diameter growth rate than trees with SL	Highly significant	Highly significant	Highly significant
Frequency of CL in genera is associated with early successional vegetation	Not significant	Not significant	Not significant
Frequency of CL in genera is associated with lower wood density	Not significant	Highly significant	Significant*
Frequency of CL in genera is associated with maximum height	Highly significant	Not significant	Highly significant

*Inverse relationship.

CL = compound leaves; SL = simple leaves.

The rapid growth hypothesis

One of the alternative hypotheses for the adaptive function of CL is that they promote rapid growth during favourable light conditions, such as those found in gaps in the canopy (Givnish, 1978, 1984; Niinemets, 1998). In the present study, the diameter growth rate (increase in diameter per year) of CL trees with was significantly greater than that of SL counterparts, and although this relationship was much stronger within the Fabaceae it was still present within the other datasets (Table 3, Fig. 3). Furthermore, the pattern is still apparent when we apply statistical tests that account for any potential influence of spatial pseudoreplication, initial diameter and/or local environmental differences at very small spatial scales (e.g. microclimate or competition).

Despite the significantly higher diameter growth rates of CL trees they do not seem to be over-represented among pioneer species as determined through the pioneer index (Table 3). The lack of relationship between pioneer status and possession of CL is consistent with the findings of Niinemets (1998), who has suggested that CL may be an important adaptation for decreasing branching and increasing rapid vertical growth among both shade-tolerant and pioneer species (Niinemets, 1998). This finding also supports the findings of Popma *et al.* (1992), who found no association between obligate gap-dependent species and CL structure in trees in a lowland tropical rain forest in Mexico. Moreover, the lack of correlation may indicate that the pioneer index may not be effectively capturing the rapid growth characteristics of trees – or, at least, not sufficiently precisely to generate a statistical differences – possibly because the plots are all from mature forest.

The association between a higher frequency of CL genera and lower wood density (when the Fabaceae are removed from the dataset) is consistent with the prediction of the rapid growth hypothesis that fast-growing trees have lower wood density, especially in early successional species that adopt the ecological strategy of growing fast and building low-density stems (Köhler *et al.*, 2000). It is interesting to note that the Fabaceae have a higher average wood density than do trees with simple leaves, demonstrating the benefits of taxonomically partitioning datasets to uncover ecological patterns that may otherwise remain hidden. These associations between traits also suggest that compound leaves might have multiple adaptive values.

CONCLUSIONS

The results presented here provide some interesting insights into the ecology and biogeography of the Amazon rain forest. Firstly, it is clear that the macrogeographical distribution of leaf organization traits does not vary in a simple way with other, more intensively studied, ecological traits of Amazonian trees. For instance, previous studies using the RAINFOR database have suggested that forests in western Amazonia have higher wood productivity (Malhi *et al.*, 2004), higher turnover (Phillips *et al.*, 2004) and lower wood density and biomass (Baker *et al.*, 2004) than forests growing on infertile soils further east. Trees with compound leaves do not show any similarly straightforward regional patterns.

Secondly, the dominance of one numerically abundant CL taxon, the Fabaceae, rendered some of the observed geographical and ecological correlates of the CL trait difficult to interpret. Thus, the fact that functioning can be strongly tied to specific taxa is an important general point that should be taken fully into account in any future biogeographical studies of this nature. Thirdly, there is some support for both the seasonal drought hypothesis and for the rapid growth hypothesis, suggesting that leaf organization may play an important and as yet largely unrecognized role in the dynamics of the Amazon rain forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary information on all plots used in this study.

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BIOSKETCH

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