

## LETTER

# Decoupled leaf and stem economics in rain forest trees

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## Abstract

Cross-species analyses of plant functional traits have shed light on factors contributing to differences in performance and distribution, but to date most studies have focused on either leaves or stems. We extend these tissue-specific analyses of functional strategy towards a whole-plant approach by integrating data on functional traits for 13 448 leaves and wood tissues from 4672 trees representing 668 species of Neotropical trees. Strong correlations amongst traits previously defined as the leaf economics spectrum reflect a tradeoff between investments in productive leaves with rapid turnover vs. costly physical leaf structure with a long revenue stream. A second axis of variation, the ‘stem economics spectrum’, defines a similar tradeoff at the stem level: dense wood vs. high wood water content and thick bark. Most importantly, these two axes are orthogonal, suggesting that tradeoffs operate independently at the leaf and at the stem levels. By simplifying the multivariate ecological strategies of tropical trees into positions along these two spectra, our results provide a basis to improve global vegetation models predicting responses of tropical forests to global change.

## Keywords

Functional diversity, leaf economics, multiple factor analysis, plant strategies, plant traits, tropical forest, wood density.

*Ecology Letters* (2010) 13: 1338–1347

## INTRODUCTION

The study of plant functional traits has contributed much to our understanding of the factors shaping species distributions (Diaz *et al.* 2004; Engelbrecht *et al.* 2007), and predicting responses of ecosystem structure and function to global changes (Diaz *et al.* 2007; Suding *et al.* 2008). Several recent advances have resulted from the integration of functional traits with traditional studies describing the performance and distribution of species

across environmental gradients (Diaz *et al.* 2004; Suding *et al.* 2005; Westoby & Wright 2006; Poorter *et al.* 2008). In particular, cross-species comparisons have revealed important axes of trait variation, building from traits such as seed size (Moles *et al.* 2005) and growth form (Diaz *et al.* 2004) to physiological (Sack & Frole 2006) and anatomical measurements (Zanne *et al.* 2010). An important recent breakthrough was the description of a leaf economics spectrum (LES) (Wright *et al.* 2004), which contrasts inexpensive short-lived leaves with rapid returns on carbon

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and nutrient investments vs. costly long-lived leaves with slow returns on investments. A separate line of evidence has suggested that an axis of variation related to several wood traits also exists (Chave *et al.* 2009) and correlates with plant performance (Poorter *et al.* 2010). Yet it remains unknown whether traits describing the function of different tissues such as leaves and wood are coordinated. An analysis of functional traits at the scale of whole plants is vital to understand the complicated relationships amongst traits, performance and species distributions (Westoby & Wright 2006). Here, we contribute an important first step: examining the relationships amongst traits associated with leaf and wood tissues.

Alternative predictions can be made for the relationship between leaf and stem traits. One possibility, derived from plant life history theory, is that leaf and stem traits are coordinated such that a single axis of variation explains most woody plant strategies. Under this hypothesis, allocation strategies of cheap or expensive tissues occur at a whole-plant level (Grime *et al.* 1997), resulting in synchronized construction costs of leaf and stem tissues. Indeed low wood density, like thin short-lived leaves, has been associated with faster growth and high-light environments primarily because of cheap construction costs (Poorter *et al.* 2010). In contrast, species with dense wood, like those with thick, long-lived leaves, tend to have higher survival rates because they tolerate stress from shade, wind, drought and herbivores (Chave *et al.* 2009).

An alternative hypothesis that we test here is that allocation strategies of leaf and stem tissues are decoupled, such that species may combine different structures and function of leaves and stems. Such a pattern would be consistent with recent observations that stem traits are better predictors of plant performance than leaf traits in adult trees (Poorter *et al.* 2008).

The few studies that have examined coordination in design across plant tissue types provide contrasting information. Freschet *et al.* (2010) found tight correlations amongst leaf, stem and root chemical composition in the dominant 40 species of a subarctic flora including seven growth forms, providing support for a single axis of trait variation. Amongst 30 common species in the Pacific Bonin Islands, however, Ishida *et al.* (2008) found strong correlations between stem tissue density and leaf mass per unit area but weak correlations between stem tissue density and leaf photosynthetic rates. The extent to which such results represent general patterns of tissue coordination will require more extensive and comprehensive sampling of many species, especially in species-rich biomes such as tropical forests.

Here, we test the hypothesis that traits related to stem economics are uncorrelated with traits defining the LES, using a dataset of unprecedented scale for Amazonian trees. We sampled 13 448 leaves and wood tissue from 4672 trees

representing 668 tropical tree species representative of lowland Neotropical forests. We use multiple factor analyses of 16 functional chemical, physiological and structural traits that play an important role in the performance of woody plants to test the predictions of intercorrelated leaf and stem traits.

## MATERIAL AND METHODS

### Trait sampling

Leaf and twig samples were collected by professional tree climbers from every tree in nine 1-ha plots across a gradient of precipitation and geological substrate in French Guiana, and herbarium vouchers were used to complete botanical determinations of each tree sampled (Baraloto *et al.* 2010). We measured a suite of 16 traits that play an important role in the performance (functioning, productivity and survival) of woody plants. Complete details of trait-sampling methods are provided in Appendix S1 of Supporting Information.

We classified most of these traits as associated with ecological strategies at the leaf or stem level (Table 1). For leaflet surface area and total leaf surface area, however, no *a priori* classification was possible. The relationship between leaf size and other leaf traits is complicated. A need for greater biomechanical support with increased leaf area may be expected, but empirical studies provide conflicting results, with observed correlations between leaf area and specific leaf area (SLA) that are positive (Niinemets 1998), negative (Shipley 1995) or variable amongst habitats (Pickup *et al.* 2005). Leaf area was not included as a trait in the landmark study of the global LES (Wright *et al.* 2004). Inclusion of leaf area in a stem economics group is also uncertain. Denser branch wood may be hypothesized to support larger leaves because of its greater biomechanical strength (Niklas 1995) and increased cavitation resistance (Hacke & Sperry 2001). However, the higher construction costs per unit volume associated with dense wood would also be predicted to favour investment in smaller leaves (Hacke & Sperry 2001; Pickup *et al.* 2005), a prediction supported by studies in both tropical forests (Wright *et al.* 2007) and temperate woodlands (Pickup *et al.* 2005). We thus do not give an *a priori* placement to variables describing leaf area in our test of decoupled leaf and stem economics spectra.

### Data analysis

We compiled a dataset with species-mean trait values, as well as an individual-level dataset, to examine the robustness of our analysis to the inclusion of intraspecific variation.

In the species-level dataset, we standardized the data to correct for the effects of local environment and ontogenetic

**Table 1** Functional traits measured in the study, and their assignment to leaf or stem trait groups. Detailed methods for functional trait measurement are provided in Appendix S1 of Supporting Information

Attribute (abbreviation)	Unit	Strategy	<i>A priori</i> group
Trunk xylem density (WdDens)	g cm <sup>-3</sup>	Stem transport, structure and defense	Stem
Trunk bark thickness (Bark)	mm	Stem transport, structure and defense	Stem
Branch xylem density (TwigDens)	g cm <sup>-3</sup>	Stem transport, structure and defense	Stem
Branch bark thickness (TwigBark)	mm	Stem transport, structure and defense	Stem
Trunk wood moisture content (WdMst)	%	Stem transport, structure and defense	Stem
Foliar N <sub>m</sub> (N)	cg g <sup>-1</sup>	Leaf resource capture	Leaf
Foliar P <sub>m</sub> (P)	µg g <sup>-1</sup>	Leaf resource capture	Leaf
Foliar K <sub>m</sub> (K)	µg g <sup>-1</sup>	Leaf resource capture	Leaf
Foliar C:N (CN)	g g <sup>-1</sup>	Leaf resource capture and defense	Leaf
Foliar <sup>13</sup> C composition (C13)	‰	Leaf resource capture	Leaf
Laminar total chlorophyll (Chlo)	µg mm <sup>-2</sup>	Leaf resource capture	Leaf
Laminar toughness (Tough)	N	Leaf resource capture and defense	Leaf
Leaf tissue density (LTD)	g cm <sup>-3</sup>	Leaf resource capture and defense	Leaf
Specific leaf area (SLA)	cm <sup>2</sup> g <sup>-1</sup>	Leaf resource capture and defense	Leaf
Laminar surface (leaflet)	cm <sup>2</sup>	Leaf resource capture	Uncertain
Entire leaf surface (leaf)	cm <sup>2</sup>	Leaf resource capture	Uncertain

stage on trait phenotypes. To do so, we used two measures of individual tree stature: diameter at breast height and overall height (measured with a laser rangefinder), and two measures of crown light exposure (CE) (Poorter & Arets 2003). We estimated CE indices, which provide an ordinal estimate of the local light environment, separately for the entire individual and for the collected twig and leaf sample. Thus, we had four intercorrelated measures of individual stature, which we collapsed into a single measure using the Non-linear Iterative Partial Least Squares algorithm, as implemented in the *ade4* package of R (Dray & Dufour 2007). Only two of the 16 traits,  $\delta^{13}\text{C}$  and bark thickness, varied significantly with this multivariate factor, and so we corrected for these correlations by substituting the residuals from linear regressions of these variables against individual stature.

Although leaf traits were measured on every individual, wood traits and chemistry were not. We therefore estimated unobserved trait values using Multiple Imputation with Chained Equations (MICE), as implemented in the *mice* package of R (van Buuren & Groothuis-Oudshoorn, Unpublished). Missing values constituted 28.6 and 13.5% of the individual- and species-level datasets, respectively. Unobserved values were estimated through predictive mean matching using all other data as predictors, rather than assigning column mean values as is done under other imputation procedures (e.g., Wright *et al.* 2004). The robustness of the data imputation procedure was evaluated by assessing the convergence of the Gibbs sampler at the heart of MICE by plotting the means and standard deviations of five imputations of data. No trends were observed in the mean or variance of the imputed data over the course of

1000 iterations. We are therefore confident in the robustness of the data resulting from the imputation procedure.

To test the hypothesis that the spectrum of stem traits is orthogonal to the spectrum of leaf traits, we used multiple factor analysis (MFA), a multivariate ordination method that permits examination of common structures in datasets with many variables that can be separated into different groups of variables (Escofier & Pagès 1990). MFA involves two steps. First, a principal component analysis (PCA) is performed on each group of variables which is then 'normalized' by dividing all its elements by the square root of the first eigenvalue obtained from the PCA. In our dataset, the groups were defined as in Table 1. Second, the normalized datasets are merged to form a unique matrix and a global PCA is performed on this matrix. The individual datasets are then projected onto the global analysis. In this way, variables in each group are permitted to maintain free covariances amongst themselves, and the relationships between groups of variables can be examined without the influence of within-group covariance. We use as a test statistic the between group correlation coefficient, RV, which is scaled from 0 if every variable in one group is completely uncorrelated with every variable in the other group(s), to 1 if the two groups are completely homothetic. Under the hypothesis of orthogonality of leaf and stem traits economics spectra, the RV coefficient of a MFA performed on groups as defined in Table 1 should be smaller than the RV of a MFA performed on randomly generated groupings of the same data. We created a sampling distribution for our test statistic using 1000 permutations of variable assignments to two groups, and

used a one-tailed test with  $\alpha = 0.05$  to test for orthogonality between leaf and stem trait groups. To examine the placement of the leaf area variables on the global ordination, we projected them afterwards on the global analysis. We conducted the same MFA analyses and permutation tests for individual and species-level datasets, both with and without data imputations, to verify the robustness of our results to within-species variation.

To test for any sampling bias in our cross-species comparisons related to their evolutionary history, we also performed species-level analysis using phylogenetically independent contrasts (PICs). We recovered a phylogenetic hypothesis for our 668 species using the PhyloMatic utility (Webb & Donoghue 2005), based on the Davies *et al.* (2004) phylogenetic hypothesis for relationships amongst angiosperm families, with polytomies applied within most families and genera. PICs were calculated in the ape module of R (Paradis *et al.* 2004), as the difference in mean trait values for pairs of sister species and nodes ( $n = 667$ ). For this analysis, branch lengths were scaled to 1.

To determine the nature of relationships both within and amongst functional traits defining leaf and stem trait groups, we examined pairwise correlations amongst all variables. We conducted this analysis for the species-level dataset both with and without PICs.

For all analyses, leaf toughness, surface area, leaf tissue density and SLA were log-transformed to more closely meet the assumption of normality. Other traits were approximately normally distributed without transformation.

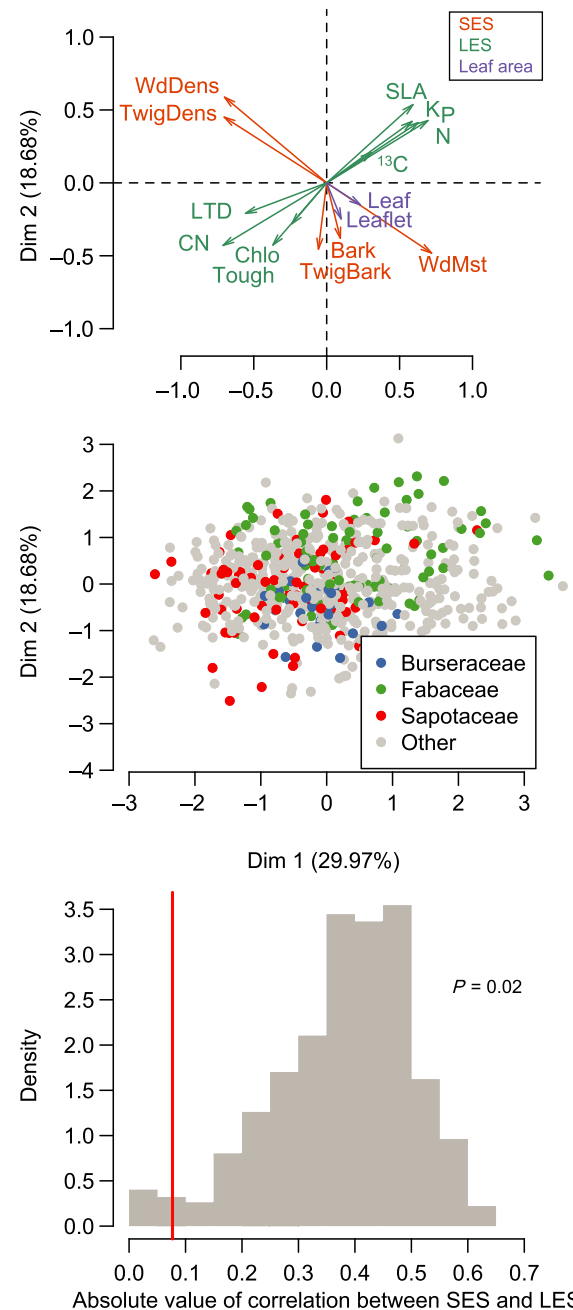
All analyses were conducted in the R 2.10 statistical platform (R Development Core Team 2010).

## RESULTS

Multiple factor analysis confirmed the strong and significant correlations of leaf traits on one hand, and wood traits on the other hand (Table 1). Furthermore, our analyses show the leaf economics and stem economics spectra to be orthogonal ( $P = 0.02$ ; Fig. 1). In other words, tradeoffs in leaf economics and stem economics occur independently. Concordant results were found when considering all individual trees, and between data with and without imputation of missing cells (Figure S1).

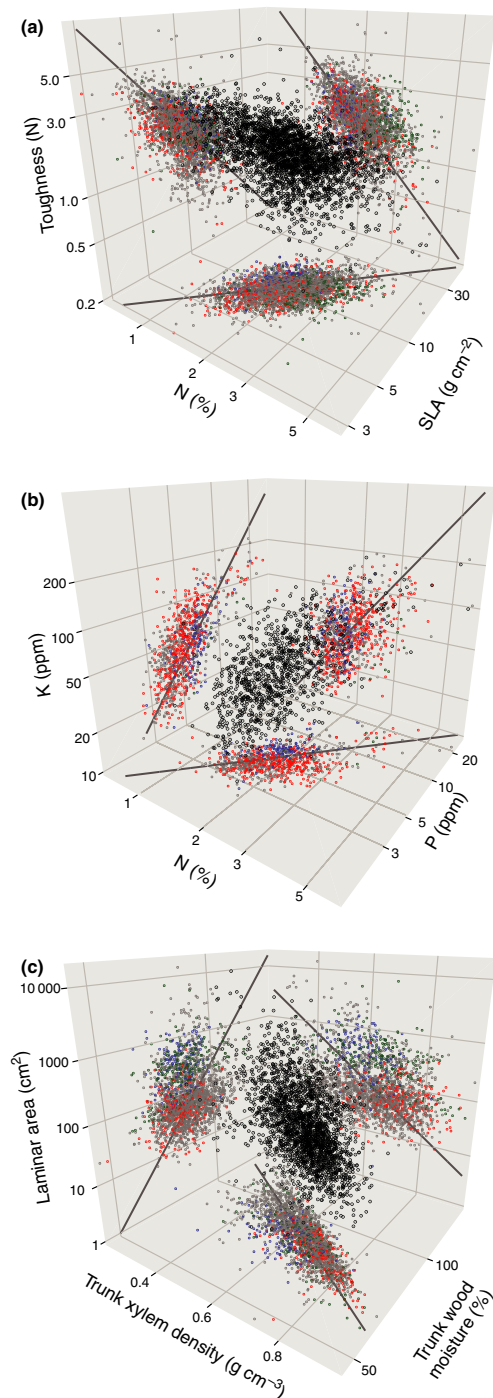
The first MFA axis thus represents the LES, running from species with thin, productive leaves with quick returns of carbon and nutrient investment, to species with dense, thick and tough leaves that have slow returns (Fig. 2a). Foliar nitrogen, phosphorus and potassium concentrations were tightly correlated with this spectrum (Fig. 2b; Table 2).

The second axis represents the stem economics spectrum (SES), which is bounded by species with high wood



**Figure 1** Functional strategies of tropical trees. (a) Trait loadings biplot illustrating the leaf economics and stem economics spectra as multiple factor dimension derived from the measurement of 16 functional traits. (b) Projection in multiple factor dimension of the 4672 individuals for which traits were measured. Fabaceae (green), Sapotaceae (red) and Burseraceae (blue) are highlighted as examples of patterns in pantropical families. (c) Observed correlation between leaf and stem trait groups (vertical line), relative to the distribution expected if traits were randomly assigned to groups.





**Figure 2** Trait correlations in tropical trees. (a) Leaf structure and chemistry in the leaf economics spectrum; (b) leaf chemistry in the leaf economics spectrum, (c) traits defining the proposed stem economics spectrum. Projected shadow lines in each panel illustrate the standardized major axis regression (SMA) relationship between each pair of traits. Fabaceae (green), Sapotaceae (red) and Burseraceae (blue) individuals are highlighted as examples of patterns in pantropical families.

tissue density for both trunks and branches and species with high stem and branch moisture content and thick bark (Fig. 2c).

The two variables describing leaf area show significant correlations with traits associated with both axes (Table 2), and their placement weakly associates them with the stem economics axis (Fig. 1). Both leaf unit (leaflet) and total leaf area tend to decrease with increasing wood density, and larger leaves also tend to be tougher (Table 2; Fig. 1).

The generality of the axes and their orthogonality is supported by analyses of three pantropical families that occupy different positions along the LES: Fabaceae, Sapotaceae and Burseraceae (Fig. 1b; Figure S3). The two axes and their relationship are largely retained across families. For example, Fabaceae tend to have thin leaves with high mineral nutrient concentrations but are represented by widespread Amazonian lineages with both dense wood (some *Swartzia*) and light wood (some *Inga*). Sapotaceae, which tend to have thicker leaves with higher C:N ratios because of C-rich latex, contain widespread species with large, dense leaves and light wood (some *Micropholis*) and smaller dense leaves with heavier wood (some *Pouteria*). Burseraceae are mostly intermediate along the LES, and the relationships within this group are the least concordant. Nevertheless, this family includes species with light wood and large leaves (*Trattinnickia*) and denser wood with smaller leaves (some *Protium*).

Generality is also supported by the constancy of the orthogonality amongst the nine sampled sites (Figure S3). These sites represent a gradient in precipitation and soil fertility, across which the distribution of community trait values varies (Baraloto *et al.* 2010) and for which the dominant species hierarchy changes almost completely amongst all pairs of plots (C. Baraloto, unpublished data). Still, the two axes and their relationship remain highly conserved.

The PIC analysis produced results largely consistent with the general species analyses (Figure S4). The notable exception involves correlations between variables describing leaf area, which show only weak correlations with stem and leaf traits in the PIC dataset even though the significant positive correlation between leaf area and leaflet area is retained (Table 2).

## DISCUSSION

The fact that leaf functional traits covary tightly is well documented across a wide array of ecosystem types (Wright *et al.* 2004, 2005). In this study, we tested whether functional traits related to the stem and branches of woody plants also covary with leaf traits. We showed that wood traits covary along a single axis of variation which we identify as the SES, but that this axis is orthogonal to the axis of leaf trait variation (LES). Life history theory predicts a correlated

**Table 2** Pairwise relationships amongst the 16 functional traits in the imputed species dataset ( $n = 668$ ). Shown are the Pearson correlation coefficients for species data (above diagonal) and phylogenetically independent contrasts (below diagonal)

	Stem economics				Leaf economics								Uncertain			
	WdDens	Bark	TwigDens	TwigBark	WdMst	N	P	K	CN	C13	Chlo	Tough	LTD	SLA	Leaf	Leaflet
Stem economics	WdDens	-0.12	<b>0.74</b>	-0.06	<b>-0.79</b>	-0.20	-0.14	-0.09	0.21	0.00	0.02	0.05	0.22	-0.12	-0.20	-0.14
	Bark	-0.08	-0.10	<b>0.29</b>	0.15	-0.04	-0.03	-0.08	0.04	0.04	0.02	-0.01	-0.08	-0.03	-0.03	0.08
	TwigDens	<b>0.67</b>	-0.02	-0.05	<b>-0.56</b>	-0.25	-0.26	-0.22	0.27	-0.09	-0.01	0.00	0.27	-0.15	<b>-0.36</b>	<b>-0.29</b>
	TwigBark	0.00	0.22	0.03	0.08	-0.06	-0.08	-0.07	0.12	0.07	0.02	0.17	0.11	-0.28	0.17	0.10
Leaf economics	WdMst	<b>-0.79</b>	0.09	<b>-0.49</b>	0.00	0.25	0.19	0.17	-0.27	0.10	-0.09	-0.11	-0.26	0.17	0.12	0.12
	N	-0.16	-0.05	-0.18	-0.05	0.21	<b>0.67</b>	<b>0.55</b>	<b>-0.93</b>	<b>0.29</b>	-0.10	<b>-0.36</b>	<b>-0.30</b>	<b>0.51</b>	0.19	-0.05
	P	-0.14	0.02	-0.19	-0.09	0.19	<b>0.61</b>	<b>0.70</b>	<b>-0.58</b>	<b>0.39</b>	-0.15	-0.23	<b>-0.33</b>	<b>0.40</b>	0.27	-0.02
	K	-0.07	-0.09	-0.20	-0.11	0.13	<b>0.50</b>	<b>0.69</b>	<b>-0.52</b>	<b>0.34</b>	-0.17	-0.15	<b>-0.45</b>	<b>0.41</b>	0.19	0.08
Uncertain	CN	0.16	0.07	0.20	0.11	-0.20	<b>-0.91</b>	<b>-0.49</b>	<b>-0.44</b>	-0.16	0.18	<b>0.39</b>	<b>0.37</b>	<b>-0.60</b>	-0.18	0.05
	C13	0.05	0.03	-0.02	0.07	0.02	0.24	<b>0.41</b>	<b>0.39</b>	-0.23	-0.11	-0.03	-0.23	0.10	0.21	0.03
	Chlo	0.00	0.00	-0.05	0.07	-0.07	-0.17	-0.24	0.10	-0.16		<b>0.38</b>	0.17	<b>-0.48</b>	0.20	0.11
	Tough	0.04	-0.01	-0.01	0.16	-0.10	<b>-0.36</b>	-0.22	-0.13	<b>0.39</b>	<b>0.43</b>		0.18	<b>-0.64</b>	<b>0.31</b>	<b>0.41</b>
	LTD	0.15	0.03	0.26	0.13	-0.17	<b>-0.34</b>	<b>-0.33</b>	<b>-0.45</b>	<b>0.38</b>	<b>0.28</b>	0.22		<b>-0.55</b>	-0.04	-0.25
	SLA	-0.08	-0.06	-0.13	<b>-0.29</b>	0.14	<b>0.48</b>	<b>0.32</b>	<b>0.36</b>	<b>-0.56</b>	0.08	<b>-0.55</b>	<b>-0.65</b>		-0.06	-0.11
	Leaf	-0.07	0.10	0.03	0.11	0.08	-0.02	0.02	-0.01	0.01	-0.05	-0.05	0.04	-0.04		<b>0.37</b>
Leaflet	-0.02	0.07	0.04	0.08	0.04	-0.04	-0.06	-0.06	0.01	0.01	0.04	-0.02	0.04	-0.02	<b>0.36</b>	

Significant correlations, based on penalty-corrected  $P$ -values, are indicated in bold. Variables are ordered by their *a priori* placement on the stem economics spectrum, leaf economics spectrum or uncertain placement. For abbreviations, refer to Table 1.

strategy collapsing into a single functional axis, with one extreme defined by low-density wood leading to cheap stem volumetric expansion, fast stem hydraulic conductance, high water supply to the leaves, high photosynthetic rates and high growth rates (i.e., the typical light-demanding or pioneer species; Grime *et al.* 1997). The opposite suite of traits would correlate with higher persistence and survival (i.e., the typical shade-tolerant species). We did not find support for this hypothesis. Rather, our analysis uncovered an additional gradient of variation defined on the one hand by species with large thick leaves and light wood (e.g., *Carapa* spp., Meliaceae); and on the other hand by species with small cheap leaves and dense wood, including many common tropical timber species such as *Aspidosperma* spp. (Apocynaceae). The many intermediate examples along these two orthogonal axes, both within and amongst families (Fig. 1), imply that strategies of leaf dynamics and strategies of stem dynamics are independent in evergreen, lowland tropical trees.

Our comprehensive analyses suggest that the orthogonality of the LES and SES is a general phenomenon amongst Neotropical trees. The ordination results were highly similar amongst analyses of individual and species-mean data, regardless of whether missing values were imputed (Figure S1), suggesting that observed patterns are also robust to within-species variation. Moreover, results were conserved across different sites that differ broadly in both floristic composition and environmental characteristics (Figure S3). Results were similar amongst three dominant pantropical families (Figure S2) and when phylogenetic contrasts were made with species-level data (Figure S4). Nevertheless, our results provide no general consensus for plant tissue design in light of recent studies in other systems (Ishida *et al.* 2008; Freschet *et al.* 2010). Below, we discuss global predictions for each axis of trait variation and for the overall result of decoupled leaf and stem economics spectra.

### Expanding the leaf economics spectrum

Our results expand the definition of the LES to include several new functional traits. Leaf toughness may be important for both physical defense against herbivores and to prolong leaf lifespan, and it has been found to correlate negatively with both herbivory rates and with sapling regeneration light requirements (Kitajima & Poorter 2010). Here, we confirm the strong and consistent placement of leaf toughness on the LES for a system where herbivore pressure is relatively high (Coley *et al.* 1985).

The tight correlations amongst foliar N, P and K concentrations, and between these nutrients and other leaf economics traits, underline the importance of foliar stoichiometry including leaf K in defining this axis of leaf

strategies (Fyllas *et al.* 2009). Notably, leaf K concentration was less tightly correlated with leaf economics in a global analysis that included 251 species of different growth forms (Wright *et al.* 2005). Given the role of leaf K in stomatal control (Roelfsema & Hedrich 2005), it would be interesting to investigate whether the tight correlations we observed in this large dataset are maintained across gradients of nutrient limitation and drought stress.

Foliar  $\delta^{13}\text{C}$  is an indicator of leaf-level water-use efficiency that might be predicted to be correlated with the LES because it reflects a tradeoff between photosynthetic rates and stomatal conductance (Seibt *et al.* 2008). However, leaf  $\delta^{13}\text{C}$  signatures did not correlate strongly with the LES in our study, nor did it correlate with stem tissue density as found amongst Bonin island plants (Ishida *et al.* 2008). In fact, foliar  $\delta^{13}\text{C}$  was weakly correlated with all other variables in our dataset both when considered globally for individuals of varying stature (Table 2), and when we corrected for individual stature in species-level analyses (Figure S1). The sensitivity of this measure to microhabitat variation may preclude its utility as a plant functional trait at the community scale in systems with a complex vertical structure such as tropical forests (Farquhar *et al.* 1989; Seibt *et al.* 2008).

### The stem economics spectrum

The existence of a SES confirms recent work examining wood and whole-stem traits (Chave *et al.* 2009; Zanne *et al.* 2010). Species with dense wood are often better protected against decay that may be mediated by pests and pathogens (Pearce 1996) and are biomechanically more stable (Niklas 1995), thus contributing to enhanced survival and longevity. Low wood density and high moisture content, on the other hand, implies cheap volumetric construction cost, facilitating rapid expansion in tree height and diameter (Chave *et al.* 2009; Anten & Schieving 2010). For tropical trees at least, lower wood density is significantly correlated with high levels of hydraulic conductance in stems and leaves (Santiago *et al.* 2004; Markesteijn 2010), suggesting that the pattern we observe for stem tissue density can be translated to an increased water supply to leaves (Ishida *et al.* 2008). Nevertheless, a recent global meta-analysis integrating species-level databases found weak correlations between wood density and vessel anatomy, which was a primary determinant of stem conductivity (Zanne *et al.* 2010). Our results underline the need for global studies integrating data for leaf and stem physiology and tissue densities for the same individuals.

Thicker bark tended to be associated with lower wood density in our analysis, with at least two potential explanations. First, if bark provides structural support then we would predict an allocation tradeoff between thick bark

and dense wood for biomechanical support. However, recent evidence suggests that the bark of tropical trees is neither strong enough nor stiff enough to provide much biomechanical support (Paine *et al.* 2010). More probably, thicker bark may represent a defense against pathogens or herbivores, particularly for species with low wood density (Paine *et al.* 2010).

Our analysis suggests that leaf area integrates information relevant to both the leaf and stem economics spectra. We found, as in several other recent studies, that laminar area and leaf area both tend to decrease with increasing wood density (Wright *et al.* 2007; Malhado *et al.* 2009), an observation consistent with dry mass allocation tradeoffs between leaves and stems. On the whole, larger leaves tend to be tougher, both when including palms that have large and tough leaves ( $r_{\text{leaf-tough}} = 0.41$ ,  $P < 0.05$ ; Table 2), and when excluding palms ( $r_{\text{leaf-tough}} = 0.37$ ,  $P < 0.05$ ). In vegetation types with lower rainfall, we might expect the association between leaf area and stem economics to become stronger because of increased risk of cavitation with increased transpiration surface (Pickup *et al.* 2005). We would also predict a decoupling of leaf area from leaf toughness if lower precipitation is accompanied by lower probability of herbivore damage risks to tissue, reducing the advantage of tougher tissue with increasing laminar size (Kitajima & Poorter 2010).

## CONCLUSIONS

The extent to which strategies of leaf dynamics and strategies of stem dynamics are coordinated has important consequences for our understanding of factors controlling species distributions and the impacts of land use and climate change (Suding & Goldstein 2008). We suggest three future steps to applying the functional trait relationships presented here to these important questions. First, in light of predicted scenarios of global change that include drought and changes in nutrient cycles (Malhi *et al.* 2008), we repeat the call for cross-species trait analyses that integrate not only leaf and stem dynamics as we report here but also the dynamic strategies of roots across gradients of soil fertility and water availability (Westoby & Wright 2006; Freschet *et al.* 2010).

Second, our results provide two suggested improvements for predictive vegetation-climate models, in which plant strategies are currently represented by discrete plant functional types (Huntingford *et al.* 2008). First, the characterization of plants on the basis of growth form and leaf tissue design should be expanded to consider stems and roots, as these tissues may be more relevant to particular ecological processes (e.g., Hickler *et al.* 2006). Second, given the clear evidence for continuous variation in functional trait combinations revealed by our study (Fig. 1), future models

should attempt to incorporate continuous variation in traits rather than discrete plant functional types.

Finally, the nature of relationships between functional traits and many ecosystem processes depends on relationships between traits and demographic parameters such as growth and survival (Suding *et al.* 2008). For long-lived plants such as tropical trees it is perhaps not surprising that stem-level traits are more important correlates of tree growth and survival than leaf-level traits (Poorter *et al.* 2008). Important advances will result from further tests of relationships between traits and demographic rates, using more complete trait databases in tropical forests and other biomes to determine the global generality of such findings amongst woody plants.

## ACKNOWLEDGEMENTS

We thank all participants of the project BRIDGE who participated in field and laboratory collection and treatment of specimens. Field research was facilitated by the Guyafor permanent plot network in French Guiana which is managed by CIRAD and ONF. Research was supported by a grant to JC and CB from the Biodiversité section of the Agence National de la Recherche, France; by NSF DEB-0743103 to CB; and by an INRA Package grant to CB. Quentin Molto and Vivien Rossi provided invaluable statistical advice. We thank Frans Bongers, Robin Chazdon, Claire Fortunel, Bill Shipley and two anonymous referees for comments on previous drafts of the manuscript.

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## SUPPORTING INFORMATION

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

**Appendix S1** Detailed description of functional trait measurements.

**Figure S1** Complete results of species- and individual-level analyses.

**Figure S2** Generality of results amongst three large pantropical families.

**Figure S3** Generality of results amongst the nine 1-ha plots.

**Figure S4** Complete results of phylogenetically independent contrasts.

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Editor, Hafiz Maherali

Manuscript received 11 May 2009

First decision made 7 June 2010

Manuscript accepted 23 June 2010