Functional Ecology

British Ecological Society

Functional Ecology 2012 doi: 10.1111/j.1365-2435.2012.02020.x

Leaf, stem and root tissue strategies across 758 Neotropical tree species

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Summary

1. Trade-offs among functional traits reveal major plant strategies that can give insight into species distributions and ecosystem processes. However, current identification of plant strategies lacks the integration of root structural traits together with leaf and stem traits.

2. We examined correlations among 14 traits representing leaf, stem and woody root tissues. Traits were measured on 1084 individuals representing 758 Neotropical tree species, across 13 sites representative of the environmental variation encompassed by three widespread habitats (seasonally flooded, clay terra firme and white-sand forests) at opposite ends of Amazonia (French Guiana and Peru).

3. Woody root traits were closely aligned with stem traits, but not with leaf traits. Altogether leaf, stem and woody root traits delineated two orthogonal axes of functional trade-offs: a first axis defined by leaf traits, corresponding to a 'leaf economics spectrum', and a second axis defined by covarying stem and woody root traits, corresponding to a 'wood economics spectrum'. These axes remained consistent when accounting for species evolutionary history with phylogenetically independent contrasts.

4. Despite the strong species turnover across sites, the covariation among root and stem structural traits as well as their orthogonality to leaf traits were strongly consistent across habitats and regions.

5. We conclude that root structural traits mirrored stem traits rather than leaf traits in Neotropical trees. Leaf and wood traits define an integrated whole-plant strategy in lowland South American forests that may contribute to a more complete understanding of plant responses to global changes in both correlative and modelling approaches. We suggest further meta-analyses in expanded environmental and geographic zones to determine the generality of this pattern.

Key-words: French Guiana, functional trade-offs, leaf economics, Peru, plant traits, tropical forest, wood economics

Introduction

Terrestrial plants are fixed organisms whose basic modular organization into shoot and root systems reflects their evolutionary history to draw resources both above-ground and below-ground (Boyce 2005). The shoot system is comprised of leaves to capture light and CO_2 as the primary photosynthetic organs, and stems that support leaves, transport water and nutrients between the root and shoot systems, and store water and nutrients (Kozlowski & Pallardy 1997). Roots anchor the plant in the soil, absorb and transport water and nutrients from the soil to the shoot system, and often store water and nutrients (Jackson *et al.* 2007). Hence, leaves, stems and roots each perform critical functions that together modulate plant survival, growth and reproduction, and ultimately determine plant performance (Ackerly *et al.* 2000).

Plant traits allow the investigation into the functions of different tissues and thus into the functional trade-offs that influence species distributions along environmental gradients (ter Steege *et al.* 2006; Engelbrecht *et al.* 2007; Kraft, Valencia & Ackerly 2008). For example, leaves with higher tissue density and toughness, but lower specific leaf area and nutrient concentrations, have lower photosynthetic rates but longer life span (Reich *et al.*

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1998b; Wright & Westoby 2002). Such costly leaves are more effectively defended against herbivores and pathogens (Coley & Barone 1996; Agrawal & Fishbein 2006; Hanley *et al.* 2007), and therefore confer slower growth but higher survival rates (Poorter & Bongers 2006). Similarly, denser wood correlates with lower sapwood conductivity, lower wood water storage and thinner bark, but greater resistance to xylem cavitation (Bucci *et al.* 2004; Santiago *et al.* 2004; Baraloto *et al.* 2010b). Denser wood requires greater construction costs (Enquist *et al.* 1999), but confers greater resistance to mechanical damage and pathogen attack, leading to slower growth and lower mortality rates (Falster 2006; Poorter *et al.* 2008; Cornwell *et al.* 2009).

Many recent studies have sought to define major plant strategies (sensu Westoby *et al.* 2002) by integrating global data sets of leaf and wood traits (Reich *et al.* 1999; Wright *et al.* 2004; Zanne *et al.* 2010). Within tissue types, traits consistently covary in what have been described as 'economics spectra' that broadly summarize trade-offs between slow-growing and fast-growing plants (Wright *et al.* 2004; Chave *et al.* 2009). Two studies have more recently integrated leaf and stem traits together in large data sets of tree species in Neotropical forests and showed that leaf and stem economic spectra were not only independent (Wright *et al.* 2007), but also orthogonal (Baraloto *et al.* 2010b), suggesting that functional trade-offs operate independently at the leaf and at the stem levels. When considering the functional trade-offs for whole-plant strategies, however, it is critical to also include roots. Hence, an important unanswered question in the understanding of plant strategies is the extent to which root traits are coordinated with leaf and stem traits.

Given the anatomical continuity of xylem and phloem tissues between stem and root systems in woody plants (Tyree & Ewers 1991; Pratt *et al.* 2007), one hypothesis is that root structural traits such as wood density are coordinated with stem structural traits. If stem structural traits are orthogonal to leaf chemical and structural traits in trees (Wright *et al.* 2007; Baraloto *et al.* 2010b), we predict that root structural traits would also be orthogonal to the same leaf traits. An alternative hypothesis is that tight coordination between leaf and root traits exists irrespective of stem traits because leaf functioning depends on the water and nutrients absorbed by the roots, while root growth in turn depends on the carbohydrates produced by the leaves (Chapin 1980). Following this second hypothesis, we predict that root structural traits would correlate positively with leaf structural traits but negatively with leaf chemical traits, while both leaf and root traits would be orthogonal to stem traits.

Tests of these alternatives to date have been limited and have provided equivocal results. Fine root structural traits do not consistently correlate with leaf structural traits across boreal, arid and temperate ecosystems, especially when both herbaceous and woody species are included (Reich *et al.* 1998a; Craine & Lee 2003; Craine *et al.* 2005; Tjoelker *et al.* 2005; Withington *et al.* 2006; Liu *et al.* 2010). More limited evidence from arctic, boreal, desert, temperate and tropical ecosystems shows coordination among leaf, stem and both fine and coarse root chemical traits, suggesting a whole-plant economics spectrum (Kerkhoff *et al.* 2006; Freschet *et al.* 2010; Li *et al.* 2010), but these studies have focused solely on nutrient contents. Currently lacking is a consensus on coordination of root structural traits with leaf and stem traits, especially tissue density which describes biomechanical support and hydraulic transport (Pratt *et al.* 2007; Chave *et al.* 2009).

Here we investigate how root structural traits coordinate with leaf and stem traits in Amazonian forests that harbour the world's highest species diversity (Groombridge & Jenkins 2002). Amazonian diversification has largely been driven by the environmental heterogeneity resulting from its complex geological history (Hoorn *et al.* 2010). In addition to the broad soil fertility and seasonality gradient from the Guianas to the western Amazon, there are three widespread habitats in Amazonian lowlands: seasonally flooded, clay terra firme and white-sand forests. These habitats represent the range of resource availability, drought and flooding stress, forest structure, and floristic compositions found throughout the Amazon region (Fine *et al.* 2010; Baraloto *et al.* 2011). The high beta diversity among these three habitats (Baraloto *et al.* 2007; Fine *et al.* 2010), associated with important changes in community functional composition (ter Steege *et al.* 2006; Kraft, Valencia & Ackerly 2008), may influence species trait correlations. This system thus provides a broad range of species traits and evolutionary histories from which a general test of hypotheses of woody plant tissue coordination can be performed.

In this study we examine how roots align with stems and leaves by analysing 14 traits representing leaf, stem and woody root tissues of 758 species of tropical trees across broad environmental gradients at opposite ends of Amazonia. We measured leaf traits pertaining to resource acquisition (light, water and nutrients) and defence against natural enemies (Wright *et al.* 2004; Agrawal & Fishbein 2006), and stem and woody root traits relating to wood structure, nutrient transport and defence (Pratt *et al.* 2007; Chave *et al.* 2009), in seasonally flooded, clay terra firme and white-sand forests in French Guiana and Peru. In particular, we investigated the following questions: (i) How are root structural traits correlated to stem and leaf traits? (ii) To what extent are the correlations between leaf, stem and woody root traits consistent among Amazonian forests with contrasting habitats and biogeographical histories?

Materials and methods

STUDY SITES

We sampled broad environmental gradients representative of lowland South American rain forests, drawing from a network of 74 modified 0·5 ha Gentry plots in French Guiana and Loreto, Peru that covers the more commonly studied clay terra firme forests in addition to seasonally flooded forests and white-sand forests (Fig. 1, see Baraloto *et al.* 2011 for more details). In all plots, we recorded: (i) taxonomic identity for all trees >2·5 cm diameter at 1·3 m height (DBH), standardizing taxonomy across regions with vouchers referenced with the Missouri Botanical Garden Herbarium, and (ii) environmental factors describing climate (mean annual rainfall and dry season length), soil (texture and chemistry) and forest structure (mean basal area, height, DBH, and density of stems in three classes: 2·5–10 cm DBH, 10–30 cm DBH and >30 cm DBH) (Fig. 1a). The first dimension of the Multivariate Factor Analysis (MFA 1) on environmental factors distinguishes French Guianan forests from Peruvian forests, with longer dry season, higher rainfall and greater forest basal area in French Guiana (Fig. 1). The second MFA dimension (MFA 2) differentiates the three habitats, with decreasing soil fertility and higher density of small stems from seasonally flooded forests to terra firme forests and finally to white-sand forests (Fig. 1). We chose 13 plots to represent the variation in environmental conditions and floristic composition in the network, with at least two plots per habitat type in each country (Fig. 1b).

TRAIT SAMPLING

Previous work showed that to represent community-level trait distributions in species-rich plant communities, trait sampling requires the effort of sampling at least one individual of each species in each plot (Baraloto *et al.* 2010a). Therefore, we measured traits on at least one individual per species in each plot, representing a total of 1084 individuals and 758 species across the 13 plots. Unidentified morphospecies were also sampled and included in our study to be as conservative as possible in our analysis (see Appendix S1 in Supporting Information for a complete list of sampled species). For each species in each plot, we chose the stem nearest to 5 cm DBH, to standardize trait measures for the majority of taxa to understorey light conditions and the small tree stage. We collected leaf, stem and woody root samples for each selected individual between July 2009 and November 2009 and we measured 14 traits related to leaf, stem and woody root morphology and function (Table 1).

Bark thickness was measured at a height of 1·4 m with increment hammers (Haglöf Sweden AB, Långsele, Sweden), which give accurate readings for bark less than approximately 15 mm thick (Paine *et al.* 2010). Leaf and stem tissues were collected from a lateral branch in the understorey. On each branch, we sampled several leaves (three leaves for structural traits, ≥5 leaves for chemical traits), aiming for leaves fully expanded with little or no damage by herbivores or pathogens, and a stem fragment in the last growth unit with a diameter of 1–2 cm. We dug at the base of each stem to sample a woody root section with a diameter of 1–2 cm, to be able to compare its structure with that of the stem. We attempted to sample roots within 50 cm of the main stem with a lateral direction of growth to control for tension wood in the tissue.

On three leaves per individual, leaf chlorophyll content was estimated using three values from a Minolta SPAD 502DL meter (Spectrum Technologies, Illinois, USA) with calibrations based on Coste *et al.* (2010); leaf thickness was measured as the mean of three measurements with a digital micrometer (Mitutoyo Instruments, Singapore), and leaf toughness was measured as the average of three punch tests with a Chatillon penetrometer (Ametek, Florida, USA). The leaves were scanned using a portable scanner (Canon LiDE 60, Canon Inc., Tokyo, Japan) and their area was determined by image analyses with WinFolia software (Regent Instruments, Toronto, Canada). The leaves were dried at 60 °C for 72 h and their dry mass was weighed to determine specific leaf area (SLA, leaf area divided by its dry mass) and leaf tissue density (LTD, dry mass divided by the product between leaf area and leaf thickness). All leaves were then pooled together and ground to fine powder using a ball mill (Retsch MM200, Retsch Gmbh &

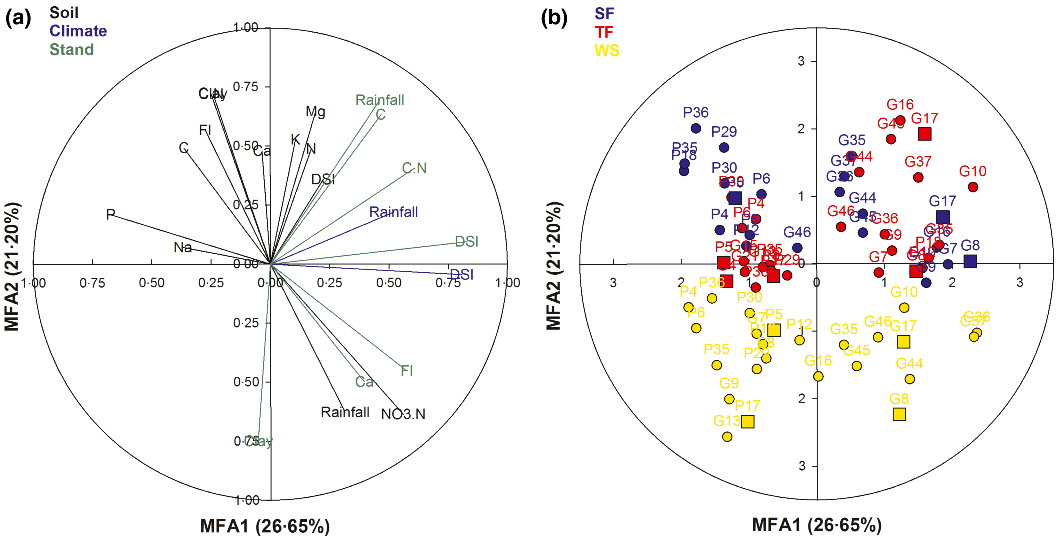

Fig. 1. Multivariate Factor Analysis (MFA) on environmental factors across the network of 74 forest plots: (a) correlation circle, (b) individual factor map. Details on environmental factors can be found in Baraloto *et al.* (2011). (a) *Climate*: Rainfall (mean annual rainfall, mm yr^{-1}) and DSI (dry season index, days); *Soil texture and chemistry*: Sand (percentage of sand,%), Silt (percentage of silt,%), Clay (percentage of clay,%), N (nitrogen,%), C (carbon,%), C.N (carbon: nitrogen ratio), NO_3.N (nitrate, ppm), P (Olsen phosphorus, ppm), K (potassium, mEq/100 g), Na (sodium, mEq/100 g), Ca (calcium, mEq/100 g), Mg (magnesium, mEq/100 g); *Forest structure*: BA (basal area >2·5 cm DBH, m² ha^{-1}), Stems2·5·10 (number of stems 2·5–10 cm DBH, ha^{-1}), Stems10·30 (number of stems 10–30 cm DBH, ha^{-1}), Stems.sup30 (number of stems >30 cm DBH, ha^{-1}), WSG (plot mean wood specific gravity), height (plot mean height, m), DBH (plot mean diameter at breast height, cm); (b) *Country*: G: French Guiana, P: Peru; *Habitat*: SF: Seasonally Flooded, TF: Terra Firme, WS: White-Sand. Squares indicate the 13 plots selected for the present study.

Table 1. List of the 14 measured traits, as well as their assignment to leaf or wood group

Trait	Abbreviation	Unit	Group	Strategy
Laminar thickness	Lthick	mm	Leaf	Resource capture and defence
Laminar toughness	Ltough	N	Leaf	Resource capture and defence
Leaf tissue density	LTD	g cm^{-3}	Leaf	Resource capture and defence
Specific leaf area	SLA	m^2 kg^{-1}	Leaf	Resource capture and defence
Leaf area	LA	cm^2	Leaf	Resource capture
Foliar Carbon	LCC	cg g^{-1}	Leaf	Resource capture and defence
Foliar Nitrogen	LNC	cg g^{-1}	Leaf	Resource capture and defence
Foliar Phosphorus	LPC	μg g^{-1}	Leaf	Resource capture
Foliar Potassium	LKC	μg g^{-1}	Leaf	Resource capture
Foliar ^{13}C composition	L13C	‰	Leaf	Resource capture
Laminar total chlorophyll	LChl	μg mm^{-2}	Leaf	Resource capture
Trunk bark thickness	Bark thick	mm	Wood	Transport, structure and defence
Stem wood density	S wood D	No unit	Wood	Transport, structure and defence
Root wood density	R wood D	No unit	Wood	Transport, structure and defence

Note: Values for trunk bark thickness are the residuals of a linear regression between trunk bark thickness and diameter at 1·3 m height for all 1084 individuals.

Co, Germany). Their carbon and nitrogen concentrations and carbon isotopic ratio were determined using an elemental analyser and mass spectrometer at the Mass Spectrometry Facility of the University of Florida. Foliar carbon isotope composition ($d^{13}C$, ‰) followed Farquhar, Ehleringer & Hubick (1989), using the conventional Pee Dee Belemnite standard. Leaf phosphorus and potassium analyses were conducted by the Soil and Plant Agricultural Laboratory at the Louisiana State University using an Inductively Coupled Spectrometer on HNO_3-H_2O_2 digests of 500 mg of plant tissue.

For stem and root wood tissue samples, outer bark was removed. For stem samples, phloem and pith wider than 1 mm in diameter were also removed (pith was negligible in root tissue samples). Stem and woody root samples were saturated with water and their saturated volume was estimated using the Sartorius density determination kit (Goettingen, Germany), which is based on the principle of water displacement. After measuring the saturated volume, samples were dried at 103 °C for 72 h, and their dry mass was determined. Stem and root basic specific gravity (Williamson & Wiemann 2010), hereafter density, was measured as the dry mass divided by the saturated volume.

DATA ANALYSIS

For statistical analyses, we first calculated the mean value of each of the 14 traits for each of the 758 species occurring in the 13 plots.

To examine the trait-by-trait correlations among all 14 traits, we performed pairwise Pearson correlation tests. We further tested the influence of species evolutionary histories on the observed correlations between groups of traits by performing pairwise correlations including phylogenetically independent contrasts (PIC). We recovered a phylogenetic tree for our 758 species using the PhyloMatic utility (Webb & Donoghue 2005), based on the Davies *et al.* (2004) phylogenetic hypothesis for relationships among angiosperm families, with polytomies applied within most families and genera. For this analysis, branch lengths were scaled to one. PIC were calculated as the difference in mean trait values for pairs of sister species and nodes (Paradis, Claude & Strimmer 2004).

To test the correlations both within and among traits defining leaf, stem and woody root tissues, we performed a principal component analysis (PCA) on all 14 traits. We conducted this analysis both with and without the PIC to account for the influence of species evolutionary histories.

To test the generality of the patterns between leaf, stem and woody root traits across contrasting habitats and biogeographical regions, we performed a PCA on the species traits measured in each plot and performed Mantel tests for similarity of pairwise trait correlation matrices among the 13 plots. The Mantel test is a permutation test for linear correlation between distance and similarity matrices summarizing pairwise similarities among plots.

All analyses were conducted in the R 2·10·0 statistical platform (R Development Core Team 2011), using the packages ade4 (Dray & Dufour 2007), ape (Paradis, Claude & Strimmer 2004) and vegan (Dixon 2003).

Results

The analysis of pairwise trait correlations showed a preliminary dichotomy of leaf traits against stem and root structural traits (Table 2, Appendix S2). Considering coordination among leaf traits, species with high SLA also have high nutrient concentrations (N, P, K), but low carbon concentration as well as low thickness, toughness and tissue density. Integrating stem and root structural traits, species with dense stems have dense woody roots (Fig. 2). Species with dense stems and woody roots also tend to exhibit low SLA and nutrient concentrations, but they can exhibit an array of leaf structural traits (*e.g.* thickness and toughness). Looking more specifically at the relationship between the densities of leaf, stem and woody root tissues, leaf tissue density does not correlate with either stem or woody root tissue density (Table 2, Fig. 2).

When including PIC in the pairwise correlations, the patterns of correlations among leaf, stem and woody root traits are generally conserved (Table 2). Hence, there seems to be no effect of species evolutionary history in the correlation patterns of traits related to leaf, stem and woody root tissues. Considering the densities of leaf, stem and woody root tissues, the densities of stem and woody root are still strongly correlated, but leaf functional traits were effectively decoupled from both of these (Table 2, Fig. 2).

Table 2. Pairwise correlations among leaf, stem and root traits.

	Lthick	Ltough	LTD	SLA	LA	LCC	LNC	LPC	LKC	L13C	LChl	Bark thick	S wood D	R wood D
Lthick		**0·477**	**−0·212**	**−0·465**	**0·187**	0·119	**−0·280**	**−0·283**	−0·028	0·009	**0·269**	0·087	0·027	0·040
Ltough	**0·518**		0·029	**−0·446**	**0·282**	**0·183**	**−0·235**	**−0·149**	−0·118	0·004	**0·272**	0·108	−0·030	0·026
LTD	**−0·218**	0·054		**−0·455**	0·041	0·088	−0·118	**−0·141**	**−0·239**	0·044	−0·019	0·072	0·010	0·093
SLA	**−0·484**	**−0·436**	**−0·443**		**−0·140**	**−0·245**	**0·425**	**0·462**	**0·357**	−0·074	**−0·227**	−0·114	−0·124	**−0·172**
LA	**0·264**	**0·283**	−0·058	**−0·148**		0·033	0·006	0·073	0·049	0·085	0·023	0·081	**−0·311**	−0·086
LCC	0·106	**0·213**	0·104	**−0·210**	0·017		−0·072	**−0·170**	**−0·260**	−0·020	0·007	0·023	0·065	0·049
LNC	**−0·221**	**−0·208**	**−0·138**	**0·376**	−0·060	−0·110		**0·413**	**0·274**	0·043	0·083	−0·099	**−0·172**	−0·118
LPC	**−0·227**	−0·119	**−0·158**	**0·413**	0·065	−0·086	**0·356**		**0·473**	**0·169**	−0·109	−0·049	**−0·344**	**−0·280**
LKC	−0·022	−0·125	**−0·280**	**0·328**	0·043	**−0·203**	**0·258**	**0·434**		0·048	−0·053	−0·004	**−0·170**	**−0·190**
L13C	0·069	−0·019	0·007	−0·088	**0·127**	−0·018	−0·009	**0·159**	0·105		−0·010	0·064	−0·048	−0·008
LChl	**0·306**	**0·293**	0·039	**−0·256**	0·005	−0·041	0·040	**−0·137**	−0·085	−0·003		0·042	0·008	−0·019
Bark thick	0·109	0·066	0·045	−0·118	0·047	0·024	−0·051	−0·028	−0·020	0·078	0·034		−0·051	−0·060
S wood D	−0·112	−0·084	0·042	−0·011	**−0·329**	0·040	−0·100	**−0·304**	**−0·133**	−0·098	−0·039	−0·080		**0·468**
R wood D	−0·014	−0·043	0·069	−0·039	−0·026	0·012	−0·031	**−0·261**	−0·125	−0·042	−0·023	−0·092	**0·442**	

Pearson correlation coefficients for species data (above diagonal) and phylogenetically independent contrasts (below diagonal) are shown in bold type when significant, following Bonferroni-corrected alpha values ($P < 0.00055$). See Table 1 for trait abbreviations.

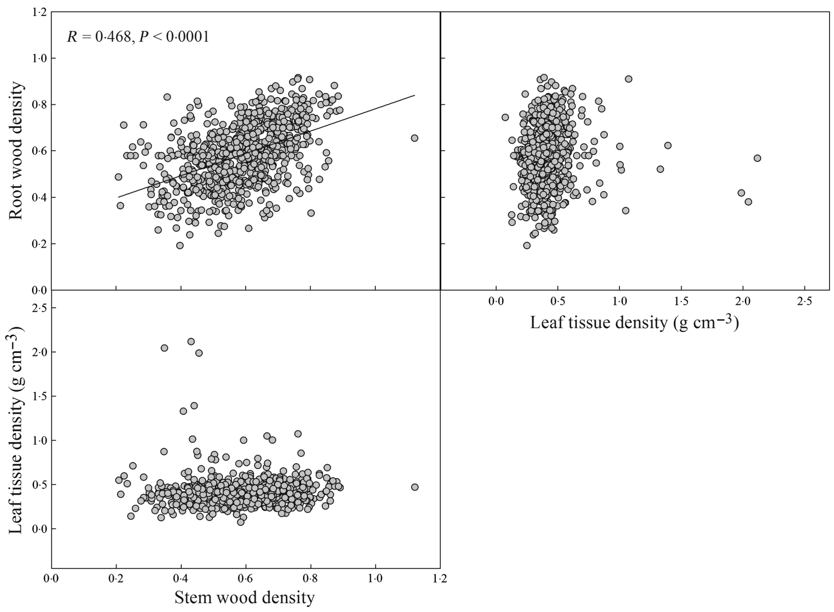

Fig. 2. Relationships between leaf, stem and woody root tissue densities in 758 tropical tree species. When the correlation was significant, Pearson correlation coefficient (R) was given with significance test and least-square regression line was drawn. Solid line indicates that the correlation is consistent when including phylogenetically independent contrasts (PIC).

The multivariate analysis of trait correlations showed that stem and root structural traits are orthogonal to leaf structural and chemical traits (Fig. 3a, Appendix S3). The first PCA axis is defined by coordinated leaf traits, opposing leaves with high SLA and high nutrient concentrations against thick, tough and dense leaves. The second axis of the PCA is defined by coordinated wood density of stems and woody roots. Bark thickness, leaf ^{13}C and chlorophyll content are not strongly correlated with either axis. When including PIC in the PCA, the patterns of correlations among leaf, stem and woody root traits are consistent (Fig. 3b, Appendix S3), further confirming that species evolutionary history did not influence the observed orthogonality between leaf and wood traits.

Pairwise trait correlation matrices were similar among the 13 plots representing a strong gradient of environmental conditions found in French Guiana and Peru (Appendix S4). The generality of coordination patterns of leaf, stem and woody root traits is supported by the consistency of the orthogonality between leaf traits on one hand and stem and root structural traits on the other along broad environmental gradients and across biogeographical regions.

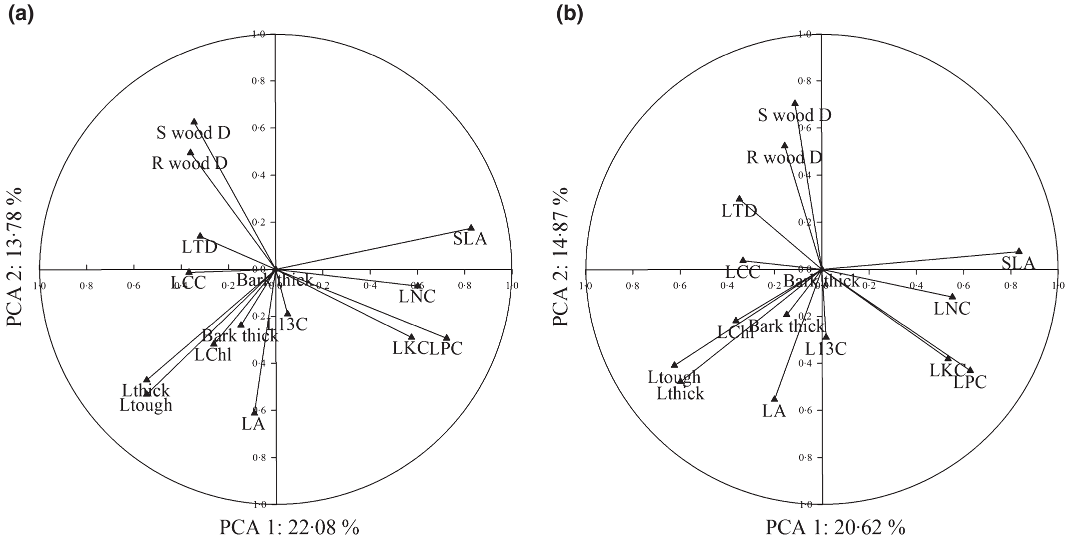

Fig. 3. Principal Component Analysis (PCA) on trait means in 758 tropical tree species: data (a) without and (b) with phylogenetically independent contrasts. See Table 1 for trait abbreviations.

Discussion

WOODY ROOTS PARALLEL TO STEMS RATHER THAN LEAVES

Plant strategies result in suites of correlated traits that arise because of functional trade-offs in resource allocation, and they can therefore be best understood from a whole-plant perspective (Westoby *et al.* 2002; Reich *et al.* 2003; Baraloto *et al.* 2010b). In this study, we examined correlations among 14 traits belonging to three vegetative tissues of trees: leaf, stem and woody root. Across 758 Neotropical tree species, we found that stem and root wood densities define a single axis of woody plant function (Table 2, Appendix S2), supporting the prediction arising from the anatomical continuity between stem and root systems (Tyree & Ewers 1991; Pratt *et al.* 2007).

Contrary to the prediction of life-history theory (Grime *et al.* 1997), but along with the findings of Wright *et al.* (2007), leaf tissue density was not correlated with either stem or woody root tissue density (Fig. 2). Hence, we found that there are two orthogonal axes of coordinated trait variation (Fig. 3, Appendix S3): leaf structural and chemical traits covary along a single axis that defines the leaf economics spectrum (Wright *et al.* 2004), while stem and root structural traits characterize another axis that defines what might best be termed the wood economics spectrum (Chave *et al.* 2009). The existence of two axes of vegetative traits suggests that Amazonian tree species can optimize their survival and growth by investing differentially in leaf and wood tissues (Baraloto *et al.* 2010b). Successful strategies in a given environment will then depend on the abiotic and biotic environmental factors filtering the local plant community (Cornwell & Ackerly 2009; Kraft & Ackerly 2010).

LEAF AND WOOD STRATEGIES ACROSS CONTRASTING HABITATS

Our study focused on three habitats that show extreme differences in resource availability and water-logging (Fig. 1). In comparison with the stable environmental conditions in clay terra firme forests, seasonally flooded forests and white-sand forests represent stressful environments in terms of flooding and drought, respectively. White-sand soils also have much lower nutrient availability than terra firme and seasonally flooded soils (Coomes & Grubb 1996; Fine *et al.* 2006; Baraloto *et al.* 2011). In our study, white-sand forests only have 6·8% and 23·4% of soil nitrogen content of terra firme and seasonally flooded forests, respectively (Baraloto *et al.* 2011).

Grime (1974, 1977, 1979) posits that two distinct strategies are associated with a gradient in resource availability: the competitive (C) strategy in high resource environments and the stress-tolerant (S) strategy in stressful and low resource environments. Both strategies are associated with traits pertaining to long life span and low investment in reproduction, but the C strategy includes high growth rate and high allocation plasticity, while the S strategy is linked to slow growth rate. Following Grime, we would expect the C strategy to be selected in terra firme forests and the S strategy to be favoured in white-sand forests, while either of these strategies could succeed in seasonally flooded forests. Thus, we would predict denser, thicker and tougher leaves, associated with denser stems and woody roots in white-sand forests.

However, we found that trait correlation patterns did not differ between the three habitats (Appendix S4), suggesting that, if white-sand forests select for species with S strategies, this does not promote coordinated leaf and wood densities in its species composition. In fact, species with trait combinations in any of the four quadrants defined by leaf and wood trait axes can establish in white-sand forests, thus maintaining the orthogonality of the two axes in this habitat. Similarly, we found that species established in terra firme and seasonally flooded forests exhibit the entire array of possible trait combinations. Hence, the orthogonality of the two trait axes is maintained in all three studied habitats (Appendix S4).

GENERALITY OF LEAF AND WOOD TRAIT AXES ACROSS AMAZONIA

Our study included traits measured across broad environmental and geographic gradients (Fig. 1), albeit within one large area of a single biome (lowland tropical moist/wet rain forest in South America). In a study of tree composition and function across Amazonia, ter Steege *et al.* (2006) showed that the high species turnover between the Guiana shield and south-western Amazonia was correlated with changes in regional soil fertility and was reflected by variation in wood density (among other plant functional traits). The environmental variation contained in our study is comparable to that encompassed in the study of ter Steege *et al.* (2006).

Yet despite differences in floristic composition among habitats and geographic regions in our study (e.g. Fine *et al.* 2010), we observe strongly conserved relationships among leaf and wood traits: the orthogonality of the two axes holds not only across the environmental gradient between three habitats but also across the geographic gradient between French Guiana and Peru (Fig. 3, Appendices S3 & S4). Hence, our experimental design confirms the previous results of Baraloto *et al.* (2010b) that were restricted to French Guianan terra firme forests, and we conclude that the orthogonality between leaf and wood economics spectra is indeed a general phenomenon in tropical trees of lowland South America.

The existence of two orthogonal axes of trait trade-offs demonstrates the need to integrate both leaf and wood trait dimensions in further studies on plant strategies along environmental gradients and geographic zones (Baraloto *et al.* 2010b). An integrated definition of plant strategies is crucial to a better understanding of plant responses to global environmental changes in both correlative and modelling approaches (Westoby & Wright 2006). The covariation of stem and root structural traits along a single axis considerably simplifies the determination of this dimension of plant strategy, as roots are often thought to be the most difficult compartment to study for practical reasons. However, we still need to test these trait relationships on other root traits, particularly fine roots, and on woody plant species from other biomes before concluding on its generality.

Acknowledgements

We thank the many colleagues who participated in field work in French Guiana, especially Marcos Ríos, Elvis Valderrama, Julien Engel, Seth Kauppinen, Alec Baxt, Benjamin Leudet, Benoit Burban, Jean-Yves Goret, Greg Lamarre and Tim Paine; and in Peru, especially Italo Mesones, Nallarett Dávila, Julio Sanchez, Julio Grandez Ríos, Fabio and Milka Casado and Tracy Misiewicz. Sandra Patiño graciously supplied some of the stem tissue analyses. We are grateful to Joe Wright, Jim Dalling and one anonymous referee for their helpful comments. Research was supported by a collaborative NSF DEB-0743103/0743800 to CB and PVAF; and by an INRA Package grant to CB.

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Received 5 March 2012; Accepted 10 May 2012
Handling Editor: Jim Dalling

Supporting information

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

Appendix S1. List of the studied species ordered alphabetically by family based on APG3 classification.

Appendix S2. Biplots of trait relationships among 14 leaf, stem and root traits in 758 tropical tree species.

Appendix S3. Correlation between the 14 leaf, stem and root traits and the first two axes of the principal component analysis on all 14 traits.

Appendix S4. Comparison of pairwise trait correlation matrices among 13 plots representing the gradient of environmental conditions found across Amazonia.

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