

Coordinated evolution of leaf and stem economics in tropical dry forest trees

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Abstract. With data from 15 species in eight families of tropical dry forest trees, we provide evidence of coordination between the stem and leaf economic spectra. Species with low-density, flexible, breakable, hydraulically efficient but cavitationally vulnerable wood shed their leaves rapidly in response to drought and had low leaf mass per area and dry mass content. In contrast, species with the opposite xylem syndrome shed their costlier but more drought-resistant leaves late in the dry season. Our results explain variation in the timing of leaf shedding in tropical dry forests: selection eliminates combinations such as low-productivity leaves atop highly vulnerable xylem or water-greedy leaves supplied by xylem of low conductive efficiency. Across biomes, rather than a fundamental trade-off underlying a single axis of trait covariation, the relationship between leaf and stem economics is likely to occupy a wide space in which multiple combinations are possible.

Key words: adaptation; functional traits; leaf deciduousness; Mexico; plant biomechanics; trade-offs; water potential; wood density; xylem hydraulic conductivity; xylem resistance to cavitation.

INTRODUCTION

A core question in plant functional ecology is the degree to which whole-plant performance depends on functional integration between parts (Ackerly 2004, Baraloto et al. 2010, Freschet et al. 2010). Functional integration is central to schemes such as that of Grime et al. (1997), who envisioned plants as deployed along a slow–fast axis of resource acquisition and utilization, in which some species have high instantaneous acquisition rates and short-lived tissues, while others have long-lived tissues with slower instantaneous acquisition rates, producing a diversity of strategies equivalent in their average long-term carbon capture rates (Marks and Lechowicz 2006). Because different patterns of functional integration would be expected to result in different whole-plant performance, it is a priority to identify covarying networks of interrelated traits that define plant structure and function within and across species (Pigliucci 2003, Olson et al. 2009).

When traits are related by a resource allocation trade-off, a pervasive covariation pattern emerges, known as an economic spectrum (Westoby et al. 2002, Reich et al.

2003). Major economics spectra have been described for leaves and stems. The leaf economics spectrum is thought to emerge from the trade-off implied by allocating space to cell walls that stiffen leaves vs. filling space with the cell lumina available for photosynthesis. This trade-off is reflected across the globe in a negative relationship between leaf life span and leaf construction costs, nutrient content, and carbon assimilation rate (Wright et al. 2004). The stem economics spectrum is underlain by a similar trade-off generated by the impossibility of filling the same volume with cell wall material and cell lumen. This trade-off means that features that depend on the cell wall fraction, such as mechanical support or herbivore resistance, will necessarily be negatively related to features that are associated with the lumen fraction, such as storage or conduction (Chave et al. 2009).

There are compelling reasons to expect that these two plant economic spectra should be tightly integrated, and most studies that have examined leaf–stem coordination bear out this expectation. Leaf traits such as stomatal conductance and leaf photosynthetic rates are associated positively with stem xylem hydraulic efficiency and negatively with wood density, in accordance with expectations regarding the interplay of xylem and leaf features in the regulation of water use (Brodribb and Feild 2000, Sperry 2000, Santiago et al. 2004, Ishida et al. 2008, Meinzer et al. 2008a, 2010, Pineda-García et al. 2011). Deciduous and evergreen species are expected to differ in their xylem hydraulic design, with drought-deciduous species being more hydraulically efficient but more vulnerable to cavitation than evergreen species;

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however, results are vague to date (Ackerly 2004, Maherali et al. 2004, Markesteijn et al. 2011). Because deciduous and evergreen leaves represent different poles of the leaf economic spectrum, this link between leaf phenology and conductive performance clearly predicts stem and leaf integration (Díaz et al. 2004, Freschet et al. 2010). In contrast, one study (Baraloto et al. 2010) found that leaf economic traits varied independently of xylem and bark density in tropical forest trees, which the authors interpreted as evidence of decoupled evolution in the stem and leaf economics spectra. The pervasiveness of the leaf–stem relationship thus remains a matter of discussion.

Plant phenotype diversity involves multiple trade-offs between traits. These trade-offs appear to allow plants to display alternative combinations of functional traits with presumably equivalent fitness within the same environment (Marks and Lechowicz 2006). Variation in xylem and leaf economy is particularly sensitive to fluctuation in water availability and temperature (Wright et al. 2004, Chave et al. 2009). Environments prone to strong contrasts in water availability would impose selection for an array of functional traits, but potentially in differing directions. One extreme might take advantage of high resource availability during favorable periods, increasing the proportion of rapidly acquisitive functional traits. The other extreme would cope with low resource availability during unfavorable periods, increasing the proportion of resource-conservative functional traits. A plethora of combinations mediated by trade-offs is expected between these two extreme functional designs.

This is the case of tropical dry forest, an environment with a marked dry season and a high prevalence of erratic dry spells during the rainy season (Pineda-García et al. 2011). To understand the coordination between leaf and stem traits it is necessary to explore covariation within a network of functional traits reflecting stem economy (e.g., hydraulics, biomechanical behavior, and water storage capacity) and leaf economy (e.g., leaf construction costs and leaf retention during the dry season). We tested the following expectations regarding the relationship between stem and leaf economics in a tropical dry forest, a community in which the majority of plants drop their leaves in response to drought. Species with low-density wood have vessels of high hydraulic efficiency but low cavitation resistance, low wood mechanical strength, and high xylem water content. Because of their low cavitation resistance, species with low-density wood, in the tropical dry forest that we studied, should drop their leaves at the first sign of drought. In contrast, species with high-density wood should be more resistant to bending, and should have lower hydraulic efficiency and greater resistance to cavitation (Hacke et al. 2001, Jacobsen et al. 2005, Pratt et al. 2007, Meinzer et al. 2010). Greater cavitation resistance means that these species should have longer

leaf retention times into the dry season, as well as costlier leaves.

We tested our hypotheses using 15 species from eight families and five orders of eudicots in a tropical deciduous forest in western Mexico, spanning the range from species that shed their leaves at the onset of the dry season to species that retain their leaves well into the dry season. This array provided quantitative data on leaf economics and phenology, as well as traits reflecting stem hydraulics, mechanical support, and construction costs. Although studies have shown that mechanical properties of wood are strongly linked to hydraulics and storage (Jacobsen et al. 2005, 2007, Pratt et al. 2007, Meinzer et al. 2008b), ours is the first to focus on the association between traits from the leaf economics spectrum and a network of traits corresponding to all three main xylem functions defining the stem economics spectrum.

In summary, we use the broad range of leaf phenologies offered by tropical dry forest trees to test for coordination between stem and leaf economics. We report several strongly significant relationships between the traits that we measured and we give reasons to suspect that these patterns of covariation unite the leaf and stem economics spectra into a common slow–fast axis of resource exploitation.

METHODS

Study site, species sampling, and variables measured

We carried out fieldwork from 2008 to 2011 in the Chamela Reserve on the western Pacific coast of Mexico. Mean annual temperature is $24.9^{\circ} \pm 8^{\circ}\text{C}$, and the average annual rainfall is 752 ± 256 mm, occurring from June to October. Leaf flushing is rapid after the first 100 mm of rainfall (Bullock and Solís-Magallanes 1990). We selected 15 deciduous species, which represent most of the dominant species at the study site, and maximize the range in leaf deciduousness and phylogenetic affinity (Appendix A).

To evaluate the coordination between stem and leaf economics, we measured 11 stem and four leaf functional and structural variables (Table 1). We selected six individuals per species in which all variables were measured. From these individuals, we detached branches 1–1.5 cm in diameter for the measurement of all physiological xylem traits. To standardize our anatomical set of measurements, we cut one $1 \times 1 \times 1$ cm disc from the basal part of each branch used to measure hydraulic traits, which was subsequently fixed in formaldehyde acetic-acid alcohol (FAA), dehydrated in alcohol, and infiltrated and embedded in paraffin (Ruzin 1999). We also marked the adjacent branches for leaf measurements.

Xylem anatomical traits and potential hydraulic conductivity (K_p)

Fixed and embedded wood discs were cut on a sliding microtome and stained with safranin. We measured

TABLE 1. Functional stem and leaf traits measured in this study.

Group	Attribute (abbreviation)	Units	References
Stem	modulus of rupture (MOR)	N/mm^2	Gere and Timoshenko (1999)
Stem	modulus of elasticity (MOE)	N/mm^2	Gere and Timoshenko (1999)
Stem	specific stem density (SSD)	g/cm^3	Kirkham (2005)
Stem	xylem water content (XWC)	%	Kirkham (2005)
Stem	specific conductivity (K_s)	$g \cdot s^{-1} \cdot MPa^{-1} \cdot mm^{-1}$	Tyree and Ewers (1991)
Stem	mean water potential at 50% loss of hydraulic conductivity (Ψ_{50})	MPa	Tyree and Ewers (1991)
Stem	hydraulically weighted vessel diameter (D_h)	μm	Carlquist (1975)
Stem	vessel density (VD)	vessels/ mm^2	Carlquist (1975)
Stem	potential conductivity (K_p)	$g \cdot s^{-1} \cdot MPa^{-1} \cdot mm^{-1}$	Poorter et al. (2010)
Stem	vessel resistance to implosion ($(t/b)^2$)		Hacke et al. (2001)
Stem	water potential at midday (Ψ_{md})	MPa	Scholander et al. (1965)
Leaf	leaf area (LA)	cm^2	Wilson et al. (1999)
Leaf	leaf mass per unit area (LMA)	g/cm^2	Wilson et al. (1999)
Leaf	leaf dry mass content (LDMC)	%	Wilson et al. (1999)
Leaf	leaf retention time (LRT, days at which 50% of the leaves were lost)	days	

tangential and radial diameters and the wall thickness of 25 pairs of vessels, as well as vessel density (VD, vessels per mm^2), using ImageJ (*available online*).⁵ We also calculated the index of resistance to implosion, $(t/b)^2$, where t is the double-wall thickness of adjacent vessels and b is the vessel lumen diameter (Hacke et al. 2001); the hydraulically weighted vessel diameter (D_h), is calculated as follows:

$$D_h = \left[\left(\frac{1}{n} \right) \sum_{i=1}^n d^4 \right]^{1/4}$$

where d is mean vessel diameter (Poorter et al. 2010). Using the Hagen-Poiseuille formula, K_p was calculated as follows:

$$K_p = \left(\left[\frac{\pi \rho_w}{128n} \right] VD \right) D_h^4$$

where ρ_w and n are the density and viscosity of water at 20°C (Poorter et al. 2010). Anatomical variables were not available for *Cochlospermum vitifolium*.

Xylem hydraulic conductivity (K_s)

During November 2010, at the onset of the dry season, we cut straight segments longer than the maximum vessel length underwater to prevent embolism entry and measured K_s using a Sperry apparatus, a low-pressure device that forces KCl solution through the stems, allowing quantification of conductivity as net flow rate/pressure gradient (Sperry et al. 1988). We estimated the maximum vessel length for each species by attaching the basal end of branches to an air compressor forcing 5 kPa of air into the stem and cutting the apical end underwater each 0.01 m until air bubbled out. Then we measured the segment length and summed 0.005 m to obtain maximum vessel length (Appendix B; see Ewers

and Fisher 1989). To measure conductivity, we connected segments to a reservoir containing a filtered (0.2 mm), degassed 10 mmol/L KCl solution, and used a pressure of 5 kPa to calculate an initial K_h , the mass flow per pressure gradient. We flushed the segments with the KCl solution using a pressure of 100 kPa for 10–20 minutes and remeasured K_h . We repeated the cycle of flushing and measuring until no increase in K_h was noted (Pockman and Sperry 2000), which usually occurred after two flushes. Finally, we divided K_h by the area of wood in cross section to calculate maximum K_s . Due to the presence of gums and latex, we were unable to obtain accurate measurements of the hydraulic properties of three species (Appendix C).

Mean water potential at which 50% of hydraulic conductivity was lost (Ψ_{50})

For each species, we generated a xylem vulnerability curve using the air injection method (Appendix C; see Sperry and Saliendra 1994). This method measures the progressive loss of hydraulic conductivity of stems sealed in steel sleeves with both ends protruding. We used segments 20% longer than the maximum vessel length to avoid potential artifacts of this technique (Appendix B; see Choat et al. 2010, Cochard et al. 2010). Vulnerability curves were constructed using 5–6 previously flushed segments. We measured hydraulic conductivity of segments after each air injection cycle using a pressure head of 5 kPa and pre-weighed vials filled with absorbent paper (Pockman and Sperry 2000). To inject air, we fitted pressure sleeves on the terminal parts of segments where they were ~ 1 cm diameter. We applied increasing pressures starting at 0.3 MPa to a maximum of 10 MPa for 10 minutes each, and measured K_h 20–40 min after pressure was removed. We evaluated Ψ_{50} for each species by fitting a four-parameter Weibull sigmoidal equation to the data (Sigma Plot 10.0; Systat 2007).

⁵ <http://rsbweb.nih.gov/ij/>

Midday water potential (Ψ_{md})

At the end of the 2010 rainy season, we measured Ψ_{md} of one terminal branch per individual sampled to measure stem and leaf variables. Measurements were taken from 12:00 to 16:00 hours with a pressure chamber (Model 1000 PMS Instrument Company, Corvallis, Oregon, USA). Branches were immediately bagged after cutting and were transported less than 15 minutes to the laboratory. This method provides a snapshot of the water status of transpiring leaves, an average of the bulk leaf and stem water potentials after stomatal closure, which is lower than the actual stem water potential (Melcher et al. 1998).

Specific stem density (SSD) and xylem water content (XWC)

We took $1 \times 1 \times 1$ cm wood samples from the segments measured for hydraulics and calculated specific stem density using the water displacement method and an analytical balance. We debarked and removed pith from samples and then oven-dried wood samples at 70°C for at least three days until constant mass. We calculated specific stem density as the ratio between dry mass and fresh volume (Kirkham 2005). We saturated in tap water for 24 h an additional six wood samples from the segments used for hydraulic measurements and oven-dried them at 70°C to constant mass, normally after three days. We calculated saturated xylem water content as the ratio between saturated mass minus dry mass over saturated mass (Kirkham 2005).

Modulus of elasticity (MOE) and modulus of rupture of wood (MOR)

We measured MOE and MOR on segments adjacent to those used for hydraulics. We wrapped branches in plastic and kept them cool until they were transferred to the laboratory. We debarked and tested segments in three-point bending with an INSTRON 3345 mechanical testing machine with a 5 kN load cell (INSTRON Corporation, Canton, Massachusetts, USA; Gere and Timoshenko 1999). Wood segments had length:diameter ratios of 20:1 to avoid shear. MOE and F_{max} , the maximum load at the moment of beam breakage, were calculated with SYSTEM IX/S INSTRON software (INSTRON Corporation, Canton Massachusetts, USA). The test segment diameter was calculated as the mean of the basal and apical diameters and a circular cross section was assumed for calculating I . MOR was calculated as $(F_{max} \times L \times R)/4I$, where L is the segment length, R is the radius, and I is the second moment of area, calculated as $I = \pi r^4/4$ (Gere and Timoshenko 1999).

Leaf retention time (LRT)

We conducted eight leaf censuses, starting on 15 October 2008 (30 days after the last 10-mm rainfall), and concluding 15 March 2009, during the late dry season.

During this period, we marked three terminal sun branches on six individuals per species and recorded the number of leaves or leaflets lost. We calculated LRT for each species (as the date on which 50% of leaf loss occurred) by fitting a sigmoidal three-parameter model to the plot of date as the independent variable and percentage leaf loss as the dependent variable (Appendix D; SigmaPlot 10.0, Systat).

Leaf area (LA), leaf mass per area (LMA), and leaf dry mass content (LDMC)

We measured LA, LMA, and LDMC on 10 fresh sun-exposed leaves per simple-leaved species and 50 leaflets per compound-leaved species. From digital images, we calculated LA using Winfolia Pro 2009 (Regent Instruments, Quebec, Canada); LMA (g/cm^2) as the ratio of leaf mass and LA; and LDMC (%) as $1 - [(\text{fresh mass} - \text{dry mass})/\text{fresh mass}] \times 100$ (Wilson et al. 1999).

Statistical analyses

The skewed distributions of SSD, K_s , $(t/b)^2$, VD, LA, and LMA required \log_{10} -transformation, whereas LRT required square-root transformation. We assessed relationships between traits using Pearson correlation. Because our main interest was finding the functional correlation structure for stem and for leaf traits, we summarized the patterns of correlation within and between the sets of stem and leaf traits using a multiple factor analysis (MFA). This ordination technique identifies the common structure among different sets of variables defined for the same individuals (Escofier and Pages 1994). MFA performs separate principal component analyses (PCA) on each set of variables. The elements of each set are then divided by the square root of the first eigenvalue of each PCA and a global PCA is then performed on the normalized data set. To assess the degree of coordination between leaf and stem traits, we used two statistics: the RV value, a coefficient between 0 and 1 derived from MFA indicating the relationship between the two sets of traits, and the Pearson correlation between the scores of the first principal component of each of the two individual PCAs. (The RV coefficient is a multivariate generalization of the R coefficient of a Pearson correlation, where the V indicates a "multivariate R.") We performed the MFA with the FactoMineR package (Lê et al. 2008) in R v.2.9 (R Development Core Team 2009), including only species with data for all variables.

To correct our correlations for phylogenetic non-independence, we calculated phylogenetically independent contrasts (PIC; Felsenstein 1985) and re-estimated correlations using the PDAP module (Midford et al. 2005) of Mesquite v.2.71 (Maddison and Maddison 2009). We reconstructed phylogenetic relationships between species using the Angiosperm Phylogeny Website (Stevens 2008), with branch lengths set to 1.0 (Appendix A).

TABLE 2. Pairwise Pearson correlations between stem and leaf traits.

	MOR	MOE	SSD	XWC	K_s	Ψ_{50}	Ψ_{md}	D_h	VD	$(t/b)^2$	K_p	LA	LMA	LDMC	LRT
MOR		0.89 ***	0.71 **	-0.74 **	-0.79 **	-0.41	-0.80 ***	-0.42	0.04	0.71 **	-0.53	-0.34	0.03	0.74 **	0.69 **
MOE	0.88 ***		0.80 ***	-0.84 ***	-0.69 **	-0.43	-0.74 **	-0.16	-0.30	0.60 **	-0.58 **	-0.50	-0.12	0.77 ***	0.78 ***
SSD	0.58 **	0.70 **		-0.98 ***	-0.61 **	-0.45	-0.83 ***	-0.25	0.21	0.78 ***	-0.75 **	-0.53 **	0.08	0.83 ***	0.80 ***
XWC	-0.66 ***	-0.77 ***	-0.96 ***		0.70 **	0.53	-0.85 ***	0.26	-0.27	-0.80 ***	0.84 ***	0.58 **	-0.11	-0.91 ***	-0.87 ***
K_s	-0.71 ***	-0.62 **	-0.54	0.73 **		0.72 **	-0.87 ***	0.60 **	-0.43	-0.78 **	0.56	-0.08	-0.59	-0.74 **	-0.66 **
Ψ_{50}	-0.40	-0.47	-0.47	0.66 **	0.81 **		0.74 **	0.57	-0.49	-0.55	0.65 **	0.05	-0.69	-0.64 **	-0.70 **
Ψ_{md}	-0.73 ***	-0.67 **	-0.74 ***	0.82 ***	0.88 ***	0.80 **		-0.44	0.10	-0.84 ***	-0.69 **	0.28	-0.38	-0.87 ***	-0.81 ***
D_h	-0.51	-0.33	-0.35	0.43	0.81 **	0.72 **	0.59 **		-0.72 **	-0.59 **	0.45 **	0.05	-0.54	-0.42	-0.47
VD	0.29	-0.04	0.11	-0.10	-0.84 ***	-0.77* **	-0.45 **	-0.77 **		0.10	0.13	0.38	0.59	-0.12	-0.12
$(t/b)^2$	0.61 **	0.48	0.70 **	-0.76 **	-0.78 **	-0.69 **	-0.79 ***	-0.79 ***	0.47 **		-0.67* **	-0.23	0.43	0.77 ***	0.80 ***
K_p	-0.47	-0.49	-0.70 **	0.83 ***	0.72 **	0.74 **	0.73 **	0.63 **	-0.24 **	-0.75 **		0.58 **	-0.28	-0.89 ***	-0.84 ***
LA	-0.35	-0.47	-0.24	0.28	0.00	0.08	0.06	0.25	-0.08	-0.04	0.22		0.37 **	-0.57 **	-0.50 **
LMA	0.04	-0.03	0.22	-0.32	-0.68 ***	-0.84 ***	-0.56 **	-0.60 **	0.58 **	0.62 **	-0.67 **	0.24		0.28	0.30
LDMC	0.71 ***	0.71 **	0.70 **	-0.85 ***	-0.84 ***	-0.75 **	-0.90 ***	-0.60 **	0.27	0.73 **	-0.87 ***	-0.27	0.52 **		0.91 ***
LRT	0.63 **	0.74 **	0.72 **	-0.84 ***	-0.69 **	-0.84 ***	-0.79 ***	-0.65 **	0.23	0.78 **	-0.83 ***	-0.33	0.54 **	0.87 ***	

Notes: Correlations based on raw data are shown above the diagonal; those based on phylogenetically independent contrasts are below the diagonal. Traits and abbreviations: modulus of rupture (MOR), modulus of elasticity (MOE), specific stem density (SSD), xylem water content (XWC), specific conductivity (K_s), mean water potential at 50% loss of hydraulic conductivity (Ψ_{50}), hydraulically weighted vessel diameter (D_h), vessel density (VD), potential conductivity (K_p), vessel resistance to implosion $(t/b)^2$, water potential at midday (Ψ_{md}), leaf area (LA), leaf mass per unit area (LMA), leaf dry mass content (LDMC), and leaf retention time (LRT). For all traits, $n = 15$, except for Ψ_{50} and K_s ($n = 12$), and for D_h , VD, $(t/b)^2$, and K_p ($n = 14$). Significant correlations are shown in boldface. ** $P < 0.01$; *** $P < 0.001$.

RESULTS

Species showed high variability in structural and functional traits (Appendix E). Most xylem and leaf traits were strongly correlated, using both raw data and PICs (Table 2). Overall, dry mass content and retention time were the leaf variables most strongly related to xylem traits. Surprisingly, leaf area did not show correlation with any leaf or xylem trait. As a consequence of the strong covariation between most traits, the first axis in the MFA accounted for 59.15% of the variance of 15 traits (Appendix F), with most variables having high loadings in the first axis (Fig. 1). In the second axis, accounting for 20.54% of the variance, leaf area, vessel density, and leaf mass per area had high loadings (Appendix F and Fig. 1). The results of individual PCAs including leaf or stem traits were very similar to the global MFA, with the same variables having high loadings in the same principal components (Appendix F).

The MFA indicated that most traits lie along a single axis. At one extreme are species with dense xylem of high mechanical stiffness and strength, high cavitation resistance, and vessels with thick walls for their diameters. These species have costly high LDMC and LMA leaves that are retained well into the dry season.

At the opposite extreme are species with xylem of low density, low mechanical strength, low cavitation resistance, vessels with thin walls for their diameters, and low LDMC and LMA leaves that are shed at the beginning of the dry season.

Finally, to depict the coordination between stem and leaf economics, we calculated the correlation between the first principal components of stem and leaf traits. Each principal component accounts for >60% of the variance within each set of variables (Fig. 2 and Appendix F). The correlation between the first principal components was $r = -0.885$ ($P < 0.001$; Fig. 2), which, along with the MFA RV coefficient of 0.719 between the sets of stem and leaf traits, suggests strong functional integration between these plant organs. Our results are congruent with the expectation of coordinated evolution of xylem and leaf traits, ranging from resource-conservative species to resource-exploitative species along a main MFA axis that describes the gradual change in xylem and leaf traits (Fig. 2).

DISCUSSION

Our results are clearly congruent with the prevailing wisdom that the leaf and stem economic spectra should be intimately linked (Brodrribb and Feild 2000, Sperry

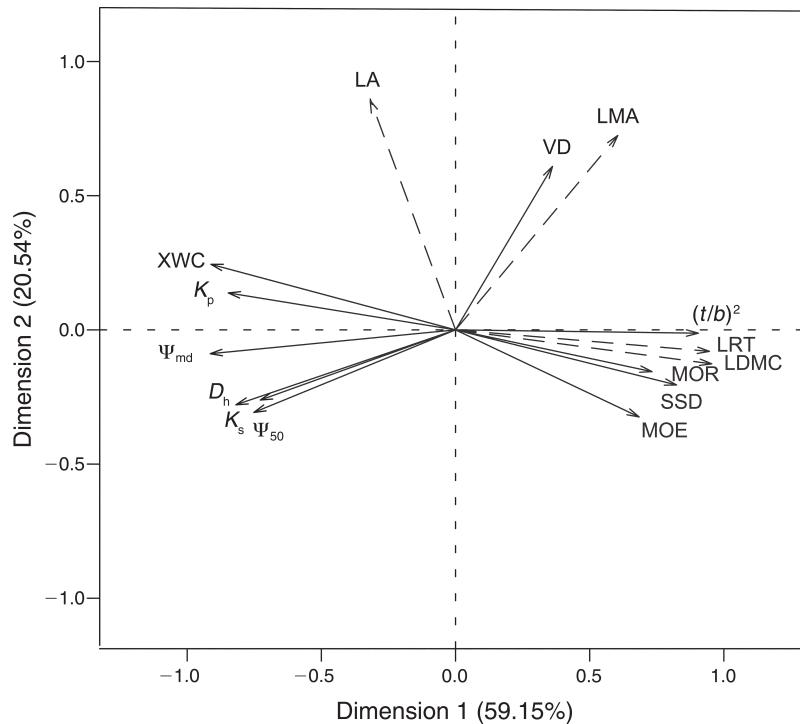


FIG. 1. Functional trait relationships on the basis of a biplot from the multiple factor analysis summarizing 11 stem structural and functional traits (solid lines) and four leaf functional traits (dashed lines) for tropical dry forest trees. Traits and abbreviations are: modulus of rupture (MOR), modulus of elasticity (MOE), specific stem density (SSD), xylem water content (XWC), specific conductivity (K_s), mean water potential at 50% loss of hydraulic conductivity (Ψ_{50}), hydraulically weighted vessel diameter (D_h), vessel density (VD), potential conductivity (K_p), vessel resistance to implosion $(t/b)^2$, water potential at midday (Ψ_{md}), leaf area (LA), leaf mass per unit area (LMA), leaf dry mass content (LDMC), and leaf retention time (LRT). Most traits significantly influenced PC1 (Dimension 1). LMA significantly influenced both components, and LA and VD significantly influenced PC2 (Dimension 2). The MFA (multiple factor analysis) between-group correlation coefficient is $RV = 0.719$. Values in parentheses in the axis labels are percentages of variance explained.

2000, Santiago et al. 2004, Ishida et al. 2008, Meinzer et al. 2008b, Freschet et al. 2010). We discuss stem–leaf coordination in terms of selection on traits that maintain plant water balance, and we also provide an explanation for the continuous variation in leaf shedding behavior observed among species of dry tropical forests. The network of structural and functional traits examined here illustrates how stem and leaf economics can be seen as integrated into a common axis of resource exploitation ranging from resource acquisitive to conservative species. Finally, we discuss ways that integration between the stem and leaf economic spectra should relate to demographic rates and ecosystem function, and ask how these constellations of trait relationships should impact studies of adaptation in plants.

Fugaciously deciduous pachycauls and tardily deciduous leptocauls

We found deciduous tropical dry forest trees to be arrayed along an axis of variation from dense-wooded, tardily deciduous species at one extreme to succulent trees that readily drop leaves at the other. Using the terms of Corner (1949) to describe stem stoutness, we call these extremes pachycauls, which bear fat stems with

low-density wood, and leptocauls, which have thin stems with high-density wood. The trait relationships that we observed probably emerge as the result of trade-offs within the stem and selection favoring functional coordination between stems and leaves. Limited space within the xylem and resources available for its construction should lead to a three-way trade-off between the main stem functions of mechanical support, water conduction, and water and photosynthate storage (Pratt et al. 2007; but see Zanne and Falster 2010). Species with lower density wood have less cell wall material and greater lumen per unit volume available for storage (Poorter et al. 2010). However, lower density wood is associated with lower capacity to resist bending, breakage, implosion, and cavitation, although vessel lumina should be wider and xylem conductivity higher (Pratt et al. 2007). In habitats with periodic drought, this tripartite trade-off has consequences for leaf phenology and leaf construction costs. For example, plants with low-density xylem with thin vessel walls are probably unable to withstand implosion and air seeding caused by highly negative xylem pressures (Hacke et al. 2001, Jacobsen et al. 2005). As a result, there is a limited window of water potentials over which these plants may

transpire without excessive cavitation, exerting selection pressure for high sapwood water storage, wide, conductively efficient vessels, high leaf photosynthetic rates, and short-lived leaves. (Brodribb et al. 2003, Ackerly 2004, Meinzer et al. 2008b). In contrast, trees with less wood water storage and safer conductive pathways will have available to them a wider temporal window across which they may transpire. However, the lower peak conductive efficiency of their vessels means that their instantaneous rates of carbon fixation will necessarily be lower than those possible in species with wider vessels. In species with narrow vessels, selection will therefore favor variants with longer lived leaves that fix carbon, albeit at lower rates, over longer periods. In accordance with these expectations, we found that an increase in conductive safety, as measured by Ψ_{50} and $(t/b)^2$, was positively associated with larger LDMC, LMA, and longer LRT during seasonal drought, and that xylem water content was negatively correlated with LRT. Species with longer LRT were associated with low wood water content, and had high wood density, MOE, and MOR.

Our results echo those of previous authors (Grime et al. 1997, Santiago et al. 2004, Ishida et al. 2008, Meinzer et al. 2008a, b, Freschet et al. 2010), suggesting that the association between leaf and xylem traits is likely to operate beyond our study site and taxa. For example, studies have found that xylem resistance to cavitation increases with wood density and decreases with xylem capacitance or maximum sapwood water content (Maherali et al. 2004, Meinzer 2008a, b, 2010, Markensteijn et al. 2010), whereas xylem cavitation resistance, stiffness, strength, and density are lower for drought-deciduous species than for evergreens in deserts and mediterranean sclerophyll shrubland (Pockman and Sperry 2000, Jacobsen et al. 2007). Results from other sites of seasonal tropical forests have led some authors to suggest that stem hydraulics and leaf phenology are not linked, basing their conclusion on wide overlaps in xylem water transport efficiency and vulnerability to cavitation between deciduous and evergreen species (e.g., Sobrado 1997, Brodribb et al. 2002, Markensteijn et al. 2010). In the present study, we provide evidence that leaf phenology behaves as a continuous ecological response correlated with stem economy. This continuous variation implies that discrete categories, such as the evergreen-deciduous dichotomy, are not representative of the whole variation in leaf and stem functional traits within seasonal tropical forests.

Coordination between stem and leaf economies in tropical dry forests

Trees can be thought of as describing a functional axis ranging from a rapid resource exploitation strategy, reflected in high hydraulic efficiency at the expense of hydraulic safety, mechanical strength, and leaf retention during drought, to a resource conservative strategy, in which species tend to bear xylem that is resistant to

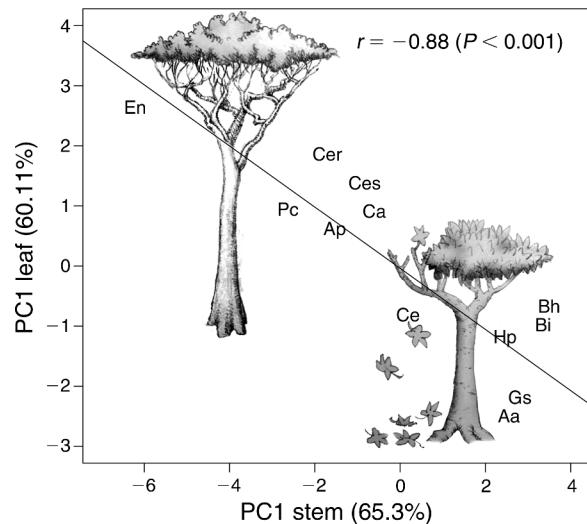


FIG. 2. Functional integration of stem and leaf traits in 12 dry tropical forest tree species as represented by the correlation between the first principal components of individual stem and leaf PCAs. The drawings represent (upper left) tardily deciduous leptocauls and (lower right) fugaciously deciduous pachycauls. Species abbreviations are: Aa, *Amphipterygium adstringens*; Ap, *Apoplanesia paniculata*; Bh, *Bursera heterosthes*; Bi, *Bursera instabilis*; Cer, *Caesalpinia eriostachys*; Ces, *Caesalpinia sclerocarpa*; Ca, *Cordia alliodora*; Ce, *Cordia eleagnoides*; En, *Esenbeckia nesiota*; Gs, *Gliricidia sepium*; Hp, *Heliocarpus pallidus*; Pc, *Piptadenia constricta*.

cavitation but of low hydraulic efficiency, as well as stiff and strong, and leaves that persist well into drought (Fig. 3). Overall, we provide evidence that leaf and stem traits are correlated, particularly in traits related to water balance during drought, such as leaf phenology and stem hydraulics. For example, LDMC and LRT, traits reflecting carbon cost and water balance in leaves, are linked with nearly all stem traits. For their part, leaf area and LMA, the only traits influencing the MFA axis 2, could be correlated with other leaf parameters, such as water balance, nitrogen balance, hydraulics, and photosynthetic rate (Poorter et al. 2009, Baraloto et al. 2010). Future research using a wider array of leaf and stem traits should clarify the degree of association between organs, providing a more detailed picture of the integration-decoupling of organ traits across ecosystems.

In the majority of plants, we expect selection to favor species that lie along the continuum that is described by the slow-fast revenue axis. However, the total range of variation expressed within communities should decrease toward drier or colder environments. For example, plants with large amounts of stem water storage resist freezing poorly (Gibson and Nobel 1986), so pachycauls probably will be mostly restricted to warm drylands (Medina 1995). Evergreen trees with low-density wood (e.g., *Ochroma* or *Cecropia*) should be restricted to frost-free areas with high water availability such as tropical rain forests, because of their very high vulnerability to

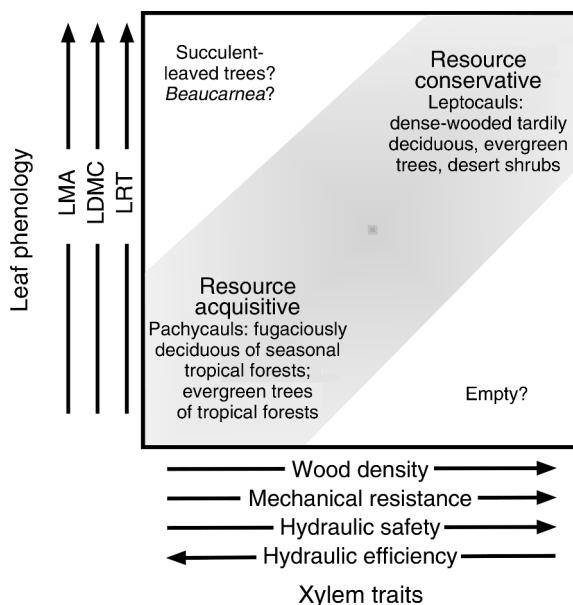


FIG. 3. Trees should lie between two extremes on a xylem traits–leaf phenology continuum: at one extreme we should find pachycauls, species with high xylem water content and low wood density, low resistance to cavitation, and low values of moduli of elasticity (MOE) and of rupture (MOR), with relatively low LMA leaves with high instantaneous C capture rates. At the other extreme, we should find leptocauls, species with low xylem water content, high wood density, high resistance to cavitation, high stem mechanical resistance, and higher LMA leaves that have lower instantaneous rates of C capture if longer-lived. The upper left and lower right areas of the functional space indicate trait combinations that would seem ontogenetically possible but of low fitness.

cavitation and frost sensitivity. Succulent evergreen trees may depart from the acquisitive-conservative axis in that they have the unusual combination of low-density, succulent tissues coupled with low resource acquisition rates (e.g., the CAM arborescent *Kalanchoe* or *Portulacaria*). Similarly, our results help to explain why combinations such as non-CAM trees with highly succulent stems with evergreen leaves should be extremely rare, such as the succulent-stemmed monocot tree *Beaucarnea*. By the same token, there are many plants with dense, stiff wood (e.g., *Dodonaea viscosa*), but because they are expected to fix CO₂ at very low rates, selection should favor long leaf retention times and higher LDMC (Fig. 3).

The different combinations of stem and leaf traits permitted in different environments should explain discrepancies between our studies and the findings of other authors. In our study we found a clear association between low-density xylem and fugacious deciduousness, and between high-density xylem and long leaf retention times. Other studies have shown no association between stem and leaf traits. Baraloto et al. (2010) examined trees in wet forest, where we would, in addition to the range present in dry forest, also expect

to find combinations such as long-lived leaves atop xylem of low density, given the low drought risk in wet forest. As a result, no linear statistical relationship would emerge from, say, study of wood density vs. leaf phenology or many other variables across a rain forest community even though the evolution of leaf and of stem features are highly contingent on one another (Sperry 2000).

The set of trait relationships that we document shows potentially important links with demographic rates of tropical dry forest trees. It seems likely that pachycauls should have high relative growth rates (RGR) and high mortality rates, as suggested by the correlations found for dry forest trees between RGR and SLA (the inverse of LMA) and mortality rates and wood density (Poorter and Bongers 2006, Poorter et al. 2008). Also, leaves and wood from pachycauls should decompose faster than those from leptocauls (Santiago 2007, Cornwell et al. 2008, Weedon et al. 2009).

Concluding remarks

Our results are congruent with the notion of a pervasive axis that runs from slow to fast resource exploitation, inevitably involving covariation between organismal parts as a result of trade-offs and correlated evolution. Given the necessary ubiquity of this covariation, the study of evolutionary trait relationships or the search for subsets of quasi-independent characters seems more justified than the search for unique central organizing characters. For example, many studies currently view wood density as such a trait (summarized in Chave et al. 2009). However, there is no evidence to suggest that this feature is any more causally “central” than any other (Zanne and Falster 2010). Instead, results such as ours suggest that evolutionary changes in a given feature, e.g., leaf deciduousness, would involve changes in the other variables, including wood density: shorter leaf retention times would be associated with selection pressure for higher instantaneous carbon fixation rates and wider vessels. Wider vessels are, in turn, associated with lower density wood. This example illustrates that wood density may be a convenient variable to measure and one that is associated with many other features (Chave et al. 2009), but there is no reason to believe that it has a sort of adaptive primacy. Instead, the question facing adaptationists in general and functional plant ecologists in particular is knowing which clusters of traits must be studied together and which can be safely examined in isolation. Such decisions are impossible until the main patterns of covariation between traits are identified and their causes are elucidated.

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SUPPLEMENTAL MATERIAL

Appendix A

Phylogenetic relationships and taxonomic information for sampled species (*Ecological Archives* E093-226-A1).

Appendix B

Maximum vessel lengths and lengths of segments used to construct vulnerability curves (*Ecological Archives* E093-226-A2).

Appendix C

Vulnerability curves for study species (*Ecological Archives* E093-226-A3).

Appendix D

Leaf retention time per species (*Ecological Archives* E093-226-A4).

Appendix E

Species list, family, and means of functional traits per species (*Ecological Archives* E093-226-A5).

Appendix F

Eigenvectors and percentage of the variance explained by the first two principal components of stem and leaf individual principal component analyses (PCA) and multiple factor analysis, MFA (*Ecological Archives* E093-226-A6).