

Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees

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Abstract In Neotropical forests, lianas are increasing in abundance relative to trees. This increased species richness may reflect a positive response to global change factors including increased temperature, atmospheric CO₂, habitat fragmentation, and drought severity; however, questions remain as to the specific mechanisms facilitating the response. Previous work suggests that lianas may gain an ecological advantage over trees through leaf functional traits that offer a quick return on investment of resources, although it is unknown whether this pattern extends to root traits and relationships with fungal or bacterial symbionts belowground. We sampled confamilial pairs of liana and tree species and quantified morphological and chemical traits of leaves and fine roots, as well as root symbiont abundance, to determine whether functional traits associated with resource acquisition differed between the two. Compared to trees, lianas possessed higher specific leaf area, specific root length, root branching intensity, and root nitrogen (N) and phosphorus (P) concentrations, and lower leaf and root tissue density, leaf and root carbon (C), root diameter, root C:P and N:P, and mycorrhizal colonization. Our study provides new evidence that liana leaf and

root traits are characterized by a rapid resource acquisition strategy relative to trees. These liana functional traits may facilitate their response to global change, raising questions about how increased liana dominance might affect ecosystem processes of Neotropical forests.

Keywords Economic spectrum · Trade-offs · Mycorrhiza · Specific root length · Specific leaf area

Introduction

Global change may alter the vegetation composition and structure of tropical forests, reducing the capacity of these ecosystems to act as a carbon (C) sink (Cramer et al. 2001) and to regulate the global climate system. One major shift in Neotropical forests concerns a steady increase in the abundance and biomass of lianas (i.e. long-lived woody climbers; Croat 1978) relative to trees (Phillips et al. 2002; Benítez-Malvido et al. 2003; Wright et al. 2004b; Schnitzer 2005; Ingwell et al. 2010; Schnitzer and Bongers 2011; Yorke et al. 2013; Laurance et al. 2014). This phenomenon may reflect a more positive response of lianas to global change factors, including increased temperature, atmospheric CO₂, fragmentation of the forested landscape, and drought severity, relative to trees, thereby allowing them to increase disproportionately (reviewed in Schnitzer and Bongers 2011). The phenomenon of liana expansion has raised questions about the biological mechanisms facilitating their increased growth, and why trees do not respond similarly to these environmental variables. For this reason, research is needed to improve our ecological understanding of lianas, and in particular, how their functional traits differ from those of trees (Cai et al. 2007; Zhu and Cao 2010; Schnitzer and Bongers 2011).

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Functional traits are measurable organismal properties that influence ecological performance (McGill et al. 2006), reflecting long-term adaptations to environmental conditions (Ackerly 2004; Lavorel and Garnier 2002). There is growing consensus that functional traits can provide insight into the diverse ecological strategies among plant species (Grime 1977; Díaz and Cabido 2001; Westoby and Wright 2006; Lavorel and Grigulis 2012), with the recognition that there are unavoidable trade-offs in strategies associated with particular suites of traits (Bloom et al. 1985; Grime et al. 1997; Reich et al. 1997; Díaz et al. 2004). Functional traits of different plant organs (i.e., leaves, stems and roots) provide information on the resource (i.e., light, water, nutrients) acquisition strategies of species (Sterck et al. 2011). For example, the leaf economic spectrum highlights trade-offs in plants between rapid acquisition and conservation of resources (Reich et al. 1999; Wright et al. 2004a; Osnas et al. 2013). This framework suggests that plants with leaf traits such as high specific leaf area (SLA; leaf area per unit of dry mass; $\text{cm}^2 \text{g}^{-1}$), low tissue density, and high nitrogen (N) and phosphorus (P) concentrations typically support high photosynthetic capacity. This strategy allows for rapid resource acquisition with a ‘quick return’ of water and nutrients on investment of dry mass. The trade-off in this strategy is that these leaf tissues typically have high maintenance costs and are poorly defended and short-lived. Alternately, plants with an opposing suite of physical and chemical traits are able to optimize a resource conservation strategy with slower returns on investment and longer-lived tissues (Reich et al. 1997, 2003; Lavorel and Garnier 2002; Díaz et al. 2004; Wright et al. 2004a).

An economic spectrum analogous to that described for leaves may exist for fine roots (Wahl and Ryser 2000; Reich et al. 2003; Lavorel et al. 2007). A particular suite of root traits may facilitate the rapid acquisition of belowground resources, but result in poor structural integrity, leading to fast root turnover (Eissenstat 1992; Ryser 1996; Eissenstat and Yanai 1997; Eissenstat et al. 2000; Craine et al. 2003). For example, high specific root length (SRL; root length per unit of dry mass, cm g^{-1}), low average root diameter, low tissue density (g cm^{-3}), high N and P concentrations, and high branching intensity (forks cm^{-1}) are commonly associated with a resource acquisitive strategy with short root life spans, and vice versa (Comas and Eissenstat 2004; Roumet et al. 2006; Holdaway et al. 2011; McCormack et al. 2012).

Root symbionts including mycorrhizal fungi and N_2 -fixing bacteria are another important component of a plant’s resource acquisition strategy. These symbioses reflect a trade-off between improved nutrient uptake and C cost to the plant. Mycorrhizal fungi may provide additional benefits, including resistance to desiccation, pathogens and herbivores (Eissenstat and Yanai 1997; Eissenstat et al. 2000).

Interestingly, plants with resource-acquisitive root traits are typically less dependent on root symbioses, possibly due to the reduced benefit of supporting costly symbioses on thin, highly branched roots that turn over quickly, and are autonomously effective at acquiring soil resources (Eissenstat 1992; Brundrett 2002; Menge et al. 2008; Comas et al. 2014; McCormack and Guo 2014). In contrast, plants with conservative root traits are not only more reliant on root symbioses for nutrient acquisition, but the symbionts themselves may affect the degree to which root traits are expressed (e.g. mycorrhizal inhibition of root branching) (Hetrick et al. 1991; Hetrick 1991; Brundrett 2002).

Functional traits provide information about the growth strategies of species that may shed light on the recent increased abundance of lianas in Neotropical forests (Schnitzer and Bongers 2011). Therefore, we investigated leaf and root functional traits of liana and tree species in a lowland tropical forest in Panama to determine whether these growth forms were characterized by different growth and resource acquisition strategies. Previous work suggests that, on a relative basis, lianas tend to have leaf traits associated with a rapid resource acquisition strategy, whereas the leaf traits of trees tend to be associated with a resource conservation strategy (Table S1). It is unknown, however, how the differences in leaf traits between lianas and trees extend to fine roots and belowground strategies for resource acquisition. Leaf and root functional traits are weakly correlated with one another across plant groups, suggesting that leaf traits provide a poor proxy for root function, and highlighting the importance of examining both above and belowground traits to fully understand plant resource strategies (Westoby and Wright 2006).

Based on our current knowledge of leaf traits for tropical lianas and trees (Table S1), we hypothesized that liana leaf traits would be characteristic of a rapid resource acquisition strategy, including lower tissue density, laminar thickness and C concentration, and higher SLA and tissue N and P concentrations than those of trees. We extended a similar hypothesis belowground and predicted that resource-acquisitive traits of liana roots would also include lower tissue density, root diameter and C concentration, and higher SRL, branching intensity and N and P concentrations than trees. For root symbionts, we hypothesized that liana roots would have lower mycorrhizal colonization and nodule biomass (Fabaceae only) than those of trees.

Materials and methods

Site description

Research took place on Barro Colorado Island (BCI), (9°9'N, 79°51'W) in the Republic of Panama. The annual

Table 1 The 12 species examined in this study organized into six confamilial tree–liana pairs

Family	Liana species	Tree species
Polygonaceae	<i>Coccoloba parimensis</i> Benth.	<i>Coccoloba manzinellensis</i> Beurl.
Rubiaceae	<i>Chomelia psilocarpa</i> Dwyer & M.V. Hayden	<i>Alseis blackiana</i> Hemsl.
Fabaceae (caes.)	<i>Clitoria javitensis</i> Benth.	<i>Platypodium elegans</i> Vogel
Combretaceae	<i>Combretum decandrum</i> Jacq.	<i>Terminalia amazonia</i> (J.F. Gmel.) Exell
Bignoniaceae	<i>Paragonia pyramidata</i> (Rich.) Bureau	<i>Tabebuia guayacan</i> (Seem.) Hemsl.
Celastraceae	<i>Prinostemma aspera</i> Miers	<i>Maytenus schippii</i> Lundell

temperature averages 27 °C, and average annual precipitation is 2600 mm, with distinct wet (May through December) and dry (January through April) seasons. The vegetation is considered tropical moist forest, with trees constituting about 27.7 % of the native species and lianas about 13 % (Croft 1978; Leigh 1999).

Leaf sampling occurred between June 2007 and January 2008 for all species (Wright et al. 2010) except the Celastraceae tree–liana pair, which was sampled in February 2013. Sampling took place in the 50-ha forest dynamics plot on BCI, which comprises 2 ha of mature secondary forest and 48 ha of old-growth forest. Lianas comprise about 25 % of the woody stems (trees and lianas), 35 % of woody species richness, and 3 % of woody basal area in this plot (Schnitzer et al. 2012). Additionally, within this plot, liana density over the last 30 years has increased nearly 140 % for stems ≥ 5 cm in diameter, while tree density has decreased 11.5 % (Schnitzer et al. 2012).

Root sampling occurred between May and July 2012 in the 25- and 6-ha plots on BCI, as root excavations are not permitted in the 50-ha plot. These adjacent forest dynamics plots are both within 700 m of the 50-ha plot where leaf sampling occurred, and are on the same upper andesitic plateau at the center of the island (Yavitt and Wieder 1988; Baillie et al. 2007). The volcanically derived soils present in all plots are relatively nutrient-poor oxisols (Lake, AVA, and Marron soil types), with similar values for total N and P and net mineralization potentials for nitrate, ammonium and phosphate (Yavitt and Wieder 1988; Baillie et al. 2007) (Table S2). The 25- and 6-ha plots comprise mature secondary forest on former agricultural lands abandoned between 1880 and 1914 (Enders 1935). Total liana abundance and biomass has not been calculated for these plots; however, our visual assessment estimates equal to slightly higher liana density in these plots and very similar species composition to the 50ha plot.

Species selection

Six confamilial tree–liana pairs (Table 1) were selected to control for phylogenetic variation that might otherwise obscure functional trait differences between growth forms. Species pairs were selected at the family level using the maximum-parsimony tree of 281 species of woody plants on BCI (Kress et al. 2009). The plant families selected are

evenly distributed across the Superrosidae and the Superasteridae. Species within families were chosen based on prevalence within the sampling area and feasibility of root and leaf sampling. In addition, for the families Fabaceae and Polygonaceae, the species selected were in the same subfamily (Caesalpinioideae) and genus (*Coccoloba*), respectively. Only liana and tree species present in all three forest dynamics plots were used.

Leaf collection and processing

Leaves were sampled from four to ten individuals for each tree and liana species (Table 1) and were collected with a shotgun from the fully sun-exposed crowns of trees and lianas. For five species, some partially shaded leaves were sampled for morphological traits due to a lack of sufficient individuals in full sunlight within the plots (*Paragonia pyramidata*, *Prinostemma aspera*, *Maytenus schippii*, *Coccoloba manzinellensis*, and *Chomelia psilocarpa*). Sampled leaves were immediately placed on ice and returned to the laboratory. We measured the following leaf functional traits: SLA ($\text{cm}^2 \text{g}^{-1}$), tissue density (g cm^{-3}), laminar thickness (cm), and total C, N, and P (%) and their ratios (C:N, C:P, N:P; %: %). SLA and tissue density were determined at three levels: the entire leaf (including the petiole and phyllodes for compound leaves), the lamina only, and a 1.483-cm² leaf disc taken to avoid veins. Chemical traits and thickness were determined for the lamina only.

Root collection and processing

Fine (<2-mm diameter) roots were sampled from ten individuals for each tree and liana species (Table 1). All individuals were sampled during the early wet season (May–July) to ensure similar soil moisture conditions. Each individual had canopy foliage exposed to direct sunlight as assessed visually using binoculars. We measured the following root functional traits: SRL (cm g^{-1}), diameter (mm), tissue density (g cm^{-3}), branching intensity (forks cm^{-1}), total C, N, and P (%) and their ratios (C:N, C:P, N:P; %: %), mycorrhizal colonization (arbuscules and/or fungal mantle; % root length), and nodule biomass (g cm^{-1} ; Fabaceae only).

For each individual tree and liana, approximately 5 g of fine roots (<2 mm-diameter) was excavated from the top

20 cm of soil and traced back to the main plant stem to ensure correct species identification (Cornelissen et al. 2003; Holdaway et al. 2011). Roots were abundant and shallow enough to allow excavation without causing significant disruption of the forest or the fine root architecture of the sample. After excavation, roots were kept moist in sealed plastic bags and transported to the laboratory for immediate processing.

Roots were rinsed with distilled water and cleaned with fine brushes to remove soil particles. For each 5-g sample, roots were split into two diameter-size classes using digital calipers: 0–1 mm to encompass lower branching order lateral roots and 1–2 mm to encompass higher branching order lateral roots (Fitter 1982; Fitter et al. 1991; Eissenstat 1992; Eissenstat et al. 2000; Pregitzer et al. 2002; Guo et al. 2008). This diameter-size class sorting system is similar to Trumbore et al. (2006), with the rationale that the smaller-size class includes roots involved in nutrient and resource acquisition and the larger-size class includes roots involved in structure and transport (Fitter et al. 1991; Eissenstat 1992; Eissenstat et al. 2000; Guo et al. 2008).

Morphological measurements

Leaves were dried at 60 °C for 72 h and weighed for dry mass (g), which was combined with leaf area (LI-300 m, leaf area meter; LI-COR, Inc., Lincoln, NE, USA) to calculate SLA ($\text{cm}^2 \text{g}^{-1}$). Lamina thickness (cm) was determined with a micrometer (TECLOCK SM112; TECLOCK Corporation, Nagano, Japan), and leaf tissue density (g cm^{-3}) was estimated as the inverse of SLA divided by laminar thickness.

Roots were scanned at 300 DPI (CanoScan LiDE210; Canon U.S.A., Inc., Melville, NY, USA) and analyzed with WinRHIZO software (Regent Instruments Inc., Quebec, Canada; 2000) to quantify total length (cm), volume (cm^3), diameter (mm) and branching intensity. Samples were then dried at 60 °C for 72 h to determine dry mass (g). Dry mass data were combined with total length and volume to calculate SRL (cm g^{-1}) and tissue density (g cm^{-3}).

Elemental determinations

Dried leaf laminas and fine roots were ground into a fine powder using a ball mill, and analyzed for total C, N and P content. We determined a single mean leaf C, N and P concentration for each species by combining an equal mass of powdered leaf tissue from each conspecific individual ($n = 4$ –10 individuals per species). Leaf tissue was analyzed at the soil analysis laboratory of the Smithsonian Tropical Research Institute. Total C and N were determined through combustion using a Flash HT elemental analyzer (continuous flow-isotope ratio mass spectrometry [CF-IRMS]; Thermo Fisher Scientific (Bremen) GmbH, Bremen, Germany), and total P was determined through acid extraction using a Lachat QuikChem flow injection analyzer

(8500; Lachat Instruments/Hach Company, Loveland, CO, USA). We determined root C, N and P concentrations for each individual ($n = 120$). Root tissue was analyzed at the analytical chemistry lab of Odum School of Ecology, University of Georgia, Athens, GA. Total C and N were determined by combustion using a CHN Carlo-Erba elemental analyzer (NA1500, Carlo-Erba Instruments, Milan, Italy). Total P was determined using acid extraction and was analyzed colorimetrically using a Alpkem rapid flow analyser (RFA-300 Series; Alpkem Corporation, Clackamas, OR, USA).

Mycorrhizal fungi

A small portion of the 0–1-mm root size class of each sample was sub-sampled and stored in 95 % ethanol (ETOH) at 4 °C for mycorrhizal assessment. These subsamples were rinsed with deionized water, cleared in a 5 % potassium hydroxide (KOH) solution at 60 °C for 4–6 h, briefly soaked in a 2 % hydrogen chloride (HCl) solution, and then stained at 60 °C for 15 min using a 0.05 % trypan blue solution (trypan blue in 2:1:1 lactic acid:water:glycerol). Stained roots were rinsed repeatedly with deionized water and stored in a de-stain solution (2:1:1 lactic acid:water:glycerol) prior to microscopic analysis. Arbuscular mycorrhizal (AM) colonization was quantified at 40× magnification using the magnified intersections method of McGonigle et al. (1990), and the presence of arbuscules was quantified (% root length). Arbuscules are the structural site of plant–fungal exchange of C for nutrients, and therefore provide a good estimate of AM activity (Brundrett 1991). Species of the genus *Coccoloba* (family Polygonaceae) are dually colonized by AM and ectomycorrhizal (ECM) fungi. ECM fungi colonize roots extracellularly, and therefore obscure the visibility of arbuscules below the ECM mantle. As a result, the presence of ECM mantle was quantified for this tree–liana pair in place of arbuscules. All mycorrhizal colonization measurements were normalized by root length (cm).

N₂-fixing nodules

For the family Fabaceae, N₂-fixing nodules were removed from roots prior to scanning, dried at 60 °C for 72 h, and weighed for dry mass (g). Dry mass data were combined with root length data from WinRHIZO to calculate nodule biomass per unit root length (g cm^{-1}).

Statistical analyses

We used linear mixed effects models to evaluate leaf and root trait differences between lianas and trees. Growth form (tree or liana) was a fixed effect, and family was a random effect. Mycorrhizal colonization was evaluated with and without the family Fabaceae, given the potential

Table 2 Results of mixed effects models comparing (a) leaf and (b) root morphological traits between trees and lianas

(a) Leaf traits	Leaf		Disc		Lamina	
	$F_{1,117}$	P	$F_{1,129}$	P	$F_{1,117}$	P
SLA (cm ² g ⁻¹)	21.759	<0.001	19.308	<0.001	17.835	<0.001
Tissue density (g cm ⁻³)	31.133	<0.001	27.586	<0.001	26.158	<0.001
Thickness (mm)	N/A		N/A		0.298	0.596
(b) Root traits	0–1 mm		1–2 mm			
	$F_{1,113}$	P	$F_{1,113}$	P		
Diameter (mm)	41.506	<0.001	0.247	0.619		
SRL (cm g ⁻¹)	54.340	<0.001	1.474	0.227		
Tissue density (g cm ⁻³)	0.439	0.508	5.778	0.017		
Branching intensity (forks cm ⁻¹)	5.986	0.016	0.032	0.858		

Numbers in **bold** represent significant differences between growth forms at $\alpha = 0.05$

Table 3 Concentration of total carbon, nitrogen and phosphorus and respective ratios in leaf and root tissue of lianas and trees

	Leaf (lamina)		Root (1–2 mm)		Root (0–1 mm)	
	Tree	Liana	Tree	Liana	Tree	Liana
C (%)	46.3 (1.3, 2.6) ^a	43.3 (1.2, 2.3) ^b	47.3 (0.37, 0.36) ^a	45.4 (0.29) ^b	45.0 (0.57, 0.56) ^a	44.4 (0.47, 0.46) ^a
N (%)	2.59 (0.48, 0.89) ^a	2.11 (0.27, 0.52) ^a	1.25 (0.05) ^a	1.19 (0.04) ^a	1.56 (0.06) ^a	1.62 (0.05) ^a
P (%)	0.12 (0.02) ^a	0.10 (0.02) ^a	0.051 (0.01) ^b	0.064 (0.01) ^a	0.064 (0.003) ^b	0.073 (0.003) ^a
C:N	19.1 (2.48) ^a	21.4 (2.48) ^a	39.7 (1.84, 1.76) ^a	36.4 (1.48, 1.43) ^b	28.8 (1.27, 1.22) ^a	27.4 (0.88, 0.86) ^a
C:P	391.9 (65.6) ^a	469.1 (65.6) ^a	983.9 (63.6, 59.8) ^a	756.9 (42.3, 40.0) ^b	702.1 (37.8, 35.9) ^a	606.8 (26.1, 5.0) ^b
N:P	21.7 (2.41) ^a	22.1 (2.41) ^a	24.7 (1.29, 1.23) ^a	20.6 (0.93, 0.89) ^b	24.4 (0.88, 0.86) ^a	22.1 (0.86, 0.83) ^b

Values are geometric means except for root and leaf P, which are arithmetic means. Values in parentheses are \pm one standard error (SE). Different letters represent significantly different trait values between growth forms as a result of the mixed-effects models at $\alpha = 0.05$

confounding effects of a second root symbiosis (N_2 -fixing bacteria) on patterns in mycorrhizal colonization (Bethlenfalvay et al. 1985, 1997). For the Fabaceae only, we compared nodule biomass per unit root length between *Clitoria javitensis* (liana) and *Platypodium elegans* (tree) with a two-tailed *t* test (Satterthwaite method due to inequality of variances). Log₁₀-transformed values were used to improve normality in all leaf morphological traits, SRL (0–1 and 1–2 mm), root diameter (0–1 and 1–2 mm), root tissue density (0–1 mm), root branching intensity (1–2 mm), leaf and root C and N, and root C:N, C:P, and N:P. Statistical analyses were performed in JMP Pro version 10.0.1 (SAS Institute Inc., Cary, NC, USA) and R version 3.0.2 software.

Results

For leaf traits, lianas had higher SLA (leaf, disc and lamina), lower tissue density (leaf, disc and lamina), and a lower percentage of total C (lamina) than trees. Laminar thickness, percentage of total N and P, and chemical ratios did not differ between trees and lianas (Tables 2, 3; Fig. 1).

For root traits in the 0–1-mm root size class, lianas had higher SRL, branching intensity, and percentage of total P, and lower mean root diameter, C:P and N:P than trees. For the 1–2-mm size class, lianas had a higher percentage of total P and lower tissue density, percentage of total C, C:N, C:P, and N:P than trees (Tables 2, 3; Fig. 2).

Across all plant families, mycorrhizal colonization did not differ between lianas and trees; however, when the family Fabaceae was removed from the analysis (see "Materials and methods"), lianas had a lower percentage of root length colonized by arbuscules or ECM mantle relative to trees ($P = 0.0126$; Fig. 3). For nodule biomass, we found no significant difference between *Clitoria javitensis* (liana) and *Platypodium elegans* (tree) ($P = 0.198$). Mean nodule values for the liana and tree species were 18.2 and 57.3 $\mu\text{g cm}^{-1}$, respectively.

Discussion

We compared root and leaf functional traits of lianas and trees in a lowland tropical forest in Panama to better

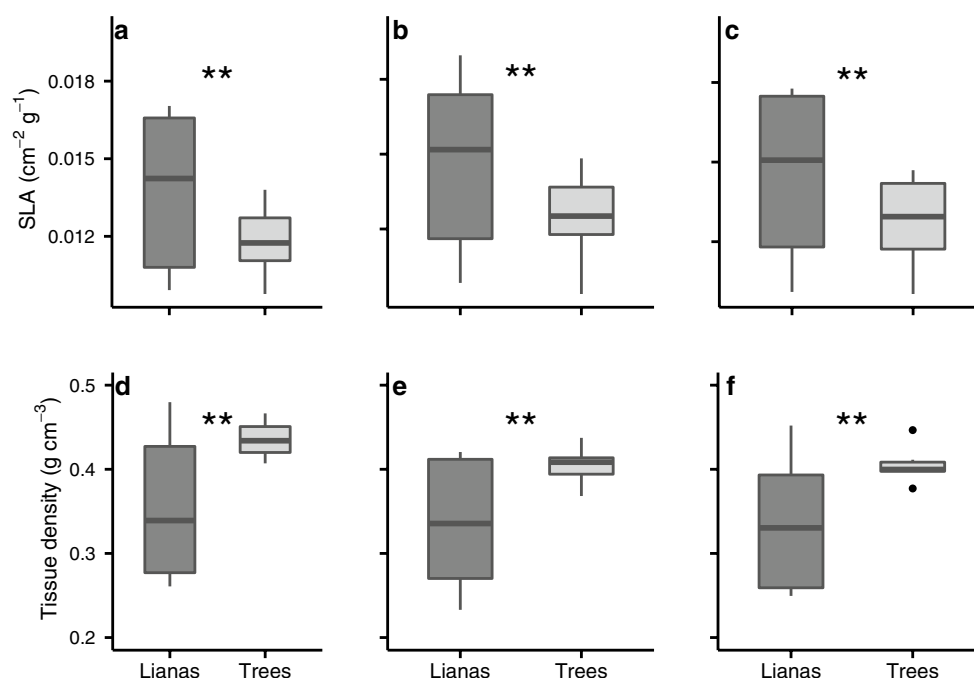


Fig. 1 Specific leaf area (**a–c**) and leaf tissue density (**d–f**) for the leaf, disc and lamina (*left, middle, and right columns, respectively*) from $n = 56$ individuals (lianas) and $n = 67$ individuals (trees). Box-plots include the median (*black line*), first and third quartiles (*bottom*

and *top* of the box, respectively), 1.5 times the interquartile range (*whiskers*), and outliers (*black points*). Asterisks indicate statistically significant differences between growth forms at $\alpha = 0.05$ (*) and $\alpha < 0.001$ (**). Laminar thickness not shown ($P = 0.68$)

understand the ecological strategies of these growth forms. We found that lianas and trees possessed leaf functional traits on opposing ends of the leaf economics spectrum, similar to observations in previous studies (Table S1). Our study also provides new evidence that the divergence in functional traits between lianas and trees extends below-ground, such that the root traits of lianas are associated with a rapid resource acquisition strategy relative to those of confamilial trees. While our findings are strong, more work would be necessary to determine whether our observations of trait differences between lianas and trees extend beyond the species in this study and across diverse tropical forests.

Leaf traits

We found that liana leaves possessed higher SLA, lower leaf tissue density, and lower leaf C concentration than trees. These results suggest that liana leaves have greater surface area available for photosynthesis at a lower expenditure of structural C, and because of this, liana leaves may be more prone to herbivory and turnover than those of trees (Eissenstat and Yanai 1997). This finding is consistent with previous studies on leaf functional traits of lianas and trees (Table S1), and argues for a direct link between changing climatic conditions—in particular, increased atmospheric CO_2 —and heightened photosynthetic capacity in lianas.

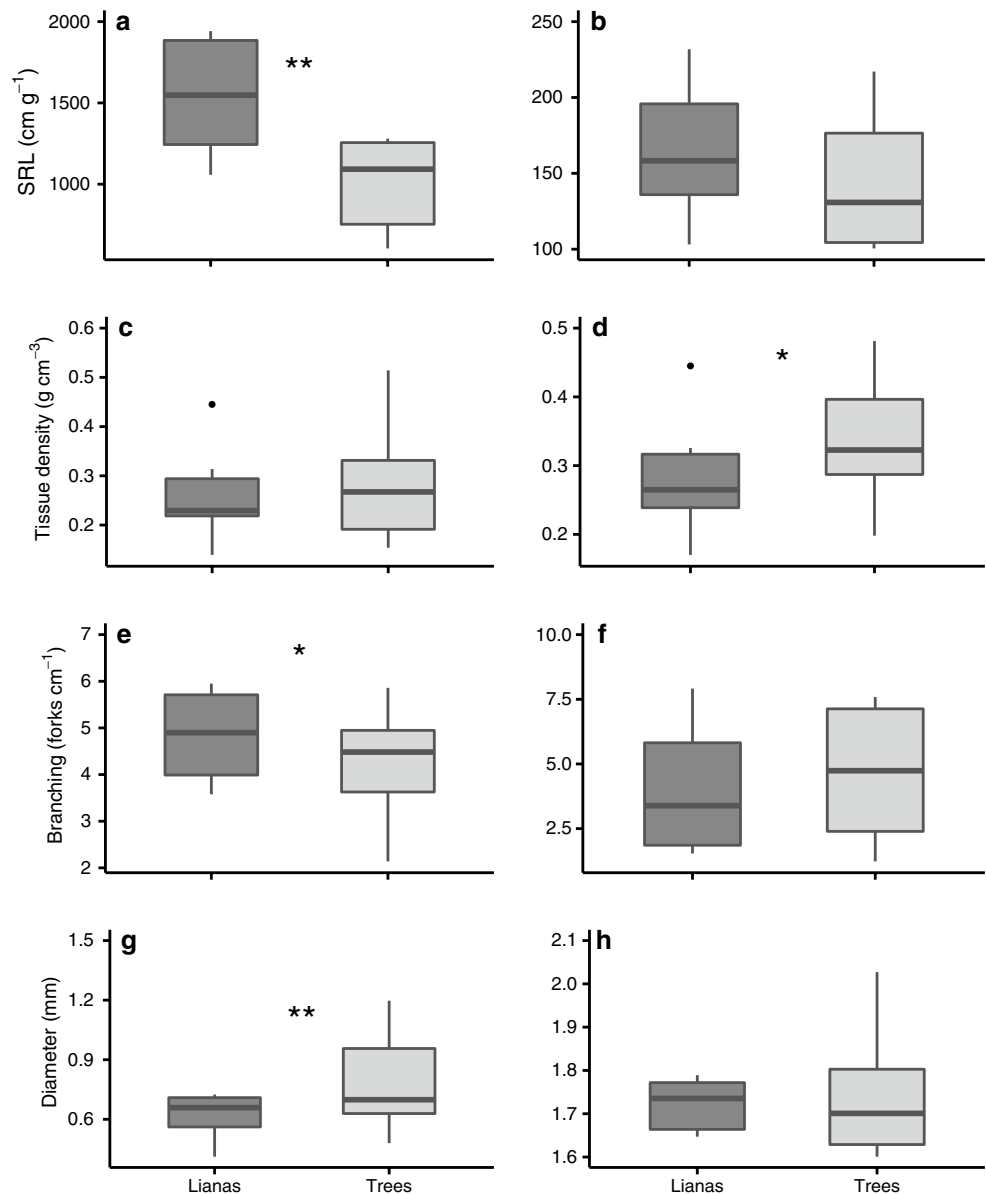
Leaf laminar thickness did not vary between lianas and trees. However, leaf thickness may not be closely related to leaf life span, and therefore does not always correlate with other leaf traits (Kitajima and Poorter 2010; Kitajima et al. 2012). Additionally, differences in SLA, tissue density and lamina thickness are difficult to resolve because they are mathematically interdependent traits ($\text{SLA} = \text{tissue density} \times \text{lamina thickness}$) (Witkowski and Lamont 1991).

We also did not observe higher leaf N and P concentrations or lower ratios of C to nutrients for lianas, although low replication in leaf chemical analyses ($n = 6$ species mean values per growth form) may have hindered our capacity to detect these relationships. Nonetheless, more labile (lower C content) liana leaf litter may stimulate nutrient cycling in soils and promote further establishment and plant growth (Dewalt et al. 2000; Tang et al. 2011).

Root traits

We observed that liana roots had lower tissue density, diameter, C content, C:N, C:P, and N:P ratios, and percentage of mycorrhizal colonization (for non-leguminous species), and had higher SRL, branching intensity, and P content than the roots of related trees for one or both size classes evaluated (0–1-mm and 1–2-mm diameters). Collectively, these findings suggest that lianas create fine roots with limited structural integrity, which as a result are likely to turn

Fig. 2 Specific root length (a, b), root tissue density (c, d), root branching intensity (e, f) and average root diameter (g, h) for the 0–1 mm (left column) and 1–2 mm (right column) root size classes for $n = 60$ individuals (lianas) and $n = 60$ individuals (trees). Boxplots include the median (black line), first and third quartile (bottom and top of the box, respectively), 1.5 times the interquartile range (whiskers), and outliers (black points). Asterisks indicate statistically significant differences between growth forms at $\alpha = 0.05$ (*) and $\alpha < 0.001$ (**)



over more quickly relative to the roots of trees (Eissenstat and Yanai 1997; Reich and Hall 2013). Rapid turnover may allow liana roots to explore the soil volume efficiently and may be less costly to the plant via low C construction costs, especially under elevated atmospheric CO_2 conditions (Caplan et al. 2014).

Our results suggest that lianas in both size classes of fine roots have morphological traits that may reduce life span and increase the capacity for resource acquisition relative to trees. For 0–1-mm roots, lianas had lower average diameter and higher SRL than trees. Differences in SRL can result from differences in tissue density or diameter, as these relationships are mathematically interdependent (Ostonen et al. 2007; Wurzbürger and Wright 2015), suggesting that the difference in SRL

between lianas and trees is driven mainly by root diameter. In the 1–2-mm root size class, however, lianas had lower tissue density than trees, with no differences in SRL or diameter. While we acknowledge that the predetermined root size class of 1–2 mm may have limited our capacity to detect differences in root diameter, and thus associated effects on SRL, our results nonetheless point to important differences in tissue density between lianas and trees.

Our findings suggest that lianas are less reliant on mycorrhizal symbionts than trees. First, we observed that among non-leguminous species, liana roots supported lower mycorrhizal colonization compared to trees. Second, we observed a negative correlation between root branching intensity and mycorrhizal colonization in

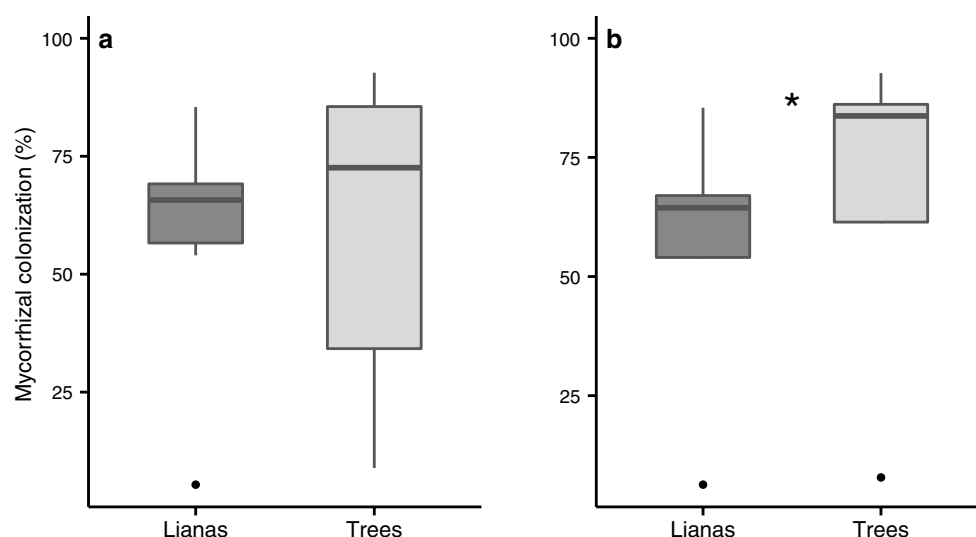


Fig. 3 Mycorrhizal colonization for the 0–1-mm root size class for $n = 42$ individuals (**a**) All families, and $n = 35$ individuals (**b**) Fabaceae removed. Boxplots include the median (black line), first and third quartile (bottom and top of the box, respectively), 1.5 times the

interquartile range (whiskers), and outliers (black points). Asterisks indicate statistically significant differences between growth forms at $\alpha = 0.05$ (*)

trees, but not in lianas (Fig. S1; $Z_{1,40} = 1.56$, $P = 0.059$). Highly branched roots may provide an advantage in belowground resource acquisition and may offset the demand for mycorrhizal symbionts, as evidenced by the negative relationship between root branching and mycorrhizal colonization in many plant species (Steeves and Sussex 1989; Hetrick 1991). Our results suggest that tree species may rely more heavily than lianas on mycorrhizal symbionts, particularly if they have low root branching intensity. Low mycorrhizal dependence could be advantageous for lianas under global change conditions (i.e. warmer temperatures, N deposition) that can accelerate nutrient mineralization by heterotrophic soil microbes, thus reducing the beneficial effect of symbiotic relationships.

Among chemical traits, liana root tissue possessed lower C:N, C:P, and N:P ratios than trees. High N content in tissues can be representative of protein concentrations associated with nutrient uptake and assimilation, while high P content increases the potential for the construction of biological compounds associated with energy and growth (sugar phosphates and nucleic acids) (Sterner and Elser 2002). Lower C can also result in decreased protection from herbivory by root exudates, as evidenced in isotopic studies (McDougall and Rovira 1970). Collectively, liana root tissue stoichiometry is complementary to their morphological traits, which are indicative of rapid root growth, nutrient uptake and assimilation, and poor structural integrity. Similar to that in leaves, the chemical composition of liana roots results in labile litter, which may enhance nutrient cycling in soils.

Ecosystem impacts

Functional traits provide an important first step in predicting the effects of global change on tropical forest community composition and structure, and hence on alteration of ecosystem function (Bardgett 2011; Reichstein et al. 2014). The results of this study raise new questions about how an increase in liana dominance might modify ecosystem processes of tropical forests. As lianas continue to increase in abundance relative to trees, their functional traits may drive changes in biogeochemical cycles. For example, higher rates of liana root turnover (as suggested by high SRL and low tissue density), as well as the lower C:N and C:P of liana litter inputs, may lead to increased root litter decomposition, soil C turnover, and mineralization of soil nutrients (Eissenstat and Yanai 1997; Gill and Jackson 2000; Reichstein et al. 2014). Stimulation of decomposers may further result in disproportionate losses of C through the priming of soil microbes (Sayer et al. 2011). Increases in plant available nutrient supply may have substantial impacts on forest productivity and could alter patterns in belowground allocation (Yavitt et al. 2011; Wurzbarger and Wright 2015). Additionally, since mycelial networks incorporate stable C in soils, the tendency for liana roots to support lower levels of mycorrhizal symbionts relative to trees may lead to further reductions in the long-term stability of soil organic C pools (De Deyn et al. 2008; Bardgett 2011). Finally, liana root and leaf traits, including high SLA and SRL, high N content and low tissue density, may improve water use efficiency, and thereby alter ecosystem water cycling, which

is particularly relevant in the context of global change-induced disruption of precipitation regimes and drought (Reichstein et al. 2014).

Conclusion

Our results provide new evidence that liana leaf and root traits are more characteristic of a rapid resource acquisition strategy than those of trees. These findings are consistent with the hypothesis that lianas are able to allocate a high proportion of their resources towards growth and resource acquisition because they rely on trees for structural support (Darwin 1867; Putz 1983; Cai et al. 2007). Liana leaf and root traits include a set of ecological trade-offs that may elucidate the mechanisms driving the increased abundance of lianas in Neotropical forests. Relative to trees, functional traits of lianas facilitate low C expenditure, rapid growth, and a high return on resource investment, which may provide them a competitive advantage under global change scenarios, including CO₂ fertilization, N deposition and physical disturbances. Increased liana abundance may ultimately change the composition of functional traits at the ecosystem level, affecting cycles of C, water, and nutrients, and the role of tropical forests in the global climate system.

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