LETTER

Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition

Gregory P. Asner[*] and Roberta E. Martin

Department of Global Ecology, Carnegie Institution for Science, 260 Panama Street, Stanford, CA, 94305, USA

*Correspondence: E-mail: gpa@ stanford.edu

Abstract

Lianas are an important growthform in tropical forests, and liana abundance and biomass may be increasing in some regions. Explanations for liana proliferation hinge upon physiological responses to changing resource conditions that would favour them over trees. Testing a chemical basis for such responses, we assessed 22 foliar traits in 778 lianas and 6496 trees at 48 tropical forest sites. Growthform differences in chemical allocation occurred on a leaf mass and area basis. Light capture-growth and maintenance-metabolism chemicals averaged 14.5 and 16.7% higher mass-based concentration in lianas than in trees globally, whereas structure and defence chemicals averaged 9.0% lower in lianas. Relative differences in chemical allocation by lianas and trees were mediated by climate with peak differences at about 2500 mm year^{-1} and 25 °C. Differences in chemical traits suggest that liana expansion could be greatest in forests undergoing increased canopy-level irradiance via disturbance and climate change.

Keywords

Canopy chemistry, growthform, leaf traits, plant functional types, tropical forest.

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INTRODUCTION

Lianas (woody vines) are a diverse group of plants found in nearly all tropical forests. They are second only to trees in terms of stand-level biomass, comprising up to 10% in some forests (Putz 1984), and they strongly influence tropical forest structure and ecosystem functioning (Schnitzer & Bongers 2002). Recent studies suggest that lianas may be increasing in abundance and biomass in some Neotropical forests with potential cascading impacts at community and ecosystem levels (reviewed by Schnitzer & Bongers 2011). Although experimental work has yet to assign specific causes to observed liana increases, putative explanations focus on liana responses to changing forest evapotranspirative (ET) balance due to changes in rainfall and temperature, boosted rates of natural and anthropogenic disturbance and atmospheric CO_2 enrichment. Each of these explanations would suggest the existence of a physiological response in lianas to changing resource conditions that favours them over trees. We thus would expect to find systematic differences in growth-related leaf traits advantaging lianas over trees under conditions of increasing water stress from rising ET demand, enhanced light or nutrient availability associated with disturbance and/or increasing atmospheric CO_2. We might also anticipate differences in leaf traits related to metabolism that would aid in energetic efficiency.

Although growth-related leaf traits may be central to understanding plant responses to environmental change, other traits are likely to be important as well. In tropical forests, plant trait evolution has taken place under enormous herbivore and pathogen pressure (Coley 1983; Fine *et al.* 2004), so structure and defence traits are key to enhancing leaf survival for future carbon gain. Yet the overall investment portfolio of a plant is also affected by resource availability, with light and rock-derived nutrients being two of the more scarce resources in humid tropical forests. As a result, trade-offs are made to allocate finite resources to traits that promote growth in lieu of structure and defence, or vice versa (Dudt & Shure 1994; Dominy *et al.* 2003; Fine *et al.* 2006). Studies seeking the most general understanding of whether traits differ among co-existing growthforms, such as lianas and trees, must therefore account for these potential investment trade-offs with respect to environmental conditions.

Leaves are a locus of chemical investment undertaken by plants to cope with their environment, including competition with co-existing individuals and species. Using numerous chemical elements, plants synthesise a wide variety of compounds in their leaves to support multiple functional strategies, which can be grouped into three broad categories: (1) light capture and growth, (2) structure and defence and (3) maintenance and metabolism (Table S1; *Supporting Information*). Light capture-growth compounds include photosynthetic pigments, such as chlorophylls and carotenoids, nitrogen (N) and phosphorus (P), as well as the immediate products of photosynthesis, such as soluble carbon compounds (Evans 1989; Chapin 1991; Niinemets *et al.* 1999). Structure-defence compounds include lignin and cellulose that support strength and longevity (Melillo *et al.* 1982), as well as phenols and tannins for chemical defence (Coley *et al.* 1993). Maintenance-metabolism elements (e.g. Ca, K, Mg, Zn, Mn, B, Fe) are those required to support and mediate myriad processes within the leaf, such as stomatal function and protein synthesis. Although it is well known that the make-up of foliar chemical portfolios varies with environmental conditions, particularly with soil fertility and climate, how co-existing growthforms differ in their chemical investments, and with respect to background environmental variability, remains poorly understood. This is particularly true for tropical lianas and trees, as a general knowledge of their chemical trait portfolios within and across contrasting sites has yet to be developed.

The relatively sparse comparative work on liana and tree leaf chemistry, and related traits such as leaf mass per area (LMA), has been carried out in site-level studies, which can produce different results based on environmental conditions. In a seasonally dry tropical forest in China, Cai *et al.* (2009) found higher N and lower LMA in lianas as compared to trees, associating these traits with enhanced rates of carbon fixation and water and nitrogen use efficiency in lianas. But in a consistently wet Panamanian forest,

Santiago & Wright (2007) observed lower carbon assimilation rates in liana foliage, and found no indication that lianas allocate more chemical resources to photosynthesis. They did find longer leaf lifespans in lianas, which when combined with evidence for greater leaf area per stem area (Gerwing & Farias 2000), suggested that lianas optimise resource use per unit stem diameter. Contrasting results in studies comparing liana and tree foliar allocation and performance may be related to climate conditions, as drier and sunnier conditions already tend to support higher background densities of lianas in tropical forests (Dewalt *et al.* 2010). However, lacking canopy chemical information among many sites has slowed our understanding of growthform-specific strategies, including those that might help to explain why liana abundances are increasing in some forests.

Here, we assessed differences in foliar chemical traits supporting light capture and growth, structure and defence, and maintenance and metabolism among co-existing lianas and trees in humid tropical forest canopies. By carefully controlling for local variation in illumination conditions, which often dominates patterns of leaf chemistry and LMA (Poorter *et al.* 2009; Messier *et al.* 2010), we developed a comparative analysis of liana and tree traits among tropical forest sites spanning a wide range of environmental conditions and floristic composition.

MATERIAL AND METHODS

Sample collection and analysis

We collected canopy samples from 7274 individuals in 48 humid tropical forest sites spanning Neotropical, Afrotropical (Madagascar) and Australasian ecoregions (Table S2; *Supporting Information*). Among sites, estimated mean annual precipitation ranges from 1313 to 6096 mm year^{-1}, elevation from 21 to 3700 m.s.l and mean annual temperature of 8–27 °C (Table S3; *Supporting Information*). Our overall sampling included 778 liana and 6496 tree specimens. The percentage of samples collected as lianas in any forest stand ranged from 4 to 41%, with a mean liana:tree sampling ratio of 15% (Figure S1; *Supporting Information*), excluding Barro Colorado Island in Panama where our local sampling included a nearly equal proportion of liana and tree species for other purposes. Lianas were distributed among 563 species, 216 genera in 69 families (Table S4; *Supporting Information*). Trees from corresponding locations were sampled from 3322 species, 807 genera in 140 families.

Owing to the strong effect of shade on foliar chemical concentrations and LMA (Poorter *et al.* 2000, 2009; Wright *et al.* 2007), and its confusing impact on growthform- and taxon-specific comparisons (Asner *et al.* 2011), we carefully controlled for full sunlight exposure. This process required that two or more trained workers agreed that the selected canopy has unobstructed exposure to the sky. Leaf collections were conducted using tree climbing, shooting and canopy crane techniques. Details on leaf collections, processing, LMA determination and chemical assays are provided in Table S5 and the text in the *Supporting Information*.

Statistical analysis

Growthform-specific differences in leaf trait values among all samples were evaluated using linear mixed models with the residual maximum likelihood method. Site selection was treated as a random factor to account for possible dependence of leaf trait measure-

ments on sampling location, whereas growthform and climate variables [Mean annual precipitation (MAP), Mean annual temperature (MAT)] and their interaction were treated as fixed effects. With the exception of phenols, tannins and $\delta^{13}C$, all leaf traits required transformation by natural logarithm. Stepwise multiple linear regressions were used to evaluate site-level variation in leaf traits with respect to MAP and MAT. At the ecoregional level, *t*-tests were used to assess the difference in trait values between liana and tree. These results are presented as the per cent difference in mean values for liana-to-tree growthforms. We used Principal Components Analysis (PCA) to determine whether leaf properties vary in a coordinated manner. The first principal axis of a PCA describes the largest degree of co-variation among variables. The PCA models were developed for: (1) all leaf traits excluding $\delta^{13}C$, (2) light capture and growth chemical traits, plus LMA, (3) structure and defence traits and (4) traits involved in maintenance and metabolism.

RESULTS

A global pattern

A summary of leaf traits for all liana and tree samples is provided on a mass basis in Table 1, and on an area basis in Table S6 (*Supporting Information*). The LMA variation in lianas and trees exceeded the range summarised for most other biomes (Poorter *et al.* 2009), confirming the exceedingly high interspecific variation recently reported for humid tropical forest canopies (Asner *et al.* 2011). Despite the high variance, LMA was an average 16% lower in lianas, indicating systematically greater photosynthetic surface area per unit leaf mass (Table 1). Similarly, nearly all light capture and growth chemicals were found in higher mass-based concentrations in lianas than in trees (Fig. 1a). A general pattern emerged, with photosynthetic pigment concentrations 17–21% higher in lianas compared with trees, and N and P concentrations 12 and 9% higher, respectively, in lianas. When evaluated on an area basis (Table S6), however, chlorophyll concentrations were similar between lianas and trees (Fig. 1a). Furthermore, N, P and soluble carbon switched from significantly higher concentrations on a mass basis to much lower concentrations on an area basis in lianas as compared with trees. On average, maintenance-metabolism chemicals were also found in higher mass-based concentrations in lianas: 21–41% higher concentration of base cations (Ca, K and Mg) and 4–11% higher concentration of other micronutrients (Zn, Mn, B and Fe) (Table 1). Most of these elements were found in a slightly lower concentration per leaf area in lianas (Fig. 1), but these differences proved statistically insignificant (Table S6). Notably, Ca was significantly more concentrated in lianas both on a mass and area basis.

We also found significant differences in growthform-specific allocation to foliar structure and defence compounds (Table 1). The three most often cited compound groups in this role – lignin, phenols and tannins – were an average 11–26% lower in mass-based concentration in lianas than in trees. In contrast to light-growth and maintenance-metabolism traits, the systematically lower investment in structure-defence compounds by lianas was consistent on both a mass and an area basis (Fig. 1a).

We used PCA to assess the degree to which our leaf trait groupings represent unique or overlapping physiological properties and processes. The first PC explained just 31 and 30% of the variance among all traits for lianas and trees, respectively (Table S7; *Supporting*

Table 1 Leaf traits on a mass basis for tropical canopy lianas and trees

Trait	Lianas					Trees				
	Mean	SD	CV	Min	Max	Mean	SD	CV	Min	Max
LMA (g m^{-2})	92.87	36.69	39.6	24.21	245.06	109.68	39.08	35.6	29.95	445.85
δ^{13}C (%) [n.s.]	−30.94	1.58	5.1	−36.20	−25.70	−30.95	1.78	5.8	−36.20	−24.10
Light capture-growth										
Chl-a (mg g^{-1})	5.78	2.42	41.9	1.20	17.89	4.84	1.82	37.7	0.99	14.18
Chl-b (mg g^{-1})	2.18	0.96	43.9	0.37	7.49	1.82	0.73	40.2	0.34	5.92
Car (mg g^{-1})	1.67	0.64	38.1	0.39	4.86	1.43	0.50	34.8	0.38	7.87
N (%)	2.20	0.78	35.6	0.66	5.49	1.98	0.68	34.3	0.56	6.12
P (%)	0.12	0.07	59.9	0.03	0.66	0.11	0.07	58.3	0.02	0.86
Water (%)	62.34	8.85	14.2	42.03	90.79	58.56	7.49	12.8	25.27	83.18
Soluble-C (%) [n.s.]	45.45	10.98	24.2	18.56	81.62	44.93	11.49	25.6	16.19	82.55
Structure-defence										
C (%)	47.81	3.35	7.0	35.20	57.40	49.24	3.23	6.6	34.70	58.90
Hemi-cellulose (%)	13.32	5.37	40.3	0.00	35.91	11.53	4.80	41.6	0.00	48.19
Cellulose (%)	19.08	5.80	30.4	6.93	49.09	18.50	5.59	30.2	3.34	44.33
Lignin (%)	21.94	8.75	39.9	2.66	64.51	24.77	10.06	40.6	2.71	63.79
Phenols (mg g^{-1})	78.40	56.81	72.5	0.00	321.57	104.51	52.84	50.6	0.00	310.81
Tannins (mg g^{-1})	37.45	27.59	73.7	0.00	215.92	46.77	25.74	55.1	0.00	236.02
Maintenance-metabolism										
K (%)	0.95	0.57	60.5	0.14	3.77	0.78	0.46	58.6	0.13	4.40
Ca (%)	1.41	1.04	73.6	0.02	6.68	0.98	0.80	81.5	0.01	8.02
Mg (%)	0.32	0.18	56.5	0.03	1.20	0.26	0.14	54.5	0.02	1.38
Zn (µg g^{-1})	18.11	16.75	92.4	3.61	236.58	17.13	55.19	322.3	1.86	2535.98
Mn (µg g^{-1})	300.72	551.57	183.4	6.22	7331.67	284.89	505.52	177.4	3.76	6594.25
B (µg g^{-1})	29.94	21.65	72.3	2.95	170.43	26.29	22.78	86.6	2.24	321.89
Fe (µg g^{-1})	96.00	193.03	201.1	9.52	2250.00	87.96	226.05	257.0	9.36	9470.68

Multivariate linear mixed models (Site [random]; growthform [fixed]) indicate statistical differences by growthform ($P < 0.05$) for all traits except for δ^{13}C and soluble-C as noted by [n.s.].
CV, absolute values of coefficient of variation, LMA, leaf mass per area; Max, maximum; Min, minimum; SD, standard deviation.

Information), indicating decorrelation among many chemicals. Moreover, a total of 15 principal components were required to explain 95% of the variance among all traits. Among light capture and growth traits alone, the first PC explained 71% (lianas) and 69% (trees) of the variation, in agreement with the leaf economics spectrum (Wright *et al.* 2004). In contrast, the first PC explained just 39–41% and 34–35% of the variance within each group of structure-defence and maintenance-metabolism traits respectively. Together, the PCA results indicate that many of our leaf chemicals represent orthogonal functional traits, and thus we carried all of them forward for further analysis and comparison.

Linear mixed modelling results indicated that site selection accounted for about 25% of the variation in LMA (Table 2), but growthform stood out as the most important factor. Among light capture and growth traits on a mass basis, growthform again accounted for most of the modelled variation with site selection and climate factors playing a distant secondary or no detectable role. One exception was P for which site accounted for 50% of the variation. On an area basis, growthform remained most important in explaining N and P; however, area-based photosynthetic pigments were determined more by site selection and climate variables (Table S8; *Supporting Information*). Similar results were found for cations associated with cellular maintenance and metabolism. On a mass basis, structure and defence traits were also best explained by growthform, whereas site selection accounted for an average 14% of the mea-

sured variation (Table 2). When calculated on an area basis, structure and defence traits remained best explained by growthform (Table S8), and neither site nor climate variables accounted for much of the chemical variation among the leaf samples.

Intersite variation

We found that the liana-to-tree (L : T) ratio of investment in mass-based light capture and growth chemicals was inversely related to MAP, and positively with MAT to a lesser degree (Fig. 2; $R^2 = 0.64$, $P < 0.001$). Additional analyses indicated that the site-level L : T ratio for photosynthetic pigments and N decreased with increasing MAP (R^2 range of 0.30–0.37, all $P < 0.02$). Area-based calculations indicated weaker relationships between L : T and MAP for all growth chemicals, owing to the compensating effect of changing LMA with climate. Nonetheless, the site-level L : T ratio for structure and defence compounds was negatively associated with MAP on both an area ($R^2 = 0.20$, $P < 0.01$) and mass ($R^2 = 0.36$, $P < 0.01$) basis. Analyses of individual chemical traits suggested that these patterns are primarily driven by changes in liana chemical allocation with climate. As precipitation increases and/or temperature decreases, liana chemistry often converges with that of trees (Figure S2).

Critically, we identified a threshold of about 2500 mm year^{-1} and 25 °C at which a shift occurs in the relative investment by lianas
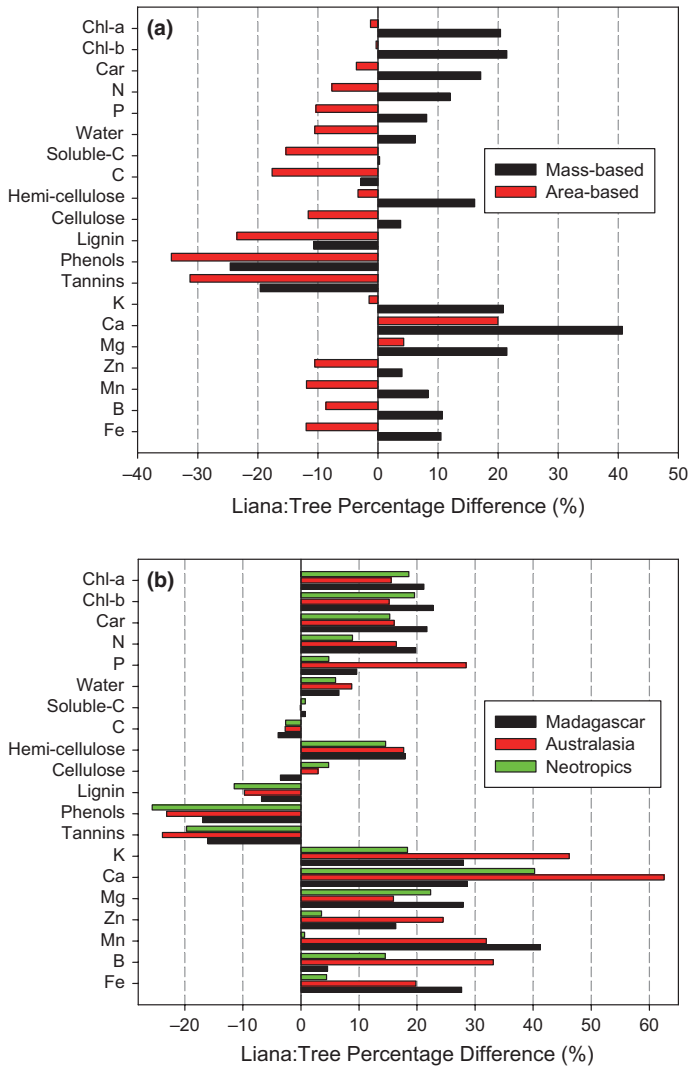
Figure 1 (a) Percentage differences in mass- and area-based chemical traits for canopy lianas and trees. (b) Breakdown of mass-based differences by ecoregion. Differences are calculated as [(L/T) × 100] − 100.

Table 2 Summary of the best multivariate linear mixed models relating leaf traits calculated on a mass basis to the random effect of site, fixed effect of growthform (liana, tree) and mean annual temperature (MAT) as a covariate. Mean annual precipitation had no significant effect on any foliar trait

Trait	r^2	RMSE	Site % variance	Growthform F	MAT F
LMA	0.28	0.13	25.4	176.4 (−)	9.9 (−)
$\delta^{13}C$	0.36	1.42	23.2		40.9 (−)
Light capture-growth					
Chl-a	0.26	0.15	24.0	133.5 (+)	
Chl-b	0.26	0.16	23.8	139.4 (+)	4.3 (+)*
Car	0.22	0.13	20.5	117.0 (+)	
N	0.21	0.13	21.8	51.2 (+)	
P	0.50	0.16	50.7	13.1 (+)	4.7 (−)*
Water	0.19	0.05	10.0	130.2 (+)	40.8 (−)
Soluble-C	0.17	0.10	13.9		26.6 (−)
Structure-defence					
C	0.27	0.03	30.3	121.4 (−)	
Hemi-cellulose	0.09	0.22	8.2	62.7 (+)	32.4 (+)
Cellulose	0.12	0.13	9.1	8.2 (+)	14.4 (+)
Lignin	0.19	0.18	19.6	39.4 (−)	
Phenols	0.13	50.50	12.4	151.7 (−)	
Tannins	0.09	24.94	8.3	72.9 (−)	
Maintenance-metabolism					
K	0.23	0.20	26.3	73.7 (+)	
Ca	0.52	0.29	40.1	106.9 (+)	
Mg	0.26	0.20	21.4	79.4 (+)	
Zn	0.13	0.26	15.9	25.8 (+)	
Mn	0.30	0.50	27.2	26.9 (+)	11.8 (−)
B	0.42	0.24	42.5	41.3 (+)	
Fe	0.54	0.22	53.0	9.8 (+)	5.8 (−)*

LMA, leaf mass per area; RMSE, root-mean-square error.
*Significant effects in the model are indicated $P < 0.001$ for all, but those marked as $P < 0.05$. The direction of the response for significant relationships is indicated in parentheses.

and trees in light capture and growth chemicals. Although this threshold is not as clear in regression models based on individual traits, it is more obvious when assessing growthform-specific differences in combined traits as shown in Fig. 2. Above 2500 mm year^{-1} and below 25 °C, light capture and growth chemicals are less likely to be elevated in liana foliage.

Ecoregional variation

Global differences in mass-based leaf traits between lianas and trees were mirrored in the groupings by Neotropical, Malagasy and Australasian ecoregions (Fig. 1b), yet some interesting exceptions became apparent. The differential investment in light capture and growth traits by lianas and trees was maximal in the Malagasy region, where LMA was nearly 25% lower and photosynthetic pigments more than 20% higher in lianas than trees ($P < 0.05$). By comparison, differences among these traits were smaller in the Neotropics and Australasia (Table S9; *Supporting Information*). The growthform-based difference in foliar N concentration was also highest in

the Malagasy region (20%), as compared with 16% in Australasia and 9% in the Neotropics ($P < 0.05$). Yet P concentrations were differentially higher in liana leaves in Australasia (28%, $P < 0.05$), and much less so in the other regions.

Opposite to regional trends in light capture-growth traits, investment differences in structure and defence by lianas as compared with trees were smallest in Madagascar (Fig. 1b). For example, foliar phenol and tannin concentrations were 25% higher in Neotropical and Australasian trees as compared with lianas, but this difference was just 15% in Madagascar ($P < 0.05$). In contrast, liana-to-tree differences in Ca and K were maximal in Australasia − up to 63% higher than in other regions ($P < 0.05$).

DISCUSSION

General liana-tree differences

Our results strongly suggest the existence of a systematic difference in chemical traits between co-existing lianas and trees at site to global scales. Independent of floristic composition, climate, soil type and other sources of environmental variation found throughout this dataset of more than 7300 canopy individuals, mass-based concentrations of leaf chemicals promoting light capture and growth were
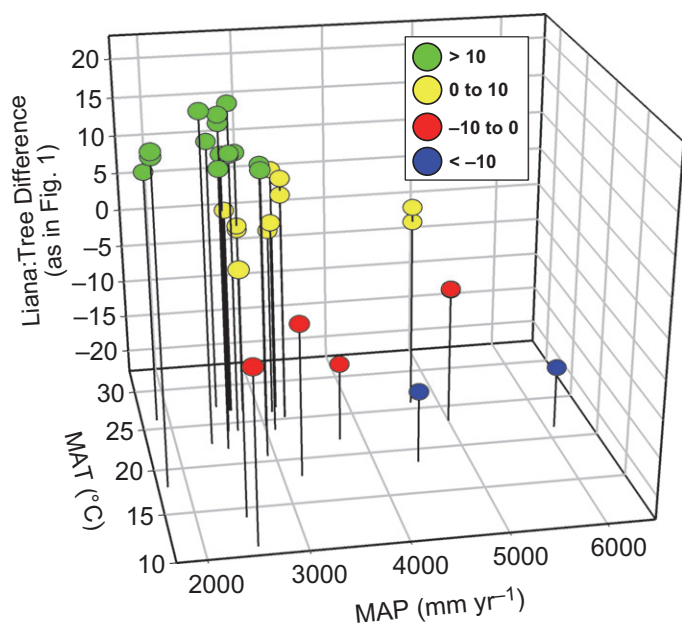
Figure 2 Relative importance of mean annual precipitation and mean annual temperature in determining liana-to-tree ratios (L:T) of light capture and growth traits on a mass basis. Colours indicate the percentage difference in allocation. Differences are calculated as $[(L/T) \times 100] - 100$.

Table 3 Mean differences in mass-based leaf chemical trait allocation between tropical canopy lianas and trees, by ecoregion and globally

	Light capture-growth	Structure-defence	Maintenance-metabolism
Global	14.5	−9.0	16.7
Ecoregion			
Madagascar	18.0	−7.7	26.4
Australasia	16.4	−9.4	35.0
Neotropics	12.4	−9.0	16.8

Differences are calculated as $[(L/T) \times 100] - 100$.

an average 14.5% higher in lianas than in trees (Table 3). Similarly, average concentrations of chemical elements supporting foliar maintenance and metabolism were 16.7% higher in lianas. In contrast, structure and defence compounds averaged 9.0% lower in concentration in lianas.

Area-based results provided an additional perspective on chemical trait differences among growthforms. Although photosynthetic pigments were found in higher mass-based concentration in lianas, this was balanced by systematically lower LMA, resulting in no general difference in area-based allocation to chlorophylls and carotenoids. This finding supports work of Poorter *et al.* (1995), Wright *et al.* (2004) and many others, showing that investment in chlorophyll scales inversely with LMA, and thus area-based investments in light capture remain similar among growthforms. However, we also found that, while N and P are in higher mass-based concentrations in lianas compared with trees, both nutrients are found in significantly lower abundance on an area basis (Fig. 1). That is, lianas maintain higher mass-based N and P investments, yet not so much as to compensate for the fact that their leaves are generally thinner. Mass-based calculations are useful when considering biogeochemical

feedbacks, such as nutrient flows supporting growth (Townsend *et al.* 2007), and our results suggest that lianas support higher rates of N and P cycling by concentrating these elements in leaves. In contrast, area-based calculations are linked to rates of carbon assimilation (Wright *et al.* 2004), and thus our results suggest that N and P requirements are lower in lianas per unit of photosynthetic surface area. Perhaps this is due to other growthform-specific factors, such as a lower overall amount of carbon required by lianas per unit energy absorbed to grow and maintain canopy position; trees may invest more N and P per unit leaf area to boost carbon production for the wood structures required to maintain sunlight canopy positions (Gerwing & Farias 2000). Note however that, had we only considered N and P, our findings on growth-related chemical traits would have suggested that carbon assimilation rates are lower on a leaf-area basis in lianas as compared with trees. However, we also discovered that Ca is found in ~ 40% higher foliar concentration on a mass and area basis in liana canopies (Tables 1 and S6). Primary production is considered Ca (or P + Ca) limited in many humid tropical forests (Vitousek & Sanford 1986; Townsend *et al.* 2008), so our results suggest that large and consistent differences in liana allocation to Ca may favour them metabolically.

In contrast to the nutrient results, leaf structure and defence compounds were found in universally lower concentrations in canopy lianas compared to trees, on both a mass and area basis (Tables 1 and S6). Moreover, growthform-specific differences in allocation to lignin, phenols and tannins were more pronounced on an area than on a mass basis (Tables 2 and S8). Although energetic and construction-cost trade-offs between growth and defence are well recognised (Coley 1983; Westbrook *et al.* 2011), patterns and potential differences among co-existing growthforms have been difficult to detect. Sapling-stage mortality or shade tolerance among growthforms is clearly linked to the trade-off between growth and defence (Poorter *et al.* 2008; Kitajima & Poorter 2010; Wright *et al.* 2010), yet here we found consistent growthform-specific differences in chemical allocation to defence among full-sunlight canopy individuals. And while differences in growthform are said to play a negligible role in the light capture- and growth-related leaf economics spectrum (Reich *et al.* 1997; Wright *et al.* 2004), trees clearly invest more to defend current and future carbon gain than do lianas.

Role of climate

Comparing allocation patterns across sites, our findings indicate that chemical differences between lianas and trees are mediated by climate conditions. The relative difference in light capture and growth traits is negatively correlated with MAP and positively related to MAT. Moreover, investments in structure and defence compounds become increasingly similar between lianas and trees, co-existing in higher precipitation conditions. This was not obvious when considering individual chemical traits along with the effect of site selection (which inherently includes climate variation among sites) (Table 2). However, when looking specifically at the growthform differences in chemical group allocation (i.e. light capture and growth), the effect of climate became much more clear (Fig. 2). This revealed a pattern suggesting that the relative difference in the rate at which climate affects leaf chemical traits varies by growthform.

We also found specific climate regimes associated with heightened investments in growth compounds by lianas as compared to trees. The peak conditions – at around 2500 mm precipitation year^{-1} and

25 °C – are broadly aligned with a high in liana abundances and basal area observed in some tropical forests (Dewalt *et al.* 2010). Schnitzer (2005) observed decreasing liana abundance with increasing MAP, although his relationship was subtle at the global scale ($R^2 = 0.10$). His and subsequent studies treated climate parameters as rough estimates, and precipitation is highly variable from year to year, so reported conditions for peak liana abundances are approximations (S. Schnitzer, pers. comm.). Likewise, our precipitation data, derived from literature sources and limited field-station records, only provides an estimate of conditions associated with peak chemical differences between co-existing lianas and trees. Moreover, chemical trait sensitivity to climate is mediated by soil fertility (Martin & Asner 2009), which was not reported here and requires investigation. Finally, although our annual climate data do not resolve the importance of seasonality, which is thought to be an additional determinant of liana abundance (Dewalt *et al.* 2010), higher MAT and lower MAP are often associated with longer dry seasons and higher annual irradiance in tropical regions (Marengo 1992; Pinker & Laszlo 1992).

Predicting growthform responses to ecological change

The pro-growth, weak-defence chemical strategy in liana foliage provides a physiological basis for evaluating the proposed causes of increasing liana abundance and biomass in some tropical forests. Such explanations have focused on rising ET demand, natural and anthropogenic disturbance rates, and atmospheric CO_2 concentrations (Schnitzer & Bongers 2011). Our results may narrow the range of potential mechanisms supporting liana proliferation. First, we found no difference in foliar $\delta^{13}C$ between lianas and trees at global, regional or site levels. Given that foliar $\delta^{13}C$ provides a metric for the ratio of photosynthesis to stomatal conductance (O'Leary 1988; Flanagan *et al.* 1996), our results suggest no systematic difference in the average water-use efficiency of lianas and trees (sensu Marshall & Zhang 1994; Beerling & Woodward 1995). This would mean that neither growthform possesses an underlying water-use advantage under either increasing ET or elevated CO_2. On the other hand, systematic differences in nutrient concentrations, particularly N, P and Ca, may favour growthform-specific responses to elevated CO_2 (Field & Mooney 1986; Niinemets *et al.* 1999).

Although increasing ET may not be a direct cause for liana proliferation in some regions, it could be indirectly related to elevated solar irradiance associated with fewer clouds and warmer temperatures (Freedman *et al.* 2001; Feeley *et al.* 2011). Increasing irradiance, combined with relatively greater allocation to growth compounds under drier and warmer conditions (Fig. 2), could strongly advantage lianas. Despite the observation that photosynthetic pigments are similar between lianas and trees on a leaf-area basis, differential requirements for and acquisition of macronutrients key to light-induced growth responses (e.g. N, P and Ca) may advantage lianas under conditions of increasing irradiance. Moreover, given the reduced allocation to foliar structure and defence in lianas, any enhanced light-stimulated carbon uptake can be dedicated to additional resource acquisition via leaf and root growth as compared to trees with greater evolved defence investments and commitments to canopy structural components. Finally, changes in irradiance and nutrient availability are also directly linked to disturbances rates (Silver & Vogt 1993; Asner *et al.* 2004), and increased disturbance has been considered as a third explanation for increasing liana abundance. The physiological response could be similar to that of

increased irradiance, but also with increased nutrient flow from detrital material or soils resulting from the disturbance (Olander *et al.* 2005). The ability of lianas to store and utilise higher concentrations of macronutrients on a mass basis, and more efficiently on an area basis, may advantage them under conditions of increased nutrient flow via disturbance. From these observations, we predict that increases in liana abundance and biomass could be largest in forests with increasing irradiance and/or rates of disturbance.

Overall, our results provide a phytochemical foundation to explore where, how and why lianas may be increasing in abundance and biomass, which may be directional, thus representing a reshuffling of canopy composition in some tropical forests. However, we also recognise that recent liana increases may be transient responses to local, regional or global changes that eventually saturate physiologically or even diminish over time. For example, growth responses to increasing CO_2 often saturate when nutrients become heavily subscribed to within the system (Hungate *et al.* 1997). Once available resources run low, other species – such as slow-growing, shade tolerant trees – may gain an advantage at the community level. On the other hand, increasing disturbance frequency, such as via logging, fire and storm events (Nelson *et al.* 1994; Cochrane & Schulze 1999; Asner *et al.* 2005), may result in sustained increases in light and nutrient resources, thereby advantaging lianas in the long run. Given that lianas live for decades or longer in tropical forests (Schnitzer *et al.* 2006), potential transient responses to recent and ongoing environmental changes will be difficult to separate from long-term, directional change in forest composition.

AUTHORSHIP

GPA and REM designed the study, collected and analysed the data, and wrote the paper.

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