Received: 8 September 2020 | Accepted: 4 November 2020

DOI: 10.1111/1365-2435.13717

RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Lianas explore the forest canopy more effectively than trees under drier conditions

José A. Medina-Vega[1,2] | Frans Bongers[1] | Stefan A. Schnitzer[2,3] | Frank J. Sterck[1]

[1]Forest Ecology and Forest Management Group, Wageningen University and Research Centre, Wageningen, The Netherlands

[2]Smithsonian Tropical Research Institute, Balboa, Republic of Panama

[3]Department of Biological Sciences, Marquette University, Milwaukee, WI, USA

Correspondence
José A. Medina-Vega
Email: jamedinavega@gmail.com

Funding information
Nederlandse Organisatie voor Wetenschappelijk Onderzoek, Grant/Award Number: 824.14.006; Smithsonian Tropical Research Institute

Handling Editor: Oscar Godoy

Abstract

1. Lianas rely on trees for support and access to high-light positions in the forest canopy, but the implications for how lianas explore the canopy compared to trees remain understudied. We present an in situ forest canopy study to test the hypotheses that: (1) lianas favour leaf display over stem investment compared to trees and (2) lianas have greater potential to colonize non-shaded, high-light areas effectively than trees.
2. We compared branches of 16 liana species with those of 16 sympatric tree species in the canopy of two lowland tropical forests with contrasting rainfall regimes in Panama using 40–50 m tall canopy cranes. One forest was relatively dry and seasonal in rainfall and associated solar radiation. The other forest was relatively wet and had a weaker seasonality.
3. We observed that lianas were more efficient in leaf display over stem investment than trees, particularly in the forest with lower precipitation and stronger seasonality. Specifically, lianas had a lower LMA (leaf mass per unit leaf area), stronger apical dominance, higher stem slenderness and fewer leaf layers than trees. In the forest with higher precipitation and weaker seasonality, lianas also had stronger apical control and fewer leaf layers than trees, but both lianas and trees were relatively similar in LMA and stem slenderness.
4. Our study shows that lianas more effectively explore the canopy than trees under drier conditions, but much less so under wetter conditions. We argue that lianas display a functional strategy that allows them to better intercept light than the tree species in forests with low precipitation and strong seasonality, while they are constrained to display such strategy at high precipitation – light-limited – sites.

KEYWORDS
allocation, canopy, leaf, lianas, stem, trees, tropical forest, woody vines

1 | INTRODUCTION

Lianas (woody vines) are an important component of tropical forests. They contribute 5%–10% of above-ground biomass (Schnitzer et al., 2011) but up to 40% of leaf productivity (Hegarty & Caballé, 1991; Phillips et al., 2002). Lianas use trees for support and access to the canopy. They place their leaves over those of their host trees and compete intensely for light and soil resources (Rodríguez-Ronderos et al., 2016; Schnitzer et al., 2005), with adverse effects on tree dynamics and forest structure. Lianas reduce tree regeneration

(Schnitzer & Carson, 2010), growth (Pérez-Salicrup et al., 2001; van der Heijden et al., 2015), reproduction (García León et al., 2018; Wright et al., 2015) and survival (Ingwell et al., 2010; Wright et al., 2015).

Lianas differ considerably from trees in terms of their physiology, anatomy and chemical attributes (Asner & Martin, 2012; Isnard & Feild, 2015; Zhu & Cao, 2009, 2010), but stem morphology is arguably the most distinct difference between lianas and trees. Trees build relatively large trunks and branch systems to support and expose their leaves. By contrast, lianas use the architecture of their host trees and are hypothesized to favour stem elongation rather than constructing a large trunk themselves (Mooney & Gartner, 1991; Paul & Yavitt, 2011; Putz, 1984; Teramura et al., 1991). The host-dependent strategy of lianas may favour the development of relatively large leaf photosynthetic surface area and biomass in the forest canopy (Mooney & Gartner, 1991; Putz, 1984; Wyka et al., 2013). These distinct morphological investment strategies in stems and leaves may allow lianas to produce slender long branches with relatively larger leaf areas than trees, favouring carbon gain with greater potential for plant growth, particularly in high-light environments (Mooney & Gartner, 1991; Putz, 1983). By contrast, these growth advantages may be less likely to be pronounced in low-light environments (Avalos & Mulkey, 1999). Nonetheless, few systematic, in situ studies have quantified and compared biomass allocation, branch development and leaf display between lianas and trees in tropical forest canopies.

The morphological investment strategies in stems and leaves of lianas relative to trees are highly variable. Lianas and trees may be more similar to each other in morphology at the juvenile stage since trees and many lianas have a vertical self-supporting structure and comparable leaf mass ratios (Cornelissen et al., 1996; Selaya et al., 2007). In more mature individuals, morphological differences become pronounced, as lianas further differentiate from trees in flexible stem properties after they begin to climb (Menard et al., 2009; Rowe & Speck, 2005). Some studies report that lianas develop more abundant leaf mass at comparable basal stem area (Gerwing & Farias, 2000; Putz, 1983) and stem mass (Ichihashi & Tateno, 2015; Wyka et al., 2013) than do trees. By contrast, Niklas (1994) reported for a set of 12 lianas, gymnosperm and pteridophyte species, that lianas do not allocate less biomass to stems than do self-supporting plants at equivalent stem diameters. Kaneko and Homma (2006) further observed comparable leaf mass ratios between a temperate *Hydrangea* liana species and congeneric shrubs, suggesting that most liana species reach similar above-ground biomass levels as those of trees at lower diameters, but tend to have relatively larger leaf area per overall plant mass and per unit cross-sectional area than trees (Cornelissen et al., 1996; Isnard & Feild, 2015; Wyka et al., 2013). These results indicate that the investments in leaf mass in lianas and trees at comparable plant sizes are highly variable. However, the more consistently observed larger leaf areas in lianas than in trees at comparable plant sizes suggest that the ability of lianas to actively display relatively larger leaf area (or mass) than trees may be associated with the lower leaf mass per unit leaf area (LMA, i.e. the carbon construction cost for producing light intercepting unit area [Poorter et al., 2009]) (Asner & Martin, 2012; Cai et al., 2009; Kazda & Salzer, 2000; Santiago & Wright, 2007; Zhu & Cao, 2010) and the lower wood density of the liana form (WD; Wyka et al., 2013), in addition to the construction of slenderer stems.

Both LMA and WD are part of a group of interconnected traits that are associated with trade-offs in growth-survival strategies along a continuum of low to high levels of resource availability (Chave et al., 2009; Díaz et al., 2016; Sterck et al., 2011; Wright et al., 2004). Species with low WD and low LMA are typically found at high resource sites and tend to have high hydraulic conductivities, photosynthetic traits and leaf areas per unit shot mass (Chave et al., 2009; Santiago et al., 2004; Wright et al., 2004, 2006). Such species have faster growth rates, quicker return of leaf construction investments (i.e. Leaf Life Span - LLS) and lower survival rates than species with high WD and high LMA, typically found at low resource sites (Chave et al., 2009; Díaz et al., 2016; Poorter et al., 2009; Wright et al., 2004). Lianas show higher growth rates than trees under favourable resource conditions (Mooney & Gartner, 1991; Paul & Yavitt, 2011; Schnitzer, 2005; Schnitzer & van der Heijden, 2019; Teramura et al., 1991), which is consistent with observed lower WD, lower LMA, higher hydraulic conductivities and higher leaf nitrogen content and photosynthetic capacity on a mass basis of the liana form (see Asner & Martin, 2012; Wyka et al., 2013; Zhu & Cao, 2009). Nevertheless, studies contrasting leaf-level attributes between lianas and trees suggest a comparable nitrogen content and photosynthetic carbon fixation on an area basis (Cai et al., 2009; Kazda & Salzer, 2000; Santiago & Wright, 2007; Wyka et al., 2013; Zhu & Cao, 2010). Furthermore, observed differences in leaf-level light capture and growth chemical traits between lianas and trees, with lianas having a greater allocation to growth compounds and a higher capacity to benefit from high irradiance than trees, tend to disappear at high precipitation – light-limited – sites (>2,500 mm/year; Asner & Martin, 2012). Consequently, the higher relative growth rates in lianas than in trees (Mooney & Gartner, 1991; Paul & Yavitt, 2011; Schnitzer, 2005; Schnitzer & van der Heijden, 2019; Teramura et al., 1991) cannot be attributed solely to higher physiological or chemical attributes responsible for photosynthesis and growth. Instead, higher growth rates in lianas than in trees may be associated, particularly, with a favoured allocation towards the development of relatively larger leaf areas and cheaper leaves, a more rapid renewal of leaves via faster turnover rates, and more efficient structural elements that facilitate better exploration and use of space in lianas than in trees.

Here we quantify and compare biomass allocation, branch development and leaf display between lianas and trees in the upper canopy of two tropical forests with contrasting rainfall regimes in Panama. One forest is characterized by relatively low precipitation and strong seasonality, and the other forest is characterized by higher precipitation and weaker seasonality (Condit et al., 2000). The 40–50 m tall canopy cranes in these forests allowed us to assess the benefits and costs associated with the host-dependent life history strategy of lianas compared to trees, and the consequences for the liana strategy of stem elongation and leaf deployment. We, therefore, evaluated exposed sun-lit branches to collect precise, replicated measurements, which is difficult for fully grown trees

or lianas dwelling in the forest canopy. Moreover, exposed canopy branches are important since they represent potential bottlenecks for the hydraulic integrity and carbon gain of entire individuals given their potential for a high-light interception but also highwater losses. We hypothesize that:

1. Lianas effectively display more leaves for a given stem investment by carrying more leaf mass (or area) for a given stem mass (or area) and by producing leaves and stem at lower structural costs realized by their lower LMA, quicker leaf turnover (LLS) and lower WD than trees.
2. Lianas produce longer branches for a given diameter and their branches are under stronger apical dominance than trees. These differences between lianas and trees may result in more rapid elongation of slenderer and less ramified branches in lianas compared to trees. Moreover, these responses allow lianas to display their leaves in a single layer on top of their tree hosts, whereas trees build and maintain crowns with multiple layers in the upper canopy.
3. Given that lianas are supposed to benefit from high-light conditions, we expected that lianas particularly show those hypothesized responses (see points 1 and 2) in the drier forest, where they could benefit from additional sunlight.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted this study in the Republic of Panama. We made observations between November 2015 and May 2017 from two canopy cranes operated by the Smithsonian Tropical Research Institute (STRI) and located in two lowland tropical forests at the opposite sides of the precipitation gradient extending across the Isthmus of Panama. Both cranes were equipped with a gondola connected to a rotating jib that allowed access to the forest canopy. One crane was located in Parque Natural Metropolitano (PNM, 8°59′41.55″N, 79°32′35.22″W, 30 m above sea level), a seasonally dry forest near the Pacific coast and Panama City. This crane gave access to 0.81 ha of forest. Annual rainfall averaged 1,864 mm and 91.8% occurred in the wet season, from May to December (means from 1995 to 2017, data provided by the Physical Monitoring Program of STRI). In this forest, monthly precipitation was >100 mm each month in the dry season, from January to April (see Appendix S1). Mean annual temperature was 26.1°C.

The second canopy crane was located in the wet evergreen forest Bosque Protector San Lorenzo, near the Caribbean coast of Panama (BPSL, 9°16′51.71″N, 128 79°58′28.27″W, 130 m above sea level). This crane gave access to 0.91 ha of forest. Annual rainfall averaged 3,292 mm and 89.8% occurred in the wet season, from May to December. The dry season in this forest was less intense than the dry season in PNM, with monthly precipitation of <100 mm each month from January to March, and 145.4 mm in April (means from 1997 to 2017). Mean annual temperature was 25.4°C. The PNM will hereafter be referred to as the dry forest and the BPSL as the wet forest (Holdridge, 1967; Murphy & Lugo, 1986).

2.2 | Species selection and branch census protocol

We randomly selected eight liana and eight tree species at each crane site (see Appendix S2) from those species with two or more canopy individuals present. Both evergreen and deciduous species were included in the design. There was no species overlap between sites, which is consistent with the strong effects of seasonal drought and soil phosphorus on regional plant species distributions (Condit et al., 2013). The dry forest has a higher proportion of deciduous species, higher litter production (Santiago & Mulkey, 2005) and higher soil extractable phosphorus (P) tightly linked with better litter quality than the wet forest (Santiago et al., 2005). The 32 species belonged to 22 families. We selected two individuals of each species and four fully exposed branches at the top of the canopy of each in November 2015. The host trees for the studied liana individuals were different from the studied tree individuals. The initial branches ranged from 30 to 70 cm in length and already had leaves present (see Appendix S3). We quantified the number of leaves and shoots present on each branch approximately every 30 days in the dry season and every 60 days in the wet season for 17 months.

2.3 | Organ-level attributes

We estimated species-specific LMA as the ratio between leaf mass and leaf area (g/cm^2), without the petiole (see Appendix S4). We estimated species-specific leaf longevity (life span) from presence/absence records of fully expanded leaves collected from each census. The median age in days of leaf death (leaf longevity, LLS) was analysed using the Kaplan–Meier method, which accounted for right-censored leaves that were removed from the census due to loss or death of the branch (Efron, 1988). We determined species-specific WD (g/cm^3) using five branch segments and the water displacement method (Cornelissen et al., 2003; Ilic et al., 2000). We collected each branch segment, of five centimetres length, at one metre from the distal end of five selected branches (with leaves) per species (see Appendix S4).

2.4 | Branch and whole-plant measurements

We measured the diameter and length on every census branch and every axillary shoot within the study branch with a digital calliper and a measuring tape respectively. Branch measurements were done at the same time as the leaf census measurements. We estimated the number of leaf layers within the crown of each selected liana and tree individual by lowering a plummet through the crown and counting the number of contacts between the plummet and leaves (MacArthur & Horn, 1969; see Appendix S5).

2.5 | Associations among traits and trait differences between life-forms

To test the hypothesis (one) that lianas produce leaves and stem at lower structural costs realized by their lower LMA, quicker leaf turnover (LLS) and lower WD than trees, we applied for each forest a one-way ANOVA to contrast LMA, LLS and WD between lianas and trees. LMA, LLS and WD were log (base e) transformed before the analyses. We also quantified the strength of the relationship between traits, for each forest, using standard Pearson correlation analyses. *p*-values for the bivariate associations were adjusted by controlling for the false discovery rate (Benjamini & Hochberg, 1995).

We calculated measures of phylogenetical signal on the traits themselves and the relationship between traits. We generated a phylogeny tree for each forest using the program Phylomatic (Webb & Donoghue, 2005). This program generated the phylogenetic trees after matching the genus and family names of our study species to those contained in the species-level phylogeny constructed by Zanne et al. (2014). We tested whether trait values were independent of phylogenetic signal via Blomberg's *K* (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999). We further tested if observed bivariate trait associations were a result of evolutionary divergences using phylogenetically independent contrasts (PIC; Felsenstein, 1985; see Appendix S6).

2.6 | Allometric relations

For each forest, we related leaf area (LA) to branch cross-sectional area (BA) and leaf biomass (LB) to stem biomass (SB) to test hypothesis one, and branch length (BL) to branch diameter (BD) to test hypothesis two (see Appendix S7). We tested whether these associations varied between life-forms (lianas vs. trees) by using linear mixed-effects models (LMMs) with a normal error distribution (see Appendix S8). For each analysis, we evaluated alternative models that included the main effects of BA, SB, BD, and their interaction with life-form (liana = 0, tree = 1). For all models, we included random intercepts for branches nested within individuals derived from multiple species to control for the nested structure of the design and dependence among repeated measurements of each branch. We also included random slopes to allow for different associations in LA ~ BA, LB ~ SB and BL ~ BD across species. Over the entire study period, branches were under the effect of one wet season and two dry seasons. We thus added the variable 'season' (dry vs. wet season) as a random intercept to control for the effect of seasonality. To control for deciduousness, we added the variable 'deciduousness' (deciduous vs. non-deciduous) as an additional random intercept. Individual plants, not species, were marked as deciduous if the mean leaf area loss, calculated from the study branches per individual, was more than 80% of their maximum attained leaf area (see Cornelissen et al., 2003) during the whole study period. For the relationships LA ~ BA and LB ~ SB, we excluded leafless branches.

2.7 | Apical dominance and the number of leaf layers in the crown

For hypothesis two, we related the number of axillary shoots (Nshoots) per branch per observation and the number of leaf layers (NLL) of each individual to life-form using generalized linear mixed-effects models (GLMMs). For the association Nshoots ~ life-form, we added the log (base e) of branch length (BL, refer to the section allometric relations) as an offset to control for differences in branch size per branch per observation. For this association, we included random intercepts as described in the section allometric relations.

For the association NLL ~ life-form, we added the log (base e) of individual height (*H*) as an offset to control for differences in *H*. *H* was defined as the (perpendicular) distance between the soil surface and the uppermost leaf of the study individual. For this association, we included random intercepts for individuals nested within species to control for the nested structure of the design and multiple observations on each individual.

2.8 | Model selection, evaluation and inference

We evaluated LMMs with the LME4 package version 1.1-23 (Bates et al., 2015) and GLMMs with the GLMMTMB package version 1.0.2.9 (Brooks et al., 2017) in R version 3.6.3 (R Core Team, 2020). Model validation was assessed graphically as detailed in Zuur and Ieno (2016) and model selection was based on the Akaike information criterion (AIC; Burnham & Anderson, 2002). For GLMMs, we used a Poisson distribution and checked for overdispersion and zero inflation. We used a negative binomial distribution if overdispersion was present. If zero inflation was present, we used a ZIP (zero-inflated Poisson) or ZINB (zero-inflated Negative binomial) model when appropriate. We considered models with $\Delta AIC < 2$ to have a substantial level of empirical support from the data (Burnham & Anderson, 2002). When two models had similar AIC values, we selected the simpler model. We estimated the precision of each fixed and random effect in all models by computing a 95% confidence interval of the parameter estimates using 1,000 nonparametric bootstrap simulations and the percentile interval method (Chernick, 2007). Parameter estimates with confidence limits that contained zero were considered as negligible at the community level.

3 | RESULTS

3.1 | Organ-level traits

LMA was lower in lianas than in trees in the dry forest ($F_{1,14} = 4.79$, $p = 0.046$) but not in the wet forest ($F_{1,14} = 0.67$, $p = 0.43$; Figure 1a). WD was similar between lianas and trees in both forests (dry forest: $F_{1,14} = 4.47$, $p = 0.053$; wet forest: $F_{1,14} = 0.83$, $p = 0.38$; Figure 1b). For leaf life span (LLS), lianas were not different from trees in the dry

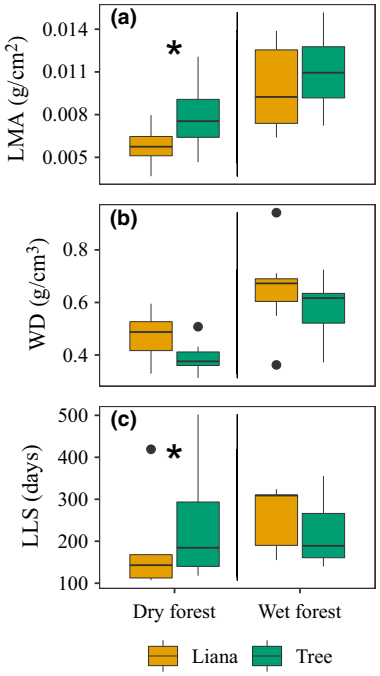

FIGURE 1 Boxplots comparing (a) leaf mass per area (LMA), (b) wood density (WD) and (c) leaf longevity (LLS) between lianas (orange) and trees (green) in a dry (PNM, the left side of the panel) and a wet (BPSL, the right side of the panel) forest in Panama. Asterisks in the left side of panels a and c indicate significant differences at the 0.05 level between lianas and trees calculated using a one-way ANOVA on the log (base e) transformed trait values. For the dry forest in panel c, we detected an outlier (Dixon's *Q* test, $Q = 0.7$, $p = 0.02$) and after excluding it, the remaining liana species had shorter LLS than trees. The dimensions are in their natural scale. Note the different vertical axes

forest ($F_{1,14} = 1.68$, $p = 0.22$). However, the species *Serjania mexicana* was an outlier (Dixon's *Q* test, $Q = 0.7$, $p = 0.02$) and after excluding it, the remaining seven liana species in the dry forest had a shorter LLS than trees ($F_{1,13} = 4.8$, $p = 0.047$, Figure 1c). In the wet forest, we did not observe differences in LLS between lianas and trees ($F_{1,14} = 1.28$, $p = 0.28$). We found a phylogenetic signal only for LLS in the dry forest (see Appendix S9).

We did not observe an association between LMA with WD and LLS, neither did we observe it for WD with LLS for both the dry and wet forest (see Appendix S10). For PICs, we observed that 30% of the variation in LLS was associated with the variation in LMA for the wet forest ($r^2 = 0.3$, r[13] = 0.54, *p*.adjusted = 0.11; see Appendix S10).

3.2 | Leaf display over stem support

For the dry forest, leaf area supported by branches was consistently higher for lianas than for trees over the entire range of observed branch cross-sectional areas (Table 1, Models A and C; Figure 2a). Leaf mass was lower for lianas than for trees in small branch sizes but this difference reversed for bigger branches (Table 1, Model C; Figure 2c). For the wet forest, leaf area supported by branches was larger for lianas than for trees at smaller branch cross-sectional areas, but this difference reversed at larger branch cross-sectional areas (Table 1, Model B; Figure 2b). For the association between leaf mass and stem mass, the leaf mass supported by branches was similar for both lianas and trees over the entire range of stem mass in the wet forest (Table 1, Model D; Figure 2d).

3.3 | Potential for canopy colonization

In the dry forest, branches were longer for lianas than for trees for any given branch diameter (Table 1, Model E; Figure 2e). For the wet forest, branches were longer for lianas than for trees only at small branch stem diameter (Figure 2f). Overall, lianas had a lower number of axillary shoots per branch than trees (Figure 3a,b; Table 1, Models G and H) and displayed their leaves in fewer layers (Figure 3c,d; Table 1, Models I and J) and within a shallower crown than trees in both forests (Figure 3e,f).

4 | DISCUSSION

We compared canopy branches for their efficiency in leaf display and structure between lianas and trees in two lowland tropical forests. We expected that lianas would be more efficient in leaf display (more leaf area or mass per branch stem area or mass, respectively) because they are reported to have slenderer stems and cheaper leaf and stem organs (lower LMA and lower WD) than trees. Also, we expected that slenderer stems and stronger apical control allow lianas to maintain leaves in single layers on top of tree branches, whereas trees have thicker stems, more ramified branches and support leaves in more layers. We discuss our results in the light of these generic predictions on differences between lianas and trees in tropical forest canopies. Since these differences varied between forests, we speculate on the possible role of resource availability (rainfall, seasonality, solar radiation and soil fertility) in modifying liana–tree differences between forests.

4.1 | Lianas had more efficient leaf display in the dry forest, but not in the wet forest

We hypothesized that lianas display leaves more efficiently than trees, and accordingly predicted that they carry more leaf area (or mass) for a given branch stem cross-sectional area (or stem mass). Also, we expected that lianas partially achieve more efficient leaf display by lower structural investment costs in leaves and stem, i.e. realized by a lower LMA, quicker leaf turnover (LLS) and lower WD than trees. Our hypothesis was supported for lianas in the dry forest, but not for lianas in the wet forest, particularly for large branch sizes.

For the dry forest, lianas increase proportionally more leaf mass with increasing branch size and have a larger leaf area per branch

TABLE 1 Summary of the fixed effects for the (generalized) linear mixed-effects models that best-fitted leaf area as a function of branch cross-sectional area (Models A and B), leaf mass as a function of stem mass (Models C and D), branch length as a function of branch diameter (Models E and F), the number of axillary shoots (Models G and H) and the number of leaf layers (Models I and J) for lianas and trees in a dry (PNM, the left columns) and a wet (BPSL, the right columns) forest in Panama

	Dry forest (PNM)				Wet forest (BPSL)			
Models	**Est.**	**Stat.**	**lci**	**uci**	**Est.**	**Stat.**	**lci**	**uci**
Leaf area ~ branch cross-sectional area			Model A				Model B	
Intercept	8.75	40.85	8.34	9.20	7.33	38.07	6.97	7.70
LifeformTree	−0.67	−2.77	−1.18	−0.20	0.58	2.20	0.05	1.08
B. cross-sectional area	0.95	11.59	0.80	1.12	0.42	3.63	0.19	0.64
LifeformTree: B. cross-sectional area	—	—	—	—	0.72	4.52	0.41	1.02
Leaf mass ~ stem mass			Model C				Model D	
Intercept	1.04	6.64	0.73	1.35	1.37	15.99	1.19	1.55
LifeformTree	0.53	2.58	0.14	0.96	—	—	—	—
Stem mass	0.74	16.40	0.65	0.84	0.56	14.11	0.47	0.63
LifeformTree: Stem mass	−0.17	−2.80	−0.29	−0.05	—	—	—	—
Branch length ~ branch diameter			Model E				Model F	
Intercept	6.03	19.49	5.44	6.64	4.86	15.60	4.28	5.48
LifeformTree	−1.40	−3.47	−2.25	−0.53	0.09	0.22	−0.80	0.96
Diameter	2.40	13.07	2.03	2.73	1.48	6.85	1.07	1.93
LifeformTree: Diameter	—	—	—	—	0.79	2.63	0.17	1.35
Number of axillary shoots			Model G				Model H	
Intercept	−4.52	−19.46	−4.74	−4.50	−4.17	−13.60	−4.31	−4.13
LifeformTree	0.63	2.14	0.57	0.77	0.95	2.61	0.89	1.06
Number of leaf layers			Model I				Model J	
Intercept	−2.47	−15.78	−2.60	−2.38	−2.26	−17.27	−2.40	−2.15
LifeformTree	1.77	8.61	1.62	1.93	1.30	8.02	1.14	1.47

Notes: Est. indicates the estimated community-level mean of each parameter. Stat. indicates the test statistic for the continuous (*t*-statistic, Model A–F) and discrete (*z*-statistic, model G–J) models. The reference level for the variable life-form is 'liana' (liana = 0, tree = 1). 'lci' indicates the lower 2.5% confidence interval and 'uci' the upper 97.5% confidence interval based on 1,000 parametric bootstraps and the percentile interval method. For the models that best fitted the number of axillary shoots (Models G and H) and the number of leaf layers (Models I and J), we added the log (base e) of branch length (BL) and the log (base e) of individual height (H) as offsets respectively. The offsets for the discrete models (Model G–J) were defined as structural predictors and their coefficients were not estimated by the models but were assumed to be one. For the continuous models (Model A–F), all variables were log (base e) transformed before the analyses. Random effects are in Appendix S11.

stem cross-sectional area than trees (Figure 2a,c). These results are consistent with our expectations. Available literature contrasting leaf mass to stem or whole plant mass between lianas and trees, however, show contrasting results. Early in ontogeny, many lianas are still in self-supporting phase and are expected to be similar to trees in terms of biomass allocation to different organs (Caballé, 1993; Putz, 1984). Supporting this idea, Cornelissen et al. (1996) reported that young lianas (and scramblers) do not differ with trees and shrubs in their leaf mass ratios (total leaf dry weight/total plant dry weight). Similar results were observed by During et al. (1994), Selaya et al. (2007), Gartner (1991) and Wyka et al. (2013), but not by Cai et al. (2007), who reported for *Bauhinia* species that young lianas have higher leaf mass ratios than trees, consistent with our observation for large sized branches in the dry forest canopy.

Later in ontogeny, when lianas are climbing, they have a more flexible stem and favour investments in leaves while trees require larger investments in their stem for maintaining structural support (Putz, 1983, 1984; Rowe & Speck, 2005). In a review of the literature, Wyka et al. (2013) reported higher investments to leaf mass at the same above-ground plant mass in mature lianas compared to mature trees. By contrast, other studies observed that mature lianas and trees did not differ in the biomass invested between leaves and stem (Kaneko & Homma, 2006; Niklas, 1994; Smith-Martin et al., 2020); they argued that a thinner but longer stem in lianas than in trees offsets any life-form difference in biomass allocation between leaves and stem (Niklas, 1994; Smith-Martin et al., 2020). In our study, the canopy branches were arguably partially in the transition from self-supporting to host-supported and may gradually develop more leaf mass for a given stem mass with increasing size (Figure 2c; Table 1, Model C).

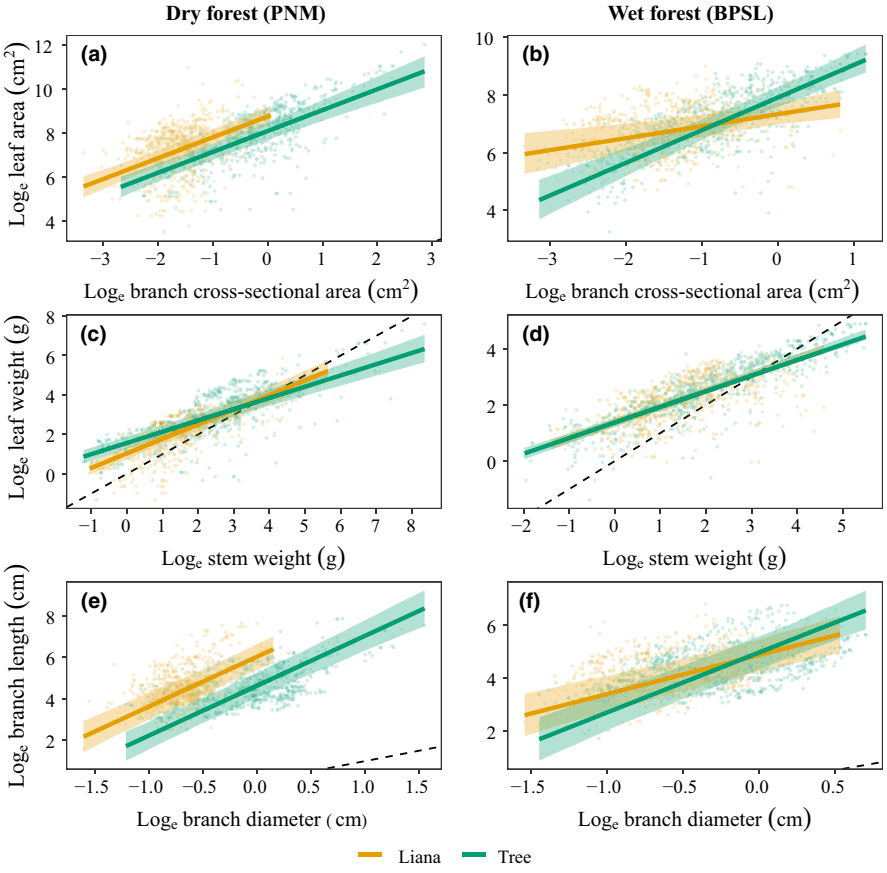

FIGURE 2 Mean predictions (solid lines) for lianas (orange) and trees (green) from the models (Table 1) that best-fitted leaf area as a function of branch cross-sectional area (panels a and b), leaf mass as a function of stem mass (panels c and d) and branch length as a function of branch diameter (panels e and f) in a dry (PNM, the left panels) and a wet (BPSL, the right panels) forest in Panama. The dots in the background indicate the observed values. A 1:1 line (dashed line) was plotted in all panels for reference. The shading around the regression lines in each panel represents 95% confidence intervals of the mean predictions based on 1,000 parametric bootstraps and the percentile interval method. All variables were log (base e) transformed before the analyses. Note the different vertical and horizontal axes

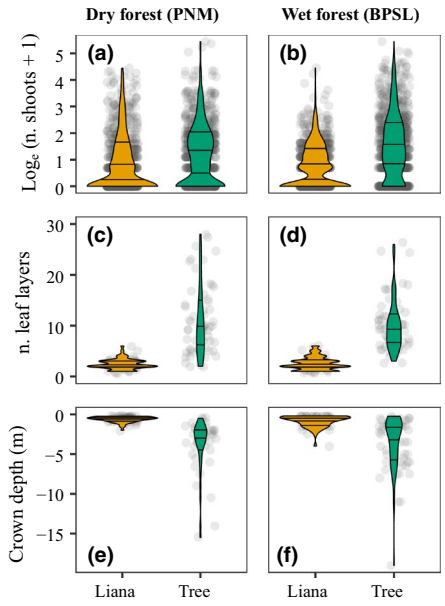

FIGURE 3 Panels a and b: violin plots comparing the number (*n.*) of axillary shoots between branches of lianas (orange) and trees (green) in a dry (PNM, panel a) and a wet (BPSL, panel b) forest in Panama. Panels c, d, e and f: violin plots comparing the number (*n.*) of leaf layers (panels c and d) and crown depth (panels e and f) between liana and tree individuals for the same dry (PNM, left panels) and wet (BPSL, right panels) forest. The horizontal lines inside the violins indicate (from low to high) the 0.25, 0.5 and 0.75 quantiles. Note the different vertical axes

The observed difference in leaf versus stem biomass investment with trees can be explained by two possible reasons: lianas had a consistent longer branch length for a given branch thickness—offsetting any life-form difference [as suggested by Niklas (1994) and Smith-Martin et al. (2020)]—and seven out of the eight liana species had shorter leaf life spans—reducing the leaf mass.

WD did not differ between lianas and trees (Figure 1b). Similar results have been observed for adult lianas and trees in Costa Rica (Werden et al., 2017) and in central Panama (Smith-Martin et al., 2019) as well as for canopy branches of lianas and trees in China (Zhang et al., 2019), but contrast with our expectation and with other studies that have shown that lianas have lower WD than trees (Chen et al., 2016; Dias et al., 2019; Zhu & Cao, 2009). Nevertheless, for seedlings, WD also tended to be similar between lianas and long-lived pioneer trees (Selaya & Anten, 2008). Consequently, a plausible explanation for the similar WD observed for lianas and trees is that the canopy branches were, at least partially, still in a self-support phase, most likely to reach other potential hosts. Overall, leaf mass to stem mass differences in canopy branches are relatively inferior due to multiple counteracting underlying factors between lianas and trees.

Our observation that lianas had a larger leaf area per branch stem cross-sectional area in the dry forest is in agreement with studies on young and mature individuals (Bullock, 1990; Cai et al., 2007; Cornelissen et al., 1996; Ewers et al., 1991; Putz, 1983; Selaya et al., 2007; Tyree, 2003; Zhu & Cao, 2009) as well as for canopy terminal twigs (Kazda et al., 2009). Larger leaf areas per biomass investment

in lianas than in trees are also reflected in the forest structure. Relative to trees, the contribution of lianas to total above-ground biomass is small (5%–10%; Schnitzer et al., 2011), but they account for as much as 40% of forest leaf area and leaf productivity (Hegarty & Caballé, 1991; Phillips et al., 2002; Schnitzer & Bongers, 2002). These differences between lianas and trees in the dry forest are consistent with a lower LMA commonly observed for lianas (Asner & Martin, 2012; Wyka et al., 2013), which was in our case also consistent with a higher leaf area per branch stem area in lianas compared to trees.

Lower LMA in lianas than in trees favours the development of larger leaf areas per unit biomass. Nevertheless, these differences between lianas and trees may not be intrinsically associated with life-form, but with life history strategy relating to shade tolerance. For instance, Cai et al. (2007) reported that the shade-tolerant liana species used in their study had similar leaf area ratios (leaf area per above-ground mass) than trees and that both, the shade-tolerant liana species and trees, had lower leaf area ratios than the light-demanding liana species. Likewise, Selaya et al. (2007) reported that seedlings of lianas and long-lived pioneer trees had similar values for leaf area ratios but higher values than the short-lived pioneers. In both studies, individuals with higher leaf area ratios had higher specific leaf areas (SLA, cm^2/g; the inverse of LMA), suggesting that differences in leaf areas per stem or whole plant investment are determined by LMA, or the costs of producing leaves, rather than life-form alone (Cai et al., 2007; Selaya et al., 2007), as also observed in this study.

For the wet forest, liana branches displayed more leaf area than tree branches at small branch sizes, as we expected and also observed in other studies (Bullock, 1990; Cai et al., 2007; Cornelissen et al., 1996; Ewers et al., 1991; Kazda et al., 2009; Putz, 1983; Selaya et al., 2007; Tyree, 2003; Zhu & Cao, 2009), but a higher leaf area in liana branches than in tree branches was not maintained with increasing branch size (Figure 2b). Probably, larger leaf areas in small liana branches may benefit lianas with (early) fast growth rates and high carbon gains (Poorter & Remkes, 1990) required to rapidly reach adequate positions in the forest canopy. With increasing branch size, the high similarity in LMA and LLS between lianas and trees may obscure any differences in leaf area display and is also consistent with the lack of differences in leaf mass versus stem mass investment observed in branches of both lianas and trees. Our results indicate that similar LMA and LLS between lianas and trees in the wet forest may obscure differences in biomass allocation patterns at the branch level since leaf mass may consistently increase with longevity in the branches of both life-forms (Ichihashi & Tateno, 2015; Reich et al., 1991). There are few examples in the literature that also no dot show differences in LMA between lianas and trees (Cai & Bongers, 2007; Castellanos et al., 1989).

4.2 | Lianas had a more efficient branch architecture for canopy colonization

We expected that lianas would produce longer branches per unit stem diameter and that branches of lianas are under stronger apical dominance than tree branches. These differences between lianas and trees may result in rapid stem elongation of slender branches, favouring a more horizontal spread of their crown and higher potential for canopy colonization when hosts are available and intervening distances are short. We indeed found evidence for a lower number of axillary shoots in liana branches than in tree branches suggesting that lianas are under stronger apical dominance than trees in both forest sites. By reducing lateral branches, the terminal branches with strong apical dominance may reduce the probability of self-shading and thus limit the existence of lower leaf layers in lianas than in trees. Less self-shading is consistent with our observations of the number of leaf layer within the crown: lianas supported leaves in a shallow single layer and can thus avoid steep light gradients and shading within their crowns. This result may refer to several individual crowns, since lianas often have multiple crowns at different canopy locations and, in some cases, even connected to different rooting points (Caballé, 1993; Cox et al., 2019; Penalosa, 1984). Trees, however, typically have leaves organized in a single multi-layered tree crown (Figure 3c,d), which is characterized by steep light gradients and by shading within lower crown parts (e.g. Horn, 1971; Sterck & Bongers, 2001; Sterck & Schieving, 2007).

For the dry forest, we also found evidence for consistently longer and slenderer (Figure 2e) branches in lianas than in trees. Longer branches per unit stem diameter and stronger apical dominance may favour lianas over trees in light acquisition since it allows them to rapidly colonize the forest canopy. Consistently longer branches in lianas than in trees at all branch sizes also suggest that lianas in the dry forest may be under consistent pressure to colonize and monopolize light interception on the forest canopy. In contrast, liana branches in the wet forest were longer than those of trees at smaller branch diameters but this difference disappeared with larger branch diameters (Figure 2f), similar to the observed changes in supported leaf area with increasing branch size for the same set of liana and tree branches (Figure 2b). An early exploration of the forest canopy and early canopy colonization via longer and slender branches may provide lianas in the wet forest with an initial advantage, which coupled to the early development of larger leaf areas also observed for the same set of liana branches, could be translated into higher growth rates and carbon accumulation required to rapidly reach adequate positions in the forest canopy. Moreover, although liana branches in the wet forest were not longer than tree branches with increasing branch diameters, lianas also produced fewer leaf layers than trees, and they positioned those leaves at a greater height than trees (Figure 3d), which was in line with our prediction.

4.3 | Forest differences explained from resource availability

What could be the reason for the inconsistent branch differences between lianas and trees in the wet versus dry forest? We speculate that forest differences in resource availability are the potential

cause. The dry forest has lower precipitation and stronger seasonality in rainfall and associated solar radiation than the wet forest (Condit et al., 2000; see Appendix S1). The dry forest has a larger proportion of dry-season deciduous species with high foliar nutrient concentrations and faster soil nutrient cycling than the wet forest (Santiago & Mulkey, 2005; Santiago et al., 2005). For the wet forest, plants favour tissues with more conservative values and longer longevities (Aerts & Chapin, 2000), most likely as a consequence of low resource availability (i.e. less light and lower soil fertility) and/or higher risks for pathogen/pest pressures, than plants in the dry forest (Coley et al., 1985; Kitajima & Poorter, 2010; Santiago & Mulkey, 2005).

The observation that lianas in the dry forest have lower LMA (Figure 1a) and lower, but phylogenetically dependent, LLS (for seven out of the eight species, Figure 1c) than trees suggests that lianas produce cheaper leaves, which is consistent with other studies at the same site (Sánchez-Azofeifa et al., 2009) and in other regions (Asner & Martin, 2012; Cai et al., 2009; Kazda & Salzer, 2000; Wyka et al., 2013; Zhu & Cao, 2010). Large investments in total leaf area are strongly associated with increases in relative growth rates (Poorter & Remkes, 1990) and thus, the capacity of lianas in the dry forest to develop larger leaf areas per biomass investment than trees is consistent with observations of higher relative growth rates in lianas than in trees in other forest sites (Mooney & Gartner, 1991; Paul & Yavitt, 2011; Schnitzer, 2005; Schnitzer & van der Heijden, 2019; Teramura et al., 1991).

Contrasting with the dry forest but consistent with a relatively low number of studies (Asner & Martin, 2015; Cai & Bongers, 2007; Castellanos et al., 1989), similar LMA (Figure 1a) and LLS (Figure 1c) between lianas and trees in the wet forest suggest that both lifeforms have similar structural investments at the leaf level for this forest. Although liana and tree branches in the wet forest do not differ in leaf display efficiency and despite having relatively similar branch structures, particularly with increasing branch size, lianas at the whole plant level may still develop larger leaf areas per unit biomass investment than trees since canopy growth in lianas is not structurally constrained as is in trees (Caballé, 1993; Cox et al., 2019; Penalosa, 1984). Low structural constraints may favour entire liana individuals with large leaf areas, but the advantage of having large leaf areas—i.e. high growth rates and carbon gain (Poorter & Remkes, 1990)—may be offset by the high costs of constructing and maintaining long-lived leaves (Kikuzawa, 1991, 1995; Reich et al., 1998).

5 | CONCLUSIONS

Our study shows that canopy branches differed more consistently between lianas and trees under drier conditions than under wetter conditions. Lianas more effectively explore the forest canopy than trees under drier conditions: this efficiency was attributed to a lower LMA, stronger apical dominance and slenderer stems, but not by differential biomass distribution between leaves and stem within branches. Under wetter conditions, lianas were less efficient in leaf display and branch slenderness, and they even tended to have a lower leaf area than trees at large branch sizes. Nevertheless, lianas carried their leaves in shallow, single layers in both forest sites, implying that they monopolize high-light spots in the canopy, whereas trees had leaves organized in deeper crowns with multiple tree layers. Since our study was limited to two forest canopies only, we call for studies that replicate more forests to test the idea that branch allometry thus contributes to the higher success of lianas over trees with reduced rainfall and increasing drought seasonality across tropical forests.

ACKNOWLEDGEMENTS

We gratefully acknowledge S. Joseph Wright for valuable support in the field, expert knowledge and helpful discussions; César Gutierrez, Dioselina Vigil, Pieter de Leeuw, Rosa Boschman, Judith de Bree, Karel Haan and Eva Gril for their contribution in data collection; Edwin Andrades and Oscar Saldaña for operating the canopy cranes and the anonymous referees who provided comments which helped to improve the quality of this manuscript. This work is part of the research project 'Explaining the rapid increase in lianas in tropical forest' with project number 824.14.006, which is financed by the Dutch Research Council (NWO) and also supported by the Smithsonian Tropical Research Institute (STRI).

AUTHORS' CONTRIBUTIONS

F.J.S., F.B. and J.A.M.-V. conceived the ideas; F.J.S., F.B. and J.A.M.-V. designed the methodology; J.A.M.-V. collected and analysed the data; F.J.S., F.B., S.A.S. and J.A.M.-V. interpreted the data; J.A.M.-V. led the writing of the manuscript with comments from F.J.S., F.B. and S.A.S. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository (Medina-Vega et al., 2020) https://doi.org/10.5061/dryad.gb5mkkwnh.

ORCID

José A. Medina-Vega https://orcid.org/0000-0001-5468-5605
Frans Bongers https://orcid.org/0000-0002-8431-6189
Stefan A. Schnitzer https://orcid.org/0000-0002-2715-9455
Frank J. Sterck https://orcid.org/0000-0001-7559-6572

REFERENCES

Aerts, R., & Chapin, F. S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research*, *30*, 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1

Asner, G. P., & Martin, R. E. (2012). Contrasting leaf chemical traits in tropical lianas and trees: Implications for future forest composition. *Ecology Letters*, *15*(9), 1001–1007. https://doi.org/10.1111/j.1461-0248.2012.01821.x

Asner, G. P., & Martin, R. E. (2015). Canopy chemistry expresses the life-history strategies of lianas and trees. In S. A. Schnitzer, F. Bongers, R. J. Burnham, & F. E. Putz (Eds.), *Ecology of lianas* (pp. 299–308). John Wiley & Sons Ltd.

Avalos, G., & Mulkey, S. S. (1999). Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest

canopy. *Oecologia*, *120*(4), 475–484. https://doi.org/10.1007/s004420050880

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate – A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, *57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Blomberg, S. P., Garland Jr., T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*(4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Brooks, M. E., Kristensen, K., Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for Zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Bullock, S. H. (1990). Abundance and allometrics of vines and self-supporting plants in a tropical deciduous forest. *Biotropica*, *22*(1), 106–109. https://doi.org/10.2307/2388726

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.

Caballé, G. (1993). Liana structure, function and selection: A comparative study of xylem cylinders of tropical rainforest species in Africa and America. *Botanical Journal of the Linnean Society*, *113*(1), 41–60. https://doi.org/10.1111/j.1095-8339.1993.tb00328.x

Cai, Z. Q., & Bongers, F. (2007). Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. *Journal of Tropical Ecology*, *23*(1), 115–118. https://doi.org/10.1017/S0266467406003750

Cai, Z. Q., Poorter, L., Cao, K. F., & Bongers, F. (2007). Seedling growth strategies in *Bauhinia* species: Comparing lianas and trees. *Annals of Botany*, *100*(4), 831–838. https://doi.org/10.1093/aob/mcm179

Cai, Z. Q., Schnitzer, S. A., & Bongers, F. (2009). Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia*, *161*(1), 25–33. https://doi.org/10.1007/s00442-009-1355-4

Castellanos, A. E., Mooney, H. A., Bullock, S. H., Jones, C., & Robichaux, R. (1989). Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. *Biotropica*, *21*(1), 41–49. https://doi.org/10.2307/2388440

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chen, Y.-J., Bongers, F., Tomlinson, K., Fan, Z.-X., Lin, H., Zhang, S.-B., Zheng, Y.-L., Li, Y.-P., Cao, K.-F., & Zhang, J.-L. (2016). Time lags between crown and basal sap flows in tropical lianas and co-occurring trees. *Tree Physiology*, *36*(6), 736–747. https://doi.org/10.1093/treephys/tpv103

Chernick, M. R. (2007). *Bootstrap methods: A guide for practitioners and researchers* (2nd ed.). Wiley-Interscience.

Coley, P. D., Bryant, J. P., & Chapin III, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, *230*(4728), 895–899. https://doi.org/10.1126/science.230.4728.895

Condit, R., Engelbrecht, B. M., Pino, D., Perez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(13), 5064–5068. https://doi.org/10.1073/pnas.1218042110

Condit, R., Watts, K., Bohlman, S. A., Pérez, R., Foster, R. B., & Hubbell, S. P. (2000). Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*, *11*(5), 649–658. https://doi.org/10.2307/3236572

Cornelissen, J. H. C., Diez, P. C., & Hunt, R. (1996). Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, *84*(5), 755–765. https://doi.org/10.2307/2261337

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. T., Morgan, H. D., Heijden, M. G. A. V. D., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380. https://doi.org/10.1071/Bt02124

Cox, C. J., Edwards, W., Campbell, M. J., Laurance, W. F., & Laurance, S. G. W. (2019). Liana cover in the canopies of rainforest trees is not predicted by local ground-based measures. *Austral Ecology*, *44*(5), 759–767. https://doi.org/10.1111/aec.12746

Dias, A. S., Oliveira, R. S., Martins, F. R., Bongers, F., Anten, N. P. R., & Sterck, F. (2019). How do lianas and trees change their vascular strategy in seasonal versus rain forest? *Perspectives in Plant Ecology Evolution and Systematics*, *40*, 125465. https://doi.org/10.1016/j.ppees.2019.125465

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., & Garnier, E. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

During, H. J., Kwant, R. A., & Werger, M. J. A. (1994). Effects of light quantity on above-ground biomass investment patterns in the vine *Lonicera periclymenum* and the shrub *Lonicera xylosteum*. *Phytocoenologia*, *24*, 597–607. https://doi.org/10.1127/phyto/24/1994/597

Efron, B. (1988). Logistic-regression, survival analysis, and the Kaplan-Meier curve. *Journal of the American Statistical Association*, *83*(402), 414–425. https://doi.org/10.2307/2288857

Ewers, F. W., Fisher, J. B., & Fichtner, K. (1991). Water flux and xylem structure in vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 127–160). Cambridge University Press.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, *125*(1), 1–15. https://doi.org/10.1086/284325

García León, M. M., Martínez Izquierdo, L., Mello, F. N. A., Powers, J. S., Schnitzer, S. A., & Edwards, D. (2018). Lianas reduce community-level canopy tree reproduction in a Panamanian forest. *Journal of Ecology*, *106*(2), 737–745. https://doi.org/10.1111/1365-2745.12807

Gartner, B. L. (1991). Relative growth-rates of vines and shrubs of western poison oak, *Toxicodendron diversilobum* (Anacardiaceae). *American Journal of Botany*, *78*(10), 1345–1353. https://doi.org/10.2307/2445273

Gerwing, J. J., & Farias, D. L. (2000). Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology*, *16*(03), 327–335. https://doi.org/10.1017/S0266467400001437

Hegarty, E. E., & Caballé, G. (1991). Distribution and abundance of vines in forest communities. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 313–336). Cambridge University Press.

Holdridge, L. R. (1967). *Life zone ecology*. Tropical Science Center.

Horn, H. S. (1971). *The adaptive geometry of trees*. Princeton University Press.

Ichihashi, R., & Tateno, M. (2015). Biomass allocation and long-term growth patterns of temperate lianas in comparison with trees. *New Phytologist*, *207*(3), 604–612. https://doi.org/10.1111/nph.13391

Ilic, J., Boland, D., McDonald, M., Downes, G., & Blakemore, P. (2000). *Wood density phase 1: State of knowledge*. Australian Greenhouse Office.

Ingwell, L. L., Wright, S. J., Becklund, K. K., Hubbell, S. P., & Schnitzer, S. A. (2010). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island. *Panama. Journal of Ecology*, *98*(4), 879–887. https://doi.org/10.1111/j.1365-2745.2010.01676.x

Isnard, S., & Feild, T. S. (2015). The evolution of angiosperm lianescence: A perspective from xylem structure-function. In S. A. Schnitzer, F. Bongers, R. J. Burnham, & F. E. Putz (Eds.), *Ecology of lianas* (pp. 221–238). John Wiley & Sons Ltd.

Kaneko, Y., & Homma, K. (2006). Differences in the allocation patterns between liana and shrub *Hydrangea* species. *Plant Species Biology*, *21*(3), 147–153. https://doi.org/10.1111/j.1442-1984.2006.00160.x

Kazda, M., Miladera, J. C., & Salzer, J. (2009). Optimisation of spatial allocation patterns in lianas compared to trees used for support. *Trees-Structure and Function*, *23*(2), 295–304. https://doi.org/10.1007/s00468-008-0277-9

Kazda, M., & Salzer, J. (2000). Leaves of lianas and self-supporting plants differ in mass per unit area and in nitrogen content. *Plant Biology*, *2*(3), 268–271. https://doi.org/10.1055/s-2000-3701

Kikuzawa, K. (1991). A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *The American Naturalist*, *138*(5), 1250–1263. https://doi.org/10.1086/285281

Kikuzawa, K. (1995). Leaf phenology as an optimal strategy for carbon gain in plants. *Canadian Journal of Botany*, *73*(2), 158–163. https://doi.org/10.1139/b95-019

Kitajima, K., & Poorter, L. (2010). Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*, *186*(3), 708–721. https://doi.org/10.1111/j.1469-8137.2010.03212.x

MacArthur, R. H., & Horn, H. S. (1969). Foliage profile by vertical measurements. *Ecology*, *50*(5), 802–804. https://doi.org/10.2307/1933693

Medina-Vega, J. A., Bongers, F., Schnitzer, S. A., & Sterck, F. J. (2020). Data From: Lianas explore the forest canopy more effectively than trees under drier conditions. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.gb5mkkwnh

Menard, L., McKey, D., & Rowe, N. (2009). Developmental plasticity and biomechanics of treelets and lianas in *Manihot* aff. *quinquepartita* (Euphorbiaceae): A branch-angle climber of French Guiana. *Annals of Botany*, *103*(8), 1249–1259. https://doi.org/10.1093/aob/mcp078

Mooney, H. A., & Gartner, B. L. (1991). Reserve economy of vines. In F. E. Putz & H. A. Mooney (Eds.), *The Biology of Vines* (pp. 161–179). Cambridge University Press.

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*(1), 67–88. https://doi.org/10.1146/annurev.es.17.110186.000435

Niklas, K. J. (1994). Comparisons among biomass allocation and spatial distribution patterns of some vine, pteridophyte, and gymnosperm shoots. *American Journal of Botany*, *81*(11), 1416–1421. https://doi.org/10.2307/2445314

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*(6756), 877–884. https://doi.org/10.1038/44766

Paul, G. S., & Yavitt, J. B. (2011). Tropical vine growth and the effects on forest succession: A review of the ecology and management of tropical climbing plants. *Botanical Review*, *77*(1), 11–30. https://doi.org/10.1007/s12229-010-9059-3

Penalosa, J. (1984). Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, *16*(1), 1–9. https://doi.org/10.2307/2387886

Pérez-Salicrup, D. R., Claros, A., Guzman, R., Licona, J. C., Ledezma, F., Pinard, M. A., & Putz, F. E. (2001). Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia. *Biotropica*, *33*(2), 324–329. https://doi.org/10.1111/j.1744-7429.2001.tb00183.x

Phillips, O. L., Vasquez Martinez, R., Arroyo, L., Baker, T. R., Killeen, T., Lewis, S. L., Malhi, Y., Mendoza, A. M., Neill, D., Vargas, P. N., & Vinceti, B. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature*, *418*(6899), 770–774. https://doi.org/10.1038/nature00926

Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*(3), 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, H., & Remkes, C. (1990). Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, *83*(4), 553–559. https://doi.org/10.1007/BF00317209

Putz, F. E. (1983). Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro basin. *Venezuela. Biotropica*, *15*(3), 185–189. https://doi.org/10.2307/2387827

Putz, F. E. (1984). The natural history of lianas on Barro Colorado Island. *Panama. Ecology*, *65*(6), 1713–1724. https://doi.org/10.2307/1937767

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reich, P. B., Tjoelker, M. G., Walters, M. B., Vanderklein, D. W., & Bushena, C. (1998). Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, *12*(3), 327–338. https://doi.org/10.1046/j.1365-2435.1998.00208.x

Reich, P. B., Uhl, C., Walters, M. B., & Ellsworth, D. S. (1991). Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia*, *86*(1), 16–24. https://doi.org/10.1007/BF00317383

Rodríguez-Ronderos, M. E., Bohrer, G., Sánchez-Azofeifa, A., Powers, J. S., & Schnitzer, S. A. (2016). Contribution of lianas to plant area index and canopy structure in a Panamanian forest. *Ecology*, *97*(12), 3271–3277. https://doi.org/10.1002/ecy.1597

Rowe, N., & Speck, T. (2005). Plant growth forms: An ecological and evolutionary perspective. *New Phytologist*, *166*(1), 61–72. https://doi.org/10.1111/j.1469-8137.2004.01309.x

Sánchez-Azofeifa, G. A., Castro, K., Wright, S. J., Gamon, J., Kalacska, M., Rivard, B., Schnitzer, S. A., & Feng, J. L. (2009). Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: Implications for remote sensing in tropical environments. *Remote Sensing of Environment*, *113*(10), 2076–2088. https://doi.org/10.1016/j.rse.2009.05.013

Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., & Jones, T. (2004). Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, *140*(4), 543–550. https://doi.org/10.1007/s00442-004-1624-1

Santiago, L. S., & Mulkey, S. S. (2005). Leaf productivity along a precipitation gradient in lowland Panama: Patterns from leaf to ecosystem. *Trees-Structure and Function*, *19*(3), 349–356. https://doi.org/10.1007/s00468-004-0389-9

Santiago, L. S., Schuur, E. A. G., & Silvera, K. (2005). Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama. *Journal of Tropical Ecology*, *21*(4), 461–470. https://doi.org/10.1017/S0266467405002464

Santiago, L. S., & Wright, S. J. (2007). Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology*, *21*(1), 19–27. https://doi.org/10.1111/j.1365-2435.2006.01218.x

Schnitzer, S. A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, *166*(2), 262–276. https://doi.org/10.1086/431250

Schnitzer, S. A., & Bongers, F. (2002). The ecology of lianas and their role in forests. *Trends in Ecology & Evolution*, *17*(5), 223–230. https://doi.org/10.1016/S0169-5347(02)02491-6

Schnitzer, S. A., Bongers, F., & Wright, S. J. (2011). Community and ecosystem ramifications of increasing lianas in neotropical forests. *Plant Signaling & Behavior*, *6*(4), 598–600. https://doi.org/10.4161/psb.6.4.15373

Schnitzer, S. A., & Carson, W. P. (2010). Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters*, *13*(7), 849–857. https://doi.org/10.1111/j.1461-0248.2010.01480.x

Schnitzer, S. A., Kuzee, M. E., & Bongers, F. (2005). Disentangling above- and below-ground competition between lianas and trees in

a tropical forest. *Journal of Ecology*, *93*(6), 1115–1125. https://doi.org/10.1111/j.1365-2745.2005.01056.x

Schnitzer, S. A., & van der Heijden, G. M. F. (2019). Lianas have a seasonal growth advantage over co-occurring trees. *Ecology*, *100*(5), e02655. https://doi.org/10.1002/ecy.2655

Selaya, N. G., & Anten, N. P. R. (2008). Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. *Functional Ecology*, *22*(1), 30–39. https://doi.org/10.1111/j.1365-2435.2007.01350.x

Selaya, N. G., Anten, N. P., Oomen, R. J., Matthies, M., & Werger, M. J. (2007). Above-ground biomass investments and light interception of tropical forest trees and lianas early in succession. *Annals of Botany*, *99*(1), 141–151. https://doi.org/10.1093/aob/mcl235

Smith-Martin, C. M., Bastos, C. L., Lopez, O. R., Powers, J. S., & Schnitzer, S. A. (2019). Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. *Ecology*, *100*(11), e02827. https://doi.org/10.1002/ecy.2827

Smith-Martin, C. M., Xu, X., Medvigy, D., Schnitzer, S. A., & Powers, J. S. (2020). Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytologist*, *226*(3), 714–726. https://doi.org/10.1111/nph.16275

Sterck, F. J., & Bongers, F. (2001). Crown development in tropical rain forest trees: Patterns with tree height and light availability. *Journal of Ecology*, *89*(1), 1–13. https://doi.org/10.1046/j.1365-2745.2001.00525.x

Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011). Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(51), 20627–20632. https://doi.org/10.1073/pnas.1106950108

Sterck, F. J., & Schieving, F. (2007). 3-D growth patterns of trees: Effects of carbon economy, meristem activity, and selection. *Ecological Monographs*, *77*(3), 405–420. https://doi.org/10.1890/06-1670.1

Teramura, A. H., Gold, W. G., & Forseth, I. N. (1991). Physiological ecology of mesic, temperate woody vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 245–286). Cambridge University Press.

Tyree, M. T. (2003). Plant hydraulics: The ascent of water. *Nature*, *423*(6943), 923. https://doi.org/10.1038/423923a

van der Heijden, G. M. F., Powers, J. S., & Schnitzer, S. A. (2015). Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(43), 13267–13271. https://doi.org/10.1073/pnas.1504869112

Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes*, *5*(1), 181–183. https://doi.org/10.1111/j.1471-8286.2004.00829.x

Werden, L. K., Waring, B. G., Smith-Martin, C. M., & Powers, J. S. (2017). Tropical dry forest trees and lianas differ in leaf economic spectrum traits but have overlapping water-use strategies. *Tree Physiology*, *38*(4), 517–530. https://doi.org/10.1093/treephys/tpx135

Wright, I. J., Falster, D. S., Pickup, M., & Westoby, M. (2006). Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiologia Plantarum*, *127*(3), 445–456. https://doi.org/10.1111/j.1399-3054.2006.00699.x

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Wright, S. J., Sun, I. F., Pickering, M., Fletcher, C. D., & Chen, Y. Y. (2015). Long-term changes in liana loads and tree dynamics in a Malaysian forest. *Ecology*, *96*(10), 2748–2757. https://doi.org/10.1890/14-1985.1

Wyka, T. P., Oleksyn, J., Karolewski, P., & Schnitzer, S. A. (2013). Phenotypic correlates of the lianescent growth form: A review. *Annals of Botany*, *112*(9), 1667–1681. https://doi.org/10.1093/aob/mct236

Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., McGlinn, D. J., O'Meara, B. C., Moles, A. T., Reich, P. B., & Reich, P. B. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*(7486), 89–92. https://doi.org/10.1038/nature12872

Zhang, L., Chen, Y., Ma, K., Bongers, F., & Sterck, F. J. (2019). Fully exposed canopy tree and liana branches in a tropical forest differ in mechanical traits but are similar in hydraulic traits. *Tree Physiology*, *39*(10), 1713–1724. https://doi.org/10.1093/treephys/tpz070

Zhu, S. D., & Cao, K. F. (2009). Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. *Plant Ecology*, *204*(2), 295–304. https://doi.org/10.1007/s11258-009-9592-5

Zhu, S. D., & Cao, K. F. (2010). Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia*, *163*(3), 591–599. https://doi.org/10.1007/s00442-010-1579-3

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636–645. https://doi.org/10.1111/2041-210x.12577

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Medina-Vega JA, Bongers F, Schnitzer SA, Sterck FJ. Lianas explore the forest canopy more effectively than trees under drier conditions. *Funct Ecol*. 2021;35:318–329. https://doi.org/10.1111/1365-2435.13717