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ABSTRACT

We test the hypotheses proposed by Gentry and Schnitzer that liana density and basal area in tropical forests vary negatively with mean annual precipitation (MAP) and positively with seasonality. Previous studies correlating liana abundance with these climatic variables have produced conflicting results, warranting a new analysis of drivers of liana abundance based on a different dataset. We compiled a pan-tropical dataset containing 28,953 lianas (≥2.5 cm diam.) from studies conducted at 13 Neotropical and 11 Paleotropical dry to wet lowland tropical forests. The ranges in MAP and dry season length (DSL) (number of months with mean rainfall <100 mm) represented by these datasets were 860–7250 mm/yr and 0–7 mo, respectively. Pan-tropically, liana density and basal area decreased significantly with increasing annual rainfall and increased with increasing DSL, supporting the hypotheses of Gentry and Schnitzer. Our results suggest that much of the variation in liana density and basal area in the tropics can be accounted for by the relatively simple metrics of MAP and DSL.

DETERMINING THE FACTORS THAT AFFECT THE DISTRIBUTION AND ABUNDANCE of plants is a central goal in ecology. At global scales, climatic variables such as mean annual rainfall and the seasonality of rainfall may be key predictors of vascular plant abundance, and have been hypothesized to affect directly or indirectly the density of many tropical forest plant groups (**Gentry 1991, Schnitzer 2005**). For example, many vascular plant life forms (*e.g.*, trees, palms, and epiphytes) are more abundant in tropical lowland forests that receive more precipitation (**Gentry 1982, 1995**). In contrast, the abundance of lianas, a key component of most tropical forests (**Schnitzer & Bongers 2002**), has been hypothesized to be negatively correlated with mean annual precipitation (MAP) and positively correlated with length of the dry season (**Gentry 1991, Schnitzer 2005**).

Tests of these hypotheses have produced contrasting results. **Schnitzer (2005)** found a negative relationship between mean annual rainfall and liana density using a pan-tropical dataset collected by A. Gentry (in **Phillips &**

Miller 2002), as well as a negative relationship between rainfall and liana density and a positive relationship with seasonality in a study conducted across the rainfall gradient of the isthmus of Panama. In contrast, **van der Heijden and Phillips (2008)** found no relationship between mean annual rainfall and liana abundance when they used a slightly modified Neotropical subset of the Gentry dataset used by **Schnitzer (2005)**. Furthermore, **van der Heijden and Phillips (2008)** also failed to find that the length of the dry season, as defined as number of consecutive months with mean rainfall <100 mm, was a significant predictor of liana abundance. Because lianas are important components of tropical forest structure and dynamics, and they may be increasing in abundance and biomass in lowland tropical and subtropical forests (**Phillips *et al.* 2002, Wright *et al.* 2004, Wright & Calderón 2006, Allen *et al.* 2007**), understanding the determinants of liana abundance and biomass may provide insights into the mechanisms that govern liana communities and help explain the reported increase in liana density (**Schnitzer 2005**).

We tested whether liana density and basal area were related to MAP and seasonality of precipitation using a newly assembled, independent, pan-tropical dataset of lianas. We examined both liana density and basal area, which are highly correlated with estimated aboveground biomass (**Schnitzer *et al.* 2006**). Our dataset spanned a large range of liana abundance, basal area, mean annual rainfall, and seasonality of rainfall in the tropics. We used this dataset to test the hypotheses of **Gentry (1991)** and **Schnitzer (2005)** that lianas are most abundant and have higher basal area in drier tropical forests (*i.e.*, <2000 mm/yr) with greater seasonality of rainfall, and that liana abundance and basal area decrease with increasing rainfall.

METHODS

We compiled liana surveys conducted in dry to wet tropical lowland sites (>500 mm MAP; <1000 m asl; 23°N–23°S latitude) located in old growth forest (**Fig. 1**). We defined old growth forest as that which had not been cleared by humans during the last 120 yr. We included only older forests because lianas are significantly more abundant in young secondary forests (<*ca* 70 yr old), whereas forests >70 yr old have similar liana densities to old growth forests (**DeWalt *et al.* 2000**). Additionally, we excluded oceanic islands because islands often have markedly lower liana diversity and abundance compared with nearby continental areas (**Gentry 1991, Rice *et al.* 2004**). Borneo is considered a continental-fragment island and therefore was included in the dataset. The dataset, including climate variables, was collected by this study's authors and assembled during a National Center for Ecological Analysis and Synthesis (NCEAS) liana working group.
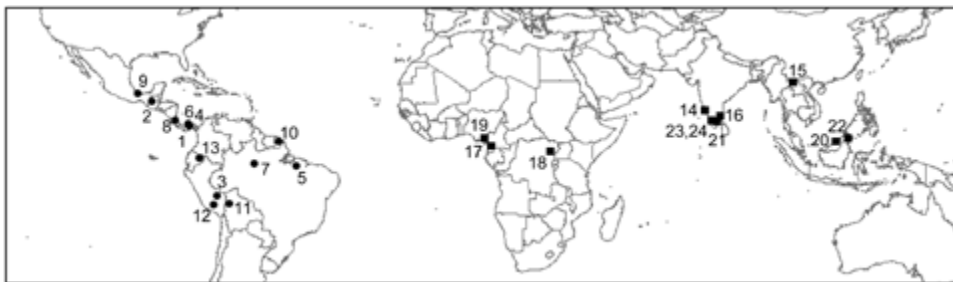

Figure 1
Map of sites used in this study. Numbers correspond to site codes listed in Table S1. Neotropical and Paleotropical sites are plotted with circles and squares, respectively.

In total, the dataset included 28,953 individual lianas ≥2.5 cm diam. from studies conducted in 24 distinct sites (Table S1): 13 in the Neotropics (7 in South America, 5 in Central America, and 1 in Mexico) and 11 in the Paleotropics (3 in Africa, 5 in India, 2 on Borneo, and 1 in China). At several sites, multiple researchers had independently conducted liana surveys. For these sites, we averaged liana density and basal area after applying the corrections explained below.

We standardized the datasets for taxonomic groups using recommendations of **Gerwing _et al._ (2006)** and **Schnitzer _et al._ (2008)**. The datasets in our analyses were modified where necessary to include only climbing woody stems that maintain connections to the ground throughout their lives. We included Smilacaceae but excluded hemiepiphytic climbers (including Araceae and Marcgraviaceae), climbing ferns, Poaceae (_e.g._, climbing bamboo), and Arecaceae (climbing palms). These groups were also excluded from the analysis of the Gentry Neotropical dataset conducted by **van der Heijden and Phillips (2008)**.

Different researchers used different points of measurement (POM) of the diameter along the liana stem, which can lead to significantly different estimates of liana abundance, basal area, and biomass (**Schnitzer _et al._ 2006**). To account for tapering of liana stems with increasing distance from roots, we applied the allometric equations in **Schnitzer _et al._ (2006)** to adjust all diameter measurements to the estimated stem diameter as if measured 130 cm from the last substantial roots. This POM, with some exceptions when branching occurs <130 cm, is recommended by the NCEAS liana working group (**Gerwing _et al._ 2006, Schnitzer _et al._ 2008**) and was the method most commonly used in the dataset (45% of the studies; Table S1). After adjusting diameter measurements, we included only lianas that were ≥2.5 cm diam. as measured (or estimated) at 130 cm from roots. We used 2.5 cm as a minimum diameter threshold for three reasons. First, this greater diameter allowed inclusion of most studies in our dataset. Second, this size allowed direct comparison with the dataset amassed worldwide by A. Gentry using a minimum diameter of 2.5 cm (**Gentry 1988, Phillips & Miller 2002**), which was the basis of several studies examining the effects of climate or edaphic factors on liana density and diversity (**Clinebell _et al._ 1995, Schnitzer 2005, van der Heijden & Phillips 2008**). Third, most lianas >2.5 cm diam. are already established in the canopy (**Kurzel _et al._ 2006**). Therefore, these lianas have been through abiotic and biotic filters of establishment and height growth and have passed through life history stages with the highest risk of mortality.

Most of the studies (79%) in our dataset followed lianas to determine which stems were connected aboveground or obviously connected belowground. Each group of connected stems was considered one individual liana, and the diameter measured was from the largest stem. We refer to these studies as those that sampled 'genets,' although no genetic testing was conducted to determine if nearby lianas with no stem connection were indeed genets (_i.e._, unique genotypes that started from seed) or separated ramets (_i.e._, clones whose origin is vegetative) of the same genet. Censuses at four sites did not follow lianas to determine whether stems were obviously connected to other stems, and thus counted each rooted stem as an individual. We refer to these studies as those that sampled 'ramets' (Table S1). To consider ramets as distinct individuals increases liana density substantially (**Putz 1984, Schnitzer _et al._ 2006**), and therefore we conducted analyses with and without the sites where ramets were included to determine whether the elevated density at those sites unduly influenced the relationship between climatic factors and liana density and basal area.

We did not correct for minor differences in sampling methodology between the datasets, such as whether all stems crossing a horizontal plane 130 cm above the ground ('crossing') or only individuals rooted within the plot ('rooted') were counted. In a study conducted in French Guiana, **Schnitzer _et al._ (2006)** found that liana density did not significantly differ when genets of rooted vs. crossing lianas were counted. Therefore, the difference in methods of using rooted vs. crossing genets probably did not affect our results. Nonetheless, we also conducted analyses on the dataset excluding sites where the crossing criterion was used.

We tested whether liana density or basal area were significantly affected by biogeographic regions (Neotropics vs. Paleotropics), by MAP, or by dry season length (DSL) using analysis of covariance (PROC GLM, Type I Sums of Squares) in SAS V. 9.1. DSL was estimated as the number of months with <100 mm/mo. DSL has been used previously as an indicator of dry conditions (_e.g._, **Phillips _et al._ 2002, van der Heijden & Phillips 2008**). Wet tropical forest transpires at least 100 mm/mo (**Hodnett _et al._ 1996, Malhi _et al._ 2002**), suggesting that plants might be water limited below this amount of precipitation. Because MAP and DSL were significantly negatively

correlated (Pearson's $r=-0.48$, $P<0.05$), we examined models with only region and MAP or DSL, and MAP* region or DSL* region, respectively, as predictor variables. When interaction terms were not significant, they were removed from the model and regressions were conducted including only main effects. We used the natural log of density, basal area, and MAP, but DSL was not transformed. Models using these variables provided the best curve fit and the residuals were distributed normally. We report statistics using transformed data, but figures are presented with back-transformed values. We used one-tailed probability values when examining the relationship between MAP or DSL on liana density and basal area because we tested hypotheses predicting a direction in effect (*i.e.*, we predicted that liana density and basal area would be negatively correlated with MAP and positively correlated with DSL).

RESULTS

The 24 sites spanned a considerable range in mean annual precipitation (MAP; 860–7250 mm/yr) and DSL (0–7 mo). Neither MAP nor DSL differed significantly between the Neotropical and Paleotropical sites (MAP: $F_{1, 22}=0.44$, $P=0.52$; DSL: $F_{1, 22}=1.27$, $P=0.27$). A total of 106.6 ha were sampled across 24 sites. The average size sampled per site (± 1 SD) was 4.4 ha (± 7.8); the median was 1.35 ha.

Liana density averaged 376 (± 330) individuals/ha (≥ 2.5 cm diam.) across the 24 sites, ranging 15-fold between 94 (Agumbe, India) and 1414 individuals/ha (Fazenda Sete, Brazil). Basal area averaged 0.71 m^2/ha (± 0.46), ranging 12-fold between 0.18 (Agumbe, India) and 2.1 m^2/ha (Fazenda Sete, Brazil).

Consistent with the hypotheses of **Gentry (1991)** and **Schnitzer (2005)**, across the tropics liana density and basal area decreased significantly with increasing precipitation and decreasing seasonality (**Fig. 2**), with each factor explaining 21–37 percent of the variance among sites (**Table 1**). Neotropical sites harbored significantly greater liana density and basal area than Paleotropical sites across MAP and DSL leading to a significant main effect of region (**Fig. 3**), which accounted for 19–20 percent of the variance among sites (**Table 1**).
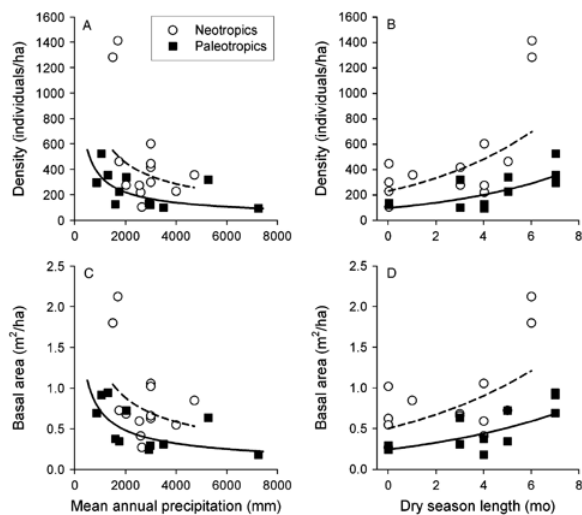

Figure 2

Relationships between liana density and (A) mean annual precipitation (MAP) and (B) dry season length (DSL) and between liana basal area and (C) MAP and (D) DSL. Note that higher values of DSL indicate greater seasonality. Liana density and basal area decreased significantly with MAP and increased with DSL; both liana community variables were higher across MAP and DSL for Neotropical sites (dashed line) than Paleotropical sites (solid line), leading to different y-intercepts but slopes for each regression did not differ. In (A), Neotropical *density*$=70,312(MAP)^{-0.663}$ and Paleotropical *density*$=34,201(MAP)^{-0.663}$. In (B),

Neotropical *density*=230 × exp(1.85[*DSL*]) and Paleotropical *density*=96 × exp(1.85[*DSL*]). In (C), Neotropical *basal area*=79.5(*MAP*)$^{0.592}$ and Paleotropical *basal area*=43.4(*MAP*)$^{0.592}$. In (D), Neotropical *basal area*=0.503 × exp(0.147[*DSL*]) and Paleotropical *basal area*=0.245 × exp(0.147[*DSL*]).

Table 1. Analysis of covariance tests of effects of region (Neotropics vs. Paleotropics), mean annual precipitation (MAP) and dry season length (DSL) on liana density and basal area. None of the interaction terms were significant and were therefore removed from the model. Type I sequential sums of squares in the GLM procedure of SAS were examined for these analyses. The proportion of total sum of squares explained by region and climatic parameters are indicated for each test (R2).

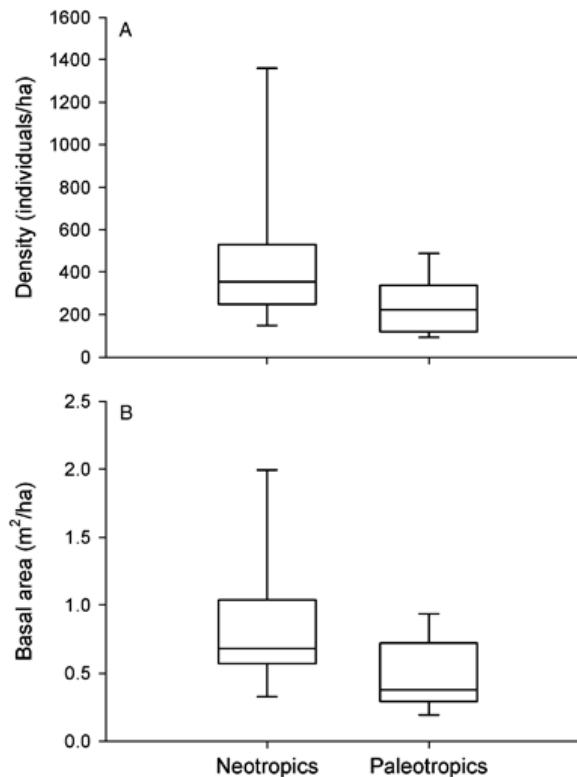| Source of variation	Ln(Density)			Ln(Basal area)		
	F [a]	*P*	*R*^{2}	*F* [a]	*P*	*R*^{2}
Region	7.08	0.015	0.20	7.04	0.015	0.19
Ln(MAP)	7.59	0.012	0.21	8.68	0.008	0.24
Region	9.56	0.006	0.20	8.27	0.009	0.19
DSL	17.6	<0.001	0.37	13.8	0.001	0.32

[a] df=1,21 for each test.

Figure 3
Box plots showing that Neotropical sites supported greater (A) liana density and (B) basal area than Paleotropical sites. Results of statistical tests are shown in **Table 1**. The 25th and 75th percentiles are represented by the lines on the box closest and farthest from zero, and the line within the box denotes the median. Error bars below and above the box indicate the 10th and 90th percentiles, respectively.

The relationships between MAP and liana density and basal area were negative and of similar magnitude for both regions of the tropics (**Fig. 2A, C**). The two Neotropical sites with the highest liana density, Oquiriquia and Fazenda Sete, influenced the relationship between MAP and density and basal area, but the negative relationship was still statistically significant even when these sites were removed (density: $F_{1, 19}$=4.40, *P*<0.05; basal area: $F_{1, 19}$=5.35, *P*<0.05). When the four sites in the Neotropics that sampled ramets were removed from

the pantropical analysis, the relationships remained significantly negative (density: $F_{1, 16}$=5.72, P<0.05; basal area: $F_{1, 16}$=5.89, P<0.05). When each region was examined separately, the relationship was statistically significant for density and basal area among Paleotropical sites (density: $F_{1, 9}$=5.07, P=0.05; basal area: $F_{1, 9}$=7.00, P<0.05) but not for density or basal area among Neotropical sites (density: $F_{1, 11}$=3.85, P=0.08; basal area: $F_{1, 11}$=2.27, P=0.16).

The relationships between DSL and liana density and basal area were positive pan-tropically ([Table 1](); [Fig. 2B, D]()) and were significant for both Neotropical (density: $F_{1, 11}$=9.55, P<0.05; basal area: $F_{1, 11}$=4.96, P<0.05) and Paleotropical sites (density: $F_{1, 9}$=7.70, P<0.05; basal area: $F_{1, 9}$=9.14, P<0.05). DSL remained significantly related to density ($F_{1, 19}$=9.20, P<0.01) and basal area ($F_{1, 19}$=6.93, P<0.05) when Oquiriquia and Fazenda Sete were removed. In addition, the relationship was significantly positive between DSL and density ($F_{1, 16}$=11.2, P<0.01) and basal area ($F_{1, 16}$=9.15, P<0.01) even when sites where ramets were sampled were excluded.

The residuals from all models including Neotropical and Paleotropical sites were similar in magnitude across the amount of area sampled per site ([Fig. 4]()). Sites that were less intensively sampled were no more likely to deviate from the predicted number of lianas or basal area than sites where greater area was sampled. In addition, area sampled did not have a significant effect on either liana variable when included as a covariate in the statistical model.
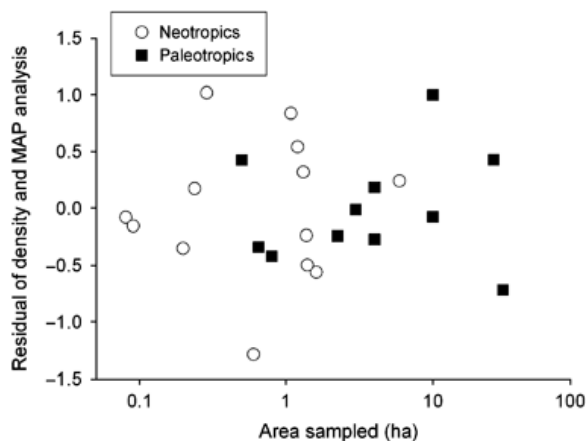

Figure 4
Plot of the area sampled against the residuals of the model examining how density was related to mean annual precipitation (MAP). The magnitude of the residuals did not change over area sampled.

DISCUSSION

Our pan-tropical dataset supports the hypotheses that mean annual precipitation (MAP) and DSL are predictors of patterns of liana density and basal area in the tropics, with each factor explaining 21–37 percent of the variance among sites after accounting for the effect of regional differences, which explained 19–20 percent. Regardless of region, liana density and basal area both decreased in continental tropical forests with increasing rainfall and decreasing seasonality.

Our results are consistent with those of **Schnitzer (2005)**, who found that lianas were more abundant in forests with the lowest rainfall and highest seasonality, but they contradict those of **van der Heijden and Phillips (2008)**, who analyzed only the Neotropical sites within the same Gentry dataset used by **Schnitzer (2005)**. MAP for the Gentry dataset ranged from 400 to 9000   mm/yr in the Neotropics (**van der Heijden & Phillips 2008**) and from 1000 to 5500   mm/yr in the Paleotropics (**Schnitzer 2005**). Whereas we and **Schnitzer (2005)** found a significant negative relationship between annual rainfall and liana density, **van der Heijden and Phillips**

(2008) found only a nonsignificant, negative trend. In addition, there was evidence in their study for a unimodal relationship between annual rainfall and liana basal area, with the highest basal area in sites of intermediate rainfall (*ca* 3100 mm/yr), whereas there was no indication of such a relationship in our dataset. They found no relationship between DSL and density, whereas we found a significant positive one. In support of our results, the site with the highest liana density in their dataset (Galerazamba, Colombia; a tropical very dry forest) received very low annual rainfall (500 mm/yr) and had the highest number of dry months (11) of all their sites.

Explaining discrepancies among studies.— There are several possible explanations for the discrepancy between the results of **van der Heijden and Phillips (2008)** and our study. First, as **van der Heijden and Phillips (2008)** suggested to explain the difference between their study and that of **Schnitzer (2005)**, the relationship between MAP and liana density and basal area may vary regionally, with a stronger pattern in the Paleotropics. Indeed, when we examined our data by region, we found a significant negative relationship between MAP and liana density and basal area for Paleotropical sites but not for Neotropical sites. However, the slope of the relationship did not differ significantly between regions, suggesting that liana density and basal area follow similar patterns with MAP in the Neotropics. The lack of a significant relationship in the Neotropics but not Paleotropics when examining the regions separately likely resulted from the smaller range of precipitation sampled in the Neotropics (1500–4725 mm/yr) than in the Paleotropics (860–7250 mm/yr), and therefore failed to capture high MAP where liana density would be lowest. In fact, when we analyzed the Paleotropical sites in our dataset within the MAP range of our Neotropical sites, the relationship between MAP and liana density and basal area were not significant. In addition, the relationship between liana density and basal area and DSL was significantly positive for both Neotropical and Paleotropical sites when examined separately. Thus, it appears the pattern between climatic variables and liana success is not necessarily stronger in the Paleotropics than Neotropics, negating that explanation for why the two datasets yield different results.

Second, the discrepancy between datasets could arise from differences in the range of climatic variation among the sites included in the two datasets. Our dataset did not include any forests with MAP <860 mm/yr, whereas the Gentry dataset included four such sites, with one as low as 400 mm/yr (Yanaigua, Bolivia; a tropical thorn woodland). However, when we analyzed the Gentry data reported in Supplement 1 of **van der Heijden and Phillips (2008)** and excluded sites >1000 m in elevation and with MAP<860, to make the dataset more analogous to our own, there was still no significant relationship between MAP and liana density. Thus, differences in climatic range variation do not explain the disparity between our study and that of **van der Heijden and Phillips (2008)**.

A third possible explanation for the discrepancy between the two studies is that the 65 sites analyzed by **van der Heijden and Phillips (2008)** each represented such a small area that each site provided an imprecise estimate of forest-level liana abundance and basal area. Although Gentry sampled across an area of several hectares in each site with 10 transects each of 2 × 50 m scattered across the landscape, the total area sampled for each site (0.1 ha) was much smaller than all but two of our sites (Cocoli and Fort Sherman, Panama). Sampling a greater area captures more of the forest spatial heterogeneity, including both gap (often with relatively high liana densities) and closed-forest sites (often with relatively low liana densities). Most of our Neotropical sites sampled much greater areas (mean=1.18 ha; median=1.35 ha) in wider transects or plots than Gentry's, and therefore likely provided more precise estimates of liana abundance and basal area. We suggest that the high sampling error likely associated with estimations of liana density and basal area in Gentry's small plots may hinder detection of underlying regional or global patterns using his dataset. To aid future intersite comparisons of liana density and basal area, we encourage the use of the standard protocols for censusing lianas proposed by **Gerwing et al. (2006)** and **Schnitzer et al. (2008)** as well as sampling areas >0.1 ha.

Explaining increasing liana density and basal area with decreasing rainfall and increasing seasonality.— If liana establishment and growth are favored by low rainfall and high seasonality leading to greater abundance and

basal area under these conditions, what is the mechanism? One possibility is that understory light levels are higher in drier tropical forests throughout the year than in wet forests, regardless of seasonality (**Condit *et al.* 2000**). Light is thought to be one of the most important factors determining liana proliferation (**Putz 1984, Schnitzer *et al.* 2000**), and thus higher year-round light or increases in light when trees become deciduous in the dry season would favor lianas in drier and more seasonal forests. **Kurzel *et al.* (2006)** suggested that the relatively high amount of light penetrating into drier forests may increase liana germination, growth, and survival in the understory, which in turn may increase liana performance and thus abundance in drier forests. Indeed, lianas are often found in greater relative abundance in high-light areas, such as forest edges and treefall gaps, than in the intact forest understory (**Putz 1984, Schnitzer *et al.* 2000, Laurance *et al.* 2001**). Lianas also proliferate in the high-light conditions following land abandonment and decline in abundance, both as seedlings and adults, as understory light levels decrease over tropical forest succession (**DeWalt *et al.* 2000, Capers *et al.* 2005**).

Although lianas may be favored by higher light in sites with lower rainfall and higher seasonality, they must also cope with drought, which occurs more often in forests with lower annual rainfall and longer dry seasons. **Schnitzer (2005)** summarized the morphological traits that may confer a growth advantage to lianas during the dry season. For example, several liana species have been found to have relatively deep roots (**Tyree & Ewers 1996, Restom & Nepstad 2004, Andrade *et al.* 2005**) and high water-use efficiency (**Cai *et al.* 2009b**). These traits may allow lianas to keep a substantial number of their leaves and grow during seasonal droughts when many competing trees are deciduous, and thereby confer a competitive advantage to lianas in drier or more seasonal tropical forests. In the seasonal forest of Barro Colorado Island, Panama, **Schnitzer (2005)** found that lianas grew seven times faster than trees in the dry season but only twice as fast in the wet season. In southwestern China, **Cai *et al.* (2009b)** found that lianas maintained relatively high rates of photosynthesis during the dry season, whereas photosynthesis in co-occurring trees dropped significantly during that time. Thus, the ability to grow during the dry season, when competing growth forms are mostly dormant, may explain why lianas are more abundant in forests with less MAP and greater DSL.

DSL and MAP may also affect the size-class distribution of trees, which could indirectly affect the liana community. If drier tropical forests have a greater density of small trees, which are more suitable hosts for lianas of all twining types (**Putz 1984, Putz & Holbrook 1991**), then drier forests may support more lianas than wetter forests. The abundance of small trees clearly varies among tropical forest plots, and its relationship to MAP and DSL is complicated (**Muller-Landau *et al.* 2006**). Pairing liana and tree surveys would help to address the relationships between climate, host availability, and liana density and basal area.

We found a strong positive relationship between DSL and liana density and basal area, but DSL, defined as the number of calendar months with long-term mean rainfall ≤100 mm/yr, may be a poor proxy for soil water availability. The beginning and end of calendar-months are artificial endpoints, and months vary in length, such that the same rainfall regime (*i.e.*, same average rain per day for 365 d in sequence) could produce different DSL simply by shifting which day corresponds to 1 January. In addition, plants growing in sites with similar dry season lengths but on soils differing in water-holding capacity do not experience the same levels of drought stress (**Engelbrecht *et al.* 2007**) because plants on low water holding-capacity soils experience drought conditions more quickly. Thus, the same DSL value in different sites may affect plants to different degrees depending on local site conditions (*e.g.*, topography, soils, winds) and distribution of rainfall during the year. Nonetheless, our results suggest that seasonality of rainfall, even if measured with DSL, is an important climatic variable needed to understand the global distribution of lianas.

Does MAP or DSL have a greater effect on liana abundance and basal area in the tropics? Models with DSL explained more of the variance (*i.e.*, had higher R^2) than those with MAP, suggesting that DSL may be a better predictor of liana density and basal area. Indeed, even with the limitations pointed out above, DSL may better

reflect the degree to which plants experience water stress. Most tropical forests have sufficient water during the wet season, so more or less rainfall during the wet season likely will not affect water availability (*i.e*., MAP can vary without changing plant water stress). However, the length of the dry season directly determines the duration of water limitation. Because MAP and DSL were highly correlated in our study, we would need more sites with high rainfall and high seasonality, *i.e*., >2000   mm/yr and >4 consecutive dry months (*e.g*., tropical monsoon forests) to separate their relative effects. In our dataset, only the Ebom site in Cameroon experiences high rainfall and high seasonality (2035   mm/yr and 5 dry mo during two dry seasons). Adding liana surveys in tropical forests that receive both high rainfall and high seasonality may help determine which factor has a greater effect on liana abundance and basal area.

Biogeographical patterns in liana distribution.— In our study, Neotropical forests harbored more lianas than Paleotropical forests, yet we do not believe that our data are robust enough to definitively claim that lianas are systematically more abundant in Neotropical forests than in Paleotropical forests. Our samples in the Neotropics were from a drier subset of the rainfall spectrum (1500–4725   mm/yr) than our samples in the Paleotropics (860–7250   mm/yr). Thus, in the Neotropics, we lacked very wet sites, such as the Choco area of Colombia, which would be predicted to have very low liana density and basal area. To compare liana abundance and basal area among biogeographical regions properly, more liana surveys need to be conducted across the Americas, Asia, and Africa with enough sites to represent the full range in climatic conditions present in each region (for such a comparison of tree diversity between Amazonia and Africa see **Parmentier *et al.* 2007**).

Conclusion.— We tested the relationship between MAP and DSL using the largest available dataset in terms of area sampled and found strong support for the hypotheses that liana density and basal area decrease with increasing rainfall and increase with increasing seasonality of rainfall. The number of sites included in our study (24) was relatively small compared with the Gentry dataset (**Phillips & Miller 2002**), but our study sites spanned a large range of rainfall and seasonality and represented all continents with tropical forest, with the exception of Australia. Our results suggest that lianas are most successful in drier tropical forests. Unexplained variation in liana abundance and basal area among sites may be attributed to other environmental factors such as differences in soils, drainage, and topography (**Proctor *et al.* 1983, Putz & Chai 1987, Gentry 1991, Laurance *et al.* 2001, Ibarra-Manríquez & Martínez-Ramos 2002, DeWalt & Chave 2004, DeWalt *et al.* 2006**); availability of suitable hosts (trellises) caused by differences in tree composition or size (**Putz 1984, Balfour & Bond 1993, Campbell & Newbery 1993**); rates and extents of large-scale disturbances, such as hurricanes (**Quigley & Platt 2003, Rice *et al.* 2004, Garrido-Pérez *et al.* 2008**); rates and extents of small-scale disturbances, such as treefall gaps (**Putz 1984, Putz & Chai 1987, Schnitzer *et al.* 2000, Schnitzer & Carson 2001**); and sampling error. Nonetheless, it appears that the liana density and basal area in a particular tropical site are strongly related to the relatively simple metrics of MAP and DSL.

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