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Abstract

Lianas reduce tree growth, reproduction, and survival in tropical forests. Liana competition can be particularly intense in isolated forest fragments, where liana densities are high, and thus, host tree infestation is common. Furthermore, lianas appear to grow particularly well during seasonal drought, when they may compete particularly intensely with trees. Few studies, however, have experimentally quantified the seasonal effects of liana competition on multiple tree species in tropical forests. We used a liana removal experiment in a forest fragment in southeastern Brazil to test whether the effects of lianas on tree growth vary with season and tree species identity. We conducted monthly diameter measurements using dendrometer bands on 88 individuals of five tree species for 24 months. We found that lianas had a stronger negative effect on some tree species during the wet season compared to the dry season. Furthermore, lianas significantly reduced the diameter growth of two tree species but had no effect on the other three tree species. The strong negative effect of lianas on some trees, particularly during the wet season, indicates that the effect of lianas on trees varies both seasonally and with tree species identity.

1 INTRODUCTION

Tropical lianas commonly proliferate following disturbance, and they are found in high densities in treefall gaps, young secondary forests, and forest fragments (Farah et al., **2014**; Lobo, Leao, Melo, Santos, & Tabarelli, **2011**; Schnitzer, **2018**; Schnitzer, Dalling, & Carson, **2000**). When in high densities, lianas can compete intensely with trees, reducing tree growth, reproduction, and diversity (García-León et al., **2018**; Schnitzer & Carson, **2010**; Toledo-Aceves, **2015**). Lianas can hinder tree regeneration due to excess weight or competition for resources, and in extreme cases, lianas can arrest succession leading to liana-dominated forests (Schnitzer et al., **2000**; Martínez-Izquierdo et al., **2016**; Tymen et al., **2016**). The reduction in tree growth and survival due to liana competition reduces forest-wide carbon accumulation and may result in future changes in forest structure and composition (Farah et al., **2014**; van der Heijden, Powers, & Schnitzer, **2015**; Schnitzer, Heijden, Mascaro, & Carson, **2014**).

Lianas appear to grow particularly well during seasonal drought (Schnitzer, **2005**; Schnitzer & van der Heijden, **2019**), which may lead to stronger competition for limited resources, particularly water. By contrast, trees grow more during the wet season (Schnitzer & van der Heijden, **2019**), when competition from lianas may actually have a larger negative effect on tree growth (van der Heijden, Powers, & Schnitzer, **2019**). However, the season in which lianas exert stronger negative effects on trees is poorly understood. Determining the seasonal effects of lianas on tree growth is particularly important because extreme climatic events, such as longer droughts, are increasing in frequency (Cai, Schnitzer, & Bongers, **2009**; DeWalt et al., **2010**; Schnitzer & Bongers, **2011**).

Lianas may also influence tree community composition by competing more intensely with some tree species than others. The differential response of tree species to liana competition may alter community composition by disadvantaging the tree species that suffer more from liana competition (Schnitzer, **2018**). Currently, it is unclear whether some tree species suffer more than others from liana competition. Some studies have argued that shade-tolerant and slow-growing tree species are more prone to liana infestation, and thus, lianas have a greater negative effect on those species (Clark & Clark, **1990**; Putz **1984a**, **1984b**, **1980**; Schnitzer et al., **2000**). Other studies have shown greater negative impacts of lianas on light-demanding and fast growth tree species than shade-tolerant and slow growth species (e.g., Visser, Muller-Landau, et al., **2018**; Visser, Schnitzer, et al., **2018**). And yet other studies have argued that all tree species respond similarly to liana competition (Alvarez-Cansino, Schnitzer, Reid, & Powers, **2015**; Martínez-Izquierdo, García, Powers, & Schnitzer, **2016**). Thus, whether different tree species differ significantly in their response to liana competition remains contentious.

Forest fragments are becoming a common forest type in the tropics and subtropics, such as the Brazilian Atlantic forest, where lianas can be particularly abundant (Turner & T Corlett **1996**; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, **2009**), and trees regenerating may be particularly vulnerable to liana infestation (Barry, Schnitzer, Breugel, & Hall, **2015**; Putz **1984a**, **1984b**; Schnitzer et al., **2000**). Despite the observed negative effects of lianas on tree performance (e.g., Alvarez-Cansino et al., **2015**; Schnitzer & Carson, **2010**; Toledo-Aceves, **2015**; García León et al., **2018**), there are little empirical data showing that lianas have a stronger negative effect with changing abiotic conditions (e.g., seasonally; van der Heijden et al., **2019**). Here, we used a 2-year liana removal experiment (September 2012 to September 2014) to evaluate the effect of lianas on the growth of host trees in a forest fragment in Southeastern Brazil. We addressed two main questions: (a) Does the effect of lianas on tree growth vary seasonally? (b) Does the effect of lianas on tree growth vary with tree species identity? Considering that in 2013/2014, Sao Paulo state experienced the strongest drought since recording started in 1961 (Coelho, Cardoso, & Firpo, **2016**), we also addressed the questions: (c) Does the effect of lianas on tree growth increase with extreme drought? and (d) Which climatic variables are correlated with tree growth after liana removal?

2 METHODS

2.1 Study area

We conducted this study in a 14-ha semideciduous seasonal forest fragment located in Piracicaba county, southeast Brazil (22°42′S, 47°37′W, 546 m a.s.l.). The region has a mean annual temperature of 20.5°C, with mean warmest and coldest months temperature of 23.3 and 16.7°C, respectively (Alvares, Stape, Sentelhas, Goncalves, & Sparovek, **2013**). Mean annual rainfall is 1,281 mm, with 50% falling between December and January (Figure **S1**). According to Köppen's classification, the region supports humid subtropical forest (Cfa). The study site was located in an agricultural–urban landscape that historically has been exposed to degradation such as logging, recurrent incursions by cattle, and fire. The most recent fire was in 1981, 32 years before the study (Venegas-Gonzalez, Arx, Chagas, & Tomazello Filho, **2015**). The forest fragment is extremely liana dense (~4,200 lianas >1 cm diam per ha, César et al., **2016**; cf. Schnitzer et al., **2012**), and it lacks a continuous canopy throughout most of the fragment. The tree community is a mix of early and late successional species (César et al., **2016**).

2.2 Tree species selection and growth evaluation

We installed dendrometer bands on 15–20 individuals of five tree species that were >7 cm in diameter at breast height (Table **1**). Initially, in year 1, we installed 50 dendrometer bands in 10 individuals per species. In the second year, we added another 40 dendrometers to the trees (88 total individuals total; 2 trees died during the second year). The target trees had similar diameters (standard deviation <4.5 cm) and heights (Table **1**). The minimum distance among trees within each treatment was five meters. We selected the tree species that were relatively abundant and thus provided enough replication. All individuals selected were located within the core area of the forest fragment and exposed to similar levels of liana infestation. The species selected were as follows: *Ceiba speciosa* (A. St.-Hil.) Ravenna; *Piptadenia gonoacantha* (Mart.) J.F. Macbr.; *Aloysia virgata* (Ruiz & Pav.) Juss*.*; *Bauhinia forficata* Benth.; and *Trichilia clausseni* C. DC.

Table 1. Characteristics of the five tree species and number of individuals per year (year 2 include trees of year 1) used in the experiment, with their respective average diameter at breast height (DBH), total height, and ecological classification

Species	Treatment	No. trees		Classification	DBH (±*SD*)	Height

		Year 1	Year 2			
Aloysia virgata—Av (Verbenaceae)	LR	5	10	NCT	12.6 (3.3)	<10 m
	NLR	5	10		10.1 (2.7)	<10 m
Bauhinia forficata—Bf (Fabaceae)	LR	5	10	NCT	11.0 (2.6)	<10 m
	NLR	5	10		8.7 (2.4)	<10 m
Ceiba speciosa—Cs (Malvaceae)	LR	5	7	CT	11.0 (4.0)	>10 m
	NLR	5	10		9.0 (1.3)	>10 m
Piptadenia gonoacantha—Pg (Fabaceae)	LR	5	9	CT	11.5 (4.5)	>10 m
	NLR	5	8		9.7 (2.4)	>10 m
Trichilia claussenii—Tc (Meliaceae)	LR	5	9	NCT	12.9 (5.1)	<10 m
	NLR	5	5		12.2 (4.4)	<10 m

Abbreviations: CT, canopy trees; DBH (Sd), diameter at breast height (standard deviation) in cm; LR, trees with liana removal; NCT, non-canopy trees; NLR, trees with non-liana removal.

The dendrometer bands were made of stainless steel ribbons (12.7 × 0.15 mm, width and thickness, respectively) with 0.2 mm precision (Botosso & Tomazello Filho, **2001**). For half of the individuals of each tree species, we cut all lianas within a 10 m radius (methods follow Tobin, Wright, Mangan, & Schnitzer, **2012**; Wright, Tobin, Mangan, & Schnitzer, **2015**). We measured tree growth monthly for 24 months, starting in September 2012. Initially, we installed 10 dendrometer bands for each species, 5 for trees in the liana removal treatment (LR) and 5 for controls (NLR). In September 2013, we added dendrometer bands to 40 additional individuals of the five-target species. We quantified the change in stem diameter based on the initial diameter of each tree individual. The total mean relative growth was calculated as a percentage of the initial size for tree species with liana removals (LR) and controls (NLR)(Mello et al., **2020**).

2.3 Data analysis

To test our first two questions, whether the effects of lianas on tree growth varies with season and species identity, we used a linear mixed model. We classified the wet season as the period with rain >100 mm per month (October to March) and the dry season as the period with <50 mm per month (June to August). The months with intermittent precipitation in between the dry and wet seasons (50–100 mm per month) were considered as a transitional season (Figure **S1**; Álvarez-Cansino et al., **2015**). We used the annualized monthly mean relative growth as our response variable, that was obtained by multiplying the 3-month season data by 4 and the 6-month season data by 2 (e.g., Schnitzer & van der Heijden, **2019**). We used treatment type (removal vs. control), season (wet, transition and dry), species (5 species), and interactions among variables as fixed factors and included year (2 years) and tree individuals (88 trees) nested on species (5 species) as random factors (Table **2**). We selected the random factors to take into account the temporal variability of years with contrasting climate and the multiple measurements of individuals per species.

Table 2. Results of the log likelihood ratio test for the linear mixed model with treatment, season, species, and interactions as fixed factors and year and individuals nested on species as random factors

Fixed effect	*df*	χ^2	Pr ($>\chi^2$)
Treatment	1	16.9893	<0.0001
Season	2	77.4950	<0.0001
Species	4	13.5832	<0.008
Treatment × season	2	6.7836	0.0336
Treatment × species	4	11.3494	0.022905

Season × species	8	10.1070	0.257594

Note: We used the annualized monthly mean relative growth for the five host species studied. Treatment was the liana removal manipulation versus control, seasons were dry, transition, and wet, and species were the five species describe in Table 1.

To test our third question, whether the effect of lianas on tree species growth varies with extreme drought, we used the tree accumulated relative growth per year as the response variable and included treatment type (removal vs. control), species (5 species), and year (normal and reduced precipitation) as fixed factors, as well as the interactions among the variables (Table **3**). We used tree individuals (88 individuals) nested on species (5 species) as random factors to account for possible spatial autocorrelation.

Table 3. Results of the log likelihood ratio test for the linear mixed model with year, treatment, species, and interactions as fixed factors and individuals nested on species as random factors

Fixed effect	*df*	χ^2	Pr ($>\chi^2$)
Treatment	1	10.9046	0.001
Year	1	12.9653	0.0003
Species	4	29.9693	<0.008
Treatment × year	1	0.487	0.485
Treatment × species	4	9.8163	0.043
Year × species	4	2.8775	0.578

Note: We used the yearly accumulated relative growth data for the five tree species studied. Treatment was the liana removal manipulation versus control, years were year 1 and year 2, and species were the five species described in Table 1.

We present a table with the values of the log likelihood ratio tests for the models. To fit the models, we log-transformed the response variables to normalize the residuals and used the function lmer() from the package *lme4*, software R (R Core Team **2017**). We present the β estimates of growth and the 95% interval confidence for the effects of treatment to control per species and year. We calculated the β estimates of growth per season excluding species from the fixed factors to allow generalization of the results. We adjusted the confidence interval based on Bonferroni correction with 98.3% CI for three post hoc comparisons.

Finally, to test out last question, whether climatic variables are correlated with tree growth after liana removal, we used generalized additive models (GAMs) to describe the effects of the climate variables precipitation, relative humidity, average temperature—Max and Min—and evapotranspiration on tree monthly relative growth. We used the package *mgcv* for GAM models in R (Wood, **2011**). Climatic data sets were obtained from a weather station located 250 m from the study area.

3 RESULTS

3.1 Effect of liana removal on tree growth

The presence of lianas in the control trees substantially limited tree diameter growth compared to trees where lianas were removed (Mean annual relative growth LR treatment = 4.51 ± 0.73, controls = 1.85 ± 0.23). After 12 months, the mean tree relative growth was 304% higher for trees with lianas removed (mean annual relative growth during year 1 LR treatment = 7.6 ± 1.8, controls = 2.5 ± 0.53). The difference in mean tree relative growth between LR and controls was 192% by the end of the second year (mean annual relative growth during year 2 LR treatment = 2.81 ± 0.42, controls = 1.46 ± 0.18. Figure **1**). Two tree species, *Ceiba speciosa* and *Piptadenia gonoacantha*, responded the strongest to liana removal compared to the other three species (mean annual

relative growth for *Ceiba speciosa* LR treatment = 8.2 ± 2.1, controls = 1.7 ± 0.5; mean annual relative growth for *Piptadenia gonoacantha* LR treatment = 7.6 ± 1.8, controls = 2.5 ± 0.53).
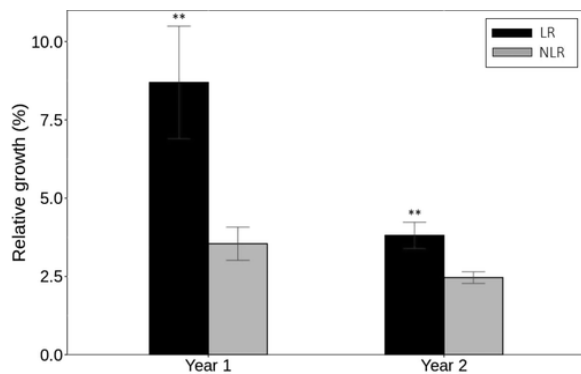

Figure 1. The total mean relative growth for all tree species as a percentage of the initial diameter size of the five tree species with liana removal (LR) and non-liana removal (NLR) in the forest fragment for year 1 and year 2 of the experiment. Sample size for the first year was LR: N = 24 and NLR: N = 24 and for the second year was LR: N = 45 and NLR: N = 43. Asterisks denote significant differences between treatments (*p < .05 and **p < .01)

3.2 Effect of liana removal by tree species and season

The interaction between season and treatment (df = 2, χ^2 = 6.516, p < .038, Table **2**) revealed a stronger effect of liana removal during the wet season (mean monthly relative growth LR treatment = 0.53 ± 0.05, controls = 0.22 ± 0.02; β_{t-c} = −0.14; 98.3% CI = 0.09, 0.21) compared to the transition (mean monthly relative growth LR treatment = 0.27 ± 0.05, controls = 0.11 ± 0.02; β_{t-c} = −0.076; 98.3% CI = −0.0005, 0.16) and dry seasons (Mean monthly relative growth LR treatment = 0.19 ± 0.03, controls = 0.07 ± 0.01; β_{t-c} = −0.076; 98.3% CI = −0.012, 0.16, Figure **2**). Moreover, the interaction between treatment and species (df = 4, χ^2 = 11.3494, p < .023, Table **2**) revealed a species-specific growth response of trees to the liana removal treatment. The species *C. speciosa* had a stronger response to liana removal during the wet season (mean monthly relative growth during wet season *Ceiba speciosa* LR treatment = 1.1 ± 0.2, controls = 0.2 ± 0.07; β_{t-c} = −0.3; 95% CI = −0.4, −0.15) compared to the transition (mean monthly relative growth during transition *Ceiba speciosa* LR treatment = 0.4 ± 0.1, controls = 0.1 ± 0.03; β_{t-c} = −0.21; 95% CI = −0.33, −0.08) and dry season (mean monthly relative growth during dry season *Ceiba speciosa* LR treatment = 0.2 ± 0.08, controls = 0.07 ± 0.04; β_{t-c} = −0.2; 95% CI = −0.32, −0.07, Figure **3**). In contrast, the species *P. gonoacantha* had a strong response to liana removal during all seasons—wet season (mean monthly relative growth during wet season *Piptadenia gonoacantha* LR treatment = 0.9 ± 0.1, controls = 0.4 ± 0.06; β_{t-c} = −0.24; 95% CI = −0.35, −0.12); transition (mean monthly relative growth during transition *Piptadenia gonoacantha* LR treatment = 0.8 ± 0.2, controls = 0.1 ± 0.04; β_{t-c} = −0.17; 95% CI = −0.29, −0.04); and dry season (mean monthly relative growth during dry season *Piptadenia gonoacantha* LR treatment = 0.5 ± 0.1, controls = 0.1 ± 0.03; β_{t-c} = −0.16; 95% CI = −0.28, −0.03). Tree growth of *Aloysia virgata, Bauhinia forficata,* and *Trichilia clausseni* did not respond to liana removal in either season (Figure **3**).
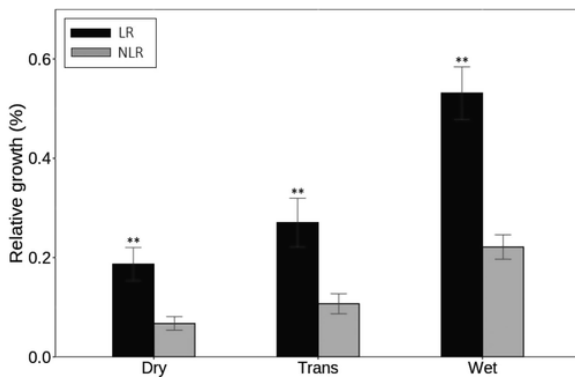
Figure 2. The total monthly mean relative growth of the tree species with liana removal (LR) and non-liana removal (NLR) in the forest fragment by season (dry: June to August; transition: April, May, and September; wet: October to March). Sample size for the first year was LR: N = 24 and NLR: N = 24 and for the second year was LR: N = 45 and NLR: N = 43. Asterisks denote significant differences between treatments (*p < .05 and **p < .01)
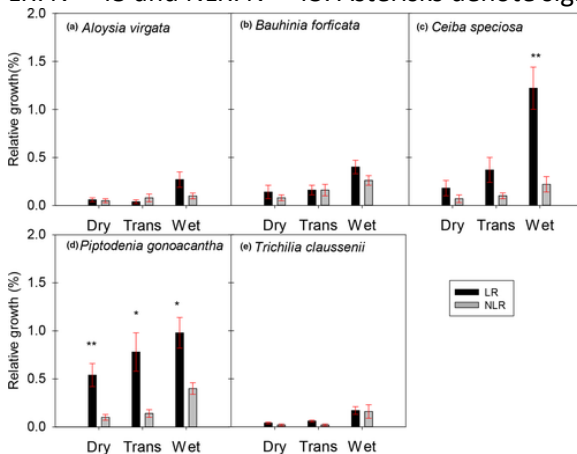

Figure 3. The monthly mean relative growth of species by season (dry: June to August; transition: April, May, and September; wet: October to March) of the five replicated tree species with liana removal (LR) and non-liana removal (NLR) in the forest fragment. The species are (a) *Aloysia virgata*, sample size N: LR = 10 and NLR = 10; (b) *Bauhinia forficata*, sample size N: LR = 10 and NLR = 10; (c) *Ceiba speciosa*, sample size N: LR = 7 and NLR = 10; (d) *Piptadenia gonoacantha*, sample size N: LR = 9 and NLR = 8; and (e) *Trichilia claussenii*, sample size N: LR = 9 and NLR = 5. Asterisks denote significant differences between treatments (*p < .05 and **p < .01)

3.3 Effect of liana removal by tree species and year

Tree growth was higher during the normal year compared to the extreme drought year; however, the non-significant interaction between treatment and year suggests no differences in the effect of liana removal on tree growth per year (df = 1, χ^2 = 0.487, p < .485, Table **3**; Figure **1**). In contrast, the per year model showed significant interaction between tree species and treatment, suggesting a species-specific response of tree growth to liana removal per year (df = 4, χ^2 = 9.8163, p < .043, Table **3**). The species *C. speciosa* had an increased diametric growth in the LR treatment compared to the control in both years (mean annual relative growth for *Ceiba speciosa* during year 1 LR treatment = 12.6 ± 4.4, controls = 2.3 ± 1.3, $\beta_{Year\ 1\ t\text{-}c}$ = −2, 95% CI = −2.9, −0.99; and year 2 LR treatment = 5.2 ± 1.1, controls = 1.4 ± 0.3, $\beta_{Year\ 2\ t\text{-}c}$ = −1.77, 95% CI = −2.7, −0.8), while *P. gonoacantha* responded the strongest during the year 1 compared to year 2 (mean annual relative growth for *Piptadenia gonoacantha* during year 1 in LR treatment = 19.8 ± 3.7, controls = 3.8 ± 1.7, $\beta_{Year\ 1\ t\text{-}c}$ = −1.02, 95% CI = −2.03, −0.012; and year 2 in LR treatment = 4.3 ± 1.1, controls = 2.3 ± 0.4, $\beta_{Year\ 2\ t\text{-}c}$ = −0.8, 95% CI = −1.73, 0.13. Figure **4**; Figure **S1**). Diametric growth of the tree species *Aloysia virgata*, *Bauhinia forficata*, and *Trichilia clausseni* did not increase following liana removal in either year (Figure **4**; Figure **S1**). Overall, all

species had a reduced diametric growth during the extreme drought year compared to the first year (β_{t-c} = −1.02; 95% CI = −1.76, −0.27; Figure **4**).
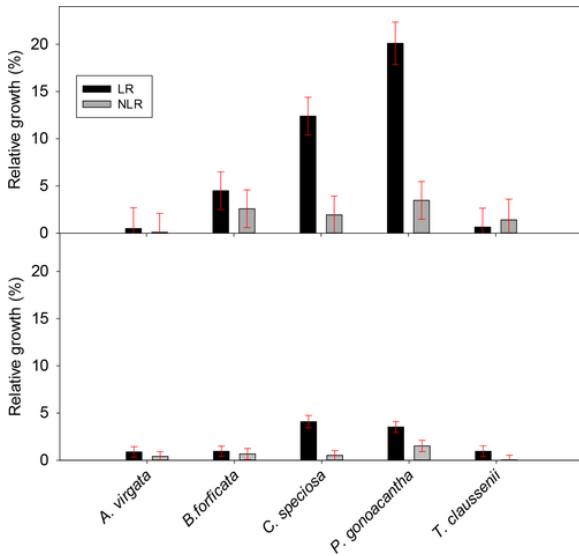

Figure 4. The total mean relative growth per species as a percentage of the initial diameter size of the five replicated tree species with liana removal (LR) and non-liana removal (NLR) in the forest fragment. Panel "a" represents the first year after the liana removal treatment. Panel "b" represents the second year after the liana removal treatment. Species are *Aloysia virgata*, sample size N: LR = 10 and NLR = 10; *Bauhinia forficata*, sample size N: LR = 10 and NLR = 10; *Ceiba speciosa*, sample size N: LR = 7 and NLR = 10; *Piptadenia gonoacantha*, sample size N: LR = 9 and NLR = 8; and *Trichilia claussenii*, sample size N: LR = 9 and NLR = 5. Asterisks denote significant differences between treatments (*p < .05 and **p < .01)

3.4 Influence of climatic variables on tree growth after liana removal treatment

According to the GAM models, some tree species with liana removal had diametric growth significantly associated with climatic variables in both the normal year (year 1: October 2012–September 2013) and the extreme drought year (year 2: October 2013–September 2014, Table **4**). We found a high percentage of variance (R^2adj) and deviance explained (%Dev) by climatic variables for four tree species, with significant values for two species during the year one of the experiment and significant values for the other two species during the year 2 of the experiment (extreme drought year—Table **4**). The species *A. virgata* and *C. speciosa* had the highest values of R^2adj (>0.65) and %Dev (>83.6) during the year 1, while *P. gonoacantha* and *T. clausenii* had the highest values of R^2adj (>0.76) and %Dev (>88.9) during the second year. Rainfall and humidity were correlated with tree growth after lianas removal during both years, being rainfall positively correlated with growth in *A. virgata*, *P. gonoacantha,* and *T. clausenii*, while humidity was positively correlated with growth in *C. speciosa* (Figure **S3**). All climatic variables had a large non-linear adjustment for the species *T. clausenii* with a particularly strong correlation with the climatic variable maximum temperature and humidity (p < .01). We did not find significant correlation between tree growth and climatic variables in the species *B. forficata*.

Table 4. General additive model (GAM) for monthly growth of trees with liana removal as function of climatic variables (maximum and minimum temperature, rainfall, humidity, and evapotranspiration)

Climatic variables	Av		Bf		Cs		Pg		Tc	
	EDF	F	EDF	F	EDF	F	EDF	F	EDF	F
Year 1										
T_{max}	1.49	1.65	1.00	0.41	1.00	3.85	1.82	2.58	1.49	0.77
T_{min}	1.00	2.01	1.00	0.27	1.00	0.75	1.00	0.01	1.62	0.44

	EDF	F	EDF	F	EDF	F	EDF	F	EDF	F
Rainfall	**1.88**	**11.1*****	1.00	0.58	1.00	3.99	1.00	0.69	1.00	0.68
Humidity	**1.00**	**8.95****	1.00	0.19	**1.88**	**8.52****	1.00	1.15	1.00	2.51
Evapotranspiration	1.00	3.28	1.00	0.94	1.00	1.33	1.00	0.72	1.00	0.42
(R^2adj)	.77		.42		.65		.42		−.02	
%Dev	88.7		67.3		83.6		72.7		50	
Year 2										
T_{max}	1.00	2.82	1.00	1.36	1.00	0.58	1.00	0.99	**1.98**	**24.8*****
T_{min}	1.00	1.78	1.00	0.09	1.00	0.28	1.48	0.60	**1.00**	**14.4***
Rainfall	1.00	2.39	1.00	1.59	1.00	1.53	**1.00**	**7.63****	**1.00**	**15.5***
Humidity	1.23	0.31	1.00	0.86	1.00	1.37	**1.00**	**26.3*****	**1.86**	**29.5*****
Evapotranspiration	1.00	3.17	1.00	1.10	1.00	0.31	1.00	0.15	**1.92**	**6.08***
(R^2adj)	.24		−.27		−.22		.76		.90	
%Dev	60.5		30.5		33.5		88.9		97.3	

Note. The approximate significance of smooth terms is reported, with estimated degrees of freedom (EDF), F statistics (and significant p values, $*p < .1$, $**p < .05$, $***p < .01$). The percentage of variance explained by climatic variables is given by the adjusted coefficient of determination (R^2adj) and deviance explained (%Dev).

4 DISCUSSION

Our finding that lianas substantially reduced tree diameter growth is consistent with other liana removal studies (reviewed by Estrada-Villegas & Schnitzer, **2018**; Toledo-Aceves, **2015**). We found that the effect of lianas on tree growth varied with species identity, where two tree species were much more sensitive to liana infestation than the other three species. Our findings are consistent with studies that found that lianas had a varying effect on different tree species (e.g., Putz **1984a**, **1984b**; Visser, Schnitzer, et al., **2018**; Wright et al., **2015**). By contrast, other studies have concluded that lianas generally have a negative effect on the growth and survival of all species. For example, in a liana removal experiment in central Panama, Martínez-Izquierdo et al. (**2016**) reported that lianas had a similar negative effect on the seedlings of all 14 tree species examined. In the same experiment, Alvarez-Cansino et al. (**2015**) reported that lianas had a similar negative effect on sap velocity and diameter growth of adults of seven canopy tree species.

The species with statistically significant diameter growth in our study are tree species that reach greater heights in the forest when compared to the other three species analyzed. For instance, *P. gonoacantha* and *C. speciosa* are both canopy trees, reaching heights of up to 20 and 30 meters, respectively (Lorenzi, **1992**). Lianas seek light by climbing into the canopy of sun-exposed trees, intercepting light, and ultimately hindering canopy tree growth and carbon storage (Mohandass, Davidar, Somasundaram, Vijayan, & Beng, **2015**; Schnitzer et al., **2014**). Botosso, Filho, Maria, & Ferreira-Fedele, (**2005**) found that lianas reduced the diametric growth of the tall canopy tree *Centrolobium tomentosum*, a species that can reach heights up to 35 m in semideciduous seasonal forests of Southeastern Brazil. In addition, dendrochronological studies in forest fragments have verified the decrease of canopy tree diameter growth following liana infestation (Godoy-Veiga et al., **2018**; Venegas-González et al., **2017**).

The lack of response to liana cutting from the non-canopy trees *T. clausseni*, *A. virgata*, and *B. forficata* could be explained by their location in the forest understory. Since lianas tend to deploy the majority of their leaves above the forest canopy (Rodríguez-Ronderos et al., **2016**), they would naturally have a much smaller effect on understory trees than on canopy trees. Indeed, using a large-scale experimental approach in a secondary forest in Panama, García León et al. (**2018**) found that lianas substantially reduced canopy tree reproduction, but not understory tree reproduction. Alternatively, the lack of response to liana cutting from non-canopy trees could

also be explained by the generally slower growth rate of more shade-tolerant understory trees, thus reducing our ability to detect a growth response within the 2-year study period.

Trees grow more during periods of high water availability, as demonstrated by the correlations of tree growth with high humidity and rainfall, and thus, they respond more to liana removal during these periods of high growth (van der Heijden et al., **2019**; Schnitzer & van der Heijden, **2019**). Unusually, low rainfall (<100 mm) during the wet season in year 2 of the study (February 2013) limited tree growth response during that year, which likely dampened the negative effects of lianas on tree growth (Figure **4**).

The effect of lianas may have been greatest for *C. speciosa* during the wet season because trees were most actively growing during this season. During the dry season, *C. speciosa* often shed their leaves and may decrease their growth, thus reducing the effect of liana competition. The non-deciduous species *P. gonoacantha* had the strongest growth during the wet season, although the effect of lianas on *P. gonoacantha* was similar for all the three seasons. In a study at the community level, van der Heijden et al. (**2019**) found that the effect of lianas on the tree community of a moist forest in Panama was similar during the wet and dry seasons (see also Schnitzer & van der Heijden, **2019**). The similar effect of lianas on *P. gonoacantha* growth across seasons compared to *C. speciosa* may suggest stronger competition by lianas on non-deciduous trees during water limiting periods.

The results from previous liana removal experiments have shown that the intense negative effect of lianas on trees should be considered when developing management recommendations for liana-dominated forests (César et al., **2016**; Estrada-Villegas & Schnitzer, **2018**; Marshall et al., **2017**; Sfair et al., **2015**; Viani, Mello, Chi, & Brancalion, **2015**). The use of liana removal for the management of forest fragments can increase tree diameter growth and carbon storage (van der Heijden et al., **2015**). Our findings indicate that lianas have an intense negative effect on tree growth in a forest fragment; however, the response of tree growth to liana removal might differ in forest fragments with distinct characteristics. Lianas are also important in the provision of resources for fauna (Adams et al., **2017**, **2019**); Morellato & Leitao, **1996**; Yanoviak & Schnitzer, **2013**), and thus, more studies are necessary to evaluate the impacts of liana removal on several forest fragments as well as on other forest community attributes before large-scale liana removal can be recommended as a viable forest management strategy (Arroyo-Rodríguez, Asensio, Dunn, Cristóbal-Azkarate, & Gonzalez-Zamora, **2015**; Restom & Nepstad, **2001**).

In summary, this study demonstrates that the negative effect of lianas on trees varies with tree species identity and may be particularly strong on tall canopy species when compared to understory trees. Furthermore, lianas compete with trees most during the wet season, when trees are particularly photosynthetically active, and have a much more muted effect during the dry season, when trees have lower activity and lianas are more active (van der Heijden et al., **2019**; Schnitzer & van der Heijden, **2019**). The recent increases in liana density and biomass in neotropical forests (Schnitzer & Bongers, **2011**) may result in even greater competition between lianas and trees, which will likely be most intense during the wet season.

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