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Abstract

Recent studies indicate that lianas are increasing in size and abundance relative to trees in neotropical forests. As a result, forest dynamics and carbon balance may be altered through liana-induced suppression of tree

growth and increases in tree mortality. Increasing atmospheric CO_2 is hypothesized to be responsible for the increase in neotropical lianas, yet no study has directly compared the relative response of tropical lianas and trees to elevated CO_2. We explicitly tested whether tropical lianas had a larger response to elevated CO_2 than co-occurring tropical trees and whether seasonal drought alters the response of either growth form. In two experiments conducted in central Panama, one spanning both wet and dry seasons and one restricted to the dry season, we grew liana (n = 12) and tree (n = 10) species in open-top growth chambers maintained at ambient or twice-ambient CO_2 levels. Seedlings of eight individuals (four lianas, four trees) were grown in the ground in each chamber for at least 3 months during each season. We found that both liana and tree seedlings had a significant and positive response to elevated CO_2 (in biomass, leaf area, leaf mass per area, and photosynthesis), but that the relative response to elevated CO_2 for all variables was not significantly greater for lianas than trees regardless of the season. The lack of differences in the relative response between growth forms does not support the hypothesis that elevated CO_2 is responsible for increasing liana size and abundance across the neotropics.

Introduction

Lianas (woody vines) are increasing in size and abundance relative to trees throughout neotropical forests (Schnitzer & Bongers, **2011**; Schnitzer *et al*., **2012**; Yorke *et al*., **2013**; Laurance *et al*., **2014**). Reported annual increases in liana abundance range from 0.23% to 7.8% over recent decades, whereas trees either underwent smaller annual increases or have declined in abundance in the same study areas (Phillips *et al*., **2002**; Chave *et al*., **2008**; Enquist & Enquist, **2011**; Schnitzer *et al*., **2012**). Liana seedling recruitment, reproduction, and leaf productivity have also increased relative to trees (Wright *et al*., **2004**; Wright & Calderon, **2006**; Benitez-Malvido & Martínez-Ramos, **2003**).

The reported increases in liana abundance have broad implications for the global carbon cycle because tropical forests account for the single largest terrestrial share (60%) of annual global carbon dioxide uptake (Pan *et al*., **2011**). The negative effect that lianas exert on tree growth, reproduction, and lifespan, combined with their very low contribution to forest biomass, suggests a future in which neotropical forests will absorb and store less atmospheric carbon dioxide annually (van der Heijden *et al*., **2013**; Schnitzer *et al*., **2015**). Lianas commonly comprise a large proportion of the woody species and stem number in tropical forests (Schnitzer *et al*., **2012**, **2015**); however, lianas constitute a small proportion of total tropical forest biomass (Putz, **1983**; Gerwing & Farias, **2000**; DeWalt & Chave, **2004**; Letcher & Chazdon, **2009**). Nevertheless, lianas have a disproportionately large negative effect on tree biomass accumulation by reducing tree diameter increment (Lowe & Walker, **1977**; Whigham, **1984**; Clark & Clark, **1990**; Grauel & Putz, **2004**; van der Heijden & Phillips, **2009**; Schnitzer *et al*., **2015**), leaf productivity (Dillenburg *et al*., **1993**; Perez-Salicrup *et al*., **2001**; Toledo-Aceves & Swaine, **2008**), sap flow velocity (Tobin *et al*., **2012**; Alvarez-Cansino *et al*., in press), and stem height (Perez-Salicrup, **2001**). Lianas also increase tree mortality (Putz, **1984**; Phillips *et al*., **2002**; Garrido-Perez *et al*., **2008**; Ingwell *et al*., **2010**; Schnitzer *et al*., **2015**) and suppress tree regeneration (Toledo-Aceves & Swaine, **2008**; Schnitzer & Carson, **2010**). Depending on the level of infestation, lianas are associated with a 1.6–1.9% excess risk of annual tree mortality (Phillips *et al*., **2002**; Ingwell *et al*., **2010**).

The causes of increasing lianas have not been empirically determined, but the main putative mechanisms include increased intensity of seasonal drought, higher rates of natural and anthropogenic disturbance, and increasing atmospheric CO_2 (Phillips *et al*., **2002**; Schnitzer & Bongers, **2011**). Increasing atmospheric CO_2 is often invoked as the primary cause of increasing lianas (e.g. Phillips *et al*., **2002**) because global atmospheric CO_2 levels have increased 40% since 1750 (IPCC, **2013**), with well over half the increase occurring since 1960 (NOAA, **2013**). Because lianas invest less in structural support, relying instead on trees for access to the high-light environment of forest canopies, their ratio of leaf area to stem or total plant biomass (LAR) is higher than in trees (Zhu &

Cao, **2009**, **2010**; Paul & Yavitt, **2011**). The high LAR of lianas may allow them to take advantage of increases in CO_2 levels to a greater extent than can trees (Schnitzer & Bongers, **2011**). Lianas and trees have similar photosynthetic capacity per unit leaf area (Asner & Martin, **2012**), therefore lianas should gain proportionally more carbon per unit of plant mass due to their relatively greater leaf area. This additional carbon should give lianas an advantage over trees through greater growth and reproduction, leading to increasing liana density, biomass, and productivity relative to trees in tropical forests.

Lianas may have a further advantage over trees under elevated atmospheric CO_2 in forests that experience seasonal drought. Liana abundance peaks in highly seasonal tropical forests (Schnitzer, **2015**; DeWalt *et al*., **2010**), apparently because of their ability to outperform trees during seasonal drought (Schnitzer, **2015**; Cai *et al*., **2009**). Elevated CO_2 may increase the water-use efficiency of plants by reducing stomatal conductance and increasing rates of photosynthesis (Battipaglia *et al*., **2012**; Cernusak *et al*., **2013**), thus allowing more carbon to be fixed per unit water lost through transpiration. Seasonal drought-adapted lianas may increase carbon fixation, and thus water-use efficiency, proportionally more than trees under elevated CO_2 because water-stress or deciduousness may limit carbon gain in many trees during periods of seasonal drought (Schnitzer & Bongers, **2011**).

To date, just three greenhouse studies of lianas provide the evidence for elevated CO_2 as an explanation for increasing liana abundance – none of which compared the response of lianas to trees. Given the technical and logistical constraints of working with adult lianas and trees, these studies test the CO_2 hypothesis at the seedling stage. For example, Granados & Körner (**2002**) found an increase in biomass for three tropical liana species grown under elevated CO_2, but found that the other measured traits did not show a consistent positive response to CO_2. Condon *et al*. (**1992**) reported that two congeneric species of tropical lianas exposed to elevated CO_2 increased in total biomass, leaf area, and height compared with ambient CO_2. Körner & Arnone (**1992**) found neither an aboveground biomass response nor an increase in leaf area index, but instead reported increased root mass under elevated CO_2 for two liana and three tree species. However, the results reported by Körner & Arnone (**1992**) did not compare the responses between the two growth forms. Due to the lack of a direct comparison of lianas and trees to elevated atmospheric CO_2 in the tropics, we are currently unable to conclude that lianas respond more than trees to increased atmospheric CO_2. Moreover, no studies have tested the combined effects of elevated CO_2 and seasonal drought on the performance of co-occurring tropical lianas and trees.

We tested the hypothesis that lianas respond more than trees to elevated atmospheric CO_2 using a phylogenetically diverse set of liana and tree species in common gardens in the Republic of Panama. We examined the growth of seedlings of twelve liana species and ten tree species grown in the ground within open-top chambers maintained at either ambient or elevated CO_2. We included seasonal drought as a factor and examined the response of both growth forms to elevated CO_2 over two studies: one conducted during the dry season only (‘dry-only’) and one conducted during both wet and dry seasons (‘wet-dry’). Specifically, we tested the hypothesis that relative to ambient CO_2: (1) lianas grow more than trees under elevated CO_2, and (2) lianas have an additional growth advantage under elevated CO_2 during seasonal drought.

Materials and methods

Site and species

We conducted the study along a forest edge at the Smithsonian Tropical Research Institute's (STRI) Experimental Outdoor Research Facility at Santa Cruz, Gamboa, in the Republic of Panama (Fig. **1**a). The location was along a secondary forest edge that was previously cleared for residential housing but never developed, and is now managed by STRI. Over the past 7 years, STRI has collected hourly readings of temperature, precipitation, and

full-sun photosynthetically active radiation (PAR) at this site (K. Winter, unpublished data). During the wet season (May–December), the monthly average daytime temperature is 27.9 °C, average monthly precipitation is 244 mm, and average daily total PAR is 25.2 mol m^{-2}. During the dry season (January–April), the monthly average daytime temperature is 29.3 °C, average monthly precipitation is 44 mm, and average daily total PAR is 33.8 mol m^{-2}.

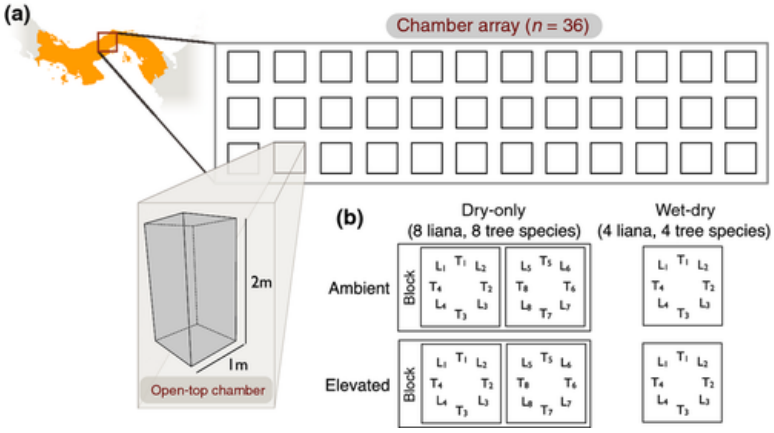

Figure 1. (a) Open-top chamber array location, layout, and dimensions. (b) experimental design and species distribution among CO_2 treatments and chambers for each experiment. L = liana, T = tree; each subscript number represents a distinct species. Species locations within each chamber for both experiments, and between chambers within block for the dry-only experiment, were randomized before planting.

We constructed an array of 36 open-top growth chambers measuring 1 m length × 1 m width × 2 m height, spaced approximately 1.5 m from each other, and wrapped with 90% shade cloth to reduce incoming sunlight and interior temperature. An air delivery system composed of three industrial blower fans attached to plastic plenums (4 m length × 1 m diameter) fed each chamber through 10 cm diameter flexible dryer ducting. Metal duct dampers controlled the ambient airflow rate through the ducting to exchange the air in each chamber once every 2 min (see Appendix S1a for details). Half of the chambers received pure CO_2 regulated through manual flow meters to a level of 780 µmol mol^{-1}. An automated sampling system and infrared gas analyser monitored levels of CO_2 in all elevated and two ambient chambers (see Appendix S1a for details). Sensors inside and outside a subset of chambers monitored temperature, light, and soil volumetric water content (VWC) throughout each experiment (see Appendix S1b for details). At the end of each experiment and after the harvest, we extracted and homogenized four soil samples from the upper 5 cm of each chamber. We analysed each homogenized sample for ammonium, nitrate, and total mineral element concentrations to assess differences in soil composition among the open-top chambers (see Appendix S1b for details). We extracted, dried, and weighed fine root material of resident vegetation growing into the chamber soil (from outside the chamber) from each of the homogenized soil samples. We describe the processing of site abiotic data in more detail in Appendix S2.

We used twelve liana and ten tree species in the two separate experiments reported here (Table **1**). We attempted to select species from among the most common species in central Panama (DeWalt *et al*., **2000**; Hubbell *et al*., **2005**; Schnitzer *et al*., **2012**) and across a range of life-history strategies (Table S1). The availability of fruits, seeds, and seedlings from Barro Colorado Nature Monument forests, and from local reforestation nurseries, also guided species selection. The liana and tree species were from a broad range of neotropical angiosperm families as a representation of the local woody plant community.

Table 1. Species (listed by family) used in the two experiments

Experiment	Lianas		Trees	
	Family	**Species**	**Family**	**Species**
Dry-only	Boraginaceae	*Tournefortia hirsutissima* L.	Apocynaceae	*Lacmelia panamensis*
Dry-only	Celastraceae	*Prionostemma asperum* (Lam.) Miers	Malvaceae	*Paquira quinata (Jacq.)* W.S. Alverson
Dry-only	Connaraceae	*Connarus turczaninowii* Triana	**Combretaceae**	***Terminalia amazonia*** (J.F. Gmel.) Exell
Dry-only	Dilleniaceae	*Davilla kunthii* A. St.-Hil.	Fabaceae (Faboideae)	*Vatairea erythrocarpa* (Ducke) Ducke
Dry-only	Loganiaceae	*Strychnos panamensis* Seem.	Meliaceae	*Cedrela odorata* L.
Dry-only	Malpighiaceae	*Stigmaphyllon lindenianum* A. Juss.	Moraceae	*Brosimum alicastrum* Sw.
Dry-only	Sapindaceae	*Paullinia pinnata* L.	**Rubiaceae**	***Calycophyllum candidissimum*** (Vahl) DC.
Dry-only	Vitaceae	*Vitis tiliifolia* Humb. & Bonpl. ex Schult.	Rubiaceae	*Randia armata* (Sw.) DC.
Wet-dry	Bignoniaceae	*Bignonia corymbosa* (Vent.) L.G. Lohmann	Bignoniaceae	*Tabebuia rosea* (Bertol.) A. DC.
Wet-dry	Connaraceae	*Connarus sp*.	Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken
Wet-dry	Fabaceae (Faboideae)	*Clitoria javitensis* (Kunth) Benth.	**Combretaceae**	***Terminalia amazonia*** (J.F. Gmel.) Exell
Wet-dry	Malpighiaceae	*Stigmaphyllon hypargyreum* Triana & Planch.	**Rubiaceae**	***Calycophyllum candidissimum*** (Vahl) DC.

Species in bold indicate those used in both studies.

Experimental design

We conducted two experiments: a 3-month 'dry-only' experiment starting February 2011, and a 7-month 'wet-dry' season experiment starting September 2011. In both the dry-only and wet-dry season experiments, we transplanted newly germinated seedlings (with at least one fully expanded true leaf and on average 15 cm in height) into the chambers and allowed them to establish for 30 days before starting the CO_2 treatment. As the liana seedlings became non-self-supporting during each experiment, trellises (2 m tall, 1.3 cm diameter bamboo poles) were added 5 cm from the rooting location of the seedling.

The dry-only CO_2 treatment began in late February 2011, 1 month after the end of the wet season that year, and ran for 90 days, until late May. Although the wet season normally starts in early May, the total precipitation during the May portion of the experiment (98 mm) was 48% below the historical average, and we did not detect a difference in soil VWC in the chambers between April and May. In the dry-only experiment, we used a randomized complete block design, in which eight species of lianas and eight species of trees were randomly assigned to one of eight subplots within a pair of chambers (block) with the restriction that four distinct liana and four distinct tree species be in each chamber (Fig. **1**b). Species-level replication was nine individuals per CO_2 treatment, resulting in 72 individuals of each growth form per CO_2 treatment. Due to the small size of the seedlings and high temperatures during the dry-only experiment, we applied supplemental water to maintain daily soil moisture at 30% VWC. For comparison, the average soil moisture in the chambers without supplemental water during the subsequent (2012) dry season was 30% VWC (Table S2).

The wet-dry season CO_2 treatment began in September 2011 and ran until the end of March 2012 (204 days). In this experiment, we used a balanced factorial design, with four species of lianas and four species of trees randomly assigned to the eight subplots within each chamber. Species-level replication was 18 individuals per CO_2 treatment, resulting in 72 individuals of each growth form per CO_2 treatment. We did not use supplemental watering during this experiment. To reduce soil nutrient heterogeneity within the chamber plots, we removed, homogenized, and returned the top 50 cm of soil from all plots. We added up to 5 cm of soil from a nearby site to each growth chamber plot to compensate for soil lost during this process and during the root excavation at the end of the previous experiment. To reduce growth of nearby adult tree roots into the chamber soil and to remove the potentially confounding effects of these roots on the seedlings, we dug, lined with plastic, and backfilled a 75-cm-deep trench around the entire site at a 1 m distance from the chamber array.

Plant measurements

At the beginning of each experiment, we harvested 12–20 extra seedlings per species not used in the experiment and measured the height of the apical bud above soil (cm), diameter at 5 cm height (mm), number of live leaves, leaf area (cm^2), and dry above- and belowground biomass (g). We used these data to estimate the biomass of the experimental seedlings allometrically at the start of the experiment (see Appendix S2a). We used the initial biomass estimates to calculate the mean relative growth rate (RGR) of the biomass of each plant during the experiment:

$$\mathrm{RGR} = \frac{\ln(M_{\mathrm{final}}) - \ln(M_{\mathrm{init}})}{t},$$

(1)

where M_{init} is the allometrically estimated dry biomass of each plant at the start of the treatment, M_{final} is the measured dry biomass at harvest, and t is the number of days between the treatment start and plant harvest.

Every fifteen days during both experiments, we measured the diameter, height, and live and dead leaf count for each plant. During the wet-dry season experiment, 3 weeks before the end of the wet season, we measured the length (cm) and width (cm) of every leaf and leaflet to calculate approximate leaf area. After the harvest, we measured 50–100 leaves from each species for length, width, and fresh leaf area using a leaf area meter (LI-3100C, LI-COR; Lincoln, NE, USA). We combined the leaf measurements with stem diameter, height, and number of live leaves to allometrically estimate the total biomass of each plant midway through the experiment (see Appendix S2a).

One week prior to the end of each experiment, and 3 weeks prior to the end of the wet season in the wet-dry experiment, we measured the maximum light-saturated photosynthetic rate (μmol CO_2 m^2 s^{-1}), stomatal conductance (mol H_2O m^2 s^{-1}), and transpiration rate (mmol H_2O m^2 s^{-1}) from the newest fully expanded leaf on all plants using a portable photosynthesis system (6400XT, LI-COR). Inside the leaf chamber of the photosynthesis system, we set light levels to 1000 μmol m^{-2} s^{-1} PAR and CO_2 concentration to the appropriate chamber target level (i.e. 390 μmol mol^{-1} or 780 μmol mol^{-1}).

At the end of each experiment, in addition to the final biweekly measurements, we harvested all plants and measured the dry biomass of leaves, stems, and roots. We measured total leaf production as the difference between the number of live leaves at the beginning and number at the end of the treatment, plus all dead leaves regardless of the mechanism of leaf loss (e.g. abscission, herbivory, pathogen). We collected approximately 200 mg of dried leaf material for each plant, which we ground to a powder and measured the ratio of carbon to nitrogen (C : N) by combustion and thermal conductivity on a Thermo Flash EA112 analyzer (CE Elantech, Lakewood, NJ, USA).

Data processing and analysis

We tested each response variable (Table 2) for categorical treatment main effects and interactions by fitting linear mixed-effects models with restricted maximum-likelihood (REML) estimation (Pinhero & Bates, 2000) using the r package 'lme4' (Bates *et al*., 2012). Treatment (elevated and ambient CO_2), growth form (liana and tree), and their interaction were fixed effects in the model. We used fixed and random effects in the model to examine growth form differences while still accounting for species-level differences. To account for chamber-to-chamber variability, we used environmental variables measured within the growth chambers as covariates in the model. Environmental variables included total PAR, average soil moisture (VWC), standard deviation of CO_2 concentration, soil ammonium and nitrate, and the fine root biomass of nonexperimental species growing into the chamber plots (Appendix S1b summarizes each covariate). To make the coefficients directly comparable, we standardized all covariates by subtracting the mean and dividing by two standard deviations (Gelman & Hill, 2007). Random effects were included for chamber to account for any extra-treatment environmental variation not captured by the covariates, and for species to account for species variation not due to growth form and treatment. For *i* individuals in the wet-dry season, we used a linear mixed-effects model of the form:

$$\mathrm{Response}_i = \alpha_{CO_2(i)}, \mathrm{GF}(i) + \delta_{\mathrm{Covariates}(i)} + \beta_{\mathrm{Chamber}(i)} + \gamma_{\mathrm{Species}(i)} + \varepsilon_i$$

(2)

where $\mathrm{Response}_i$ is one of the measured plant response variables (Table 2). Fixed effects $\alpha_{CO_2(i)}, \mathrm{GF}(i)$ represent the set of regression coefficients for each treatment and their interaction, and $\delta_{\mathrm{Covariates}(i)}$ represent the environmental variables used as covariates. The crossed random effects structure $\beta_{\mathrm{Chamber}(i)}$ and $\gamma_{\mathrm{Species}(i)}$ allow the regression intercepts to vary, and ε_i are the residual model errors. For *i* individuals in the dry-only experiment, we used a model of the form:

$$\mathrm{Response}_i = \alpha_{CO_2(i)}, \mathrm{GF}(i) + \delta_{\mathrm{Covariates}(i)} + \beta_{\mathrm{Block}(i)} + \gamma_{\mathrm{Species}(i)} + \varepsilon_i$$

(3)

where each term is the same as in (2) except the random effect $\beta_{\mathrm{Block}(i)}$ is used to allow intercepts to vary by block rather than chamber to reflect the block design of this experiment.

Table 2. Bullets indicate variables measured in the experiments and used as the response variables in the model, broken down by variable category and experiment

Response variable	**Experiment**			
	Dry-only	**Wet-dry**	**Wet-half**	**Dry-half**
Growth change				
Height (cm)	•	•	•	•
Diameter (cm)	•	•	•	•
Leaf area (cm^2)	•	•	•	•
Total leaf production (#)	•	•	•	•
Leaf loss (#)	•	•	•	•
Biomass change				
Leaf biomass (g)	•	•		
Stem biomass (g)	•	•		
Root biomass (g)	•	•		
Total biomass (g)	•	•	•	•
Relative growth rate		•	•	•

Allocation ratios				
Leaf area ratio ($cm^2\ mg^{-1}$)	•	•	•	•
Leaf mass area ($mg\ cm^{-2}$)	•	•		
Specific leaf area ($cm^2\ mg^{-1}$)	•	•		
Root : shoot ratio	•	•		
Leaf : stem ratio	•	•		
Physiology				
Max photosynthetic rate ($\mu mol\ CO_2\ m^2\ s^{-1}$)	•		•	•
Stomatal conductance ($mol\ H_2O\ m^2\ s^{-1}$)	•		•	•
Transpiration ($mmol\ H_2O\ m^2\ s^{-1}$)	•		•	•
Foliar C : N ratio		•		

The wet-half and dry-half experiments are subsets of the Wet–Dry experiment.

We tested one alternate random effects structure for the models with only $\gamma_{\mathrm{Species}(i)}$ as the random intercept. We chose the optimal random effects structure for each response variable using likelihood ratio tests in a simplified model containing only covariates. When chamber-to-chamber variation was small to nonexistent, this alternate 'species-only' random effects structure was selected in accordance with the principle of parsimony.

To generate *P*-values for each model coefficient, we used code adapted from Moore (**2010**) that iteratively fits reduced fixed effects models and compares them to the full fixed effects model using a likelihood ratio test. These models are all fit using maximum-likelihood estimation instead of REML because REML estimates are not comparable among models with different fixed effects structures (Pinhero & Bates, **2000**). When the interaction or a main effect term was not significant, the term(s) was removed and the model refit using the same procedure as above.

We used bootstrapping to obtain model estimates and standard errors that are robust to non-normality and nonconstant variance of the errors. We bootstrap resampled the residuals of each model, refit the original interaction model, and extracted the least squares means. We used the r package 'lsmeans' (Lenth, **2013**) to calculate the least squares means for each level of CO_2 and growth form in the interaction model. This process was repeated 1000 times for each response variable. From these data, we calculated the mean response and standard error at each treatment level combination (growth form × CO_2), the mean effect size (i.e. log response ratio) of CO_2 separately for lianas and trees, and the 95% confidence interval of each effect size following the method of Hedges *et al*. (**1999**). We performed all data processing and analysis in the open-source statistical software program r (R Core Team, **2013**).

Results

Among the 19 growth and physiological response variables analysed in the experiments, there were no significant differences in the relative effect of CO_2 on lianas vs. on trees (Table **3**). While lianas tended to have a larger relative response to elevated CO_2, the lack of a significant interaction between CO_2 and growth form can be clearly seen across all response variables (Figs **2** and **3**). We found very few variables in which the two growth forms differed significantly, even when pooling the data across CO_2 treatments (Table **3**). The substantial intra- and interspecific variation in the experiment shows that common species of these two growth forms do not respond in a clear and predictable manner to elevated CO_2. Full results from the linear mixed model estimations are presented in Tables **4** and **5**.

Table 3. Likelihood ratio test results for the interaction between CO_2 and growth form (GF) and for a main effect of CO_2 and GF separately. The random effects structure used for each model is given (see table footnotes for description)

Response variable	**Experiment**															
	Dry-only				**Wet-dry**				**Wet half**				**Dry half**			
	Interaction	**Main Effect**		**Random structure[1]**	**Interaction**	**Main Effect**		**Random structure[1]**	**Interaction**	**Main Effect**		**Random structure[1]**	**Interaction**	**Main Effect**		**Random structure[1]**
		CO_2	**GF**			**CO_2**	**GF**			**CO_2**	**GF**			**CO_2**	**GF**	
Growth change																
Stem length (cm)	ns	ns	ns	2	ns	ns	ns	1	ns	ns	ns	1	ns	ns	ns	2
Diameter (cm)	ns	**0.040**	ns	2	ns	ns	ns	1	ns	ns	ns	2	ns	ns	ns	1
Leaf area (cm^2)	ns	ns	ns	1	ns	**0.038**	ns	2	ns	ns	ns	2	ns	**0.034**	ns	2
Total leaf production (#)	ns	ns	ns	1	ns	ns	ns	1	ns	ns	**0.035**	2	ns	ns	ns	1
Leaf loss (#)	ns	ns	ns	2	ns	ns	ns	2	ns	ns	ns	2	ns	ns	ns	2
Biomass change																
Leaf biomass (g)	ns	ns	ns	1	ns	**0.008**	ns	2	–	–	–	–	–	–	–	–
Stem biomass (g)	ns	ns	ns	1	ns	**0.007**	ns	2	–	–	–	–	–	–	–	–
Root biomass (g)	ns	**0.018**	ns	1	ns	ns	ns	2	–	–	–	–	–	–	–	–
Total biomass (g)	ns	ns	ns	1	ns	**0.012**	ns	2	ns	ns	ns	2	ns	**0.017**	ns	2
Relative growth rate	–	–	–	–	ns	ns	ns	1	ns	ns	ns	1	ns	**0.044**	ns	1
Allocation ratios																

Leaf area ratio ($cm^2\ mg^{-1}$)	ns	ns	ns	1	ns	ns	**0.016**	2	ns	ns	ns	1	ns	ns	ns	2
Leaf mass area ($mg\ cm^{-2}$)	ns	**0.025**	ns	2	ns	ns	ns	2	–	–	–	–	–	–	–	–
Specific leaf area ($cm^2\ mg^{-1}$)	ns	ns	ns	2	ns	ns	ns	2	–	–	–	–	–	–	–	–
Root : shoot ratio	ns	ns	ns	2	ns	ns	ns	2	–	–	–	–	–	–	–	–
Leaf : stem ratio	ns	ns	ns	2	ns	ns	ns	2	–	–	–	–	–	–	–	–
Physiology																
Max photosynthetic rate ($\mu mol\ CO_2\ m^2\ s^{-1}$)	ns	**<0.001**	ns	1	–	–	–	–	ns	**<0.001**	ns	1	ns	**<0.001**	ns	1
Stomatal conductance ($mol\ H_2O\ m^2\ s^{-1}$)	ns	ns	ns	2	–	–	–	–	ns	ns	ns	1	ns	**0.001**	ns	1
Transpiration ($mmol\ H_2O\ m^2\ s^{-1}$)	ns	ns	**0.038**	1	–	–	–	–	ns	ns	ns	1	ns	**0.019**	ns	1
Foliar C : N ratio	–	–	–	–	ns	ns	ns	2	–	–	–	–	–	–	–	–

[1]Random effects structures 1: $(\beta_{\mathrm{Chamber}(i)} + \gamma_{\mathrm{Species}(i)})$, 2: $(\gamma_{\mathrm{Species}(i)})$. Significant effects are highlighted in bold. The wet-half and dry-half experiments are subsets of the Wet–Dry experiment.

ns denotes nonsignificant effects; '–' indicates variables not measured in a particular experiment or subset.

Table 4. Mixed model estimates of liana and tree response to CO_2 treatment, per cent change of response, and effect size for growth, biomass, allocation ratio, and physiological variables between the dry-only and wet-dry experiments

	Dry-only								**Wet-dry**							
	Lianas				**Trees**				**Lianas**				**Trees**			
	Ambient	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**
Growth change																
Stem Length (cm)	μ 19.9	26.9	35.1	0.30	6.1	8.4	37.0	0.32	90.2	107.9	19.7	0.18	21.4	25.8	20.8	0.19
	σ 3.4	3.8	CI_{95} ± 0.43		3.5	3.8	CI_{95} ± 1.43		4.0	4.1	CI_{95} ± 0.11		4.2	4.0	CI_{95} ± 0.49	
Diameter (cm)	0.05	0.07	27.8	0.25	0.10	0.13	22.5	0.20	0.15	0.18	19.8	0.18	0.18	0.21	17.2	0.16
	0.01	0.01		0.41	0.01	0.01		0.22	0.01	0.01		0.21	0.01	0.01		0.17
Leaf area (cm^2)	153.5	242.2	57.8	0.46	198.0	293.2	48.1	0.39	807.5	1079.3	33.7	0.29	653.6	819.6	25.4	0.23
	31.2	32.4		0.48	32.4	31.6		0.38	99.1	102.7		0.30	104.4	99.6		0.39
Total leaf production (#)	5.0	10.3	103.7	0.71	4.6	6.0	29.9	0.26	18.7	27.5	47.3	0.39	31.1	35.8	14.8	0.14
	1.5	1.5		0.64	1.5	1.6		0.81	2.9	2.6		0.36	2.8	3.0		0.24
Leaf loss (#)	1.5	1.7	11.1	0.11	1.7	1.3	−21.9	−0.25	3.2	3.4	6.6	0.06	8.4	7.6	−10.3	−0.11
	0.3	0.2		0.43	0.24	0.24		0.46	0.5	0.5		0.43	0.5	0.5		0.18
Biomass change																
Leaf biomass (g)	0.51	0.91	78.1	0.58	0.60	0.85	41.7	0.35	2.27	3.64	60.4	0.47	1.82	2.41	32.6	0.28
	0.11	0.11		0.47	0.10	0.11		0.41	0.35	0.33		0.35	0.36	0.35		0.48
Stem biomass (g)	0.37	0.72	95.5	0.67	0.44	0.69	58.2	0.46	2.63	5.20	97.6	0.68	1.10	1.69	32.6	0.28
	0.08	0.09		0.51	0.09	0.09		0.46	0.55	0.55		0.46	0.53	0.54		1.13
Root biomass (g)	0.40	0.62	55.3	0.44	0.47	0.57	21.4	0.19	1.65	2.51	52.4	0.42	0.61	1.14	87.2	0.63
	0.04	0.05		0.25	0.04	0.05		0.24	0.51	0.58		0.72	0.49	0.53		1.80
Total biomass (g)	1.28	2.25	75.5	0.56	1.51	2.09	38.4	0.32	6.57	11.36	73.0	0.55	3.53	5.11	44.7	0.37

	0.22	0.23		0.39	0.23	0.21		0.36	1.20	1.16		0.41	1.19	1.19		0.80
Relative growth rate	–	–	–	–	–	–	–	–	0.0124	0.0134	8.4	0.08	0.0104	0.0111	7.3	0.07
									0.0004	0.0004		0.09	0.0004	0.0004		0.10
Allocation ratios																
Leaf area ratio ($cm^2\ g^{-1}$)	0.12	0.11	−8.0	−0.08	0.11	0.10	−10.3	−0.11	0.13	0.12	−12.1	−0.13	0.19	0.17	−9.3	−0.10
	0.005	0.005		0.12	0.005	0.005		0.13	0.02	0.02		0.38	0.02	0.02		0.29
Leaf mass area ($mg\ cm^{-2}$)	3.89	4.12	5.8	0.06	3.82	4.00	4.7	0.05	3.45	3.89	12.8	0.12	3.58	3.18	−11.1	−0.12
	0.09	0.09		0.06	0.08	0.09		0.06	0.30	0.33		0.24	0.32	0.31		0.26
Specific leaf area ($cm^2\ mg^{-1}$)	0.30	0.29	−5.2	−0.05	0.29	0.28	−4.6	−0.05	0.32	0.28	−10.8	−0.11	0.42	0.37	−12.3	−0.13
	0.01	0.01		0.09	0.01	0.01		0.09	0.04	0.04		0.35	0.04	0.04		0.27
Root : shoot ratio	1.72	1.83	6.1	0.06	1.25	1.17	−6.2	−0.06	0.33	0.26	−21.5	−0.24	0.30	0.34	13.0	0.12
	0.12	0.12		0.19	0.13	0.13		0.29	0.06	0.06		0.57	0.06	0.06		0.42
Leaf : stem ratio	1.59	1.56	−2.2	−0.02	1.29	1.31	1.1	0.01	1.27	1.20	−5.4	−0.06	1.77	1.70	−3.9	−0.04
	0.07	0.08		0.13	0.07	0.07		0.15	0.12	0.11		0.26	0.11	0.12		0.19
Physiology																
Max photosynthetic rate ($\mu mol\ CO_2\ m^2\ s^{-1}$)	5.92	8.04	35.9	0.31	5.09	6.96	36.8	0.31	–	–	–	–	–	–	–	–
	0.32	0.32		0.13	0.31	0.33		0.15								
Stomatal conductance ($mol\ H_2O\ m^2\ s^{-1}$)	0.15	0.15	−2.25	−0.01	0.11	0.08	−27.1	−0.32	–	–	–	–	–	–	–	–
	0.01	0.01		0.18	0.01	0.01		0.30								
Transpiration ($mmol\ H_2O\ m^2\ s^{-1}$)	2.22	2.12	−4.8	−0.03	1.76	1.38	−22.0	−0.25	–	–	–	–	–	–	–	–
	0.12	0.12		0.16	0.12	0.12	37.0	0.22								

Foliar C : N ratio	–	–	–	–	–	–	–	–	17.2	18.1	5.2	0.05	13.7	14.3	4.4	0.04
									0.6	0.6		0.09	0.5	0.5		0.10

These values take into account the environmental covariates and random effects used in the model. '–' indicates variables not measured in a particular experiment.

Table 5. Mixed model estimates of liana and tree response to CO_2 treatment, per cent change of response, and effect size for growth, biomass, allocation ratio, and physiological variables between the wet-half and dry-half of the wet-dry experiment

	Wet-half								**Dry-half**							
	Lianas				**Trees**				**Lianas**				**Trees**			
	Ambient	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**	**Ambient**	**Elevated**	**% Δ**	**Eff. size**
Growth change																
Stem Length (cm)																
μ	26.0	31.3	20.7	0.19	6.0	6.7	9.5	0.09	63.1	76.2	20.7	0.19	15.6	20.0	28.1	0.25
σ	3.5	3.3		CI_{95} ± 0.33	3.5	3.4		CI_{95} ± 1.43	4.3	4.4		CI_{95} ± 0.17	4.5	4.4		CI_{95} ± 0.71
Diameter (cm)	0.05	0.05	15.6	0.15	0.05	0.06	16.0	0.15	0.10	0.12	17.9	0.16	0.13	0.15	17.3	0.16
	0.01	0.01		0.29	0.01	0.01		0.26	0.01	0.01		0.23	0.01	0.01		0.18
Leaf Area (cm^2)	192.2	217.8	13.4	0.13	246.9	252.2	2.2	0.02	629.2	863.6	37.3	0.32	414.7	570.5	37.6	0.32
	17.5	16.9		0.23	17.2	17.7		0.19	84.8	85.3		0.33	86.6	88.3		0.51
Total leaf production (#)	4.0	4.3	9.3	0.09	9.9	10.5	6.2	0.06	14.9	23.4	56.7	0.45	21.3	26.0	22.1	0.20
	0.7	0.6		0.44	0.7	0.6		0.18	2.4	2.3		0.37	2.4	2.4		0.29
Leaf loss (#)	0.7	0.9	26.3	0.23	1.8	2.1	17.7	0.16	2.6	2.7	3.3	0.03	6.9	5.7	−17.6	−0.19
	0.2	0.2		0.72	0.2	0.2		0.28	0.5	0.5		0.49	0.5	0.5		0.21

Biomass change																
Leaf biomass (g)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stem biomass (g)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Root biomass (g)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total Biomass (g)	1.24	1.41	14.3	0.13	1.40	1.44	2.9	0.03	6.93	11.17	61.21	0.48	3.65	5.20	42.4	0.35
	0.10	0.10		0.20	0.10	0.10		0.19	1.09	1.14		0.37	1.18	1.17		0.77
Relative growth rate	0.015	0.015	4.7	0.05	0.014	0.014	1.9	0.02	0.009	0.011	17.1	0.16	0.007	0.009	21.1	0.19
	0.001	0.001		0.13	0.001	0.001		0.12	0.001	0.001		0.13	0.001	0.001		0.16
Allocation ratios																
Leaf area ratio ($cm^2\ g^{-1}$)	0.13	0.13	−0.9	−0.01	0.19	0.19	1.3	0.01	0.083	0.076	−8.5	−0.09	0.104	0.104	0.2	0.00
	0.01	0.01		0.15	0.01	0.01		0.11	0.017	0.016		0.59	0.017	0.018		0.47
Leaf mass area ($mg\ cm^{-2}$)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Specific leaf area ($cm^2\ mg^{-1}$)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Root : shoot ratio	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leaf : stem ratio	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Physiology																
Max photosynthetic rate	5.57	7.94	42.7	0.36	5.86	7.58	29.3	0.26	6.21	8.87	42.7	0.36	5.73	8.85	54.4	0.43

(μmol CO_2 m^2 s^{-1})																
	0.18	0.18		0.08	0.18	0.17		0.07	0.26	0.27		0.10	0.27	0.28		0.11
Stomatal conductance (mol H_2O m^2 s^{-1})	0.12	0.14	17.6	0.16	0.16	0.17	10.0	0.10	0.10	0.06	−38.2	−0.48	0.11	0.09	−19.2	−0.21
	0.01	0.01		0.15	0.01	0.01		0.12	0.01	0.01		0.22	0.01	0.01		0.19
Transpiration (mmol H_2O m^2 s^{-1})	1.50	1.71	14.1	0.13	1.89	2.01	6.5	0.06	1.69	1.25	−25.9	−0.30	1.79	1.62	−9.5	−0.10
	0.07	0.06		0.12	0.07	0.07		0.10	0.08	0.07		0.14	0.08	0.08		0.13
Foliar C : N ratio	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

These values take into account the environmental covariates and random effects used in the model. '-' indicates variables not measured in a particular subset of the experiment.

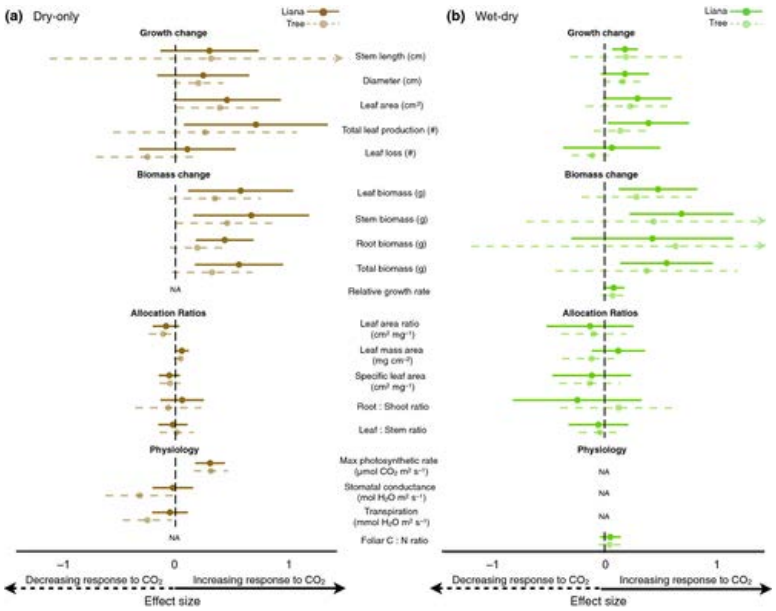

Figure 2. Effect size response to CO_2 for growth variables, biomass variables, allocation ratios, and physiological variables in the (a) dry-only and (b) wet-dry experiments. Due to the large effect of seasonality on gas-exchange measurements, the wet-dry physiology is presented in Fig 3. Positive/negative effect sizes indicate an increased/decreased response to CO_2. Points represent the mean effect size; lines represent the 95% confidence interval. Arrows denote confidence intervals that extend beyond the boundaries of the figure.

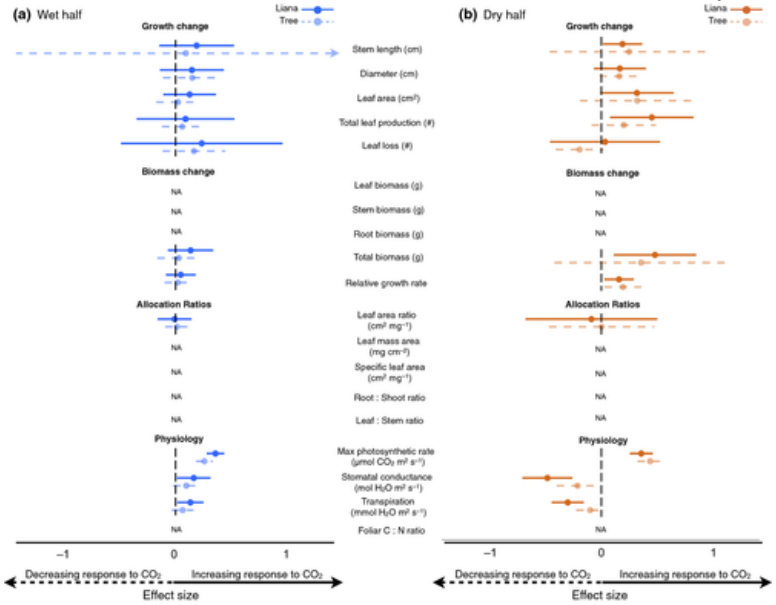

Figure 3. Effect size response to CO_2 for growth variables, biomass variables, allocation ratios, and physiological variables in the (a) wet-half and (b) dry-half of the wet-dry season experiment. Positive/negative effect sizes indicate an increased/decreased response to CO_2. Points represent the mean effect size; lines represent the 95% confidence interval. Arrows denote confidence intervals that extend beyond the boundaries of the figure.

While no significant differences between growth forms were found, a number of response variables had a significant and large CO_2 fertilization effect when pooled across growth form (Table **3**). The clear response of lianas and trees to elevated CO_2 is evidence that validates the design of our experimental array and CO_2 treatment procedures. In the dry-only experiment, four response variables showed a significant response to elevated CO_2 when growth forms were pooled (Table **3**). Stem diameter increased significantly (24.7%), even though this was only a change of <1 mm in diameter. Root mass increased significantly (37.4%), while the

aboveground biomass components (leaf and stem mass) did not show a significant increase in response to elevated CO_2. Leaf mass per area, a measure of a plant's investment in (or cost of) light interception (Poorter *et al*., **2009**), significantly increased 5.4%. The significant increase in maximum photosynthetic rate of 37.3%, combined with no significant change in stomatal conductance or transpiration, suggests an increase in water-use efficiency for both lianas and trees.

The wet-dry season experiment, which ran for twice as long as the dry-only experiment but included half the number of species, also resulted in several significant differences between elevated and ambient CO_2 when growth forms are pooled (Table **3**). Significant leaf-level responses to elevated CO_2 included a 31.5% increase in leaf area and a 49.0% increase in leaf mass. Stem biomass increased significantly by 84.6%, the largest percentage increase of all the variables. Total plant biomass increased significantly over the study period, with an increase of 64.8% in response to elevated CO_2. Within the wet–dry season experiment, none of the growth or biomass response variables showed a significant response to elevated CO_2 during the wet half of the experiment. However, in the dry half of the experiment, leaf area, total plant biomass, and RGR all increased significantly in response to elevated CO_2 (37.2%, 69.8%, and 19.0%, respectively).

Elevated CO_2 caused significant increases in maximum photosynthetic rate in both the wet and dry halves of the wet-dry season experiment when pooling growth forms, with a 36.0% increase in the wet half and a 48.2% increase in the dry half. In the wet half, stomatal conductance and transpiration showed no significant response to CO_2, whereas in the dry season, stomatal conductance decreased significantly (28.9%) and transpiration decreased significantly (19.5%). These results indicate that water-use efficiency increased in both seasons (less so in the wet half) in response to CO_2 but did not differ between lianas and trees.

Random effects of chamber and species

Examining the random effects selected by the likelihood ratio test for the analysis of each response variable (Table **3**), we found that crossed random effects (chamber and species) were selected less often (n = 25) than the only species as a random effect (n = 30). This indicates that a minority of response variables had sufficient among-chamber variation not related to treatment to include chamber as a random effect in addition to species. Thus, for only these response variables did the micro-environments of the chambers differ enough to cause detectable variation in plant growth unrelated to CO_2 level or species, but was accounted for by the inclusion of chamber as a random effect. More often only species was selected as a random effect, indicating either little among-chamber extra-treatment variability, or the environmental covariates measured throughout the experiment sufficiently explained the chamber-to-chamber variability.

Discussion

This study is the first comprehensive comparison of tropical liana and tree responses to elevated CO_2, and we did not find empirical support for the hypothesis that lianas respond more than trees to elevated CO_2. Based on the lack of any significantly stronger relative responses by lianas to elevated CO_2 across the variables measured, our data do not support the hypothesis that increasing atmospheric CO_2 is a direct mechanism underlying the reported increase in neotropical liana size and abundance. If lianas had an inherent advantage over trees under elevated CO_2, we would expect a strong response at the leaf level, which is the locus of CO_2 absorption and carbon fixation. However, lianas did not invest more than trees in photosynthetic tissue under elevated CO_2. For all leaf variables measured in each experiment, lianas and trees invested a similar amount of resources when exposed to elevated CO_2. We found a moderate increase in leaf area and leaf biomass in response to elevated CO_2 during the wet-dry experiment, but this increase did not differ between lianas and trees. In the dry-only experiment, both lianas and trees invested similarly in the leaf-level cost of light interception (leaf mass per area). Previous studies also found that lianas responded to elevated CO_2, but these studies did not simultaneously compare the response of trees.

The change in biomass and height in response to elevated CO_2 was also similar for both lianas and trees. We therefore find no support for the hypothesis that the high leaf area ratio (LAR) strategy of lianas necessarily confers an advantage under elevated CO_2. This hypothesis has been suggested as one of the underlying mechanisms explaining the reported increase in lianas (Mohan *et al*., **2006**; Körner, **2009**; Schnitzer & Bongers, **2011**; Schnitzer, **2014**). In fact, lianas and trees either had a very similar LAR, or trees had significantly larger LAR than lianas at the end of each experiment.

Lianas did not show a larger relative physiological response to elevated CO_2 during seasonal drought than trees, regardless of their reported higher water-use efficiency at ambient CO_2 levels, wider vessel elements, and potentially deeper root systems (Foster & Brooks, **2005**; Schnitzer, **2015**; Domingues *et al*., **2007**; Cai *et al*., **2009**; Chen *et al*., **2015**). Many lianas retain their leaves and are able to increase their relative growth during the dry season (Putz & Windsor, **1987**; Schnitzer, **2015**), whereas many trees are deciduous or reduce their photosynthetic activity (Condit *et al*., **2000**; Schnitzer, **2015**; Cai *et al*., **2009**). We anticipated lianas to take advantage of increased water-use efficiency that elevated CO_2 imparts on plants (Battipaglia *et al*., **2012**). However in the first reported gas exchange measurements conducted on tropical lianas under elevated CO_2, we found no significant differences in the relative increase in maximum photosynthetic rate between lianas and trees in either the wet or dry seasons. Similarly, we did not find any significant differences in the relative decrease in stomatal conductance and transpiration shown by lianas and trees. In both studies, we found increases in water-use efficiency, but there was no difference between lianas and trees. The lack of physiological differences between lianas and trees in response to CO_2 is reflected in their similar growth response, which runs contrary to our hypothesis that a greater increase in the water-use efficiency of lianas compared to trees would offset dry season-induced growth reductions in lianas.

Our study focused on liana and tree seedlings, therefore our conclusions are limited to this life-history stage. Most recent research that found evidence of increasing lianas in neotropical forests was conducted on adult stems (Schnitzer & Bongers, **2011**; Schnitzer, **2014**), but there is also some evidence for the increase at the seedling stage as well (Benítez-Malvido & Martínez-Ramos, **2003**). By the end of the wet–dry experiment, most of the lianas were climbing the trellises provided and were no longer self-supporting. The response to changes in resource availability should at least be consistent with an adult climbing liana. If elevated CO_2 was the main mechanism driving an increase in the size and abundance of lianas relative to trees, we might expect to find some effects at this earlier life stage. Ideally, co-occurring adult lianas and trees should be experimentally exposed to elevated CO_2 to resolve confounding effects of ontogeny. However, our data do not lend support to the hypothesis that elevated CO_2 is directly responsible for the observed increase in liana size and abundance.

While the interaction between elevated CO_2 and light availability was not included in our experimental design, we acknowledge its potential importance. Granados & Körner (**2002**), the only published work on tropical liana response to elevated CO_2 and light, found that lianas only increased in biomass under elevated CO_2 when grown under low light. In addition, three temperate zone studies found a larger liana response to CO_2 under low light (Körner, **2009**). The advantage when light is limiting may allow lianas to escape the low-light understory and proliferate in the high-light canopy faster than trees can. However, total daily average PAR in the wet–dry study and in the low-light level of Granados & Körner (**2002**) was similar (1.6 and 1.8 mol m^{-2}, respectively). Since neither study achieved the low-light level of the understory of a closed canopy neotropical forest (0.2–1.0 mol m^{-2}; Chazdon & Fetcher, **1983**), further study of the interaction between understory light levels, plant growth form, and elevated CO_2 is needed.

Our results for the 12 liana and 10 tree species are reported at the growth form level; however, species-specific responses to CO_2 are not uniform. For example, in the dry-only experiment, the liana *Stigmaphyllon lindenianum* increased in biomass 322% under elevated CO_2 relative to ambient, while the liana *Paullinia pinnata* showed a biomass decrease of 19%. In the same experiment, the tree *Cedrela odorata* increased in

biomass 111% under elevated CO_2 relative to ambient, while the tree *Paquira quinata* showed a biomass decrease of 15%. The large species-level variation and the generally small difference in liana and tree mean response to CO_2 (Figs **2** and **3**) led to a lack of any significant differences in growth forms. Lianas are a diverse plant growth form in tropical forests with 162 species from 36 families present on the 50-ha plot alone at Barro Colorado Island in Panama (Schnitzer *et al*., **2012**), so it is not surprising to find large variation in the response among species. It is possible that the reported increase in liana size and abundance is caused by a subset of species, which may differ among regions of the neotropics. Unfortunately, temporal censuses of lianas to date have not included species-level data. Not only are temporal species censuses needed, but any further study of lianas under elevated CO_2 should be focused on those liana species that show increases in size and abundance relative to trees over time.

We conclude that elevated CO_2 does not appear to be the main mechanism behind the reported increase in lianas, yet we cannot rule it out entirely. Other global change mechanisms such as increasing length and severity of seasonal drought, changes in soil nutrient cycles, and changes in temperature may interact with increasing atmospheric CO_2 to produce the reported increase in lianas. As with any perturbation to a natural system, the underlying mechanisms and their effects on ecosystems are likely to be complex and interactive. For example, elevated CO_2 may indirectly influence liana abundance by increasing tree productivity and mortality, which could result in higher forest-level disturbance (Phillips & Gentry, **1994**). The majority of liana species respond strongly to disturbance and liana diversity appears to be maintained by disturbance (Schnitzer & Carson, **2001**; Dalling *et al*., **2012**; Ledo & Schnitzer, **2014**). Further experimentation on the mechanisms underlying increasing lianas in the neotropics should therefore be multifactorial and include species selected based on the results of temporal censuses.

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