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# Lianas always outperform tree seedlings regardless of soil nutrients: results from a long-term fertilization experiment

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**Abstract.** Lianas are a prominent growth form in tropical forests, and there is compelling evidence that they are increasing in abundance throughout the Neotropics. While recent evidence shows that soil resources limit tree growth even in deep shade, the degree to which soil resources limit lianas in forest understories, where they coexist with trees for decades, remains unknown. Regardless, the physiological underpinnings of soil resource limitation in deeply shaded tropical habitats remain largely unexplored for either trees or lianas. Theory predicts that lianas should be more limited by soil resources than trees because they occupy the quick-return end of the “leaf economic spectrum,” characterized by high rates of photosynthesis, high specific leaf area, short leaf life span, affinity to high-nutrient sites, and greater foliar nutrient concentrations. To address these issues, we asked whether soil resources (nitrogen, phosphorus, and potassium), alone or in combination, applied experimentally for more than a decade would cause significant changes in the morphology or physiology of tree and liana seedlings in a lowland tropical forest. We found evidence for the first time that phosphorus limits the photosynthetic performance of both trees and lianas in deeply shaded understory habitats. More importantly, lianas always showed significantly greater photosynthetic capacity, quenching, and saturating light levels compared to trees across all treatments. We found little evidence for nutrient  $\times$  growth form interactions, indicating that lianas were not disproportionately favored in nutrient-rich habitats. Tree and liana seedlings differed markedly for six key morphological traits, demonstrating that architectural differences occurred very early in ontogeny prior to lianas finding a trellis (all seedlings were self-supporting). Overall, our results do not support nutrient loading as a mechanism of increasing liana abundance in the Neotropics. Rather, our finding that lianas always outperform trees, in terms of photosynthetic processes and under contrasting rates of resource supply of macronutrients, will allow lianas to increase in abundance if disturbance and tree turnover rates are increasing in Neotropical forests as has been suggested.

**Key words:** Barro Colorado Nature Monument, Panama; chlorophyll fluorescence; fertilization; lianas; Neotropics; nitrogen; nutrient limitation; phosphorus; photosynthetic performance; plant architecture and morphology; potassium; tropical forest.

## INTRODUCTION

Lianas and trees are the two dominant plant growth forms in tropical forests, and there is a growing body of evidence suggesting that lianas are increasing relative to trees in Neotropical forests (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, S. J. Wright et al. 2004, Chave et al. 2008, Foster et al. 2008, Schnitzer and Bongers 2011, Yorke et al. 2013, Schnitzer 2015). We are not sure why. Regardless, these increases in liana abundance will almost certainly have important consequences for forest biodiversity and global carbon budgets (Bunker et al. 2005, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Schnitzer et al. 2014). Indeed, Schnitzer and Carson (2010) and Schnitzer et al.

(2014) demonstrated unequivocally that when lianas increase in abundance and displace trees, forest-wide aboveground carbon storage can be reduced by as much as 18%. While exceptions exist, lianas are typically a fast-growing, light-limited growth form associated with high-light, nutrient-rich, and disturbed habitats, including forest edges, canopy gaps, and logged forests (Putz 1984, Schnitzer et al. 2000, Schnitzer and Carson 2010). Moreover, they can represent more than a third of all woody species in tropical forests (Pérez-Salícru et al. 2001, Gentry 2009, Schnitzer et al. 2012).

Lianas differ from trees in critical patterns of biomass allocation and other key life-history traits. For example, in their climbing form, lianas rely on other vegetation as trellises to gain access to the canopy, and thus they typically invest proportionally less resources into woody stem tissue than trees, and proportionally more resources toward leaves and roots (Putz 1983, Suzuki 1987, Castellanos et al. 1989, Niklas 1994, Gerwing and Farias 2000, Hättenschwiler 2002, Santiago and Wright 2007).

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This biomass allocation pattern of canopy-level lianas (lianas with at least partial foliage in the forest canopy) results in lianas having greater specific leaf area (SLA) and photosynthetic rates ( $A_{\max}$ ) than trees (Zhu and Cao 2009, 2010, Han et al. 2010, Asner and Martin 2012, Santiago et al. 2015). The abundance of canopy-level lianas often increases with soil fertility (e.g., Proctor et al. 1983, Putz 1983, 1985, Putz and Chai 1987, Balfour and Bond 1993, Bruijnzeel and Proctor 1995) and lianas show higher foliar nutrient concentrations compared to trees (Cai and Bongers 2007, Kusumoto and Enoki 2008, Zhu and Cao 2010, Asner and Martin 2012). This suggests that canopy-level lianas are far more nutrient-limited than trees, yet the few in situ experimental nutrient enrichment studies available have found either modest support for this (Hättenschwiler 2002) or no differences at all between the life forms (Cai et al. 2008).

While canopy-level trees and lianas differ strongly in terms of leaf traits, morphology, and physiology, the degree to which seedlings differ is unclear. In early ontogenetic stages, lianas typically exist without a trellis and both trees and lianas have to survive for years within deeply shaded understory habitats; under these conditions they appear strikingly similar in terms of morphology and architecture (Putz 1983). Thus, there appears to be broad overlap in the patterns of growth, survival, and habitat preferences of the seedlings of both lianas and trees (Gilbert et al. 2006). Consequently, contrasting resource uptake and allocation may not occur in early developmental stages where light remains the primary limiting resource, and most differences between trees and lianas may only develop late in ontogeny.

While light may be the most limiting resource in tropical forest understory habitats, it has recently become clear that seedlings of some woody species are also co-limited by soil nutrients. Limitation varies among species (Denslow et al. 1987) and among soil resources including nitrogen (N), phosphorus (P), or potassium (K), and in some cases limitation is caused simultaneously by multiple soil resources (Bloom et al. 1985, Ceccon et al. 2004, Holste et al. 2011, Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Indeed, recent work on the tree seedling *Alseis blackiana* (Helms.; Rubiaceae) demonstrated that photosynthesis, stomatal conductance, and photosynthetic yield were limited by N, P, and K, respectively, even in deep shade (Pasquini and Santiago 2012). In a separate study at the same site, K limited tree seedling growth (Santiago et al. 2012). For liana seedlings, however, both the degree of nutrient limitation, as well as whether liana seedlings are more or less limited by soil resources than tree seedlings, remains unknown.

Here, we test in situ the hypothesis that nutrients limit photosynthetic physiology of liana seedlings to a greater degree than tree seedlings. If lianas and trees differ, we would demonstrate that, in spite of their apparent

similarities in seedling morphology, physiological divergence happens early in ontogeny, and if not, then physiological differences must develop after they find a trellis and begin ascending into the canopy. Furthermore, testing our hypothesis may provide insight into the underlying mechanism for the increase in lianas in many Neotropical forests. Nutrient deposition, particularly of nitrogen, is increasing throughout the tropics (reviewed by Hedin et al. 2009, Hietz et al. 2011), and tree turnover rates also appear to be increasing (Phillips et al. 2004), as are rates of human disturbances and deforestation (e.g., reviewed by Laurance 2008, Wright 2010). All of these are likely to favor lianas, particularly if they gain an advantage early in ontogeny.

To test our hypothesis, we are using a fully factorial experiment where N, P, and K have been added to large replicated forest plots for more than a decade. We compare how soil resources impact the physiology and morphology of seedlings of a phylogenetically diverse group of lianas and trees from 13 plant families. We hypothesize that (1) lianas will show greater responses to soil nutrients than trees because of their ability to allocate more to growth vs. structural support, (2) lianas will be limited by different soil resources than trees, and (3) lianas in very early developmental stages prior to acquiring a trellis will have contrasting patterns of plant architecture (e.g., internode length and leaf angle) compared to trees. Our goal is to determine whether liana and tree seedlings are constrained by the same or different resources or combinations of resources and link this to key aspects of photosynthetic physiology and seedling architecture. Ultimately, we link our findings back to recent evidence that strongly suggests lianas are not only increasing in abundance throughout the Neotropics, but also altering patterns of carbon storage and sequestration (e.g., Schnitzer et al. 2014, Schnitzer 2015).

## MATERIALS AND METHODS

### *Study site*

We performed this research in seasonally moist, semi-deciduous, tropical forest located on the Gigante Peninsula (9°06'3" N, 79°50'37" W) within the Barro Colorado Nature Monument (BCNM) in central Panama (Appendix A: Fig. A1). The dry season occurs between January and April, during which less than 10% of the 2600 mm of average annual rainfall occurs. Our investigation took place from March through April 2010. Soils on the Gigante Peninsula are Oxisols and Inceptisols similar to Typic Eutrudox soils on adjacent Barro Colorado Island (Turner et al. 2012; B. L. Turner, *personal communication*). In terms of N, P, and K availability, soils at this site are relatively fertile for lowland tropical soils (Yavitt et al. 2009, Wright et al. 2011). Tree composition and stature (tree heights up to 45 m) in this forest are characteristic of mature (>200 yr) tropical secondary forest in central Panama (Wright et al. 2011).

### Experimental design

We used a long-term nutrient addition experiment where N, P, and K have been added in a full  $2 \times 2 \times 2$  factorial design with four replicates of each of eight treatments (control, N, P, K, NP, NK, PK, and NPK). The four replicates were placed perpendicular to a slight topographical gradient (36 m in elevation from southwest to northeast corner of site), because tree distributions and soil properties parallel this gradient (Yavitt et al. 2009, Wright et al. 2011). We used a balanced, incomplete-block design, where N, P, K, and NPK treatments were blocked vs. NP, NK, PK, and control treatments within each replicate (Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). This design minimizes uncontrolled error due to spatial heterogeneity and allows evaluation of main effects and two-way interactions, but limits power to evaluate the three-way interaction (Winer et al. 1991). Nutrients were added four times annually during the wet season for a total of  $125 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  as coated urea  $[(\text{NH}_2)_2\text{CO}]$ ,  $50 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  as triple super phosphate  $[\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}]$ , and  $50 \text{ kg K} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  as potassium chloride (KCl) starting in 1998 (12 yr of nutrient addition). The 32 experimental plots were each  $40 \times 40 \text{ m}$  in area and were separated by at least 40 m to minimize nutrient leaching into neighboring plots, with the exception of two plots separated by 20 m and located on opposite sides of a 3 m deep stream. In this same study site, long-term N fertilization led to increased soil acidity (0.8 unit decrease in soil pH; Corre et al. 2010), which may affect availability of P and other soil nutrients.

### Species

We selected seven liana and six tree species from 13 plant families because they were common in the study plots. The lianas were *Bauhinia guianenses* Aubl. (Fabaceae: Caesalpinioideae), *Coccoloba parimensis* Benth. (Polygonaceae), *Dolichocarpus dentatus* (Aubl.) Standl. (Dilleniaceae), *Maripa panamensis* Hemsl. (Convolvulaceae), *Paullinia fibrigera* Radlk. (Sapindaceae), *Phryganocydia corymbosa* (Vent.) Bureau ex. K. Schum (Bignoniaceae), and *Prionostemma aspera* (Lam.) Miers. (Celastraceae). The trees were *Alseis blackiana* Hemsl. (Rubiaceae), *Desmopsis panamensis* (B. L. Rob.) Saff. (Annonaceae), *Heisteria concinna* Standl. (Olacaceae), *Oenocarpus mapora* H. Karst. (Arecaceae), *Sorocea affinis* Hemsl. (Moraceae), and *Tetragastris panamensis* (Engler) Kuntze (Bursaceae). Nomenclature follows Garwood (2009). Individual seedlings were chosen haphazardly based on the first sightings of the study species within each plot. All liana seedlings were self-supporting (free-standing) and did not exhibit searcher shoots (sensu Putz and Holbrook 2009).

### Physiological measurements

Chlorophyll fluorescence measurements were used because they are highly correlated with carbon assimilation

rates (especially maximum electron transport; Maxwell and Johnson 2000), and we confirmed this relationship for one of our focal species (*A. blackiana*; Pasquini and Santiago 2012). We measured chlorophyll fluorescence of mature, fully expanded leaves using a photosynthesis yield analyzer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany). We sampled one leaf from one individual of the 13 species in each of the 32 plots (mean leaves sampled per plot = 12.4, total leaves sampled = 397). We constructed chlorophyll fluorescence light response curves using photon flux density (PFD) values of 0, 34, 97, 202, 324, 499, 700, 1067, and  $1471 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  to slowly bring the light up to the highest level. We measured the electron transport rate (ETR), which is an in vivo measure of overall capacity to provide energy to photosynthetic carboxylation reactions. We also measured photochemical quenching ( $q_p$ ); the proportion of open photosystem II (PSII) reaction centers and a proxy of the efficiency of PSII. We obtained the maximum electron transport rate ( $\text{ETR}_{\text{max}}$ ) and  $q_p$  at the highest light level (PFD =  $1471 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ). ETR was determined as

$$\text{ETR} = \frac{F'_m - F_s}{F'_m} \cdot \text{PFD} \cdot f \cdot \alpha \quad (1)$$

where  $F'_m$  is maximal fluorescence measured by a saturation pulse at each light level,  $F_s$  is steady-state fluorescence,  $f$  is a factor that represents the partitioning of photons between photosystems II and I (PSII and PSI) and is assumed to be 0.5, which indicates equal distribution of excitation energy between the two photosystems (Maxwell and Johnson 2000), and  $\alpha$  represents the fraction of photons absorbed by a leaf and is assumed to be 0.84 as an average for a variety of  $C_3$  leaves (Björkman and Demmig 1987, Stenke and Santiago 2011). Photochemical quenching was determined as

$$q_p = \frac{F'_m - F_s}{F'_m - F'_0} \quad (2)$$

where  $F'_0$  is minimum fluorescence of each illuminated sample determined during a brief dark interval following a saturation pulse (see Fig. 1 for an example of a fluorescence light response curve).

### Morphological measurements

We measured leaf angle, leaf thickness, internode length, and petiole length to characterize seedling morphology. Crown depth, perpendicular crown width, and seedling height were measured and used to calculate crown depth and crown area, relative to height. Leaf angle was measured using a protractor with a weighted thread as the angle of the leaf measured along the midvein from petiole attachment to leaf tip where a  $90^\circ$  leaf angle is parallel to the ground and perpendicular to the main stem (leaf angle  $>90^\circ$  indicates that leaf at an obtuse angle relative to the ground). We measured leaf thickness on an area of the leaf without major veins

using a digital micrometer (IP 65; Mitutoyo, Mizonokuchi, Japan). Additionally, one leaf from each seedling was collected and measured for leaf area (leaf petiole was removed) using a leaf area meter (LI-3100; Li-Cor Biosciences, Lincoln, Nebraska, USA). Leaves were then oven dried at 60°C for 48 h and weighed to determine SLA.

#### Light availability

Light availability in the tropical forest understory is heterogeneous due to a mosaic of canopy gaps and branch falls of differing ages and sizes. Because photosynthetic processes in the understory are primarily light-limited (Percy 1988), we estimated light availability directly above each of the 397 seedlings using hemispherical canopy photographs taken with a digital camera (Coolpix 4500; Nikon, Tokyo, Japan) mounted with a fisheye lens (Fisheye Converter FC-E8 0.21×; Nikon).

#### Data analyses

We analyzed ETR light response curves for saturating photon flux density ( $\text{PFD}_{\text{sat}}$ ) using Photosyn Assistant (version 1.1; Dundee Scientific, Dundee, UK), as described by Prioul and Chartier (1977). Hemispheric canopy photographs were analyzed for total light transmittance ( $T_{\text{tot}}$ ; proportion of above-canopy ambient light transmitted through the canopy) using Gap Light Analyzer (Frazer et al. 1999). We used a general linear model in SAS (proc glm, version 9.2; SAS Institute, Cary, North Carolina, USA) to determine whether liana and tree seedlings overall were found in differing light environments. Physiological and morphological data were analyzed by mixed linear models in SAS (proc mixed). The mixed linear model procedure was used rather than the general linear model procedure to yield Akaike information criterion (AIC) values for each model. Models were run on individual leaf physiological and morphological measures with fixed main effects of form (liana vs. tree), species nested within form, single nutrient main effects (N, P, K), two-way nutrient interactions ( $\text{N} \times \text{P}$ ,  $\text{N} \times \text{K}$ ,  $\text{P} \times \text{K}$ ), nutrient by growth form interactions ( $\text{N} \times \text{form}$ ,  $\text{P} \times \text{form}$ ,  $\text{K} \times \text{form}$ ), and  $T_{\text{tot}}$  (to control for heterogeneity of the light environment). Random effects were statistical replicate (Rep) and block nested within replicate. For similar analyses, see Pasquini and Santiago (2012) and Wright et al. (2011). Models that included effects of species as well as growth form were compared using AIC values (Appendix B: Tables B1–B6). Standard data transformations (natural log, square root, and arcsine) were performed to meet the assumption of normality as determined by the Shapiro-Wilk  $W$  statistic.  $T_{\text{tot}}$  are proportional data and were logit-transformed accordingly (Warton and Hui 2011). To control for Type I error ( $\alpha$ -error) in the multiple comparisons, we used family discovery rate (FDR) corrections, as described by Pike (2011) to adjust significant  $P$  values; FDR-

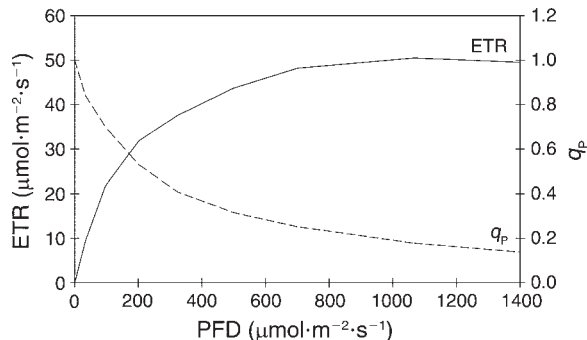


FIG. 1. Example chlorophyll fluorescence light response curve generated by the Mini-PAM photosynthesis yield analyzer showing electron transport rate (ETR; solid line) and photochemical quenching ( $q_p$ ; dashed line,  $q_p$  is a unitless quantity), for increasing levels of photon flux density (PFD).

corrected values are reported in *Results*, Figs. 2–7, and Tables 1 and 2.

## RESULTS

### Model selection

Mixed linear models were performed in two different ways, with and without species included. For all physiological and morphological variables, the model including species was a better fit to the data as determined by comparing AIC values (Appendix B: Tables B1–B6). Therefore, the findings based on the model with species included are presented.

### Physiological indices of performance

Lianas performed substantially better than trees for all physiological metrics (14–21% greater; Table 1, Fig. 2A–C). As expected, seedling photosynthetic performance was affected by light availability ( $T_{\text{tot}}$ ; Table 1), and thus it is important to note that mean understory light availability did not differ significantly between liana and tree seedlings (lianas,  $6.0\% \pm 0.6\%$  [SE]; trees,  $5.8\% \pm 0.7\%$ ;  $F_{1,395} = 0.08$ ,  $P = 0.78$ ; Appendix C: Fig. C1). In addition, species within growth forms differed significantly in physiological performance (Table 1).

Nutrient additions, especially P alone, enhanced photosynthetic physiology, whereas N or K addition never did. P addition increased  $\text{ETR}_{\text{max}}$  by 9.6% (Table 1, Fig. 3). P addition also caused a marginally significant increase in  $q_p$  (8.8%,  $P = 0.033$ ; Table 1). Surprisingly, when K was added in combination with P, it decreased the benefit to performance caused by adding P alone, as indicated by consistent significant  $\text{P} \times \text{K}$  interactions (Table 1, Fig. 4A–C). Specifically, P and K together decreased the benefit of adding P alone for  $\text{ETR}_{\text{max}}$ ,  $\text{PFD}_{\text{sat}}$ , and  $q_p$  by 7.6%, 9.2%, and 10.2%, respectively (Table 1, Fig. 4A–C). Nutrient additions enhanced the physiological performance of both lianas and trees to a similar degree (i.e., no significant interaction between growth form and nutrient addition). For the effects of all

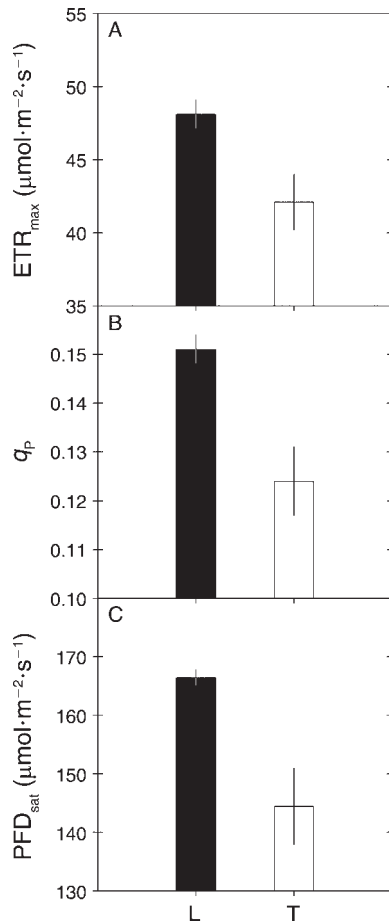


FIG. 2. Significant main effects of growth form for (A) maximum electron transport rate ( $ETR_{max}$ ), (B)  $q_p$ , and (C) saturating photon flux density ( $PFD_{sat}$ ). Lianas (L) and trees (T) are represented by solid and open bars (means  $\pm$  SE,  $N=32$  plots), respectively. All nutrient treatments are pooled. Effects were significant using the family discovery rate (FDR) corrected  $P$  value;  $P < 0.0237$ .

nutrient treatment combinations on the physiological responses of trees vs. lianas, see Appendix C: Fig. C2.

#### Plant architectural traits

Lianas and tree seedlings were significantly ( $P < 0.0115$ ) different from each other for all but one metric of plant architecture (Table 2, Fig. 5A–F). Liana crowns were 32.0% deeper, their leaves were 10.5% thicker, their internodes were 27.3% longer, and their petioles were 111.2% longer than trees (Table 2, Fig. 5A–D). Tree leaf angles were 3.9% greater, and they had 9.2% greater SLA than lianas (Table 2, Fig. 5E, F). Tree crowns were only marginally larger than liana crowns (12.9%,  $P = 0.024$ ; Table 2). Surprisingly, light availability ( $T_{tot}$ ) had little impact on seedling architecture, except for SLA (Table 2). Species within growth forms differed significantly in seedling architecture (Table 2). Liana seedlings averaged  $28.2 \pm 0.9$  cm in height and tree seedlings

averaged  $29.6 \pm 1.0$  cm in height (overall seedling height was  $28.9 \pm 0.7$  cm).

Adding nutrients alone or in combination caused very few significant changes in seedling morphology (Table 2, Fig. 6A, B). Specifically, adding K caused a significant but small increase (6.5%) in SLA, and P alone and K alone caused marginally significant but fairly substantial increases in leaf angle (P, 10.6%,  $P = 0.046$ ; K, 10.0%,  $P = 0.042$ ; Table 2). If these results were additive for P and K, then adding P and K together should have caused an even greater increase in leaf angle; however this did not occur. Instead, leaf angles were close to control levels when P and K were added together (significant  $P \times K$  interaction; Table 2, Fig. 6B). We did detect one case where nutrient additions caused the opposite response between lianas vs. trees; P addition caused petiole length to increase (15.6%) for lianas but decrease (15.7%) for trees (significant growth form  $\times$  P interaction; Table 2, Fig. 7). Nonetheless, the strong signal here is that nutrient amendments had little impact on seven different metrics of seedling morphology. For the effects of all nutrient treatment combinations on the architectural traits of trees vs. lianas, see Appendix C: Figs. C3 and C4.

#### DISCUSSION

To our knowledge, this is the first study to demonstrate that the early seedling stages of common species of lianas substantially outperform (from 14% to 21%) common species of trees for three key photosynthetic metrics regardless of macronutrient availability. Increasing nutrient supply rates for P alone increased the performance of both lianas and tree seedlings to a similar degree, but adding K with P dragged this

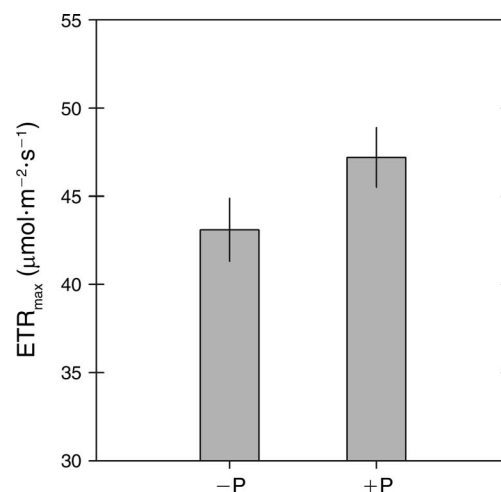


FIG. 3. Significant (FDR-corrected  $P < 0.0237$ ) main effect of P addition for  $ETR_{max}$ . Liana and tree seedlings are pooled; bars represent means  $\pm$  SE,  $N=16$  plots. Treatments without P (–P; C, N, K, and NK) and treatments with P (+P; P, NP, PK, and NPK) are also pooled.

performance benefit down. Regardless, the take home message here is that long-term nutrient amendments never benefited lianas more than trees for any macronutrient or any macronutrient combination. Also, and somewhat surprisingly, N addition never caused any significant change in any physiological or morphological metric. In addition, we were surprised that lianas and trees were architecturally quite different from each other even during the free-standing seedling stages when they appear morphologically quite similar (Table 2, Fig. 5A–F; Putz 1983). Nutrient enrichment did not change this in any way. Thus, these early morphological differences were robust and did not change even under long-term and sharply contrasting soil nutrient supply rates. We suggest that our findings are broadly applicable because we studied a phylogenetically diverse array of 13 species from 13 families. Overall, our findings demonstrate that liana seedlings growing in deep shade are always capable of higher photosynthetic performance than tree seedlings under ambient light levels and under sharply contrasting levels of macronutrients (e.g., N vs. P vs. K) or under ambient nutrient levels. Thus, the advantage of having a liana growth habit occurs very early ontogenetically prior to any use of a trellis for support. Our results provide strong evidence that P limits photosynthetic performance of seedlings of both trees and lianas in deeply shaded understory habitats.

*P limits photosynthetic performance but P and K together do not*

Adding P caused a significant increase in one of three measures of photosynthetic performance ( $ETR_{max}$ ; Table 1, Figs. 3 and 4A) and a marginally significant increase in a second measure ( $q_p$ ; Table 1, Fig. 4B). Adding K also increased photosynthetic performance, but this increase was never significant (Table 1, Fig. 4A–C). Surprisingly adding P and K together decreased photosynthetic performance relative to the addition of P alone (significant  $P \times K$  interaction) when it should have caused an increase in performance if the effect of each macronutrient alone was additive (Table 1, Fig. 4A–C). While the mechanistic basis of this is not clear, we suggest that it is likely linked to alterations in stomatal control that occur with additions of K.

Our results build on past studies that demonstrated that soil resources limit plant performance even in deeply shaded habitats (Cai et al. 2008, Kaspari et al. 2008), but here we identify which macronutrients were limiting or co-limiting. P addition enhanced  $ETR_{max}$  because P is known to increase biochemical efficiency of the light reactions of photosynthesis and promote enhanced carbon assimilation rates (Kirschbaum and Tompkins 1990, Raaimakers et al. 1995). Previous studies at this site demonstrate unequivocally that multiple soil resources co-limit trees in deep shade and we extend these results to seedlings of lianas. Thus, even a growth form that is quite light demanding and fast growing can still be limited by soil resources when light

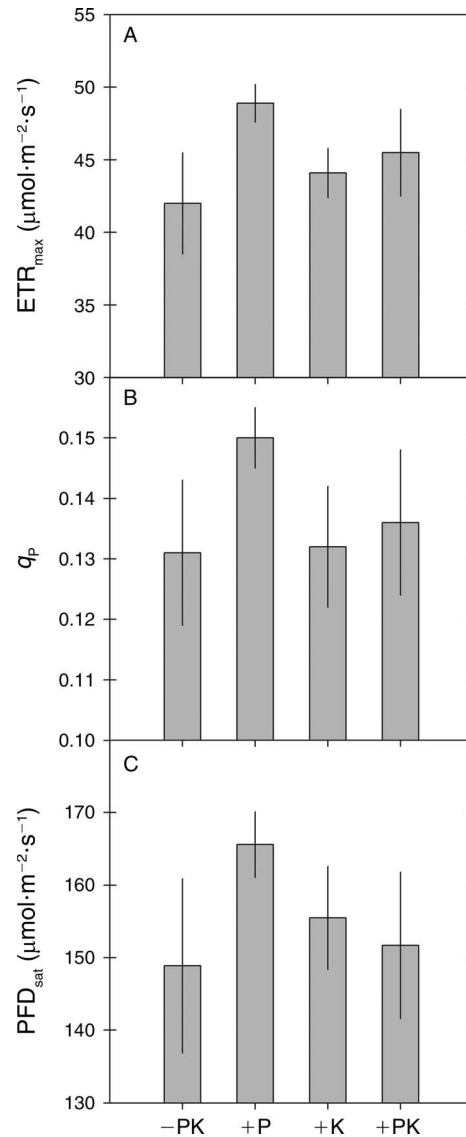


FIG. 4. Significant (FDR-corrected  $P < 0.0237$ )  $P \times K$  interactions for (A)  $ETR_{max}$ , (B)  $q_p$ , and (C)  $PFD_{sat}$ ; see Fig. 2 for definitions. Liana and tree seedlings are pooled. Treatments without P or K (–PK; C and N), P treatments (+P; P and NP), K treatments (+K; K and NK), and treatments with both P and K (+PK; PK and NPK) are also pooled. Bars represent means  $\pm$  SE,  $N = 8$  plots.

is at very low levels. We could not detect any impact of N additions on physiological performance. Nonetheless, N, P, K,  $P \times K$ ,  $N \times P$ , and  $N \times K$  all have been shown at times to limit physiological performance, growth rate, or both, among woody species (this study, Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Still, our results strongly point to P as the key limiting or co-limiting soil resource within the understory. Overall, we demonstrate that light can no longer be considered the only limiting resource in deeply shaded tropical habitats.

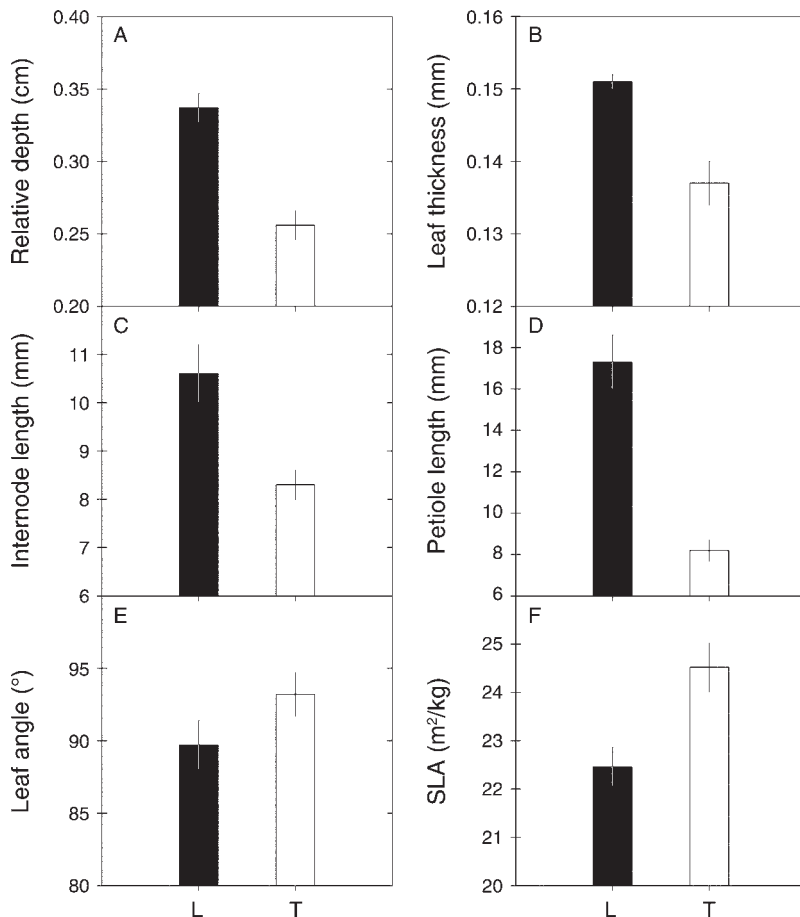


FIG. 5. Significant (FDR-corrected  $P < 0.0115$ ) main effects of growth form for (A) relative crown depth, (B) leaf thickness, (C) internode length, (D) petiole length, (E) leaf angle, and (F) specific leaf area (SLA). See Fig. 2 for arrangement of graphs.

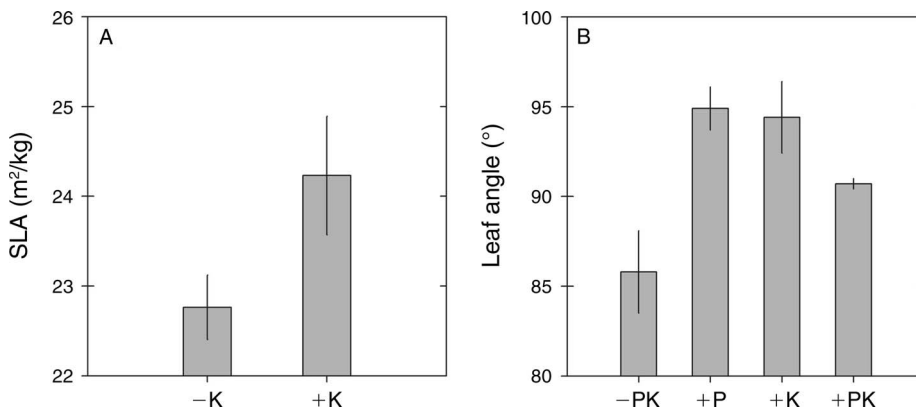


FIG. 6. Significant (FDR-corrected  $P < 0.0115$ ) (A) main effect of K for SLA and (B) interaction of  $P \times K$  for leaf angle. Lianas and tree seedlings are pooled. Panel (A) represents a significant main effect of K, where treatments without K (-K; C, N, P, and NP) and treatments with K (+K; K, NK, PK, and NPK) are pooled ( $N = 16$  plots). Panel (B) represents a significant  $P \times K$  interaction where treatments without P or K (-PK; C and N), P treatments (+P; P and NP), K treatments (+K; K and NK), and treatments with both P and K (+PK; PK and NPK) are pooled ( $N = 8$  plots). Bars represent means  $\pm$  SE.



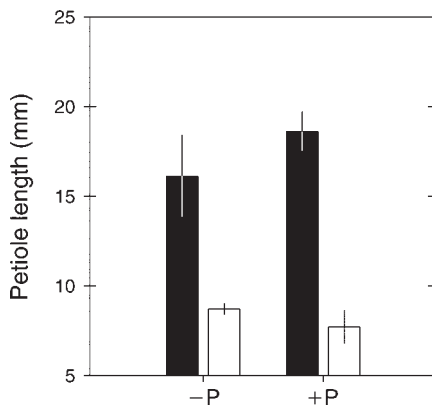


FIG. 7. Significant (FDR-corrected  $P < 0.0115$ ) interaction of  $P \times$  growth form for petiole length. Lianas and trees are represented by solid and open bars, respectively. Treatments without P (-P; C, N, K, and NK) and treatments with P (+P; P and PK, NP, and NPK) are pooled by growth form. Bars represent means  $\pm$  SE,  $N = 16$  plots.

#### *Liana and tree seedling architectures are markedly different*

Lianas are classified as a separate growth form from trees because they are structural parasites and require trellises to reach the canopy. Nonetheless, it was unknown whether key architectural traits contrast between seedlings of lianas and trees prior to lianas acquiring a trellis and prior to sending up searcher shoots. Here, counter to conventional wisdom, we show that liana seedlings differ for a suite of architectural traits. Nutrient additions rarely caused changes in any of these traits, at least while these seedlings were in deep shade. Thus, differences in liana architecture are expressed before lianas have located a trellis or before they rapidly increase growth rates under conditions of higher light availability (Den Dubbelden and Oosterbeek 1995). The height at which lianas begin to utilize external support is usually between 30 and 40 cm in lowland tropical forests of Southeast Asia and Latin America (Putz and Holbrook 2009). The average height of seedlings used in this study (29.1 cm) was close to this range, but all study individuals were self-supporting.

We found that lianas had significantly lower SLA and thicker leaves compared to trees (Table 2, Fig. 5B and F); in contrast, lianas that have reached the canopy typically have significantly higher SLA and thinner leaves than trees (Lambers and Poorter 1992, Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015). Thus, ontogenetic trait shifts appear to be occurring for these important leaf structural traits. Leaves with low SLA are more costly to build and high SLA is a characteristic of fast-growing plants (Lambers and Poorter 1992, Baruch and Goldstein 1999). Low SLA is also associated with both reduced susceptibility to herbivores (Poorter et al. 2009) and increased leaf lifespan (I. J. Wright et al. 2004). Low SLA and thick leaves of liana seedlings may allow them

to persist for long periods in the understory until they can access the canopy.

#### *The physiology of lianas and their increase in Neotropical forests*

There is compelling evidence that lianas are increasing in Neotropical forests (e.g., Schnitzer [2015] and citations therein). Here, we demonstrate that a phylogenetically diverse group of lianas had enhanced physiological performance compared to a phylogenetically diverse group of tree species (Table 1, Fig. 2A–C). Thus, our findings extend previous research that found greater performance ( $A_{\max}$ ) by canopy-level lianas (Zhu and Cao 2009, 2010, Han et al. 2010, Asner and Martin 2012, Santiago et al. 2015) to very early seedling stages in the understory. We also demonstrated greater  $q_P$  in liana seedlings relative to tree seedlings (Table 1, Fig. 2B), which suggests that lianas are able to maximize the amount of incoming solar radiation utilized for photosynthesis. This would confer an advantage in photosynthetic carbon assimilation to lianas in rapidly changing light conditions seen in the understory due to short, high-intensity sunflecks (Chazdon 1988, Percy 1988). Overall our results suggest that any changes in fertility, whether natural or anthropogenic, will not disproportionately favor lianas because lianas already outperform trees regardless of fertility, and lianas and trees responded similarly to nutrient additions (only one significant growth form by nutrient interaction; Tables 1 and 2). Thus our results do not support nutrient loading as a mechanism of increasing liana abundance in the Neotropics. Rather, our finding that lianas always outperform trees under sharply contrasting rates of

TABLE 1. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on leaf physiological traits for liana and tree seedlings.

Effects	$ETR_{\max}$	$q_P$	$PFD_{\text{sat}}$
Form	<b>0.0003</b>	<b>&lt;0.0001</b>	<b>0.0006</b>
Species (form)	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
$T_{\text{tot}}$	<b>0.0012</b>	<b>&lt;0.0001</b>	<b>0.0014</b>
N	0.8286	0.3554	0.9483
P	<b>0.0129</b>	0.0333	0.3415
K	0.5808	0.1896	0.4405
N $\times$ P	0.0552	0.2328	0.1382
N $\times$ K	0.6880	0.9682	0.6790
P $\times$ K	<b>0.0079</b>	<b>0.0112</b>	<b>0.0126</b>
N $\times$ form	0.1400	0.3081	0.4305
P $\times$ form	0.6397	0.1915	0.7753
K $\times$ form	0.9657	0.6398	0.9068
Sample size	394	393	394

Notes: Traits include maximum electron transport rate ( $ETR_{\max}$ ;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), photochemical quenching ( $q_P$ ; unitless), and saturating photon flux density ( $PFD_{\text{sat}}$ ;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Data presented are  $P$  values for fixed effects. Values in boldface type are statistically significant using the family discovery rate (FDR) corrected  $P$  value ( $P < 0.0237$ ). Form refers to liana vs. tree. Total light transmission ( $T_{\text{tot}}$ ) refers to proportion of above-canopy ambient light transmitted through canopy.

TABLE 2. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on morphological traits for liana and tree seedlings.

Effect	Crown depth (cm)	Crown area (cm <sup>2</sup> )	Leaf thickness (mm)	Leaf angle (°)	Internode length (mm)	Petiole length (mm)	SLA (m <sup>2</sup> /kg)
Form	< <b>0.0001</b>	0.0239	< <b>0.0001</b>	<b>0.0066</b>	<b>0.0028</b>	< <b>0.0001</b>	< <b>0.0001</b>
Species (form)	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>
<i>T</i> <sub>tot</sub>	0.9091	0.7875	0.6700	0.2957	0.6846	0.3155	<b>0.0099</b>
N	0.4538	0.3545	0.5213	0.2738	0.4407	0.2033	0.3867
P	0.0850	0.3086	0.2669	0.0461	0.4054	0.9743	0.6409
K	0.4931	0.5922	0.8357	0.0420	0.4519	0.2500	<b>0.0007</b>
N × P	0.6973	0.2865	0.7166	0.2418	0.0295	0.8915	0.1889
N × K	0.9349	0.5107	0.1359	0.3454	0.5180	0.0793	0.1729
P × K	0.8540	0.8786	0.2692	<b>0.0002</b>	0.8828	0.4362	0.1663
N × form	0.1443	0.0673	0.9326	0.7639	0.9454	0.8491	0.4990
P × form	0.6641	0.0879	0.6836	0.1787	0.5860	<b>0.0091</b>	0.0975
K × form	0.9091	0.1972	0.9299	0.9715	0.2206	0.0901	0.0710
Sample size	388	390	381	382	383	390	393

Notes: Data presented are *P* values for fixed effects. Values in boldface type are statistically significant using the FDR-corrected *P* value (*P* < 0.0115). Crown depth and area are both relative to height, leaf angle is measured with regard to the main stem, and SLA stands for specific leaf area.

resource supply of macronutrients or their combination will allow lianas to increase in abundance if disturbance rates are increasing in Neotropical forests as some have suggested (Phillips et al. 2004). Moreover, an increase in liana abundance will likely lead to lower forest-wide storage of carbon because lianas often displace trees and only replace 24% of the biomass (Schnitzer et al. 2014).

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1660.1.sm>