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

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12 **Abstract**

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

35 resource supply of macronutrients, will allow lianas to increase in abundance if disturbance and
36 tree turnover rates are increasing in Neotropical forests as has been suggested.

37

38 Keywords: Barro Colorado Nature Monument, Panama; Chlorophyll Fluorescence; Fertilization;
39 Neotropics; Nitrogen; Nutrient Limitation; Phosphorus; Photosynthetic Performance; Plant
40 Architecture; Plant Morphology; Potassium; Tropical Forest

41

42 **Introduction**

43 Lianas and trees are the two dominant plant growth forms in tropical forests and there is a
44 growing body of evidence suggesting that lianas are increasing relative to trees in Neotropical
45 forests (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright, S. J. et al.
46 2004, Chave et al. 2008, Foster et al. 2008, Schnitzer and Bongers 2011, Yorke et al. 2013,
47 Schnitzer 2015). We are not sure why. Regardless, these increases in liana abundance will
48 almost certainly have important consequences for forest biodiversity and global carbon budgets
49 (Bunker et al. 2005, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Schnitzer et al.
50 2014). Indeed, Schnitzer and Carson (2010) and Schnitzer et al. (2014) demonstrated
51 unequivocally that when lianas increase in abundance and displace trees, forest-wide above-
52 ground carbon storage can be reduced by as much as 18%. While exceptions exist, lianas are
53 typically a fast-growing, light-limited growth form associated with high-light, nutrient-rich, and
54 disturbed habitats, including forest edges, canopy gaps, and logged forests (Putz 1984, Schnitzer
55 et al. 2000, Schnitzer and Carson 2010). Moreover, they can represent more than a third of all
56 woody species in tropical forests (Pérez-Salicrup et al. 2001, Gentry 2009, Schnitzer et al. 2012).

57 Lianas differ from trees in critical patterns of biomass allocation and other key life
58 history traits. For example, in their climbing form, lianas rely on other vegetation as trellises to

59 gain access to the canopy, and thus they typically invest proportionally less resources into woody
60 stem tissue than trees, and proportionally more resources toward leaves and roots (Putz 1983,
61 Suzuki 1987, Castellanos et al. 1989, Niklas 1994, Gerwing and Farias 2000, Hättenschwiler
62 2002, Santiago and Wright 2007). This biomass allocation pattern of canopy-level lianas (lianas
63 with at least partial foliage in the forest canopy) results in lianas having greater specific leaf area
64 (SLA) and photosynthetic rates (A_{\max}) than trees (Zhu and Cao 2009, Han et al. 2010, Zhu and
65 Cao 2010, Asner and Martin 2012, Santiago et al. 2015). The abundance of canopy-level lianas
66 often increases with soil fertility (e.g., Proctor et al. 1983, Putz 1983, 1985, Putz and Chai 1987,
67 Balfour and Bond 1993, Bruijnzeel and Proctor 1995) and lianas show higher foliar nutrient
68 concentrations compared to trees (Cai and Bongers 2007, Kusumoto and Enoki 2008, Zhu and
69 Cao 2010, Asner and Martin 2012). This suggests that canopy-level lianas are far more nutrient-
70 limited than trees, yet the few *in situ* experimental nutrient enrichment studies available have
71 found either modest support for this (Hättenschwiler 2002) or no differences at all between the
72 life forms (Cai et al. 2008).

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

82 While light may be the most limiting resource in tropical forest understory habitats, it has
83 recently become clear that seedlings of some woody species are also co-limited by soil nutrients.
84 Limitation varies among species (Denslow et al. 1987) and among soil resources including
85 nitrogen (N), phosphorus (P), or potassium (K) and in some cases limitation is caused
86 simultaneously by multiple soil resources (Bloom et al. 1985, Ceccon et al. 2004, Holste et al.
87 2011, Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Indeed, recent work
88 on the tree seedling, *Alseis blackiana* (Helms.; Rubiaceae), demonstrated that photosynthesis,
89 stomatal conductance, and photosynthetic yield were limited by N, P, and K, respectively, even
90 in deep shade (Pasquini and Santiago 2012). In a separate study at the same site K limited tree
91 seedling growth (Santiago et al. 2012). For liana seedlings, however, both the degree of nutrient
92 limitation, as well as whether liana seedlings are more or less limited by soil resources than tree
93 seedlings, remains unknown.

94 Here we test the hypothesis *in situ* that nutrients limit photosynthetic physiology of liana
95 seedlings to a greater degree than tree seedlings. If lianas and trees differ, we would demonstrate
96 that in spite of their apparent similarities in seedling morphology, physiological divergence
97 happens early in ontogeny, and if not, then physiological differences must develop after they find
98 a trellis and begin ascending into the canopy. Furthermore, testing our hypothesis may provide
99 insight into the underlying mechanism for the increase in lianas in many Neotropical forests.
100 Nutrient deposition, particularly of nitrogen, is increasing throughout the tropics (reviewed by
101 Hedin et al. 2009, Hietz et al. 2011), tree turnover rates also appear to be increasing (Phillips et
102 al. 2004) as are rates of human disturbances and deforestation (e.g., reviewed by Laurance 2008,
103 Wright 2010). All of these are likely to favor lianas particularly if they gain an advantage early
104 in ontogeny.

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

118

119 **Materials and Methods**

120

Study site

121 We performed this research in seasonally moist, semi-deciduous, tropical forest located
122 on the Gigante Peninsula (9°06'31" N, 79°50'37" W) within the Barro Colorado Nature
123 Monument (BCNM) in central Panama (Appendix A: Fig. A1). The dry season occurs between
124 January and April during which less than 10% of the 2600 mm of average annual rainfall occurs.
125 Our investigation took place from March through April 2010. Soils on the Gigante Peninsula are
126 Oxisols and Inceptisols similar to Typic Eutrudox soils on adjacent Barro Colorado Island
127 (Turner et al. 2012, B. L. Turner personal communication). In terms of N, P, and K availability,

128 soils at this site are relatively fertile for lowland tropical soils (Yavitt et al. 2009, Wright et al.
129 2011). Tree composition and stature (tree heights up to 45 m) in this forest are characteristic of
130 mature (> 200 y) tropical secondary forest in central Panama (Wright et al. 2011).

131 *Experimental design*

132 We used a long-term nutrient addition experiment where N, P, and K have been added in
133 a full $2 \times 2 \times 2$ factorial design with 4 replicates of each of 8 treatments (control, N, P, K, NP,
134 NK, PK, NPK). The 4 replicates were placed perpendicular to a slight topographical gradient
135 (36 m in elevation from southwest to northeast corner of site) because tree distributions and soil
136 properties parallel this gradient (Yavitt et al. 2009, Wright et al. 2011). We used a balanced,
137 incomplete-block design, where N, P, K, and NPK treatments were blocked versus NP, NK, PK,
138 and control treatments within each replicate (Wright et al. 2011, Pasquini and Santiago 2012,
139 Santiago et al. 2012). This design minimizes uncontrolled error due to spatial heterogeneity and
140 allows evaluation of main effects and two-way interactions, but limits power to evaluate the
141 three-way interaction (Winer et al. 1991). Nutrients were added 4 times annually during the wet
142 season for a total of $125 \text{ kg N ha}^{-1} \text{ y}^{-1}$ as coated urea $[(\text{NH}_2)_2\text{CO}]$, $50 \text{ kg P ha}^{-1} \text{ y}^{-1}$ as triple super
143 phosphate $[\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}]$ and $50 \text{ kg K ha}^{-1} \text{ y}^{-1}$ as potassium chloride (KCl) starting in 1998
144 (12 years of nutrient addition). The 32 experimental plots were each $40 \times 40 \text{ m}$ in area and were
145 separated by at least 40 m to minimize nutrient leaching into neighboring plots, with the
146 exception of two plots separated by 20 m and located on opposite sides of a 3-m deep stream. In
147 this same study site, long-term N fertilization lead to increased soil acidity (0.8 unit decrease in
148 soil pH; Corre et al. 2010), which may affect availability of P and other soil nutrients.

149 *Species*

150 We selected seven liana and six tree species from 13 plant families because they were
151 common in the study plots. The seven lianas were *Bauhinia guianenses* Aubl. (Fabaceae –
152 Caesalpinioideae), *Coccoloba parimensis* Benth. (Polygonaceae), *Doliocarpus dentatus* (Aubl.)
153 Standl. (Dilleniaceae), *Maripa panamensis* Hemsl. (Convolvulaceae), *Paullinia fibrifera* Radlk.
154 (Sapindaceae), *Phryganocydia corymbosa* (Vent.) Bureau ex. K. Schum (Bignoniaceae) and
155 *Prionostemma aspera* (Lam.) Miers. (Celastraceae). The trees were *Alseis blackiana* Hemsl.
156 (Rubiaceae), *Desmopsis panamensis* (B. L. Rob.) Saff. (Annonaceae), *Heisteria concinna* Standl.
157 (Olacaceae), *Oenocarpus mapora* H. Karst. (Arecaceae), *Sorocea affinis* Hemsl. (Moraceae) and,
158 *Tetragastris panamensis* (Engler) Kuntze (Bursaceae). Nomenclature follows Garwood
159 (2009). Individual seedlings were chosen haphazardly based on the first sightings of the study
160 species within each plot. All liana seedlings were self-supporting (free-standing) and did not
161 exhibit searcher shoots (*sensu* Putz and Holbrook 2009).

162 *Physiological measurements*

163 Chlorophyll fluorescence measurements were used because they are highly correlated
164 with carbon assimilation rates (especially maximum electron transport, Maxwell and Johnson
165 2000) and we confirmed this relationship for one of our focal species (*Alseis blackiana*; Pasquini
166 and Santiago 2012). We measured chlorophyll fluorescence of mature, fully expanded leaves
167 using a photosynthesis yield analyzer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany).
168 We sampled one leaf from one individual of the 13 species in each of the 32 plots (mean leaves
169 sampled per plot = 12.4, total leaves sampled = 397). We constructed chlorophyll fluorescence
170 light response curves using photon flux density (PFD) values of 0, 34, 97, 202, 324, 499, 700,
171 1067 and 1471 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to slowly bring the light level up to the highest light level. We
172 measured the electron transport rate (ETR), which is an *in vivo* measure of overall capacity to

173 provide energy to photosynthetic carboxylation reactions. We also measured photochemical
174 quenching (q_p). q_p is the proportion of open photosystem II (PSII) reaction centers and is a proxy
175 of the efficiency of PSII. We obtained the maximum electron transport rate (ETR_{max}) and q_p at
176 the highest light level ($PFD = 1471 \mu\text{mol m}^{-2} \text{s}^{-1}$). ETR was determined as:

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

177
178
179
180 where F'_m is maximal fluorescence measured by a saturation pulse at each light level and F_s is
181 steady-state fluorescence. f is a factor that represents the partitioning of photons between
182 photosystems II and I (PSII and PSI) and is assumed to be 0.5, which indicates equal distribution
183 of excitation energy between the two photosystems (Maxwell and Johnson 2000), and α
184 represents the fraction of photons absorbed by a leaf and is assumed to be 0.84 as an average for
185 a variety of C_3 leaves (Björkman and Demmig 1987, Stemke and Santiago 2011).

186 Photochemical quenching was determined as:

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

187
188
189
190 where F'_0 is minimum fluorescence of each illuminated sample determined during a brief dark
191 interval following a saturation pulse (see Fig. 1 for an example of a fluorescence light response
192 curve).

193 *Morphological measurements*

194 We measured leaf angle, leaf thickness, internode length, and petiole length to
195 characterize seedling morphology. Crown depth, perpendicular crown widths, and seedling

196 height were measured and used to calculate crown depth and crown area, relative to height. Leaf
197 angle was measured using a protractor with a weighted thread as the angle of the leaf measured
198 along the midvein from petiole attachment to leaf tip where a 90° leaf angle is parallel to the
199 ground and perpendicular to the main stem (leaf angle > 90° indicates that leaf at an obtuse angle
200 relative to the ground). We measured leaf thickness on an area of the leaf without major veins
201 using a digital micrometer (IP 65, Mitutoyo Corp., Mizonokuchi, Japan). Additionally, one leaf
202 from each seedling was collected and measured for leaf area (leaf petiole was removed) using a
203 leaf area meter (LI-3100, Li-Cor Biosciences, Inc., Lincoln, Nebraska, USA). Leaves were then
204 oven dried at 60°C for 48 hours and weighed to determine SLA.

205 *Light availability*

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

212 *Data analyses*

213 We analyzed ETR light response curves for saturating photon flux density (PFD_{sat}) using
214 Photosyn Assistant (version 1.1, Dundee Scientific, Dundee, UK) as described by Prioul and
215 Chartier (1977). Hemispheric canopy photographs were analyzed for total light transmittance
216 (T_{total} ; proportion of above-canopy ambient) using Gap Light Analyzer (Frazer et al. 1999). We
217 used a general linear model in SAS (proc glm; version 9.2, SAS Institute Inc., Cary, North
218 Carolina, USA) to determine whether liana and tree seedlings overall were found in differing

219 light environments. Physiological and morphological data were analyzed by mixed linear
220 models in SAS (proc mixed). The mixed linear model procedure was used rather than general
221 linear model procedure to yield Akaike Information Criterion (AIC) values for each model.
222 Models were run on individual leaf physiological and morphological measures with fixed main
223 effects of form (liana versus tree), species nested within form, single nutrient main effects (N, P,
224 K), two-way nutrient interactions ($N \times P$, $N \times K$, $P \times K$), nutrient by growth form interactions (N
225 \times form, $P \times$ form, $K \times$ form), and T_{total} (to control for heterogeneity of the light environment).
226 Random effects were statistical replicate (Rep) and block nested within replicate. For similar
227 analyses see Pasquini and Santiago (2012) and Wright et al. (2011). Models that included effects
228 of species as well as growth form were compared using AIC values (Appendix B: Tables B1-
229 B6). Standard data transformations (natural log, square root, and arcsine) were performed to
230 meet the assumption of normality as determined by the Shapiro-Wilk W -statistic. T_{total} are
231 proportional data and were logit transformed accordingly (Warton and Hui 2011). To control for
232 type I error (α -error) in the multiple comparisons we used Family Discovery Rate (FDR)
233 corrections described by Pike (2011) to adjust significant P -values; FDR corrected values are
234 reported in the notes associated with each table.

235

236 **Results**

237

Model selection

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

242 *Physiological indices of performance*

243 Lianas performed substantially better than trees for all physiological metrics (14-21%
244 greater; Table 1, Fig. 2A-C). As expected, seedling photosynthetic performance was affected by
245 light availability (T_{total} ; Table 1) and thus it is important to note that mean understory light
246 availability did not differ between liana and tree seedlings (Lianas: $6.0 \pm 0.6\%$ SE, Trees: $5.8 \pm$
247 0.7% SE, $F_{1,395} = 0.08$, $P = 0.78$; Appendix C: Fig. C1). In addition, species within growth
248 forms differed significantly in physiological performance (Table 1).

249 Nutrient additions, especially P alone enhanced photosynthetic physiology, whereas N or
250 K addition never did. P addition increased ETR_{max} by 9.6% (Table 1, Fig. 3). P addition also
251 caused a marginally significant increase in q_P (8.8%, $P = 0.033$; Table 1). Surprisingly, when K
252 was added in combination with P it decreased the benefit to performance caused by adding P
253 alone as indicated by consistent significant $P \times K$ interactions (Table 1, Fig. 4A-C).
254 Specifically, P and K together decreased the benefit of adding P alone for ETR_{max} , PFD_{sat} , and q_P
255 by 7.6%, 9.2%, and 10.2%, respectively (Table 1, Fig. 4A-C). Nutrient additions enhanced the
256 physiological performance of both lianas and trees to a similar degree (i.e., no significant
257 interaction between growth form and nutrient addition). For the effects of all nutrient treatment
258 combinations on the physiological responses of trees versus lianas see Appendix C (Fig. C2).

259 *Plant architectural traits*

260 Lianas and tree seedlings were significantly different from each other for *all but one*
261 *metric* of plant architecture (Table 2, Fig. 5A-F). Liana crowns were 32.0% deeper, their leaves
262 were 10.5% thicker, their internodes were 27.3% longer, and their petioles were 111.2% longer
263 than trees (Table 2, Fig. 5A-D). Tree leaf angles were 3.9% greater, and they had 9.2% greater
264 SLA than lianas (Table 2, Fig. 5E-F). Tree crowns were only marginally larger than liana

265 crowns (12.9%, $P = 0.024$; Table 2). Surprisingly, light availability (T_{total}) had little impact on
266 seedling architecture except for SLA (Table 2). Species within growth forms differed
267 significantly in seedling architecture (Table 2). Liana seedlings averaged 28.2 ± 0.9 cm in height
268 and tree seedlings averaged 29.6 ± 1.0 cm in height (overall seedling height was 28.9 ± 0.7 cm).

269 Adding nutrients alone or in combination caused very few significant changes in seedling
270 morphology (Table 2, Fig. 6A-B). Specifically adding K caused a significant but small increase
271 (6.5%) in SLA, and P alone and K alone caused marginally significant but fairly substantial
272 increases in leaf angle (P: 10.6%, $P = 0.046$, K: 10.0%, $P = 0.042$; Table 2). If these results were
273 additive for P and K, then adding P and K together should have caused an even greater increase
274 in leaf angle; however this did not occur. Instead, leaf angles were close to control levels when P
275 and K were added together (significant $P \times K$ interaction; Table 2, Fig. 6B). We did detect one
276 case where nutrient additions caused the opposite response between lianas versus trees; P
277 addition caused petiole length to increase (15.6%) for lianas but decrease (15.7%) for trees
278 (significant growth form \times P interaction; Table 2, Fig. 7). Nonetheless, the strong signal here is
279 that nutrient amendments had little impact on seven different metrics of seedling morphology.
280 For the effects of all nutrient treatment combinations on the architectural traits of trees versus
281 lianas see Appendix C (Figs. C3 and C4).

282

283 **Discussion**

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

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

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

305 Adding P caused a significant increase in one of three measures of photosynthetic
306 performance (ETR_{max} ; Table 1, Fig. 3 and 4A) and a marginally significant increase in a second
307 measure (q_p ; Table 1, Fig. 4B). Adding K also increased photosynthetic performance, but this
308 increase was never significant (Table 1, Fig. 4A-C). Surprisingly adding P and K together
309 decreased photosynthetic performance relative to the addition of P alone (significant $P \times K$
310 interaction) when it should have caused an increase in performance if the effect of each

311 macronutrient alone was additive (Table 1, Fig. 4A-C). While the mechanistic basis of this is not
312 clear, we suggest that it is likely linked to alterations in stomatal control that occur with additions
313 of K.

314 Our results build on past studies that demonstrated that soil resources limit plant
315 performance even in deeply shaded habitats (Cai et al. 2008, Kaspari et al. 2008) but here we
316 identify which macronutrients were limiting or co-limiting. P addition enhanced ETR_{max} because
317 P is known to increase biochemical efficiency of the light reactions of photosynthesis and
318 promote enhanced carbon assimilation rates (Kirschbaum and Tompkins 1990, Raaimakers et al.
319 1995). Previous studies at this site demonstrate unequivocally that multiple soil resources co-
320 limit trees in deep shade and we extend these results to seedlings of lianas. Thus, even a growth-
321 form that is quite light-demanding and fast-growing can still be limited by soil resources when
322 light is at very low levels. We could not detect any impact of N additions on physiological
323 performance. Nonetheless, N, P, K, $P \times K$, $N \times P$ and $N \times K$ all have been shown at times to
324 limit physiological performance, growth rate, or both, among woody species (current study,
325 Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Still, our results strongly
326 point to P as the key limiting or co-limiting soil resource within the understory. Overall, we
327 demonstrate that light can no longer be considered the only limiting resource in deeply shaded
328 tropical habitats.

329 *Liana and tree seedling architecture are markedly different*

330 Lianas are classified as a separate growth form from trees because they are structural
331 parasites and require trellises to reach the canopy. Nonetheless, it was unknown whether key
332 architectural traits contrast between seedlings of lianas and trees prior to lianas acquiring a trellis
333 and prior to sending up searcher shoots. Here, counter to conventional wisdom, we show that

334 liana seedlings differ for a suite of architectural traits. Nutrient additions rarely caused changes
335 in any of these traits at least while these seedlings were in deep shade. Thus differences in liana
336 architecture are expressed before lianas have located a trellis or before they rapidly increase
337 growth rates under conditions of higher light availability (Den Dubbelden and Oosterbeek 1995).
338 The height at which lianas begin to utilize external support is usually between 30-40 cm in
339 lowland tropical forests of Southeast Asia and Latin America (Putz and Holbrook 2009). The
340 average height of seedlings used in this study (29.1 cm) was close to this range, but all study
341 individuals were self-supporting.

342 We found that lianas had significantly *lower* SLA and *thicker* leaves compared to trees
343 (Table 2, Fig. 5B and F); in contrast, lianas that have reached the canopy typically have
344 significantly *higher* SLA and *thinner* leaves than trees (Lambers and Poorter 1992, Cai et al.
345 2009, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015). Thus ontogenetic trait
346 shifts appear to be occurring for these important leaf structural traits. Leaves with low SLA are
347 more costly to build and high SLA is a characteristic of fast growing plants (Lambers and
348 Poorter 1992, Baruch and Goldstein 1999). Low SLA is also associated with both reduced
349 susceptibility to herbivores (Poorter et al. 2009) and increase leaf lifespan (Wright, I. J. et al.
350 2004). Low SLA and thick leaves of liana seedlings may allow them to persist for long periods
351 in the understory until they can access the canopy.

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

353 There is compelling evidence that lianas are increasing in Neotropical forests (e.g.,
354 Schnitzer 2015 and citations therein). Here we demonstrate that a phylogenetically diverse
355 group of lianas had enhanced physiological performance compared to a phylogenetically diverse
356 group of tree species (Table 1, Fig. 2A-C). Thus our findings extend previous research that

357 found greater performance (A_{\max}) by canopy-level lianas (Zhu and Cao 2009, Han et al. 2010,
358 Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015) to very early seedling stages in
359 the understory. We also demonstrated greater q_p in liana seedlings relative to tree seedlings
360 (Table 1, Fig. 2B), which suggests that lianas are able to maximize the amount of incoming solar
361 radiation utilized for photosynthesis. This would confer an advantage in photosynthetic carbon
362 assimilation to lianas in rapidly changing light conditions seen in the understory due to short,
363 high intensity sunflecks (Chazdon 1988, Pearcy 1988). Overall our results suggest that any
364 changes in fertility, whether natural or anthropogenic, will not disproportionately favor lianas
365 because lianas already outperform trees regardless of fertility and lianas and trees responded
366 similarly to nutrient additions (only one significant growth form by nutrient interaction, Tables 1
367 and 2). Thus our results do not support nutrient loading as a mechanism of increasing liana
368 abundance in the Neotropics. Rather, our finding that lianas always outperform trees under
369 sharply contrasting rates of resource supply of macronutrients or their combination will allow
370 lianas to increase in abundance if disturbance rates are increasing in Neotropical forests as some
371 have suggested (Phillips et al. 2004). Moreover, an increase in liana abundance will likely lead
372 to lower forest-wide storage of carbon because lianas often displace trees and only replace 24%
373 of the biomass (Schnitzer et al. 2014).

374

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Running head: Lianas always outperform trees (Pasquini et al.)

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- 583

584

APPENDIX A

585

Figure showing map of study area.

586

587

APPENDIX B

588

Mixed linear model results for the factorial, incomplete-block design comparing statistical model that includes species and statistical model that does not include species.

589

590

591

APPENDIX C

592

Figures showing the average of total transmission of light above liana and tree seedlings

593

used in study, and responses to full-factorial nitrogen, phosphorus, and potassium addition

594

compared to unfertilized controls for physiological and morphological traits.

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

	ETR _{max}	q _P	PFD _{sat}
Form	0.0003	<0.0001	0.0006
Species (Form)	<0.0001	<0.0001	<0.0001
T _{total}	0.0012	<0.0001	0.0014
N	0.8286	0.3554	0.9483
P	0.0129	0.0333	0.3415
K	0.5808	0.1896	0.4405
N × P	0.0552	0.2328	0.1382
N × K	0.6880	0.9682	0.6790
P × K	0.0079	0.0112	0.0126
N × Form	0.1400	0.3081	0.4305
P × Form	0.6397	0.1915	0.7753
K × Form	0.9657	0.6398	0.9068
Sample size	394	393	394

597 Data presented are *P*-values for fixed effects. Bolded values are statistically significant using the
 598 Family Discovery Rate (FDR) corrected *P*-value ($P < 0.0237$). Total light transmission (T_{total} ;
 599 proportion of above-canopy ambient), maximum electron transport rate (ETR_{max}; $\mu\text{mol m}^{-2} \text{s}^{-1}$),
 600 photochemical quenching (q_P ; unitless), and saturating photon flux density (PFD_{sat}; $\mu\text{mol m}^{-2} \text{s}^{-1}$).
 601 ¹).

Running head: Lianas always outperform trees (Pasquini et al.)

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

	Rel. depth	Rel. area	Thickness	Angle	Internode	Petiole	SLA
Form	<0.0001	0.0239	<0.0001	0.0066	0.0028	<0.0001	<0.0001
Species (Form)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
T_{total}	0.9091	0.7875	0.6700	0.2957	0.6846	0.3155	0.0099
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	0.0007
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	0.0002	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	0.0091	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

604 Data presented are P -values for fixed effects. Bolded values are statistically significant using the Family Discovery Rate (FDR)

605 corrected P -value ($P < 0.0115$). Total light transmission (T_{total} ; proportion of above-canopy ambient), relative crown depth (cm),

Running head: Lianas always outperform trees (Pasquini et al.)

606 relative crown area (cm^2), leaf thickness (mm), leaf angle (degrees from main stem), internode length (mm), petiole length (mm), and
607 specific leaf area (SLA; m^2/kg).

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608 **Figure Legends**

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

612

613 Fig. 2. Significant main effects of growth form for (A) maximum electron transport rate
614 (ETR_{max}), (B) photochemical quenching coefficient (q_p), and (C) saturating photon flux density
615 (PFD_{sat}). Lianas and trees are represented by L and black bars, and T and open bars,
616 respectively. All nutrient treatments are pooled. Bars represent means (± 1 SE, $N = 32$ plots).

617

618 Fig. 3. Significant main effect of P addition for maximum electron transport rate (ETR_{max}).
619 Liana and tree seedlings are pooled. Treatments without P (C, N, K, and NK) and treatments
620 with P (P, NP, PK, and NPK) are also pooled. Bars represent means (± 1 SE, $N = 16$ plots).

621

622 Fig. 4. Significant $P \times K$ interactions for (A) maximum electron transport rate (ETR_{max}), (B)
623 photochemical quenching coefficient (q_p), and (C) saturating photon flux density (PFD_{sat}). Liana
624 and tree seedlings are pooled. Treatments without P or K (C and N), P treatments (P and NP), K
625 treatments (K and NK) and treatments with both P and K (PK and NPK) are also pooled. Bars
626 represent means (± 1 SE, $N = 8$ plots).

627

628 Fig. 5. Significant main effects of growth form for (A) relative crown depth, (B) leaf thickness,
629 (C) internode length, (D) petiole length, (E) leaf angle, and (F) specific leaf area (SLA). Lianas
630 and trees are represented by L and black bars, and T and open bars, respectively. Bars represent

631 means (± 1 SE, $N = 32$ plots).

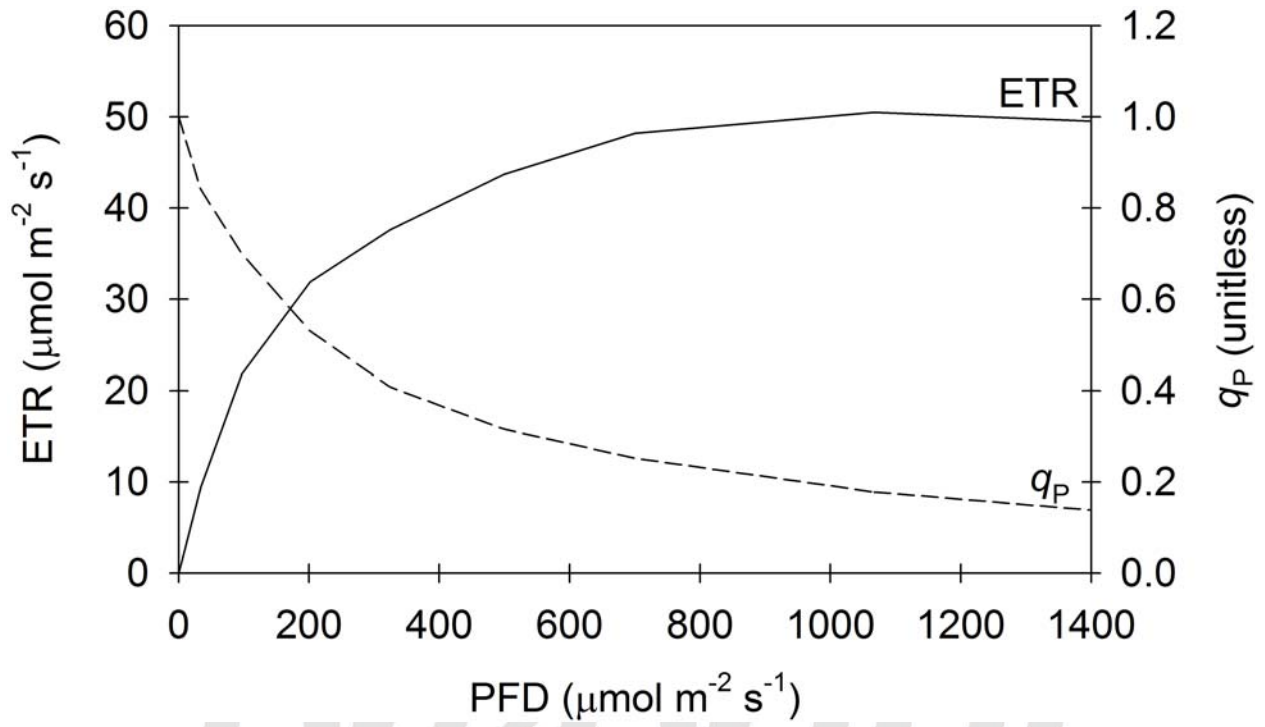
632

633 Fig. 6. Significant main effect of K for (A) specific leaf area (SLA) and significant interaction of
634 $P \times K$ for (B) leaf angle. Lianas and tree seedlings are pooled and represented by L and T,
635 respectively. Panel A represents a significant main effect of K, where treatments without K (C,
636 N, P, and NP) and treatments with K (K, NK, PK, and NPK) are pooled ($N = 16$ plots). Panel B
637 represents a significant $P \times K$ interaction where treatments without P or K (C and N), P
638 treatments (P and NP), K treatments (K and NK) and treatments with both P and K (PK and
639 NPK) are pooled ($N = 8$ plots). Bars represent means (± 1 SE).

640

641 Fig. 7. Significant interaction of $P \times$ growth form for petiole length. Lianas and trees are
642 represented by L and black bars, and T and open bars, respectively. Treatments without P (C, N,
643 K, and NK) and treatments with P (P and PK, NP and NPK) are pooled by growth form ($N = 16$
644 plots). Bars represent means (± 1 SE).

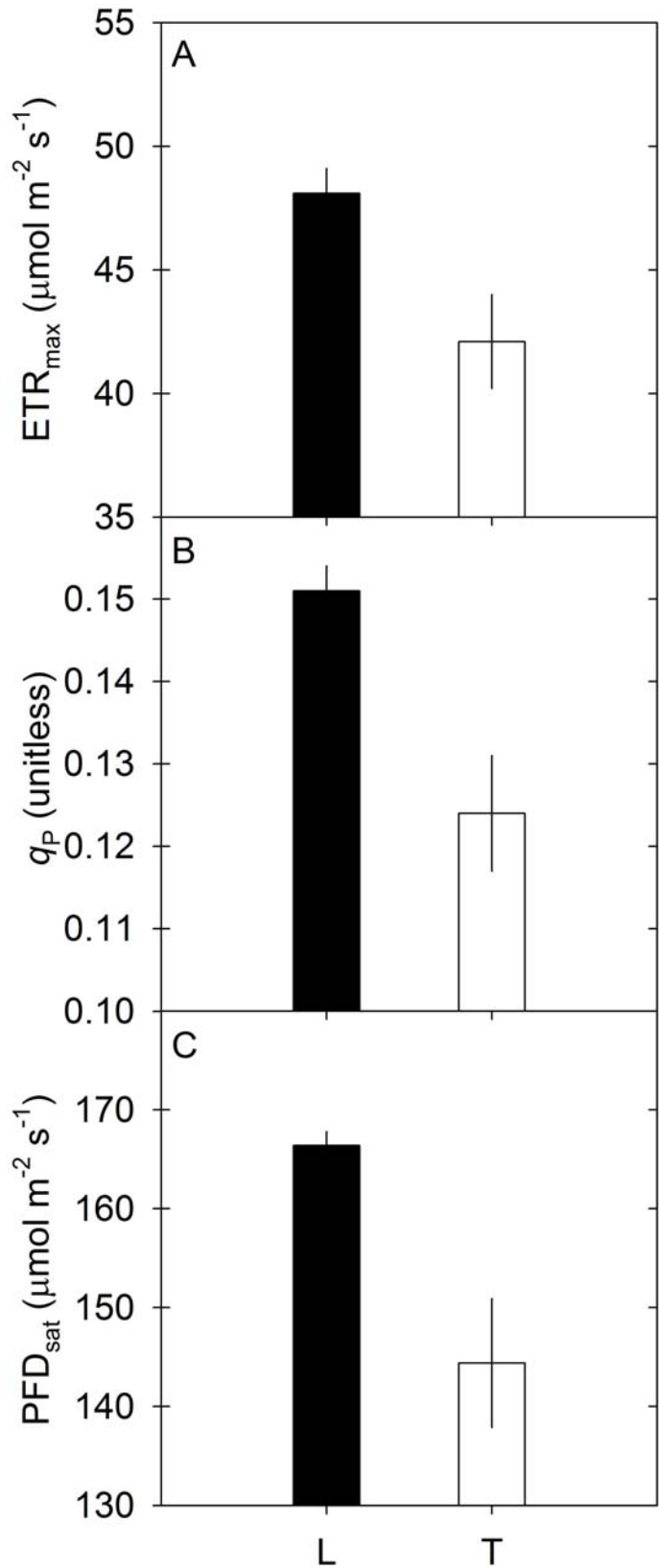
645 Figure 1



646

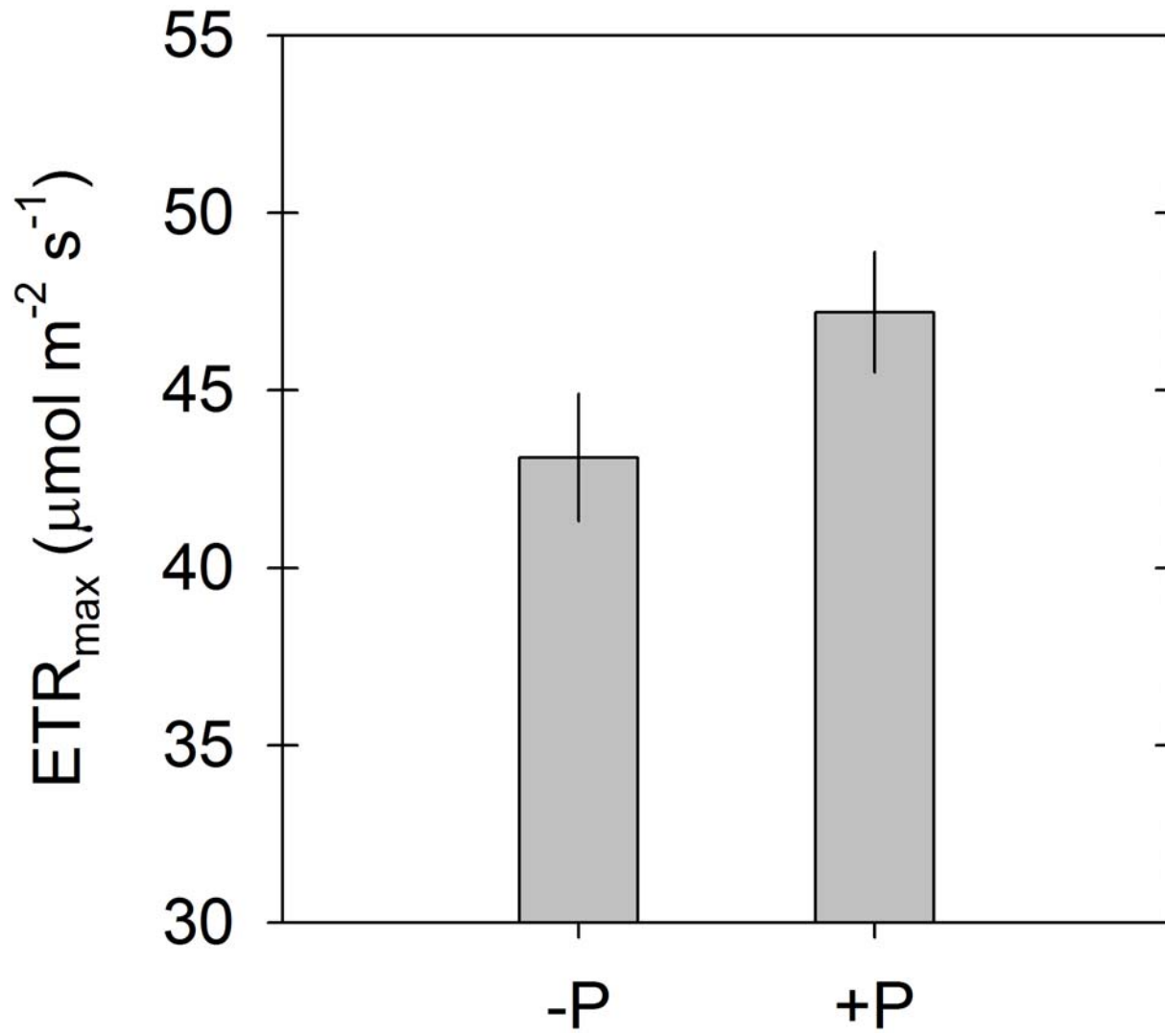
Preprint

647 Figure 2



648

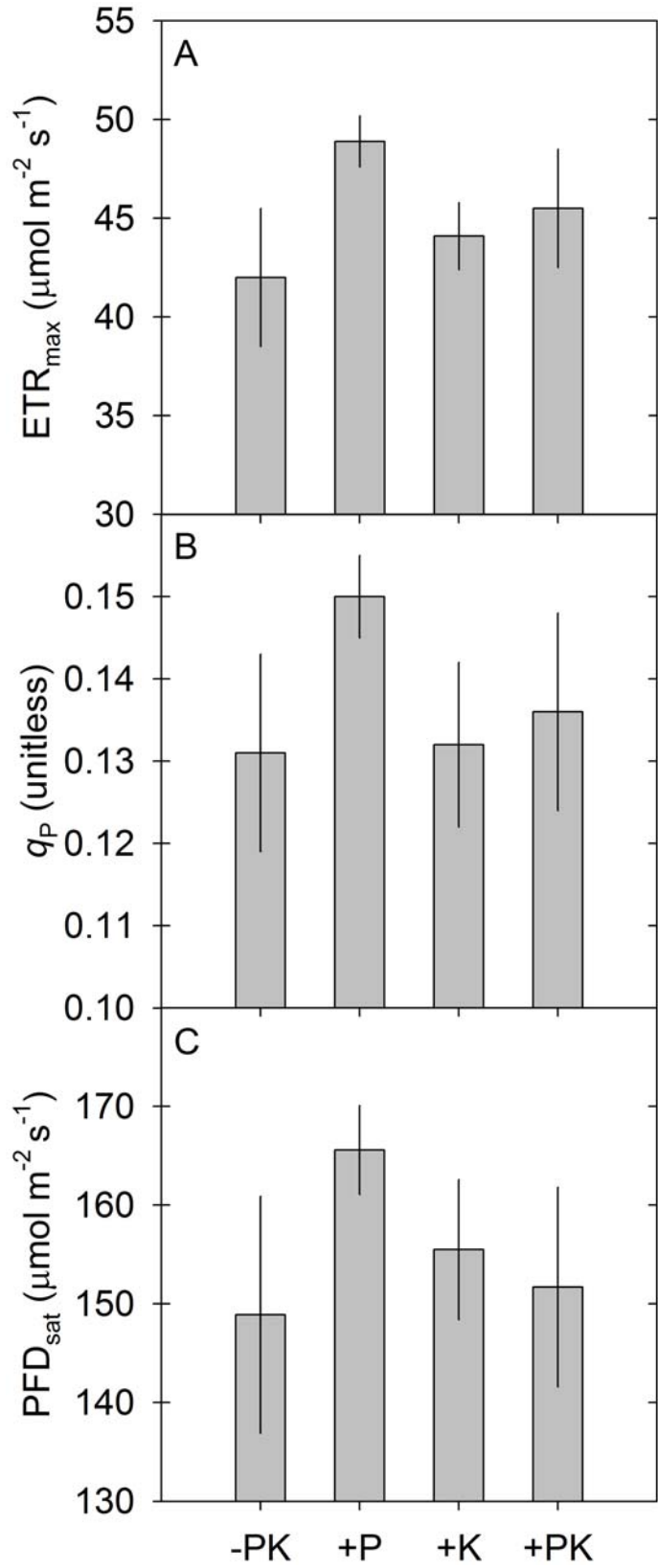
649 Figure 3



650

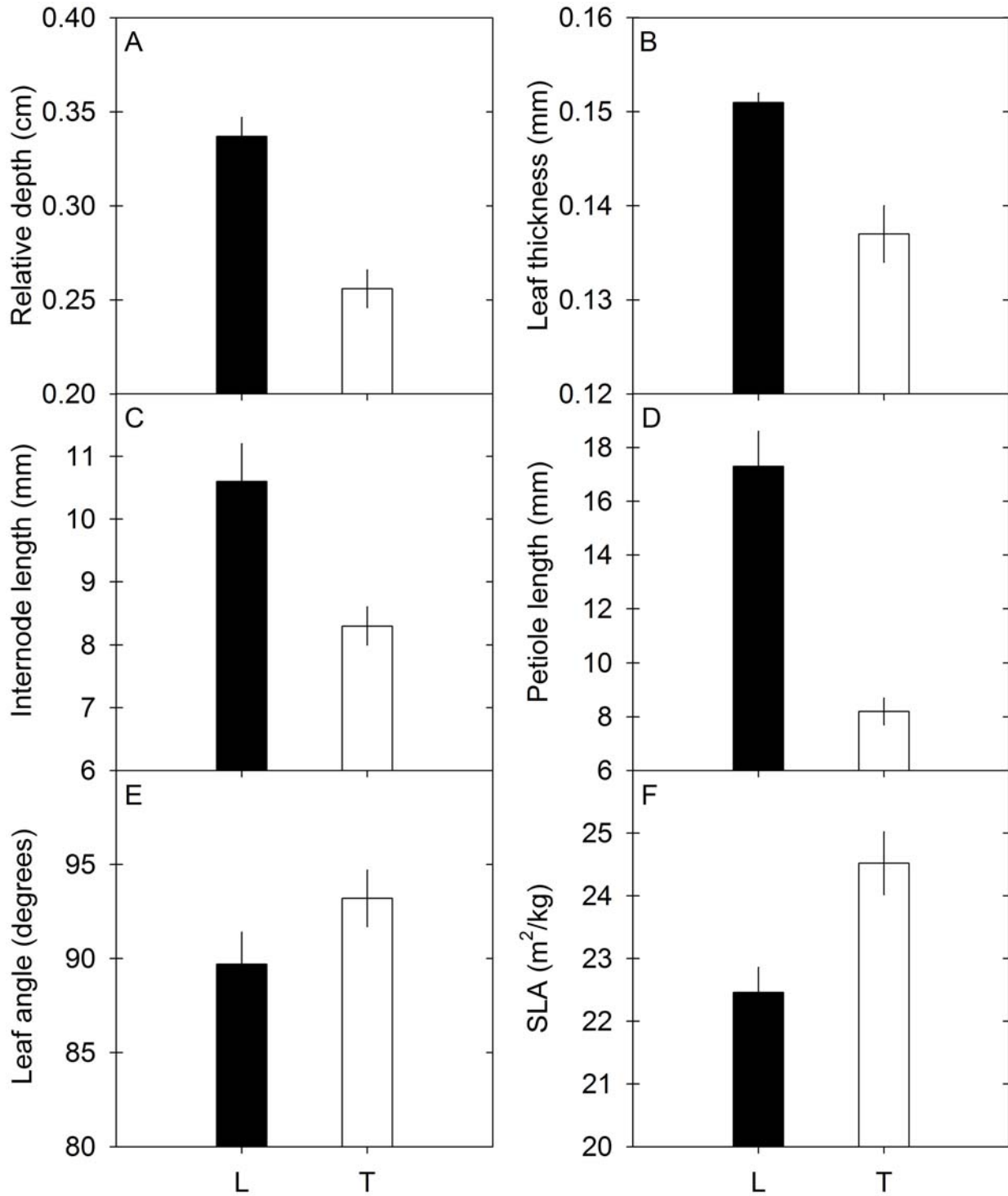
651

652 Figure 4



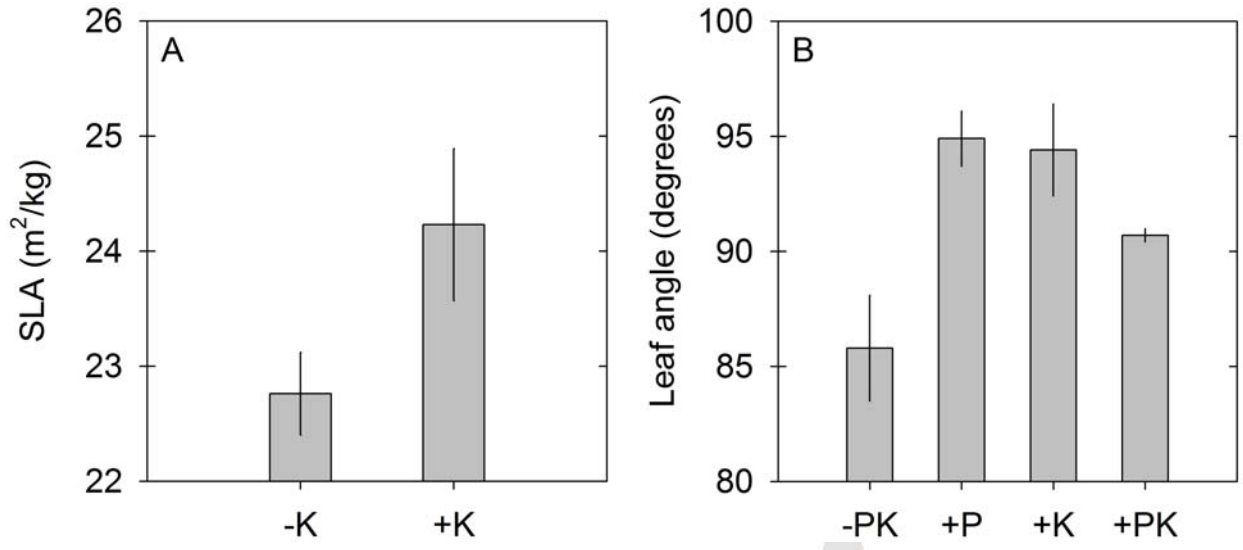
653

654 Figure 5



655

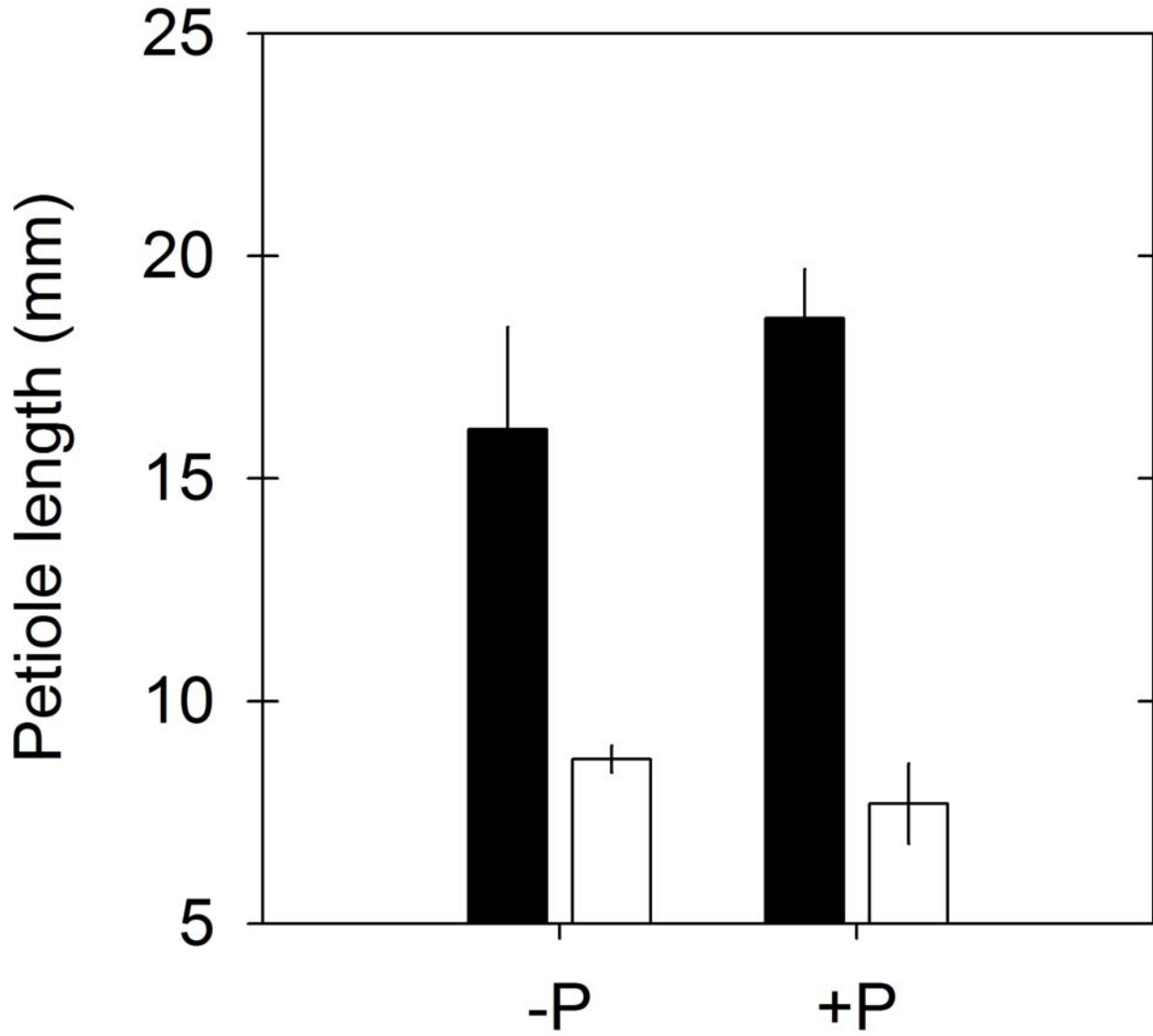
656 Figure 6



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preprint

658 Figure 7



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