

PHOTOSYNTHETIC AND MORPHOLOGICAL ACCLIMATION OF SEEDLINGS OF TROPICAL LIANAS TO CHANGES IN THE LIGHT ENVIRONMENT¹

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- **Premise of the study:** Few studies have analyzed the physiological performance of different life stages and the expression of ontogenetic niche shifts in lianas. Here, we analyzed the photosynthetic and morphological acclimation of seedlings of *Stigmaphyllon lindenianum*, *Combretum fruticosum*, and *Bonamia trichantha* to distinctive light conditions in a tropical dry forest and compared their response with the acclimation response of adult canopy lianas of the same species. We expected acclimation to occur faster through changes in leaf photochemistry relative to adaptation in morphology, consistent with the life history strategies of these lianas.
- **Methods:** Seedlings were assigned to the following light treatments: high light (HH), low light (LL), sun to shade (HL), and shade to sun (LH) in a common garden. After 40 d, HL and LH seedlings were exposed to opposite light treatments. Light response curves, the maximum photosynthetic rate in the field (A_{max}), and biomass allocation were monitored for another 40 d on leaves expanded before transfer.
- **Key results:** Photosynthetic responses, A_{max} , and biomass of *Stigmaphyllon* and *Combretum* varied with light availability. Physiological characters were affected by current light environment. The previous light environment (carryover effects) only influenced A_{max} . Morphological characters showed significant carryover effects. *Stigmaphyllon* showed high morphological and physiological plasticity. Sun-exposed seedlings of this liana increased stem biomass and switched from self-supporting to climbing forms.
- **Conclusions:** Acclimation in seedlings of these lianas is consistent with the response of adult lianas in the canopy in direction, but not in magnitude. There was no evidence for ontogenetic niche shifts in the acclimation response.

Key words: canopy ecology; lianas; ontogenetic niche shift; photosynthetic plasticity; Panama; seedling ecology; shade avoidance; tropical dry forests.

Lianas are ubiquitous elements of tropical and temperate forests and are well distributed across plant families (Schnitzer and Bongers, 2002). Similar to the case for trees, liana taxonomic diversity should reflect a wide range of functional types and regeneration strategies (Gallagher et al., 2011), which changes as succession progresses (Letcher and Chazdon, 2012). However, most lianas are considered typical pioneers based on their photosynthetic performance, fast growth, and preference for colonizing disturbed habitats, forest edges, canopy gaps, and the top of the canopy (Avalos and Mulkey, 1999a; Sanches and Válio, 2002; Avalos et al., 2007; Toledo-Aceves and Swaine, 2008; Ledo and Schnitzer, 2014). Despite their pioneer character as adults, many lianas germinate in the shaded forest understory, and as seedlings, they start as self-supporting plants and can tolerate variable periods of deep shade while storing

resources to climb to the forest canopy (Nabe-Nielsen, 2002; Feild and Balun, 2008; Sanches and Válio, 2002; Letcher and Chazdon, 2012; Celis and Avalos, 2013).

It is not clear how consistently lianas maintain their pattern of resource use, habitat choice, and regeneration strategy throughout their ontogeny. Adult lianas respond rapidly to light changes and heterogeneous light conditions (Avalos and Mulkey, 1999a; Ledo and Schnitzer, 2014) by investing more biomass in leaves relative to supporting tissues as compared with trees (Putz, 1984; Castellanos, 1991), which maximizes light interception, enhances mobility, and facilitates the colonization of disturbed habitats (Paul and Yavitt, 2011). In contrast, seedlings may show very restricted physiological responses not necessarily comparable with those of adults, especially when resources are limited. Therefore, it is reasonable to expect the expression of ontogenetic niche shifts, as lianas move from shaded conditions in the understory to well-lit conditions along forest edges, canopy gaps, and the top of the canopy. However, very few studies have discussed differences in physiological performance among different life stages in lianas, from the understory to the canopy. The evidence for ontogenetic niche shifts in tropical plants is still inconclusive (Poorter et al., 2005; Gilbert et al., 2006), and it is likely that most species have intermediate light requirements and benefit from moderate light early in life (Wright et al., 2003).

In this study, we measured the light acclimation capacity of young seedlings of three twining lianas in response to contrasting

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light conditions and compared their response with the acclimation response of adults of the same species described previously (Avalos and Mulkey, 1999a; Avalos et al., 2007). Most studies on seedling ecology have focused on the responses of already established seedlings, or juveniles (*sensu* Garwood, 1996; Whitmore, 1996; Baraloto et al., 2005), whereas very few have examined the implications of initial morphology on seedling establishment and its role determining the ecological amplitude of tropical species (Kitajima, 1994, 1996a, b), especially when compared with adults. Our aim here is to evaluate the consistency of the regeneration span of these lianas in which adults behave like light-demanding species (Avalos and Mulkey, 1999a; Avalos et al., 2007).

We expect initial light conditions to determine the extent of adjustment to subsequent light changes. Thus, the magnitude of phenotypic differences in response to light changes should be higher in seedlings that started growth under high light. Light-demanding species will perform poorly in the shade, while species able to withstand the shade will express more conservative strategies, showing fewer phenotypic differences across habitats. Expanding our knowledge on the range of responses expressed by lianas to the continuum of light environments found in tropical forests, especially in early regeneration stages, is crucial to understand the increased abundance of lianas in neotropical forests (Wright et al., 2004) and their role in carbon cycling and to predict the future behavior of rainforest ecosystems under global warming scenarios (Schnitzer and Bongers, 2002; Malhi and Phillips, 2004; Malhi, 2012; Van der Heijden et al., 2013).

MATERIALS AND METHODS

Study site—This research was conducted in central Panama at Parque Natural Metropolitano, a 100–150-yr-old tropical dry forest. The site has an average annual rainfall of 1740 mm and a well-defined dry season (December through late April). Here, the Smithsonian Tropical Research Institute maintains a cantilevered construction crane that allows repeated, nondestructive access to the upper canopy from a suspended cage (Parker et al., 1992).

Study species—The neotropical liana *Stigmaphyllon lindenianum* A. Juss. (Malpighiaceae) is abundant throughout the study area as well as in trees under the crane. *Combretum fruticosum* (Loefl.) Stunz (Combretaceae) and *Bonamia trichantha* Hallier f. (Convolvulaceae) were the most abundant twining lianas on trees under the crane during the wet season of 1994 and the dry season of 1995 (Avalos and Mulkey, 1999b; Avalos et al., 2007). Canopy lianas of *C. fruticosum* and *B. trichantha* show alternative leaf phenotypes. Leaves produced during the wet season have lower photosynthetic capacity relative to those produced during the dry season (Avalos et al., 2007). Although the information on the ecology of seedlings is limited, we have found that *S. lindenianum* and *C. fruticosum* germinate both in large gaps and in shaded environments, whereas *B. trichantha* is found only in conditions of direct sunlight. As adults, the three species are associated with high light habitats. All are twining lianas with very narrow stems (~1 cm in diameter). Hereafter, the species are referred to by their generic designation.

Growth conditions—Seeds were collected from at least 10 reproductive individuals throughout Parque Metropolitano and from lianas growing on trees under the crane during the dry season. Seeds were taken to the greenhouse of the Smithsonian Tropical Research Institute in Panama City and allowed to germinate under moderate sun conditions in flats filled with alluvial soil taken from the field site. Seeds were watered daily via a sprinkler system. *Combretum* and *Bonamia* started to germinate after 10–12 d, whereas *Stigmaphyllon* required 28 d to emerge. Immediately after germination, each seedling was transplanted to a flexible plastic bag with a mixture of vermiculite and peat moss soil. These containers were large enough to minimize the adverse effects of root binding and provided appropriate conditions before transplant into the common garden.

Sequence of sun and shade treatments—After developing the third leaf node (8–10 cm in stem length), 1-mo-old seedlings were randomly assigned to one of four light sequences (HH, HL, LH, and LL) in a common garden set up at Parque Metropolitano. Seedlings of all species were self-supporting when experiments started. Lianas under the high to low sequence (HL) began under sun and after 40 d were exposed to shade by relocating the shade cloth during the second part of the experiment. Responses to new light conditions were monitored for another 40 d. Seedlings under the low to high sequence (LH) were subjected to the opposite transfer. Seedlings in the high light (HH) and low light groups (LL) were maintained only under sun or shade during the entire experimental period. The experiment lasted 10 and a half weeks and included 76 lianas in *Combretum*, 72 in *Bonamia*, and 109 in *Stigmaphyllon* after removing damaged seedlings by herbivory or manipulation. Plants were watered when necessary, and sprayed with an insecticide when signs of herbivory were detected.

Common garden experiment—Transplant to the common garden took place in May of 1997 (start of wet season). Tree trunks and other plant debris were cleared from an area of 30 × 30 m to expose the soil surface. The first 40 cm of soil of an area of 20 × 4.5 m were removed, homogenized, and cleared of roots to provide homogeneous conditions for seedling planting. In addition, branches from neighboring trees and lianas overtopping the experimental area were cut to secure homogeneous illumination. Shade treatments were created with 63% neutral greenhouse shade cloth put over shade houses made of bamboo poles 1.8 m tall.

Seedlings were planted in four contiguous subplots of 5 × 4.5 m, keeping homogeneous soil and light conditions.

To quantify relative differences in photosynthetic photon flux density (PPFD) among plots, we used four quantum light sensors (Li-190SA, Li-COR, Lincoln, Nebraska, USA) positioned on the ground in the middle of each plot. The light sensors were hooked to a Li-1000 datalogger (Li-COR) programmed to scan PPFD levels at 1-min intervals, starting at 8:00 and ending at 16:00 solar time. Since the goal was to measure relative differences in PPFD to categorize plots rather than to compile a record of light variation at the site, the measurements were done for 2 days 2 weeks before, and for 2 days 2 weeks after the switch in light conditions. Before the light transfer, HH and HL plots received an average of 720 and 1045 $\mu\text{mol PPFD m}^{-2}\text{s}^{-1}$, whereas LL and LH plots received 136 and 270 $\mu\text{mol PPFD m}^{-2}\text{s}^{-1}$, respectively. This was sufficient to separate high light from low light plots. The distribution of PPFD during the day differed little for plots exposed to similar light conditions. After the transfer of light treatments, average PPFD levels of sun environments (HH and LH) were close to 1700 $\mu\text{mol PPFD m}^{-2}\text{s}^{-1}$, whereas in shade treatments irradiance values remained under 100 $\mu\text{mol PPFD m}^{-2}\text{s}^{-1}$.

Response variables—We monitored changes in leaf structure, physiology, and patterns of biomass allocation in seedlings before and after the switch in light treatments. Physiological measurements were restricted to those leaves flushed and fully expanded under sun or shade at the start of the experiment. Although new leaves were produced after the transfer of light treatments, they were not present in sufficient numbers across light sequences and, thus, were not included in the analyses of photosynthetic variation. Morphological traits included the total biomass distributed to roots, stems, and petioles, leaves, root to shoot ratio, leaf to stem ratio, and leaf to total mass ratio as determined from the individual dry mass for half of the replicates in each treatment, harvested after 40 d of development before the light switch, and at the end of the experiment, 40 d after the light transfer. We took special care in collecting all root material (including fine roots) by washing them in situ. All plant material used in biomass measurements was stored and dried in an oven at 60°C for 2 d until constant mass prior to measurement. Stem length was measured at the beginning and at the end of the second part of the experiment during the light transfer.

Photosynthetic light response curves—To characterize the photosynthetic capacity of seedlings, we collected leaf discs right after dawn from fully expanded leaves, then stored them in a darkened, humidified container. This material was brought immediately to the laboratory for measurement of dark respiration rate ($\mu\text{mol CO}_2\text{-m}^{-2}\text{s}^{-1}$), light compensation point ($\mu\text{mol PPFD m}^{-2}\text{s}^{-1}$), apparent quantum yield (Q), and photosynthetic rate at light saturation ($\mu\text{mol O}_2\text{-m}^{-2}\text{s}^{-1}$) from light response curves measured with an oxygen electrode (Hansatech Instruments, Norfolk, UK) using 10% CO_2 at 28°C. Leaf specific mass (LSM) was determined from the leaf discs used in the oxygen electrode. Two sets of light curves were obtained, one before and one after the transfer of light treatments. Oxygen electrodes measure the rate of oxygen evolution, which is

stoichiometrically equivalent to the rate of carbon fixation. We also measured A_{\max} (the maximum photosynthetic rate under field conditions in $\mu\text{mol CO}_2\text{-m}^{-2}\text{s}^{-1}$) using fully expanded leaves and a portable photosynthesis system (Li-6400, Li-COR) set to an ambient CO_2 concentration of 386 μmol , a water vapor concentration of 24–28 mol, and a light intensity of 1500 $\mu\text{mol PFD}\text{-m}^{-2}\text{s}^{-1}$ keeping the temperature in the cuvette close to ambient temperature (30°C).

Statistical analyses and test of hypotheses—Before transfers—Suites of morphological and photosynthetic characters were highly correlated. Thus, we consolidated these variables using a principal component analysis (PCA). This procedure removed the correlation among variables and improved the statistical power of subsequent analyses. Differences in morphological and photosynthetic characters between sun and shade treatments were tested using a two-way ANOVA applied to the scores of the principal components. We used two ANOVA models. The first one measured differences in the principal components resulting from photosynthetic characters (dark respiration rate, light compensation point, Q , photosynthetic rate at light saturation and LSM), whereas the second model tested differences in the components derived from morphological characters between sun and shade environments. Root to shoot and leaf to mass ratios were analyzed separately from the rest of the biomass allocation variables since they resulted from the combination of variables already included in the PCA. Tukey's honestly significant difference (HSD) was used as post hoc test after finding significant main effects.

After transfers—During the second part of the experiment, a crossover design was used to test the effects of present light environment (light treatment after the transfer), the effects of exposure to previous light conditions (carryover effects), and the interaction between previous and present light treatments (which is analogous to a test of the effect of light sequence) on physiological and morphological characters. Carryover effects are the effects of the first light environment that persist and influence phenotypic responses in subsequent periods of measurement (Ratkowsky et al., 1993). We used the following crossover design:

$$Y_{ijk} = \mu + \text{Sp}_i + t_j + \beta_j + (t\beta)_{ij} + e_{ijk},$$

where Y_{ijk} is the response of the seedling of the species i within the current light environment j after being exposed to the previous light conditions k , μ is the population parameter, Sp_i is the species effect, t_j is the effect of present light

treatment, β_j is the effect the previous light treatment, $(t\beta)_{ij}$ is the interaction between previous and present light treatments (i.e., the effect of light sequence), and e_{ijk} is the error term. The first crossover model tested the significance of present and previous light treatments on the principal components emerging from physiological variables, whereas the second model tested for differences in the components coming from morphological characters. We considered acclimation to low and high light to occur if the response of HL and LH seedlings matched that of LL and HH seedlings after the transfer. Principal components were normalized using the Box–Cox method when necessary (Quinn and Keough, 2002) to conform to the normal distribution and equality of variances. All statistical analyses were done using JMP 10.0 Statistical Software (SAS Institute, Cary, North Carolina, USA).

RESULTS

Photosynthetic responses before transfers—Photosynthetic rates at light saturation in the three lianas varied little among light treatments before the transfer (Table 1). The lowest rates were observed in *Bonamia*. Q , LSM, compensation points, and respiration rates showed little variation among treatments. Before the light transfer, we found two principal components, which explained 64% of the variation in photosynthetic parameters. The first component (40.56% of the variation) was dominated by the photosynthetic rate at light saturation and Q , whereas the second component (23.65%) was dominated by respiration rate. Both components were normally distributed. The first component showed no differences between species and light environments (two-way ANOVA, $r^2 = 0.15$, $F_{5,33} = 1.17$, $P = 0.34$), whereas the second component showed significant differences only among species ($r^2 = 0.32$, $F_{2,33} = 4.88$, $P < 0.01$), with shade seedlings of *Bonamia* diverging from seedlings of *Combretum* and *Stigmaphyllon* (Tukey HSD, $P < 0.05$).

The magnitude of A_{\max} was higher under high light treatments for all species, with *Stigmaphyllon* showing the highest rates, followed by *Combretum* (Fig. 1A). Differences were

TABLE 1. Photosynthetic responses in seedlings of the lianas *Bonamia* (BM), *Combretum* (CF), and *Stigmaphyllon* (SL) before and after the light transfer in a common garden set in Parque Natural Metropolitan, Panama. Values are averages (\pm SE); N = sample size.

Treatment and species	Q (apparent quantum yield)	LSM ($\text{cm}^2\text{-g}^{-1}$)	Saturation ($\mu\text{mol O}_2\text{-m}^{-2}\text{s}^{-1}$)	Compensation ($\mu\text{mol PFD}\text{-m}^{-2}\text{s}^{-1}$)	Respiration ($\mu\text{mol CO}_2\text{-m}^{-2}\text{s}^{-1}$)	N
High light						
BM	0.01 (0.004)	0.003 (0.0004)	5.4 (0.7)	10.88 (1.7)	-2.1 (0.2)	6
CF	0.03 (0.0006)	0.004 (0.0004)	9.71 (1.2)	14.22 (1.98)	-2.16 (0.3)	7
SL	0.03 (0.004)	0.005 (0.004)	9.28 (1.6)	13.47 (2.89)	-1.2 (0.2)	7
Low light						
BM	0.02 (0.008)	0.004 (0.0004)	5.6 (1.11)	15.71 (3.84)	-3.08 (0.74)	6
CF	0.02 (0.002)	0.006 (0.003)	7.43 (0.8)	13.02 (1.81)	-1.70 (0.21)	7
SL	0.02 (0.006)	0.001 (0.0002)	7.37 (1.71)	18.18 (2.66)	-1.57 (0.4)	7
Permanent high light						
BM	0.03 (0.007)	0.004 (0.0006)	10.5 (2.47)	2.6 (1.8)	-0.84 (0.42)	3
CF	0.04 (0.004)	0.005 (0.0005)	14.44 (1.7)	13.2 (0.93)	-2.14 (0.28)	4
SL	0.02 (0.001)	0.003 (0.0004)	13.7 (2.01)	22.44 (2.82)	-1.5 (0.11)	5
High to low light						
BM	0.03 (0.002)	0.004 (0.0003)	7.08 (0.2)	5.4 (3.5)	-2 (0.008)	2
CF	0.04 (0.001)	0.004 (0.0002)	10.5 (0.93)	8 (0.66)	-1.28 (0.12)	4
SL	0.03 (0.004)	0.002 (0.0004)	7.41 (0.41)	15.9 (7.1)	-1.18 (0.4)	2
Low to high light						
BM	0.01 (0.006)	0.004 (0.001)	7.15 (1.94)	2.9 (1.53)	-1.3 (0.41)	4
CF	0.04 (0.004)	0.004 (0.0002)	10.79 (1.86)	12.56 (1.85)	-2 (0.2)	4
SL	0.04 (0.005)	0.003 (0.0001)	12.56 (1.6)	18.45 (2.02)	-2.24 (0.34)	4
Permanent low light						
BM	0.01 (0.004)	0.004 (0.0001)	4.8 (0.26)	1.73 (1.63)	-0.8 (0.33)	3
CF	0.04 (0.006)	0.003 (0.0001)	7.11 (0.98)	8.83 (1.68)	-1.52 (0.14)	3
SL	0.03 (0.002)	0.001 (0.0002)	7.67 (3.18)	11.6 (1.15)	-2.16 (0.9)	3

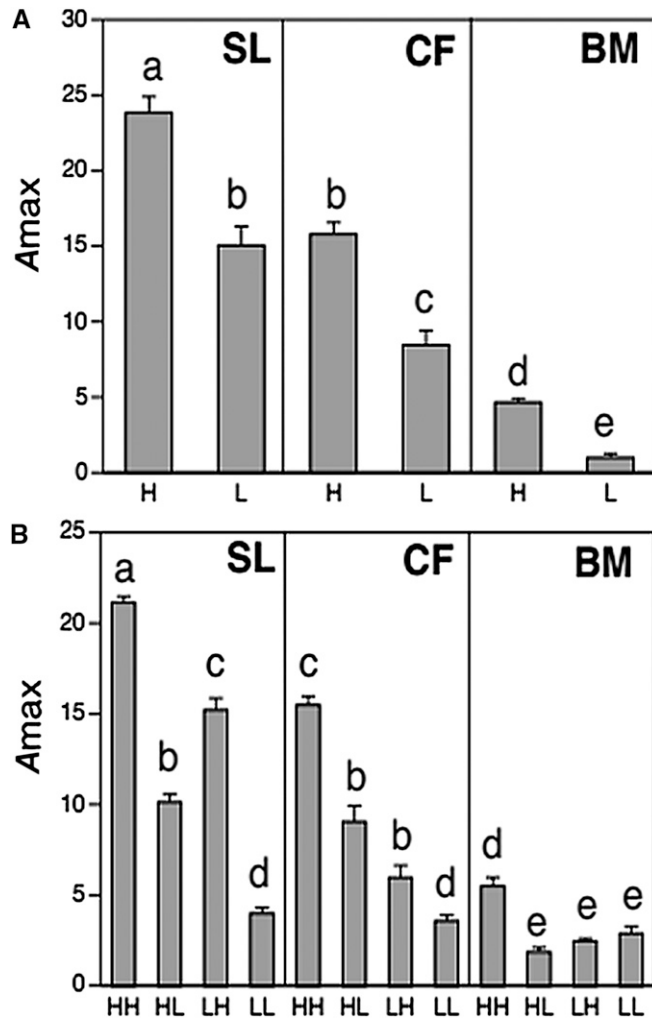


Fig. 1. Differences among species and light treatments in A_{max} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (A) before and (B) after the light transfer treatments. Abbreviations refer to species names (SL: *Stigmaphyllon*, CF: *Combretum*, BM: *Bonamia*). Letters above bars indicate statistical significance at $P < 0.05$ following Tukey's HSD test. Error bars refer to ± 1 SE.

significant among species (two-way ANOVA, $r^2 = 0.67$, $F_{2,105} = 27.82$, $P < 0.0001$) and light treatments ($F_{1,105} = 7.06$, $P = 0.009$).

Photosynthetic responses after transfers—We extracted two principal components from the second set of photosynthetic parameters, which explained 71% of the variation. The first component (47%) was dominated by photosynthetic rate at light saturation, whereas the second one (24%) was dominated by LSM. Both components were normally distributed. In the crossover design for the first component ($r^2 = 0.61$) there was a significant species effect ($F_{2,29} = 9.48$, $P = 0.0007$), with *Bonamia* separating from *Combretum* and *Stigmaphyllon* (Tukey HSD, $P < 0.05$; Fig. 2). The current light treatment had a significant effect on this component ($F_{1,29} = 7.4$, $P = 0.01$), whereas carryover effects were not significant. *Stigmaphyllon* and *Combretum* varied their photosynthetic responses as a function of increasing or decreasing light (Fig. 2). The second component presented significant differences only among species ($r^2 = 0.57$,

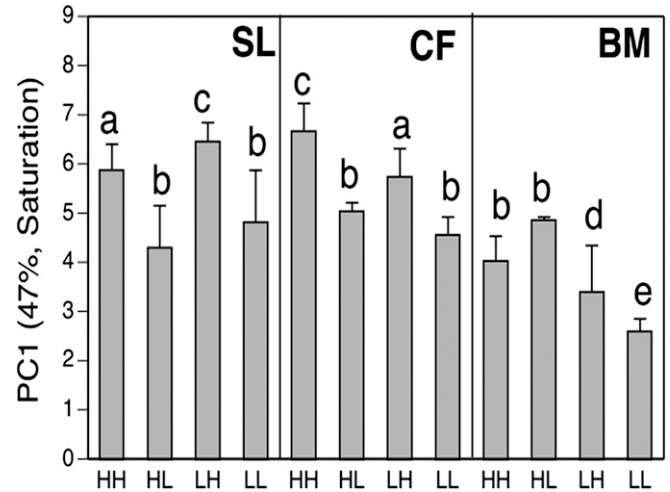


Fig. 2. Differences among species and light treatments in photosynthetic variables combined in a principal component dominated by the photosynthetic rate at light saturation ($\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) before the light transfers. Abbreviations refer to species names as in Fig. 1. Letters above bars indicate statistical significance at $P < 0.05$ following Tukey's HSD test. Error bars refer to ± 1 SE.

$F_{2,29} = 16.38$, $P < 0.0001$) with *Stigmaphyllon* diverging from *Combretum* and *Bonamia*.

The A_{max} responses after the light transfer maintained the overall differences among species and light treatments observed before the light transfer, with *Stigmaphyllon* showing the highest rates under HH (Fig. 1B). *Stigmaphyllon* varied A_{max} as a function of light availability, decreasing A_{max} under shade and increasing it under high light. *Combretum* maintained low A_{max} under shade, whereas LH seedlings did not surpass A_{max} relative to HL seedlings. In *Bonamia* A_{max} was higher under HH, but no differences were observed among the rest of the light treatments (Fig. 2). The lianas responded to previous as well as to present light treatments (Table 2), but current light conditions had a stronger effect relative to the previous light environment.

Biomass distribution before transfers—Access to high light increased seedling biomass across species (Table 3). Under high light, *Stigmaphyllon* and *Combretum* more than doubled the biomass of *Bonamia*, whereas under shade *Stigmaphyllon* had the lowest biomass. Biomass allocated to leaves under high light was the dominant allocation compartment in *Stigmaphyllon* and *Combretum*. *Bonamia* maintained consistently small

TABLE 2. Crossover design measuring the effects of exposure to present and previous light treatments (carryover effects) on A_{max} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in seedlings of *Stigmaphyllon*, *Combretum*, and *Bonamia* in a common garden experiment set in Parque Natural Metropolitan, Panama ($r^2 = 0.83$).

Source	F ratio	P
Species	$F_{2,373} = 186.98$	<0.0001
Previous light treatment (carryover effects)	$F_{1,373} = 162.60$	<0.0001
Current light treatment	$F_{1,373} = 226.37$	<0.0001
Previous light treatment \times species	$F_{2,373} = 22.28$	<0.0001
Current light treatment \times species	$F_{2,373} = 57.84$	<0.0001
Light sequence	$F_{2,373} = 11.82$	0.0007
Light sequence \times species	$F_{2,373} = 4.17$	0.01

TABLE 3. Biomass distribution in liana seedlings before and after the light transfer under high and low light environments. Abbreviations refer to species names (SL: *Stigmaphyllon*, CF: *Combretum*, BM: *Bonamia*). Values are averages (± 1 SE) of dry mass in grams; N = sample size.

Species	Leaves	Stems	Roots	Biomass	Root/shoot	Leaf/mass	N
High light							
BM	0.024 (0.004)	0.046 (0.004)	0.06 (0.003)	0.17 (0.02)	0.7 (0.08)	0.15 (0.02)	20
CF	0.17 (0.01)	0.06 (0.006)	0.07 (0.006)	0.30 (0.02)	0.31 (0.02)	0.54 (0.01)	27
SL	0.22 (0.03)	0.12 (0.01)	0.08 (0.01)	0.42 (0.06)	0.25 (0.02)	0.48 (0.01)	46
Low light							
BM	0.028 (0.002)	0.04 (0.002)	0.047 (0.003)	0.14 (0.006)	0.5 (0.02)	0.20 (0.01)	40
CF	0.093 (0.01)	0.041 (0.005)	0.054 (0.01)	0.18 (0.02)	0.43 (0.06)	0.48 (0.01)	29
SL	0.033 (0.003)	0.02 (0.001)	0.022 (0.002)	0.08 (0.007)	0.42 (0.02)	0.38 (0.02)	35
Permanent high light							
BM	0.04 (0.01)	0.06 (0.01)	0.06 (0.005)	0.18 (0.02)	0.6 (0.08)	0.19 (0.05)	3
CF	0.25 (0.06)	0.12 (0.02)	0.10 (0.02)	0.48 (0.11)	0.3 (0.03)	0.50 (0.02)	10
SL	0.76 (0.12)	0.55 (0.11)	0.41 (0.06)	1.73 (0.28)	0.3 (0.06)	0.45 (0.02)	21
High to low light							
BM	0.02 (0.004)	0.05 (0.008)	0.04 (0.01)	0.13 (0.02)	0.59 (0.1)	0.12 (0.01)	3
CF	0.13 (0.02)	0.07 (0.01)	0.08 (0.01)	0.28 (0.06)	0.36 (0.04)	0.51 (0.01)	9
SL	0.2 (0.02)	0.14 (0.04)	0.06 (0.01)	0.4 (0.1)	0.21 (0.02)	0.50 (0.01)	17
Low to high light							
BM	0.03 (0.003)	0.04 (0.003)	0.04 (0.001)	0.14 (0.008)	0.48 (0.02)	0.21 (0.02)	17
CF	0.04 (0.01)	0.02 (0.01)	0.03 (0.01)	0.10 (0.01)	0.41 (0.04)	0.44 (0.01)	4
SL	0.04 (0.004)	0.04 (0.01)	0.02 (0.001)	0.10 (0.01)	0.29 (0.04)	0.34 (0.04)	13
Permanent low light							
BM	0.02 (0.005)	0.04 (0.008)	0.06 (0.006)	0.16 (0.01)	0.66 (0.06)	0.14 (0.01)	9
CF	0.08 (0.01)	0.04 (0.006)	0.06 (0.01)	0.18 (0.03)	0.52 (0.04)	0.45 (0.02)	11
SL	0.06 (0.01)	0.05 (0.009)	0.04 (0.008)	0.14 (0.02)	0.4 (0.09)	0.42 (0.01)	11

seedlings across treatments. We consolidated biomass distribution (mass of leaves, stems, roots, and overall biomass) in one principal component, which explained 86% of the variation across species. The coefficients of the eigenvectors for this component were similar among variables and ranged 0.45 to 0.53 indicating high correlation among morphological variables. Accordingly, we termed this component “biomass”. This component was normalized with the Box–Cox transformation and was entered as a response variable into a two-way ANOVA using species, light treatment, and their interaction, as main effects. Differences were found among species and light treatments ($r^2 = 0.56$, Table 4, Fig. 3A). *Stigmaphyllon* showed the steepest differences between sun and shade groups, *Combretum* had moderate differences, and *Bonamia* did not show differences among light environments (Fig. 3A).

Biomass distribution after transfers—After the light transfer, biomass distribution was consolidated into one principal component, which explained 91% of the variation. The loadings of this component ranged from 0.47 to 0.52, showing high correlation among roots, leaves, stems, and overall biomass. The scores of this component were normalized using the Box–Cox procedure. A two-way ANOVA (Table 5, Fig. 3B) applied to the transformed scores showed significant differences among species, light sequences, and their interaction. The highest biomass

was found in *Stigmaphyllon* under continuous high light. Both *Stigmaphyllon* and *Combretum* varied the magnitude of biomass as a function of light conditions, although LL seedlings showed higher biomass than LH seedlings in both lianas. *Bonamia* showed a weaker response to differences in light availability after the transfer, and no differences were found among treatments (Fig. 3B). Current light treatment did not affect biomass allocation. None of the effects for which the current light treatment was involved influenced seedling biomass (Table 5). Similar to *Bonamia* and *Combretum*, shade seedlings of *Stigmaphyllon* showed little growth over the course of the experiment.

Root to shoot ratio—Root to shoot ratios were higher in sun seedlings of *Bonamia* relative to *Combretum* and *Stigmaphyllon* before the transfer (Table 3, $r^2 = 0.33$, $F_{2,123} = 26.89$, $P < 0.0001$). Differences were found among species under sun conditions, whereas shade seedlings of *Stigmaphyllon* and *Combretum* had similar root to shoot ratios (Tukey HSD, $P < 0.05$). The tendency was maintained after the transfer in light treatments. Root to shoot ratios were transformed using the Box–Cox procedure to correct for lack of normality. There was only a significant effect of species (Table 3, $r^2 = 0.45$, $F_{2,176} = 32.20$, $P < 0.0001$), with *Bonamia* showing higher ratios relative to *Stigmaphyllon* and *Combretum*. Differences among sequences and carryover effects were not significant.

Leaf to mass ratio—This variable showed a strong effect of species ($F_{2,123} = 202.51$, $P < 0.0001$), light treatment ($F_{1,123} = 7.96$, $P < 0.006$) and the interaction species \times light treatment ($F_{2,123} = 9.43$, $P < 0.0002$) before the light transfer (Table 3; Fig. 4). The highest leaf to mass ratios were found in *Combretum* and *Stigmaphyllon* under sun and shade conditions, whereas *Bonamia* showed the lowest ratio (Fig. 4A). After the transfer, differences were significant among species ($F_{2,175} = 135.86$, $P < 0.0001$; Fig. 4B) with *Combretum* and *Stigmaphyllon* showing

TABLE 4. Two-way ANOVA measuring the effects of species and light treatment on biomass allocation before the light transfer in seedlings of *Stigmaphyllon*, *Combretum*, and *Bonamia* in a common garden set in Parque Natural Metropolitan, Panama.

Source	F ratio	P
Species	$F_{2,123} = 7.51$	0.0008
Light treatment	$F_{1,123} = 82.60$	<0.0001
Species \times light treatment	$F_{2,123} = 26.11$	<0.0001

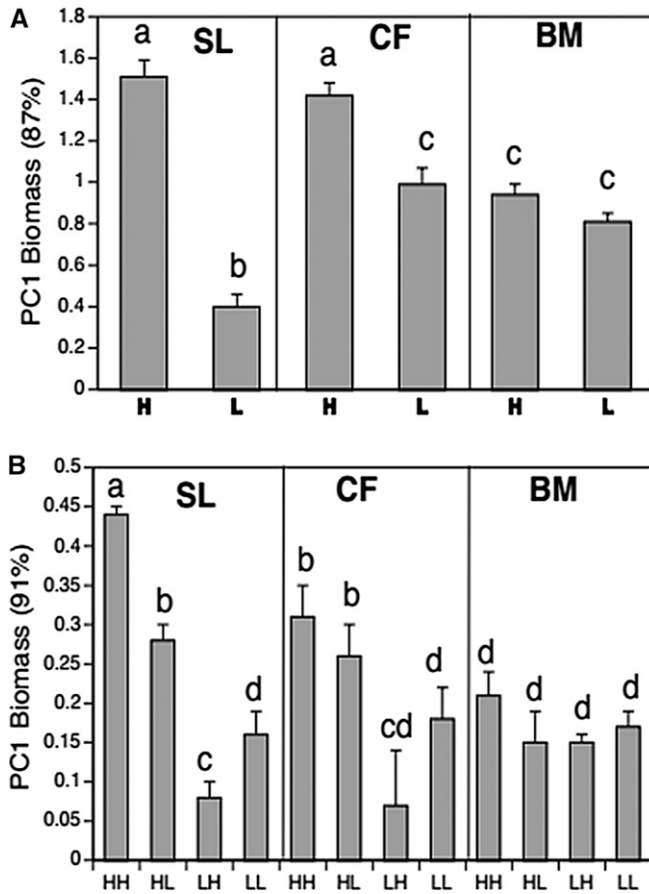


Fig. 3. (A) Differences among species and light treatments of high light (H) and low light (L) in biomass allocation variables consolidated using PCA before the light transfer in *Stigmaphyllon* (SL), *Combretum* (CF), and *Bonamia* (BM). (B) Differences in biomass allocation variables after the light transfer combined into one principal component according to sequence of light treatments. Different letters above bars show statistical significance at $P < 0.05$ (Tukey's HSD). Error bars refer to ± 1 SE.

higher ratios in HH and HL relative to *Bonamia*. Exposure to previous light environment had a significant effect ($F_{1,175} = 8.60, P < 0.003$), whereas the current light conditions did not affect leaf to mass ratios. *Bonamia* showed a weak response to light treatments, and only seedlings under HH had a slightly higher ratio relative to the rest of the light treatments.

Changes in stem length—Differences among species in stem length were significant ($r^2 = 0.34, F_{2,213} = 27.63, P < 0.0001$) and were driven by the increase in stem length of *Stigmaphyllon* under the HH and HL sequences (Fig. 5). Stem length was not affected by present light conditions, but was influenced by previous light environments ($F_{1,213} = 4.97, P < 0.02$). HH and HL seedlings were taller than LL and LH seedlings in *Stigmaphyllon* ($F_{2,213} = 6.37, P < 0.002$). *Bonamia* did not show significant increases in stem length, whereas *Combretum* had shorter seedlings only under the LL treatment. In contrast, in *Stigmaphyllon* initial exposure to sun conditions facilitated the accumulation of sufficient biomass to express the climbing response. After the light transfer, 17 *Stigmaphyllon* seedlings, taller than 15 cm, shifted from self-supporting to climbing forms. These seedlings were responsible for the steep

TABLE 5. Crossover model measuring the effects of species exposure to present and previous light conditions (carryover effects) on biomass allocation of seedlings of *Stigmaphyllon*, *Combretum*, and *Bonamia* in a common garden experiment set in Parque Natural Metropolitano, Panama ($r^2 = 0.60$).

Source	F ratio	P
Species	$F_{2,115} = 4.20$	0.01
Previous light treatment (carryover effects)	$F_{1,115} = 46.50$	<0.0001
Current light treatment	$F_{1,115} = 0.36$	0.54
Previous light treatment \times species	$F_{2,115} = 9.05$	0.0002
Current light treatment \times species	$F_{2,115} = 0.81$	0.44
Light sequence	$F_{1,115} = 14.76$	0.0002
Light sequence \times species	$F_{2,115} = 1.02$	0.36

increase in stem length and the high variation observed in the HH and HL groups where some plants increased stem length by 88% in less than 2 wk.

DISCUSSION

Acclimation is a complex response whose expression scales with the extent of light changes, spanning several orders of magnitude, from sunflecks to canopy gaps, and from days to

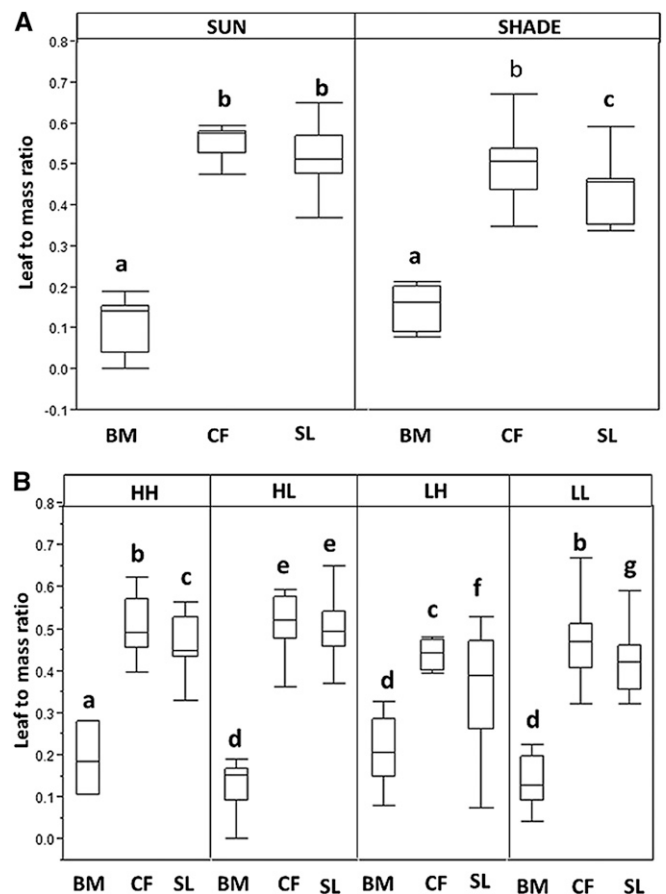


Fig. 4. Leaf to mass ratio (A) before and (B) after the light transfer in *Stigmaphyllon* (SL), *Combretum* (CF), and *Bonamia* (BM). Letters above box plots indicate statistical significance at $P < 0.05$ following Tukey's HSD test.

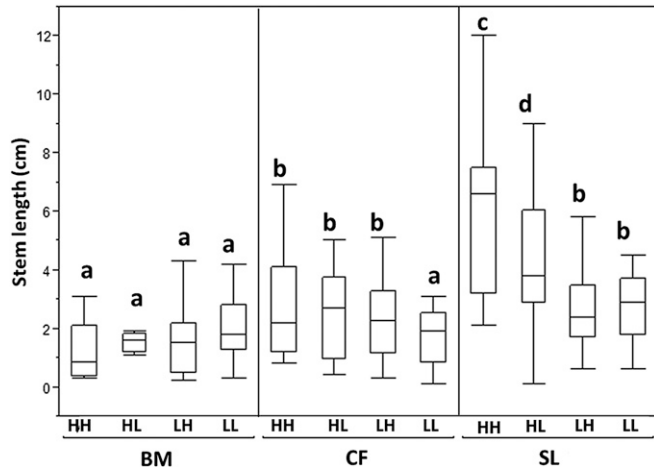


Fig. 5. Box plots representing the extent of variation in stem length increase between the beginning and end of the second part of the experiment during the light transfer. Abbreviations refer to species names (BM: *Bonamia*, CF: *Combretum*, SL: *Stigmaphyllon*). Letters above box plots indicate statistical significance at $P < 0.05$ following Tukey's HSD test.

months (Pearcy, 2007). Changes that take place over days are initially dealt with through the adjustment of the photosynthetic apparatus of mature, expanded leaves, present before the light change. These changes involve the rearrangement of within-leaf resource allocation, including leaf anatomy and nitrogen redistribution (Hikosaka and Terashima, 1996; Evans and Poorter, 2001). Morphological adjustment takes place once physiological responses have stabilized after longer time scales (days to weeks) and involve the reorganization of biomass allocation, plant architecture and leaf display, as well as the production of leaves adapted to the new light conditions (Chazdon and Kaufmann, 1993; Turnbull et al., 1993; Oguchi et al., 2003, 2005). However, in seedlings growing in the shaded understory, small size results in less leaf and root area, limiting the capacity to absorb light and nutrients and modifying biomass allocation rapidly. Here, the final acclimation response will depend on the intensity and direction of the light change, as well as on the seedling capacity to adjust existent foliage to new light conditions, given competing trade-offs among morphological and physiological characters (Evans and Poorter, 2001; Oguchi et al., 2005). For these reasons, we expected initial light conditions to determine morphological adjustment and to influence the extent of physiological responses to subsequent light changes (significant carryover effects).

The overall physiological and morphological responses of the lianas analyzed in this study conformed to these expectations. Photosynthetic variables showed small differences between sun and shade treatments before the light transfer, but after the switch, variables like saturation and respiration rates (integrated into one principal component), moved in the direction of light availability, especially in the lianas *Stigmaphyllon* and *Combretum*. Carryover effects on physiological variables were not significant or were weaker than the effect of current light environment, as in the case of A_{\max} . Physiological responses were mostly determined by the current light conditions. As discussed later, the physiological and morphological response of *Bonamia* was very limited and was more consistent

with a stress response, especially within the LL and LH treatments, which showed the lowest Q values (Table 1).

The direction of the photosynthetic responses in seedlings of *Stigmaphyllon* was similar to that of adult lianas subjected to the same sequence of light treatments in the canopy (Avalos and Mulkey, 1999a). However, seedlings exposed to sun conditions had photosynthetic rates at light saturation equivalent in magnitude to that of adult lianas exploiting shaded canopy microhabitats (Avalos and Mulkey, 1999a; Avalos et al., 2007). Photosynthetic capacities in seedlings were thus significantly limited compared with that of adults. In these seedlings, A_{\max} better reflected the extent of environmental differences, especially in *Stigmaphyllon*, and was affected by previous light conditions, but the last light treatment had a stronger effect. The magnitude of A_{\max} was similar to the photosynthetic saturation rates of adult canopy lianas in *Stigmaphyllon* and *Combretum*. *Bonamia*, in contrast, showed a very restricted A_{\max} and overall photosynthetic responses, even for seedlings maintained under continuous sun or exposed to an initial period of high light.

Stigmaphyllon and *Combretum* acclimated to a light increase or decrease using leaves produced and expanded in the previous light environment, as it has been observed in adults of these species (Avalos and Mulkey, 1999a; Avalos et al., 2007). In these lianas, adults have shown postexpansion acclimation mostly to a light increase (Avalos and Mulkey, 1999b; Avalos et al., 2007). Of the three lianas, *Bonamia* showed the most restricted response. Adults of this species are typical shade-avoiders and aggressively pre-empt the canopy by reaching peaks in leaf production quickly, which creates very dark conditions within the canopy of their host trees. In addition, canopy lianas of *Bonamia* decrease leaf life span and finally drop their leaves in shaded microhabitats while increasing leaf production in well-lit sites (Avalos et al., 2007). This behavior corresponds to an opportunistic, shade-avoiding character and implies lack of capacity to adapt already expanded leaves to shade. The limited adjustment to shade in seedlings and canopy lianas is congruent with the habitat choice of *Bonamia*, which prefers forest edges, large gaps, and the top of the canopy.

Patterns of biomass allocation were mostly influenced by exposure to previous light conditions, and thus, carryover effects were significant. *Stigmaphyllon* was the most sensitive to light differences, increasing biomass in sites of greater irradiance. *Combretum* followed a similar pattern, but to a lesser degree, since it did not show the high biomass accumulation observed in *Stigmaphyllon*. Exposure to a previous period of high light facilitated biomass increase in *Stigmaphyllon*, which extended stem length, became unstable, and shifted from self-supporting to climbing forms. This behavior is similar to that of the ecotypic forms of western poison oak *Toxicodendron diversilobum* (i.e., Gartner, 1991a, b), in which vines showed higher leaf biomass and longer stems than self-supported shrubs. However, in *Ipomoea purpurea*, the climbing habit was expressed with more intensity in the shade, where plants showed reduced branching and increased stem length more than plants in the sun (Gianoli, 2003). In this latter study, sun plants were reproductive and thus showed a strikingly different strategy of biomass allocation relative to shade plants. Given sufficient resources to accumulate biomass, shade plants can develop longer and more slender stems than plants in the sun (Gartner, 1991b; Den Dobbelen and Oosterbeek, 1995; Leicht-Young et al., 2011). In our case, seedlings showed higher respiration rates relative to canopy lianas (Avalos and Mulkey, 1999a; Avalos et al., 2007) and were clearly limited by reduced biomass accumulation in the shade.

High respiration rates, combined with a limited leaf and root area, most likely limited biomass increase across light treatments, especially in *Bonamia*.

The higher root to shoot ratios of *Bonamia* relative to *Combretum* and *Stigmaphyllon* and the relatively low leaf to mass ratio, limits this liana to well-lit environments at the beginning of the regeneration cycle. High root to shoot ratios are indicative of habitat specialization, being predominant in species adapted to dry habitats, such as drier slopes or drier forest types (Garwood, 1996). It is likely that plants in the understory of the dry forest of Parque Metropolitano experience prolonged periods of drought during the dry season. Under these conditions, small seedlings that did not produce a large shoot during the wet season benefit from higher root allocation, which favors access to deeper, more humid soil. For lianas of tropical dry forests (which often die back during the dry season), higher root allocation enhances root storage, which is important to support new growth during the wet period (see Condon et al., 1992). Lianas are among the most deeply rooted species in tropical forests (Holbrook and Putz, 1996; Andrade et al., 2005), a condition that gives them access to the water necessary to maintain an extensive leaf area using very narrow stems.

The seedling and adult lianas studied here exhibit characteristics typical of pioneer species (Bazzaz and Carlson, 1982; Bazzaz, 1996; Wright et al., 2004; Paul and Yavitt, 2011). In the understory, seedling survival and growth depend on morphological traits that enhance defense against herbivores or pathogens, such as tougher leaves and a well-developed root system. Similar to our case, high respiration costs for root construction and maintenance result in lower carbon gain in shade-intolerant species (see Kitajima, 1994). Acclimation at the physiological level increases the chances for biomass accumulation before the resource is depleted by canopy closures or overtaken by other plants, and buffers seedling mortality in low-resource environments. In contrast, the response to long-term light changes depends on the production of new organs and loss of tissues formed in the previous light environment or on the post expansion acclimation of the same tissues (Kamaluddin and Grace, 1992). The final response is determined by the interaction between morphology and function, since acclimation depends on physiological, as well as morphological plasticity. Although there are a few instances in which seedlings of pioneer species can survive prolonged periods in the shade (i.e., Dalling et al., 2001), for the most part, light-demanding species perform poorly under prolonged shade.

Understanding the expression of niche differentiation throughout ontogeny (ontogenetic niche shifts), as an adaptation mechanism to the continuum of light environments in tropical forests, faces enormous challenges given the diversity of life forms and functional roles of tropical plants. In this study, we did not find strong evidence supporting ontogenetic niche shifts. Seedlings expressed a range of physiological and morphological responses to changing light conditions consistent with their light-demanding character as adults. The amount and direction of phenotypic changes across a gradient of light conditions must be considered when judging the plasticity of morphological and physiological characters in relation to regeneration strategy and ontogenetic stages (Strauss-Debenedetti and Bazzaz, 1996). For instance, the response of *Bonamia* was very restricted in relation to the response of *Stigmaphyllon*, which reacted faster to light variation. Both responses were consistent with the strategy of resource use and habitat selection of these species in the canopy. Since lianas are increasing

in abundance and biomass across the tropics (Schnitzer and Bongers, 2011; Laurance et al., 2014) and have significant impacts on carbon sequestration in these ecosystems (Van der Heijden et al., 2013), the analysis of their adaptation to successional gradients, especially during the initial stages of regeneration, is crucial to improve the management of disturbed habitats. This knowledge is becoming urgent as tropical environments are increasingly dominated by secondary forests, a favorite habitat for lianas (Laurance et al., 2014).

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