

## Colonization Strategies of Two Liana Species in a Tropical Dry Forest Canopy

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### ABSTRACT

Lianas impose intense resource competition for light in the upper forest canopy by displaying dense foliage on top of tree crowns. Using repeated access with a construction crane, we studied the patterns of canopy colonization of the lianas *Combretum fruticosum* and *Bonamia trichantha* in a Neotropical dry forest in Panama. *Combretum fruticosum* flushed leaves just before the rainy season, and its standing leaf area quickly reached a peak in the early rainy season (May–June). In contrast, *B. trichantha* built up foliage area continuously throughout the rainy season and reached a peak in the late rainy season (November). Both species displayed the majority of leaves in full sun on the canopy surface, but *C. fruticosum* displayed a greater proportion of leaves (26%) in more shaded microsites than *B. trichantha* (12%). Self-shading within patches of liana leaves within the uppermost 40–50 cm of the canopy reduced light levels measured with photodiodes placed directly on leaves to 4–9 percent of light levels received by sun leaves. Many leaves of *C. fruticosum* acclimated to shade within a month following the strongly synchronized leaf flushing and persisted in deep shade. In contrast, *B. trichantha* produced short-lived leaves opportunistically in the sunniest locations. Species differences in degree of shade acclimation were also evident in terms of structural (leaf mass per area, and leaf toughness) and physiological characters (nitrogen content, leaf life span, and light compensation point). Contrasting leaf phenologies reflect differences in light exploitation and canopy colonization strategies of these two liana species.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>

*Key words:* *Bonamia trichantha*; *Combretum fruticosum*; light acclimation; Panama.

LIANAS FORM A DISTINCTIVE STRUCTURAL ELEMENT OF TROPICAL FOREST CANOPIES and exhibit a variety of mechanisms of ascension, growth patterns, physiological strategies, and morphologies (Schnitzer & Bongers 2002). Lianas can comprise 25 percent of upright, understory stems (Putz 1984), contribute significantly to species diversity and productivity (Gentry & Dodson 1987, Hegarty 1991), influence forest regeneration (Pinard & Putz 1993, Schnitzer *et al.* 2000, Phillips *et al.* 2005), and compete for water (Pérez-Salicrup & Barker 2000) and light with host trees (Clark & Clark 1990). In a tropical dry forest, 30 percent of the canopy surface surveyed under a canopy crane was occupied by liana foliage (Avalos & Mulkey 1999b). Lianas represent one of the most dynamic life forms of tropical forests, often reproducing clonally and exploiting all forest layers from the canopy surface to the deepest soil strata where roots are found (Holbrook & Putz 1996). Because lianas have proportionally less support biomass than trees (Holbrook & Putz 1996), they should be better able to exploit heterogeneous canopy light conditions through flexible extension growth. Unfortunately, most studies of lianas and their impact on forest regeneration are based on ground surveys, which are inherently limited. From the ground, it could be difficult to distinguish liana and tree leaves, and liana stem density does not necessarily correlate with liana leaf area displayed on top of the canopy. Limited accessibility to the forest canopy has historically constrained *in situ* studies of phenology and

physiology of liana leaves, even though such studies would provide insight into canopy interactions between lianas and trees, as well as among different liana species.

Leaf phenology and shoot architecture influence the quality of the light environment experienced by individual leaves throughout their lifetime, and thus, are linked to species differences in leaf life span and leaf functional traits (Kikuzawa 1995, Kitajima *et al.* 2005). Some plants continue shoot extension throughout the growing season continuously producing new leaves on the sunniest portion of the crown. In these species, leaves become increasingly shaded as they age, and photosynthetic rates decline rapidly as nitrogen and other mobile nutrients are reallocated to new leaves (*e.g.*, Hikosaka *et al.* 1994, Kitajima *et al.* 2002). Consequently, leaf life span may be short in these species, because the potential of mature leaves to acclimate to shade is morphologically constrained (Oguchi *et al.* 2003), and inefficient self-shaded leaves senesce as their net carbon balance approaches zero (Ackerly 1999). This strategy, found among many pioneers, opportunistically exploits the highest light availability and allows rapid growth rates. The opposite strategy is to produce leaves in a seasonal flush, which results in quick self-shading of many leaves even before they become fully mature. Consequently, crowns of species following this strategy consist of both sun and shade acclimated leaves that persist for a prolonged time, often throughout the growing season. Such species produce a greater crown leaf area index (Canham *et al.* 1994, Montgomery & Chazdon 2001, Kitajima *et al.* 2005), exerting strong resource competition for light by casting denser shade below. Both strategies

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have been found among tree species (Kikuzawa 1995, Kitajima *et al.* 2005). However, we are unaware of published studies on the phenological and physiological diversity of leaves among liana species. This type of functional diversity must be ultimately linked to their strategies of light competition with each other, and with their host canopy trees.

Here, we report the patterns of canopy colonization, leaf distribution, leaf phenology, and gas exchange properties of two lianas *Combretum fruticosum* (Loefl.) Stuntz (Combretaceae) and *Bonamia trichantha* Hallier f. (Convolvulaceae). These are the two most common lianas in the area accessed by the canopy crane at Parque Natural Metropolitan, Panama (Avalos & Mulkey 1999b). The two species differ in seasonality of leaf production and patterns of microhabitat use, providing an opportunity to explore how their leaf phenology may be linked to their light exploitation strategies, leaf distribution under sun and shade microhabitats within the canopy, shade acclimation potential, and leaf life span. Our ultimate goal is to examine how these functional leaf traits determine the ability of lianas to cast shade and compete for light with host trees.

## METHODS

**STUDY SITE.**—The study was conducted in the Parque Natural Metropolitan, near Panama City, Panama (8°59' N, 79°33' W, elevation 150 m). This 265-ha site is covered with a 100- to 150-yr old stand of tropical dry forest with a canopy height of 30–40 m. The majority of annual rainfall (mean = 1800 mm, ACP 2002) occurs during the rainy season from May through mid-December. The upper canopy of this forest was approached from above with a 42-m tall construction crane. The forest under the crane is dominated by long-lived species that can persist in mature stands, such as *Anacardium excelsum* (Anacardiaceae) and *Luehea seemannii* (Tiliaceae), as well as the early successional species *Castilla elastica* and *Cecropia longipes* (Moraceae). Crown architecture, foliage distribution, and light utilization patterns of the seven most common tree species are reported in Kitajima *et al.* (2005), while details of their leaf phenology, leaf life span, and photosynthetic traits are reported in Mulkey *et al.* (1995) and Kitajima *et al.* (1997a, b, 2002).

**LEAF PHENOLOGY.**—Leaf production, standing leaf number, and survival were determined from monthly censuses of canopy branches of both liana species from early May 1994 to July 1995. Across multiple tree crowns of each species, we located eight patches within each of which we could distinguish sun (leaves displayed at the canopy surface) and shade foliage (leaves belonging to the same liana located at approximately 40–50 cm beneath the uppermost leaves). This resulted in a total sample size of 40 branches developed from a single new shoot extension at the beginning of the growing season for *C. fruticosum* (a total of 890 leaves) and 30 branches for *B. trichantha* (a total of 752 leaves). All leaves produced on these branches were marked with water-based permanent markers. Marked leaves on 21 and 19 branches of *C. fruticosum* and *B. trichantha*, respectively, were censused monthly to calculate leaf life span. The rest of the branches provided leaf material for destructive sampling when nec-

essary. While our samples most likely included multiple individuals, and we traced them down to the ground whenever possible, actual genet identity could have been lost due to mechanical or herbivory damage.

**LIGHT GRADIENT WITHIN LIANA PATCHES.**—Daily variation in photosynthetic flux density (PFD) was measured with GaAsP photodiode (G1118, Hamamatsu, Japan) positioned in the middle of the adaxial surface of individual leaves subsampled in both sun and shade microsites. The photodiodes were calibrated against a quantum light sensor (Li-190SA, Li-COR, Lincoln, Nebraska, U.S.A.) under open-sky conditions. Total daily PFD was calculated from 5 min averages for PFD sampled every 5 sec and recorded with LI-1000 data loggers. Care was taken to maintain the natural leaf angle and orientation during the measurements. For typical leaf and solar angles, cosine-error correction for these sensors would have little effect on estimated total daily PFD (Percy *et al.* 1990). The LI-1000 dataloggers were left in the field for five consecutive days, and were moved to different patches of the two species every 2 wk, resulting in a total of 18 and 19 d for sun and shade leaves of *C. fruticosum*, and 16 d each for sun and shade leaves of *B. trichantha* between June 21 and July 24, 1994. Data collected by sensors found in inappropriate positions, or fallen off the leaf, were discarded.

**DISTRIBUTION OF FOLIAGE UNDER SUN AND SHADE CONDITIONS.**—In the early rainy season (July 1994), we measured the proportion of leaves displayed under distinctive sun and shade microenvironments within the patches of *C. fruticosum* and *B. trichantha* using a dismountable plastic cubic frame (40 × 40 × 40 cm) constructed with PVC pipes. This cube was first placed to include sun leaves within 40 cm of the canopy surface. All leaves inside the cube in this topmost position were counted and designated as sun leaves. The cube was then disassembled, except for the bottom square, and reassembled using the former bottom square as the new top square to count all leaves enclosed within the next 40 cm of the canopy. This process was repeated downward until the most shaded leaves were counted. All leaves positioned more than 40 cm below the canopy surface were designated as shade leaves.

**STRUCTURAL PROPERTIES AND PHOTOSYNTHETIC LIGHT RESPONSE OF SUN AND SHADE LEAVES.**—From branches monitored for leaf survival, fully expanded leaves were sampled to determine leaf area with a LI-3000 leaf area meter (Li-COR). Leaf-specific mass per area (LMA) was determined from 2-cm diameter leaf discs dried at 60°C until constant weight. Leaf toughness, *sensu* Coley (1983), was measured as the force of penetration of a 3-mm diameter rod attached to a spring scale of 1000 g capacity into the leaf lamina, and was expressed in weight units (g). This is not a measurement of fracture toughness as defined by material science, but it is a relative measure that is ecologically relevant, as long as the operator uses the spring scale in a consistent manner across samples of similar thickness (Choong *et al.* 1992). Nitrogen contents were determined with a Perkin-Elmer CHNO/S Model II elemental analyzer (Perkin-Elmer, England). To compare photosynthetic light curves

among species and light environments, 10 cm<sup>2</sup> leaf discs were taken right after dawn from mature sun and shade leaves (at least 1 mo after reaching full expansion) in the early rainy season (July 2004). Discs were brought back to the lab in a darkened and humidified container for immediate measurement of dark respiration and light response curves with a leaf-disk oxygen electrode (Hansatech Instruments, Norfolk, UK), as described in Kitajima *et al.* (1997b). The light curve parameters (apparent quantum yield, dark respiration rate, compensation point, and photosynthesis rate at light saturation) were estimated for each leaf by fitting a nonrectangular hyperbola using Photosynthesis Assistant© v. 1.1.2 (Dundee Software, Dundee, UK).

**STATISTICAL ANALYSES.**—The effects of species and light environments on individual trait values were analyzed with two-way ANOVA. A two-way MANOVA was used to examine the effects of species and light environment on photosynthetic parameters. MANOVA corrects *F* values and accounts for reduced degrees of freedom due to the autocorrelation of these physiological characters and is a more conservative analysis than separate two-way ANOVAs for each response variable. Tests of hypotheses using MANOVA are more accurate than univariate tests, even after correcting alpha levels using the Bonferroni approach (Freund *et al.* 1986). A Kolmogorov–Smirnov test was used to measure differences in the shape of the trajectory of the hourly variation in PFD for leaves of *C. fruticosum* and *B. trichantha* at the top of the canopy, and 40 cm below the canopy surface under shade conditions. A *t*-test was used to measure differences in the average leaf area within a liana species under sun and shade environments. All analyses were done using SAS and JMP IN statistical software (SAS Institute, Cary, North Carolina).

## RESULTS

**LEAFING PHENOLOGY AND DISTRIBUTION.**—*Combretum fruticosum* and *B. trichantha* showed contrasting patterns of leaf phenology (Fig. 1). In *C. fruticosum*, most leaves were produced in April during the dry-to-wet season transition. Standing leaf number reached its maximum in May–June, and subsequently declined steadily until January–March, when the species became mostly deciduous. In contrast, *B. trichantha* produced leaves continuously between July and November and built up standing leaf number until November, the last month of the rainy season. Afterwards, leaf production ceased and standing leaf number steadily declined until April (Fig. 1). However, this species was never completely deciduous, and continued producing new branches, and thus, new leaves in other canopy sites in May and June. The branches we tagged at the start of the experiment ran out of leaves and were deciduous during these months even though newer branches of the same, as well as other individuals, maintained leaves in May and June. Both species flowered towards the end of the dry season.

During mid-rainy season (early August) *C. fruticosum* held 74 percent of its leaves in sun and 26 percent in shade (Table 1).

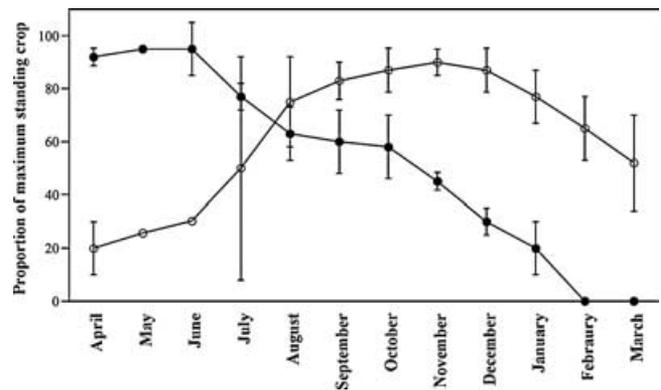


FIGURE 1. Standing leaf area for *Combretum fruticosum* (open circles) and *Bonamia trichantha* (closed circles) in a tropical dry forest canopy in central Panama. Values are means ( $\pm$  SD) for replicate branches of current leaf area standardized by the maximum leaf area observed for each branch.

A well-developed canopy patch of *C. fruticosum* was characterized as a dense shrubby crown. Leaves produced at the start of the rainy season survived for almost 6 mo under sun, but leaf life span was reduced to 3.5 mo when leaves became shaded (Table 1). In contrast, *B. trichantha* had a more open crown, with a thin leaf layer carpeting the canopy surface, colonizing mostly well-lit environments and displaying most leaves under full sun, with only 12 percent of leaves displayed in the shade (Table 1). Leaf life span of *B. trichantha* was shorter than *C. fruticosum* for both sun and shade leaves, although the difference in life span for sun and shade foliage was more pronounced in *B. trichantha* (Table 1).

**LIGHT GRADIENT WITHIN LIANA PATCHES.**—The light environment of sun leaves did not differ between species (Kolmogorov–Smirnov

TABLE 1. Structural properties, life span and distribution of leaves of two liana species, *C. fruticosum* and *B. trichantha*, in sun and shade environments in the during the wet season in a tropical dry forest in central Panama. Mean ( $\pm$ SD). See Methods for sample size.

		Percentage of total leaf area	Leaf area (cm <sup>2</sup> )	Leaf mass per area (g/m <sup>2</sup> )	Leaf toughness (g)	Leaf life span (days)
<i>C. fruticosum</i>	Sun	74.0	23.6 (6.4)	68.0 (6.0)	247 (31)	172 (60)
	Shade	26.0	24.0 (6.9)	43.0 (13.0)	153 (39)	103 (51)
<i>B. trichantha</i>	Sun	87.9	77.6 (18.6)	65.0 (11.0)	226 (34)	136 (36)
	Shade	12.1	60.0 (20.9)	57.0 (11.0)	245 (42)	48 (14)

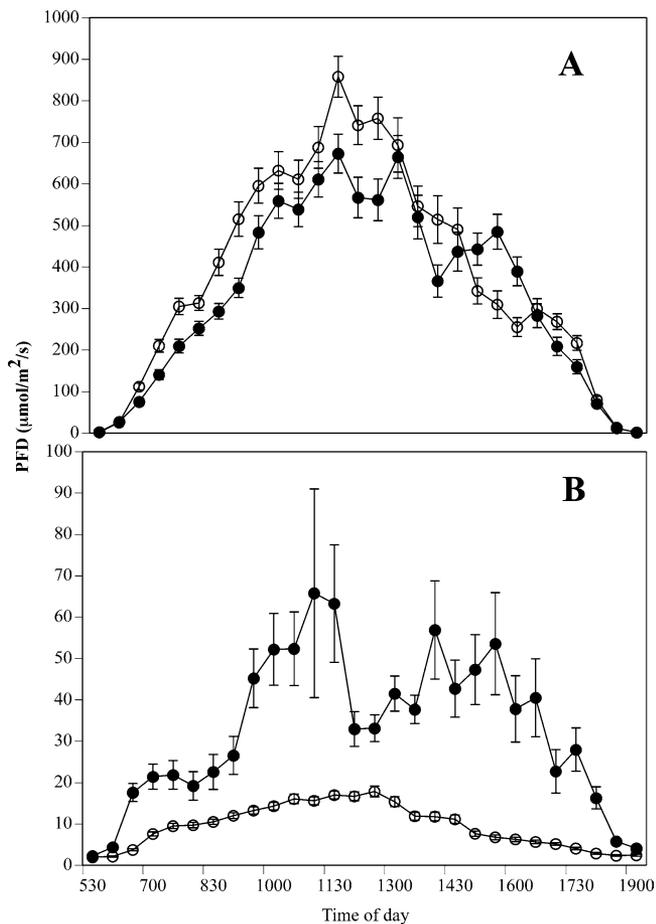


FIGURE 2. Hourly variation in PFD for leaves of *Combretum fruticosum* (open) and *Bonamia trichantha* (closed) at the top of the canopy (A) and 40 cm below the canopy surface under shade conditions (B), during the wet season of 1994. Error bars indicate  $\pm$  SE (smaller than the size of the symbol for *C. fruticosum* in shade).

test = 1.52,  $P = 0.93$ ; Fig. 2A, Table 2). However, shade leaves of the two species experienced different light environments (Kolmogorov–Smirnov test = 18.28,  $P < 0.0002$ ; Fig. 2B). Self-shading reduced PFD to only 4 percent of PFD received by sun leaves in *C. fruticosum*, while shade leaves of *B. trichantha* received 9 percent of PFD received by sun leaves (Table 2). The majority of shade leaves of *C. fruticosum* were found at very low PFD ( $\leq 150 \mu\text{mol}/\text{m}^2/\text{s}$ ; Fig. 3A).

LEAF STRUCTURAL TRAITS.—The area of individual leaves did not differ between sun and shade environments for *C. fruticosum* (Table 1;  $t$ -test = 0.28,  $P = 0.78$ ,  $df = 86$ ). Sun leaves were significantly larger than shade leaves for *B. trichantha* (Table 1;  $t$ -test = 3.3,  $P = 0.001$ ,  $df = 52$ ). LMA was higher in sun relative to shade leaves in both species ( $F_{1,77} = 8.9$ ,  $P < 0.0001$ ). LMA did not differ significantly between the two species for sun leaves. LMA was significantly greater for *B. trichantha* than for *C. fruticosum* for shade leaves ( $F_{1,76} = 30$ ,  $P < 0.0001$ ). Thus, differences in LMA

between sun and shade leaves were greater for *C. fruticosum* than for *B. trichantha*. Likewise, differences in leaf toughness between sun and shade leaves were greater for *C. fruticosum* than for *B. trichantha* (Table 1). Overall nitrogen content per unit leaf area ( $\text{mg}/\text{m}^2$ ) was higher in sun leaves than in shade leaves ( $F_{1,15} = 43.1$ ,  $P < 0.0001$ ), and higher in *B. trichantha* than in *C. fruticosum* for both, sun and shade leaves ( $F_{1,15} = 24.4$ ,  $P < 0.0002$ ; Table 2). Nitrogen per unit leaf mass ( $\text{g}/\text{g}$ ) showed similar trends (data not shown)—higher for sun than in shade ( $F_{1,15} = 10.5$ ,  $P < 0.005$ ), and for *B. trichantha* than for *C. fruticosum* ( $F_{1,15} = 15.3$ ,  $P < 0.001$ ).

PHOTOSYNTHETIC LIGHT RESPONSE CURVES.—MANOVA for four light curve parameters (apparent quantum yield, dark respiration rate, compensation point, and photosynthesis rate at light saturation) indicated highly significant differences between sun and shade leaves (Hotelling–Lawley trace<sub>3,13</sub> = 11.0,  $P < 0.0007$ ). However, there was no significant difference between the two species (Hotelling–Lawley trace<sub>3,13</sub> = 0.2,  $P = 0.46$ ; Fig. 4), nor a significant interaction between species and light environments (Hotelling–Lawley trace<sub>3,13</sub> = 3.1,  $P = 0.85$ ). *A posteriori* univariate ANOVAs indicated significant differences between sun and shade leaves for light saturated photosynthetic rates ( $F_{1,18} = 28.1$ ,  $P < 0.001$ ), dark respiration rates ( $F_{1,18} = 4.8$ ,  $P = 0.044$ ), and light compensation points ( $F_{1,18} = 6.4$ ,  $P = 0.023$ ), all being higher for sun leaves (Table 2). Apparent quantum yields did not differ significantly between sun and shade leaves ( $F_{1,18} = 4.3$ ,  $P = 0.06$ ).

## DISCUSSION

Self-shading created steep light gradients within canopy patches of the two liana species. Just 40–50 cm below the canopy surface, light at the leaf surface was reduced to 4–9 percent of canopy surface values. These lianas appear to create steeper light gradients within their crowns than do canopy trees, although no data have been collected for canopy trees in a manner strictly comparable to this study. Average light extinction was only 61 percent 50 cm below the uppermost canopy surface of an emergent *A. excelsum* tree at our study site (Kitajima *et al.* 2005). A similar degree of light extinction occurred but only over much greater distances into the canopy in the absence of liana cover when light was measured for horizontal planes along the vertical gradient (*e.g.*, 94% over 5 m; Johnson & Atwood 1970, Yoda 1974, Kitajima *et al.* 2005). Leaf position within the terminal branches of trees did not predict light extinction (Kitajima *et al.* 2005), suggesting that canopy trees, in contrast to lianas, employ a “light sharing strategy” to optimize light utilization within their large crowns.

The strong degree of self-shading and steep light gradients observed in these two lianas will starve the terminal shoots of host-tree branches of light. Avalos *et al.* (1999) found significantly lower light transmittance through individual liana leaves than through tree leaves at the same study site. Liana colonization tends to be very localized (*e.g.*, Campbell & Newberry 1993) and dependent on forest structure (Chalmers & Turner 1994). Because many lianas apparently form a thin layer covering the crown of host trees, low

TABLE 2. Photosynthetic light curve parameters, nitrogen content, and PFD for leaves of *C. fruticosum* and *B. trichantha* developed in sun and shade environments in the canopy. Means ( $\pm$  SD) calculated for 3–7 leaves per species per environment for photosynthetic parameters determined with a leaf-disk oxygen electrode, and for 4–6 leaves for nitrogen.

		Dark respiration ( $\mu\text{mol O}_2/\text{m}^2/\text{s}$ )	Light compensation ( $\mu\text{mol}/\text{m}^2/\text{s}$ )	Maximum photosynthesis ( $\mu\text{mol O}_2/\text{m}^2/\text{s}$ )	Apparent quantum yield	Nitrogen ( $\text{mgN}/\text{m}^2$ )	PFD ( $\mu\text{mol}/\text{m}^2/\text{s}$ )
<i>C. fruticosum</i>	Sun	-0.57 (0.39)	5.8 (3.0)	26.5 (8.9)	0.095 (0.022)	1.56 (0.19)	399 (405)
	Shade	-0.28 (0.19)	2.1 (1.0)	8.6 (5.0)	0.129 (0.58)	0.91 (0.19)	17 (22)
<i>B. trichantha</i>	Sun	-0.89 (0.47)	11.1 (7.6)	23.6 (5.9)	0.087 (0.019)	2.08 (0.17)	400 (444)
	Shade	-0.25 (0.59)	3.9 (1.9)	7.2 (2.2)	0.125 (0.053)	1.39 (0.31)	36 (80)

light transmission is not disadvantageous for lianas. In contrast, for trees that form multi-layered canopies, greater light penetration must be favored, so that leaves positioned lower in the crown also receive light. It is remarkable that the two liana species created such dense local shade within 1–2 mo of leaf flush in *C. fruticosum* and *B. trichantha*, respectively.

The phenological differences between the two liana species were linked to their strategy of light exploitation, capacity for shade-acclimation, and ability to maintain leaves in the shade. *Combretum fruticosum* flushed leaves just before the rainy season and its foliage area was maximal during the early rainy season (May–June). In contrast, *B. trichantha* had slower foliage development during the

rainy season, with standing leaf number peaking in the late rainy season (November). Many leaves of *C. fruticosum* must have quickly acclimated to shade during the synchronized leaf flush, even before they reached full physiological maturity. In contrast, *B. trichantha* successively developed leaves under full sun conditions, and leaves that became self-shaded were quickly abscised probably due to constraints on the acclimation of fully mature leaves (Oguchi *et al.* 2003). As a consequence, the degree of shade experienced by *C. fruticosum* is much greater than that experienced by *B. trichantha* (Figs. 2 and 3). The greater degree of shade acclimation in *C. fruticosum* relative to *B. trichantha* is also reflected in greater relative changes in LMA, light compensation points, leaf toughness, and

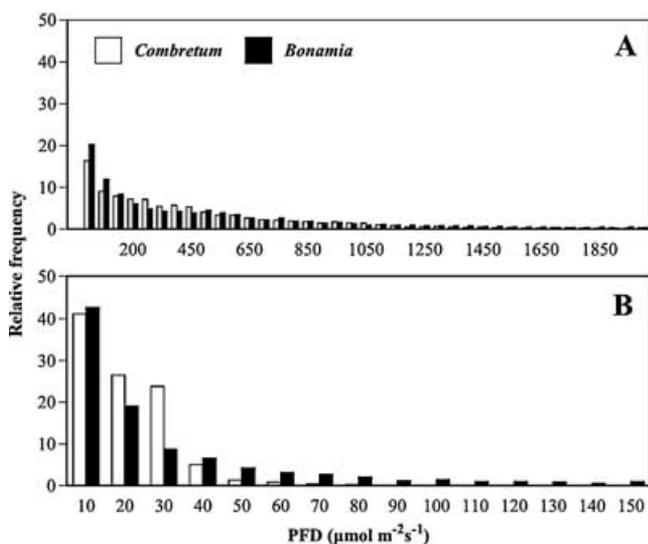


FIGURE 3. Frequency distribution of PFD received by sun (A) and shade leaves (B) within the crowns of *Combretum fruticosum* (closed) and *Bonamia trichantha* (open) at Parque Natural Metropolitano, Panama, wet season 1994.

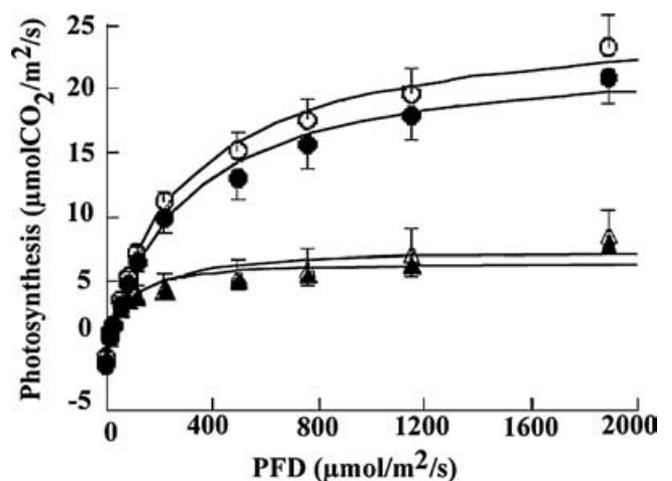


FIGURE 4. Photosynthetic light response curves for sun (circle) and shade (triangle) leaves of *C. fruticosum* (closed) and *B. trichantha* (open). Each point represents the mean of 4–7 leaves per light environment per species, with bars indicating the standard deviation. Nonrectangular hyperbolic models were fitted to the mean values.

nitrogen per unit of leaf area between sun and shade leaves (Tables 1 and 2). The synchronous leaf flushing of *C. fruticosum* enabled a greater degree of shade acclimation and a multi-layered leaf display, which permitted more complete light utilization and a greater degree of competitive impact on light environment of the host tree. Leaf flushing during the transition from dry to wet season will also enhance competitiveness, preempting light before many trees produce leaves during the early rainy season. In contrast, *B. trichantha* opportunistically grows to the most well-lit portion of the canopy and quickly sheds shaded leaves. This should permit faster growth rates, especially where canopy light availability is dynamic due to rapid growth of host branches and other lianas, but minimizes the competitive impact on the host tree. *Combretum fruticosum* and *B. trichantha* share a similar capacity for acclimation between extreme sun and shade canopy environments relative to other canopy lianas studied at the site (*i.e.*, *Stigmaphyllon lindenianum*, Avalos & Mulkey 1999a). However, *S. lindenianum* showed small changes in leaf structure, having a higher capacity for postexpansion acclimation.

In summary, our results demonstrate that lianas aggressively compete for light through local light monopolization in the canopy. The two liana species differed in strength of light competition and degree of opportunistic exploitation of full sun in relation to their leaf production phenology. Recent analyses suggest sharp increases in liana abundance and productivity in many tropical forests (Phillips *et al.* 2002, Wright *et al.* 2004), possibly as a result of increased disturbances and climate change. Thus, understanding the functional basis of the competitive strategies of lianas is important for predicting the future of tropical forest community dynamics, especially in relation to human disturbance.

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