Contribution of Lianas to Plant Area Index and Canopy Structure in A Panamanian Forest

M. Elizabeth Rodríguez-Ronderos
Marquette University

Gil Bohrer
The Ohio State University

Arturo Sanchez-Azofeifa
The Ohio State University

Jennifer S. Powers
University of Minnesota

Stefan A. Schnitzer
Marquette University, stefan.schnitzer@marquette.edu

Reports

Contribution of lianas to plant area index and canopy structure in a Panamanian forest

M. Elizabeth Rodríguez-Ronderos,[1,2,3] Gil Bohrer,[4] Arturo Sanchez-Azofeifa,[4,5] Jennifer S. Powers,[3,6] and Stefan A. Schnitzer[1,3,7]

[1]*Department of Biological Sciences, Marquette University, Milwaukee, Wisconsin 53203 USA*
[2]*Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53211 USA*
[3]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panamá*
[4]*Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, Columbus, Ohio 43210 USA*
[5]*Department of Earth and Atmospheric Sciences and Alberta Centre for Earth Observation Sciences (CEOS), University of Alberta, Edmonton, Alberta T6G 2E3 Canada*
[6]*Departments of Ecology, Evolution and Behavior and Plant Biology, University of Minnesota, St. Paul, Minnesota 55108 USA*

Abstract. Lianas are an important component of tropical forests, where they reduce tree growth, fecundity, and survival. Competition for light from lianas may be intense; however, the amount of light that lianas intercept is poorly understood. We used a large-scale liana-removal experiment to quantify light interception by lianas in a Panamanian secondary forest. We measured the change in plant area index (PAI) and forest structure before and after cutting lianas (for 4 yr) in eight 80 m × 80 m plots and eight control plots (16 plots total). We used ground-based LiDAR to measure the 3-dimensional canopy structure before cutting lianas, and then annually for 2 yr afterwards. Six weeks after cutting lianas, mean plot PAI was 20% higher in control vs. liana removal plots. One yr after cutting lianas, mean plot PAI was ~17% higher in control plots. The differences between treatments diminished significantly 2 yr after liana cutting and, after 4 yr, trees had fully compensated for liana removal. Ground-based LiDAR revealed that lianas attenuated light in the upper- and middle-forest canopy layers, and not only in the upper canopy as was previously suspected. Thus, lianas compete with trees by intercepting light in the upper- and mid-canopy of this forest.

Key words: canopy structure; competition; ground-based LiDAR; LAI-2000; leaf area index (LAI); lianas; light attenuation; Panama; plant area index (PAI); secondary tropical forest; trees; wood area index (WAI).

INTRODUCTION

Light is one of the most limiting resources in lowland tropical forests (Graham et al. 2003, Kitajima et al. 2005). The amount of photosynthetic active radiation that reaches the top of a mature tropical forest canopy can be high (>1,000 mol m^{-2} s^{-1}); however, this intense light is extinguished rapidly as it is transmitted from the canopy to the understory, where only ~1% of the incident light reaches the lower portion of the forest (Chazdon and Fetcher 1984). To maximize light interception, plants deploy leaves at the top of the forest canopy and stratify additional layers of leaves below the canopy (Kitajima et al. 2005). Researchers have estimated forest light interception by determining tree leaf contribution to the forest canopy and from optical measurements of leaf area index (LAI; total amount of leaf area per unit ground area m^2), canopy cover, leaf litter production, and by manually harvesting leaves (e.g., Asner et al. 2003, Kalacska et al. 2005, Clark et al. 2008). Plant stems and branches may also decrease light availability, but they are often overlooked in studies of light interception (Kalacska et al. 2005, Sánchez-Azofeifa et al. 2009). As the contribution of woody material from stems (wood area index, WAI) increases, light availability and canopy openness decreases (Sánchez-Azofeifa et al. 2009). The combination of LAI and WAI is plant area index (PAI), which is a measure of the total light interception by plants (Sánchez-Azofeifa et al. 2009).

Most of the light in tropical forests is intercepted by trees, which constitute the majority of the biomass, leaf area, and basal area in tropical forests. For example, in a tropical wet forest in Costa Rica, Clark et al. (2008)

directly quantified leaf area by harvesting leaves from the forest floor to the top of the canopy in 54 vertical transects and found that trees contributed more than 50% to forest leaf area. In a seasonal tropical forest in Panama, (Avalos and Mulkey 1999) used a canopy crane to access to the top portion of the canopy and reported that tree leaf canopy cover was as high as 78.4% during the dry season. Also in Panama, Wright et al. (2004) estimated that trees contributed 83% to 89% to the woody plant leaf litter productivity.

Lianas (woody vines) may also contribute substantially to light attenuation in lowland tropical forests, despite their relatively small fraction of forest biomass and basal area (Schnitzer et al. 2012, 2014, 2015, Van der Heijden et al. 2015). Lianas commonly comprise 25% of the woody stems and can contribute significantly to forest productivity (Schnitzer and Bongers 2002, Van der Heijden et al. 2013). For example, in a wet forest in Costa Rica, lianas contributed 12.1% to the total leaf area (Clark et al. 2008), even though liana density was relatively low in this forest (Mascaro et al. 2004, Yorke et al. 2013). Lianas may be particularly important to forest productivity in seasonal forests, where lianas are most abundant (e.g., Schnitzer 2005). In a seasonal tropical forest in Panama, Avalos and Mulkey (1999) reported that lianas contributed up to 40% of the leaf canopy cover. On Barro Colorado Island, Panama, lianas contributed 11% to 17% to the forest-level leaf productivity (Wright et al. 2004), and 25% to the woody stem density (stems ≥1 cm diameter; Schnitzer et al. 2012, 2015). Lianas also contribute to forest wood area index (WAI); Sánchez-Azofeifa et al. (2009) reported that lianas contributed considerably to the wood area index in tropical dry forests in Mexico, Costa Rica, and Brazil.

The contribution of lianas to tropical forest plant area index may be an indication of their competitive effects on trees. Lianas compete intensely with trees, reducing tree recruitment, growth, reproduction, and survival, as well as ecosystem-level carbon storage (Grauel and Putz 2004, Schnitzer and Carson 2010, Schnitzer et al. 2014, Van der Heijden et al. 2015, Martínez-Izquierdo et al. 2016). Lianas are thought to compete with trees by attenuating light mainly at the top of the canopy (Ingwell et al. 2010, Toledo-Aceves 2015). However, the contribution of lianas to forest-level PAI and light interception remains poorly understood. Furthermore, liana abundance may be increasing in neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015), and thus their contribution to forest dynamics and light interception is likely to increase.

We quantified the contribution of lianas to forest light interception using a large-scale experimental liana-removal manipulation in the Republic of Panama. We tested the idea that lianas attenuate light predominantly near the top of the forest canopy, where they are thought to deploy the majority of their leaves. We also hypothesized that PAI of the liana-removal plots would approach that of the control plots after liana cutting, but not entirely return to pre-cutting levels because lianas fill inter-crown spaces that result from crown shyness (Putz et al. 1984). We measured PAI before liana cutting, 6 weeks after liana cutting, and then annually for 4 yr. We quantified the speed at which trees compensated from liana removal in terms of the recovery of forest PAI to the pre-manipulation state. We also measured the 3-dimensional structure of the forest canopy using ground-based LiDAR before and annually for 2 yr after liana cutting to determine where lianas intercepted light along the vertical forest canopy gradient.

Materials and Methods

We conducted this experiment on Gigante Península, a protected mainland forest that is part of the Barro Colorado Nature Monument, in the Republic of Panamá (9°9′ N, 79°51′ W). The forest at this site is a 60-yr-old secondary seasonal tropical forest in an area that was used previously for fruit production and pastures (Leigh 1999). Rainfall averages 2616 mm per year, with 90% of the rain falling from May until December and a distinct dry season from December until April (Leigh 1999, Schnitzer and Carson 2010, Álvarez-Cansino et al. 2015).

Liana removal treatment

In 2008, we established 16 80 m × 80 m plots in portions of the forest that were similar in terms of the terrain and the number and size of lianas and trees (Álvarez-Cansino et al. 2015, Reid et al. 2015, Van der Heijden et al. 2015, Martínez-Izquierdo et al. 2016). We measured the diameter of all trees and lianas ≥1 cm diameter in the central 60 × 60 m area of each plot. In April 2011, we cut all lianas in eight randomly selected plots, with the remaining eight plots serving as non-manipulated controls. We cut lianas near the forest floor using machetes, without removing lianas from the canopy to avoid tree damage (follows Schnitzer and Carson 2010, Schnitzer et al. 2014). Nearly all of the liana stems had fallen within 1 yr of cutting lianas. Because lianas resprout copiously after being cut (Schnitzer et al. 2004), we recut stems every 3–4 months in the removal plots. We also visited the control plots with the same frequency as the removal plots to avoid a researcher visitation effect (Cahill et al. 2001, Schnitzer et al. 2002).

Measurement of plant area index (PAI) and forest structural complexity

We calculated mean per-plot Plant Area Index (PAI) as the sum of LAI and WAI (Leblanc and Chen 2001, Kalacska et al. 2005). We measured LAI and WAI in all plots 15 d before cutting lianas (March 2011), 6 weeks afterwards (May 2011), and then annually for 4 yr. All measurements were collected during the dry season (in March) except for 2014, which were collected during the wet season (June) due to logistic constraints. In each plot, we used a LI-COR LAI-2000 plant canopy analyzer

(LI-COR, Lincoln, NE, USA, Welles and Norman 1991) to measure PAI along a uniform grid of seven rows and seven columns (49 points) total, within the center 60 m × 60 m of the plot. To ensure that the open-sky measurements did not intercept forest leaf area and that the within-forest measurements did not include the shadow of the operator, we restricted light measurements to the northern half of the sensor (i.e., 180° cap) and we positioned the sensors directly north for each measurement. At every sampling period, we measured the plots in the same order to ensure consistent and comparable measurements. The point measurements were at 0.5 and 1 m above the soil surface (98 total measurements per plot). Simultaneously, we collected full-sun light measurements every 30 s with a second LAI-2000 outside of the forest on the edge of Lake Gatun as a full-sun comparison (follows Schnitzer and Carson 2010). We measured PAI during the early morning and early evening, or during the day if it was uniformly overcast, which are ideal measurement conditions (LI-COR 1990).

We characterized the canopy structural complexity in each plot using a ground-based portable canopy light detection and ranging (LiDAR) system (Parker et al. 2004). The LiDAR system consisted of a near-infrared pulsed-laser (>3,000 pulses per second) that recorded the vegetative surfaces distributed at different heights of the forest canopy (Parker et al. 2004, Hardiman et al. 2011). The LiDAR system was moved through the forest 1 m above the ground along transects with fixed spacing at a constant rate, and the light return points were recorded continuously. In all 16 plots, we measured LiDAR 1 week before liana cutting and one and 2 yr afterwards (March 2011, 2012, and 2013) along 13 60 m transects that were spaced 5 m apart and spanned the area of each plot. We processed LiDAR returns into vertical columns from 1 m above the ground to the top of the canopy for each transect (780 vertical columns per plot) in each plot using MATLAB (MATLAB 2012). Two yr of post-cutting measurements were sufficient to quantify the contribution of lianas to forest structure.

Data analysis

We used LI-COR FV2000 Analysis Software to pair the full-sun and within-forest sensor data and to convert the differences between the measurements into PAI (LI-COR 1990). To calculate PAI values, we used the horizontal uniform canopy model and the first four zenith angles (0–60°). The results were consistent between the two measurement heights (50 cm and 1 m); thus, we calculated PAI based on the mean two different heights at each point.

To assess whether PAI differed between the removal and control plots before liana manipulation, we used a Mann Whitney-U test (R Core Team 2015). We analyzed the change in PAI in the liana-removal and control plots using a linear mixed effect (LME) model with repeated measures of the same plots over time with treatment (removal or control) and time as fixed effects, and plot as a random effect (Zuur et al. 2009, R: nlme package, Pinhero et al. 2015). We used the same model to examine whether the coefficient of variation (CV) differed between treatments and over time. The mean decrease in PAI following liana cutting compared to the control plots indicated the amount of PAI contributed by lianas.

Prior to cutting lianas, more than 98% of the canopy area sampled by LiDAR was dense enough to saturate the signal below the top of the canopy (i.e., the LiDAR signal did not penetrate beyond the top of the canopy). We excluded the columns that did not saturate before the liana manipulation (<2% of the columns). Within the saturated columns, we constructed vertical plant surface density profiles for the pre-cut measurement and for each of the 2 yr following liana cutting to visualize the change in plant surface area. We grouped the columns into six different categories based on their saturation height: 0–5, 5–10, 10–15, 15–20, 20–25, and 25–41 m. The decrease in the fraction of plant surface density after liana cutting in the liana-removal plots compared to the control plots indicated the contribution of lianas to forest structure in each of the vertical categories.

We analyzed the change in the fraction of plant surface density in each of the 2 yr following liana cutting at each saturation-height category using a linear mixed effect model (LME; Zuur et al. 2009, R: nlme package, Pinheiro et al. 2015). The linear mixed effect model included treatment (removal or control) and time as fixed effects, and individual plots were included as a grouping variable in the random effects component, since columns within plots were measured repeatedly over time. The contribution of each random and fixed effect was assessed by a manual stepwise AIC of the models. We used restricted maximum likelihood (REML) to compare nested models for which random variables differed, and maximum likelihood (ML) to compare nested models for which fixed effects differed. Models were considered competitive when $\Delta AIC \leq 2$. If ties occurred, we used a correction for AIC where the number of parameters and log-likelihood where taken in account (Arnold 2010). We used normalized residuals based on the REML fit to validate the final model (Zuur et al. 2009).

RESULTS

Plant area index

Prior to cutting lianas, light interception (PAI) did not differ between the removal and control plots (Mann Whitney-U Paired t-test; $W_{(14)} = 41$, $P > 0.05$, Fig. 1). Six weeks after cutting lianas, however, mean PAI was ~20% higher in the control plots than in the liana-removal plots relative to the pretreatment measurements. Specifically, PAI decreased 16.6% in the liana-removal plots and increased 3.2% in control plots ($Z_{(18)} = -4.20$, $P < 0.01$; Fig. 1a). One yr after liana cutting, PAI was ~17% higher in the control plots; PAI decreased 21.3% in the liana-removal plots and 4.5% in control plots relative to the
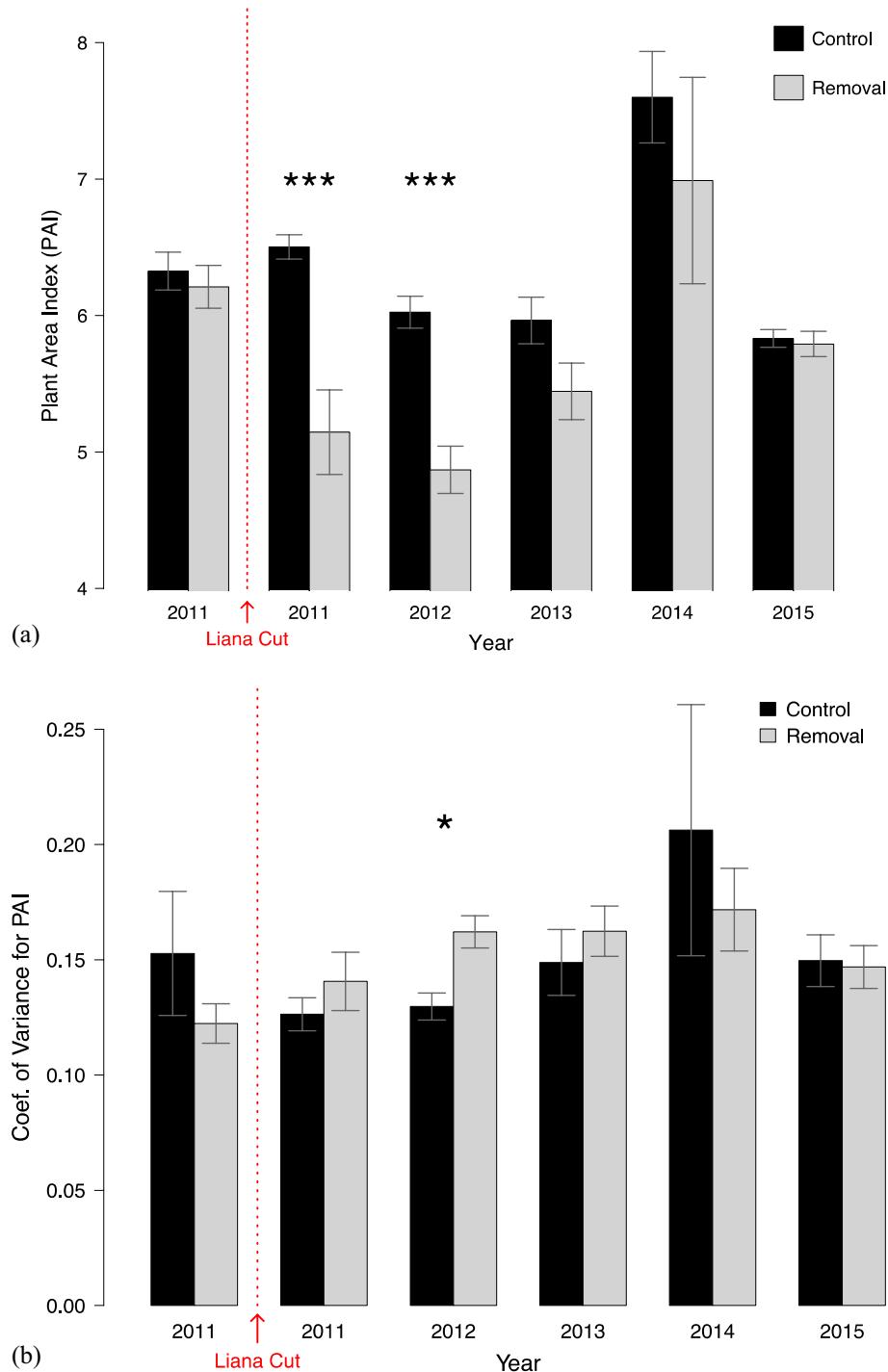
FIG. 1.   (a) Mean plant area index (PAI) and (b) the coefficient of variation (CV) in PAI for eight control plots (black bars) and eight liana-removal plots (light bars) on Gigante Peninsula, Panama. Data were collected using a LiCOR LAI-2000 optical system. Error bars represent one standard error. *P < 0.05; **P < 0.01; ***P < 0.001.

pretreatment measurements ($Z_{(18)}$ = −5.44, P < 0.01; Fig. 1a). Two yr after liana cutting (in 2013), the differences between treatments were no longer significant and, by the fourth year (2015), mean PAI was nearly identical between treatments (Fig. 1a). One yr following liana cutting, within-plot variation (CV) in PAI was significantly higher in the liana removal plots, but this effect was not evident in years 2–4 (Fig. 1b), presumably because trees had begun to compensate for the loss of liana leaves and stems.
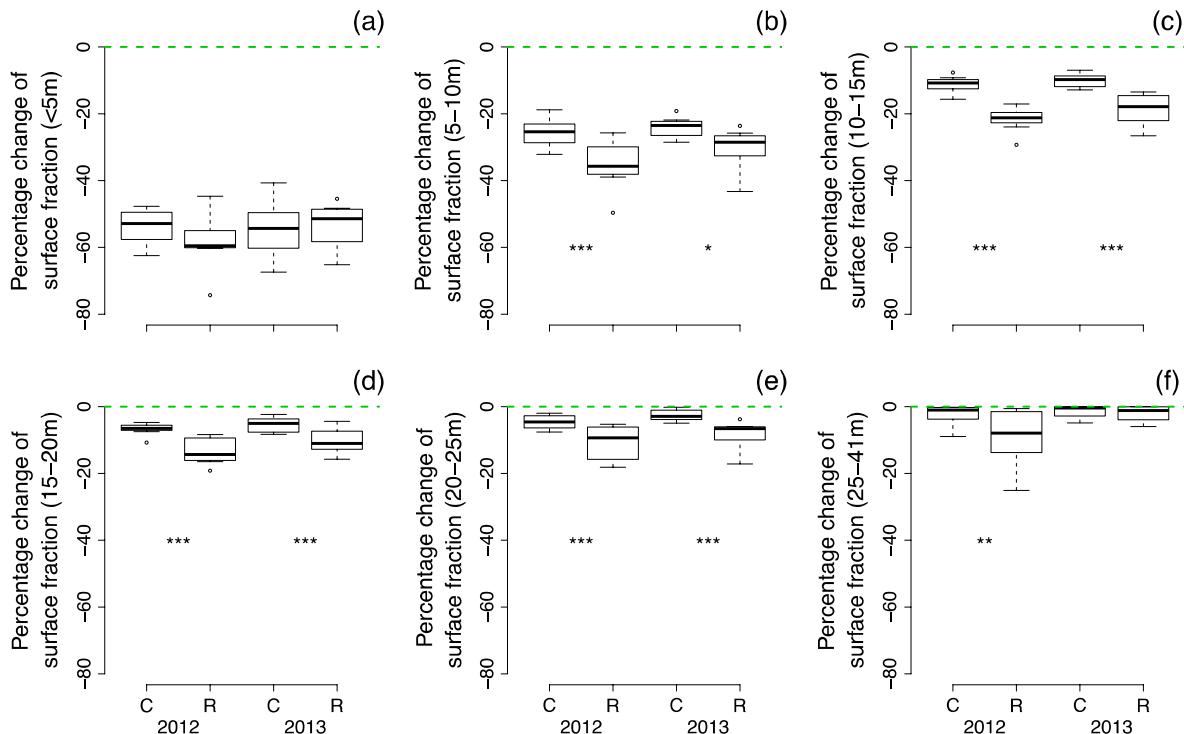
Fig. 2. The percent change in light attenuation plant surface fraction over 2 yr in control and removal plots after liana removal in sixteen 80 × 80 m plots on Gigante Peninsula, Panama. Liana removal plots are marked "R" and control plots "C". Data were collected using a portable LiDAR system 1 m above the forest floor along 13 equally-spaced transects within each plot, and processed for each 1-m long column within each transect. The same transects were repeated each year after the liana removal treatment for 2 yr. The forest vertical strata (within each column) were binned in six different height categories, according to the vertical height above ground where the LiDAR signal saturated in 2011 in each of the columns, before the liana removal: (a) <5 m, (b) 5–10 m, (c) 10–15 m, (d) 15–20 m, (e) 20–25 m and (f) 25–41 m. The change of the fraction of light-attenuating plant surface within each height layer up to the saturation height was calculated (in percent) for each column and averaged among all columns of the same saturation height layer and treatment type (R or C). Box-and-whiskers plot indicates the mean and distribution of these values. Significance of the difference between removal and control plots is marked by asterisks: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Forest structural complexity

In the lowest stratum of the forest (1–5 m), there was no difference between treatments after liana removal with respect to canopy structure, indicating that there were few liana stems and leaves intercepting light near the forest floor (Fig. 2a). In each of the higher forest stratum (above 5 m), however, the liana removal plots had significantly less light-intercepting plant structures than did the control plots (compared to the pretreatment measurements), indicating that lianas had occupied both the middle and upper portions of the forest (Fig. 2b–e). Differences in canopy structure were still significant 2 yr after liana removal for the middle and upper portions of the canopy (Fig. 2b–e), except for the highest portion of the upper canopy (25–41 m; Fig. 2f).

DISCUSSION

Lianas attenuated approximately 20% of the light penetration in this tropical forest. However, trees responded rapidly to the decrease in PAI following liana cutting, and 4 yr after the treatment trees had completely compensated for the fraction of PAI that lianas had previously contributed. Our hypothesis that the PAI would never return to pre-cutting conditions in the liana-removal plots was predicated on the idea that crown shyness maintains spaces among tree crowns (e.g., Putz et al. 1984), and that lianas can uniquely fill these inter-crown spaces. Contrary to our hypothesis, trees compensated entirely for the loss in liana PAI within 4 yr, which may have been due to trees in the canopy expanding laterally to take the space vacated by lianas, as well as plants in the understory expanding their crowns and increasing their leaf area.

The significant increase in the variation in PAI 1 yr following liana cutting may have been due to the patchy distribution of liana density and size (e.g., Dalling et al. 2012, Schnitzer et al. 2012, Ledo and Schnitzer 2014). Large lianas may have had a particularly strong effect on light interception in the forest, since large lianas can attenuate a lot of light over a limited area, and the removal of a large liana may allow copious light penetration into the understory, thus increasing the variation in PAI. The high variation in PAI, however, was present only 1 yr after cutting lianas, supporting the hypothesis

Reports

that trees compensate rapidly for the loss of liana stems and leaves. We were surprised at the speed at which trees compensated entirely after liana removal in terms of light interception, suggesting that competition for light is a powerful interaction between lianas and trees (Grauel and Putz 2004, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Álvarez-Cansino et al. 2015, Toledo-Aceves 2015).

Lianas were once thought to intercept light mainly at the top of the forest canopy, deploying their leaves over those of their host trees (e.g., Ogawa et al. 1965, Avalos and Mulkey 1999, Ingwell et al. 2010, Álvarez-Cansino et al. 2015). However, our data indicate that lianas contribute to forest structure and light interception throughout the upper- and mid-canopy layers of the forest. Because we restricted our analyses to the saturated columns, we were not able to determine the precise contribution of lianas to the very top layer of the canopy. Nonetheless, lianas were clearly present in the top stratum of the forest (25–41 m), and differences in forest structure in the top stratum between removal and control plots were present after 1 yr but absent after 2 yr, possibly because trees rapidly replaced lost liana leaves in the upper canopy, where light is most abundant. By contrast, the lack of replacement of lost liana structure in the mid-canopy after 2 yr may indicate that liana stems attenuated light in the mid-canopy. Liana stems loop through the forest and may be an important component of light interception (Sánchez-Azofeifa et al. 2009). Alternatively, trees may have been slow to add leaves to the mid-canopy because deploying leaves in the low-light environment of the mid-canopy would provide a relatively low return on their investment. In either case, our data indicated that some combination of liana leaves and stems intercept light in all but the lowest strata of the forest.

Our finding that lianas contributed ~20% to the plant area index (PAI) is comparable to other studies. For example, in a separate study in treefall gaps on Gigante Peninsula, LAI was ~16.5% higher before cutting lianas compared to 1 month afterwards (Schnitzer and Carson 2010). In the nearby old-growth forest of BCI, lianas contributed 17% to the forest leaf litter production (Wright et al. 2004). In the old-growth tropical wet forests at La Selva Biological Station, Costa Rica, lianas contributed up to 12% to the forest leaf area (Clark et al. 2008). The La Selva forest, however, had much lower liana abundance than the seasonal forests in central Panama (Mascaro et al. 2004, Yorke et al. 2013). Lianas are particularly abundant in secondary forests and seasonal forests compared to wet forests (DeWalt et al. 2000, Schnitzer 2005, Barry et al. 2015), which may also account for the discrepancy between our finding and that of Clark et al. (2008). Furthermore, neither Clark et al. (2008) nor Wright et al. (2004) included wood area index, which may explain their lower estimates of light interception by lianas.

Our findings indicate that lianas attenuate a significant amount of light in this tropical forest, and that lianas

intercepted light throughout the forest's vertical strata, not only at the top of their host trees, as was suspected previously. Competition for light between lianas and trees appears to be intense; trees compensated fully to the loss of liana structure within 4 yr, and faster in the upper layers of the canopy. If liana abundance continues to increase in neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015), then we would expect a further reduction in tree leaf area and possibly changes in canopy structure in the mid- and upper strata of these forests.

Literature Cited

Álvarez-Cansino, L., S. A. Schnitzer, J. P. Reid, and J. S. Powers. 2015. Liana competition with tropical trees varies seasonally but not with tree species identity. Ecology 96:39–45.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Asner, G. P., J. M. Scurlock, and J. A. Hicke. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Global Ecology and Biogeography 12:191–205.

Avalos, G., and S. S. Mulkey. 1999. Seasonal changes in liana cover in the upper canopy of a neotropical dry forest. Biotropica 31:186–192.

Barry, K. E., S. A. Schnitzer, M. van Bruegal, and J. S. Hall. 2015. Rapid liana colonization and community development along a secondary forest chronosequence. Biotropica 47:672–680.

Cahill Jr., J. F., J. P. Castelli, and B. B. Casper. 2001. The herbivory uncertainty principle: visiting plants can alter herbivory. Ecology 82:307–312.

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553–564.

Clark, D. B., P. C. Olivas, S. F. Oberbauer, D. A. Clark, and M. G. Ryan. 2008. First direct landscape-scale measurement of tropical rain forest leaf area index, a key driver of global primary productivity. Ecology Letters 11:163–172.

Dalling, J. W., S. A. Schnitzer, C. Baldeck, K. E. Harms, R. John, S. A. Mangan, E. Lobo, J. B. Yavitt, and S. P. Hubbell. 2012. Resource-based habitat associations in a neotropical liana community. Journal of Ecology 100:1174–1182.

DeWalt, S. J., S. A. Schnitzer, and J. Denslow. 2000. Density and diversity of lianas along a seasonal tropical forest chronosequence in central Panama. Journal of Tropical Ecology 16:1–19.

Graham, E. A., S. S. Mulkey, K. Kitajima, N. G. Phillips, and S. J. Wright. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. Proceedings of the National Academy of Sciences 100:572–576.

Grauel, W. T., and F. E. Putz. 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. Forest Ecology and Management 190:99–108.

Hardiman, B. S., G. Bohrer, C. M. Gough, C. S. Vogel, and P. S. Curtis. 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92:1818–1827.

Ingwell, L. L., S. Joseph Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 yr of tree growth and mortality on Barro Colorado Island, Panama. Journal of Ecology 98:879–887.

Kalacska, M. E., G. A. Sánchez-Azofeifa, J. C. Calvo-Alvarado, B. Rivard, and M. Quesada. 2005. Effects of season and successional stage on leaf area index and spectral vegetation indices in three mesoamerican tropical dry forests. Biotropica 37:486–496.

Kitajima, K., S. S. Mulkey, and S. J. Wright. 2005. Variation in crown light utilization characteristics among tropical canopy trees. Annals of Botany 95:535–547.

Leblanc, S. G., and J. M. Chen. 2001. A practical scheme for correcting multiple scattering effects on optical LAI measurements. Agricultural and Forest Meteorology 110:125–139.

Ledo, A., and S. A. Schnitzer. 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. Ecology 95:2169–2178.

Leigh Jr., E. G. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, Oxford.

LI-COR. 1990. LAI-2000 plant canopy analyzer. Instruction manual. LI-COR, Lincoln, Nebraska, USA.

Martínez-Izquierdo, L., M. M. Garcia-León, J. S. Powers, and S. A. Schnitzer. 2016. Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest. Ecology 97:215–224.

Mascaro, J., S. A. Schnitzer, and W. P. Carson. 2004. Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica. Forest Ecology and Management 190:3–14.

MATLAB. 2012. MATLAB and statistics toolbox release. The MathWorks Inc, Natick, Massachusetts, USA.

Ogawa, H., K. Yoda, K. Ogino, and T. Kira. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand. II. Nature and Life in Southeast Asia 4:49–80.

Parker, G. G., D. J. Harding, and M. L. Berger. 2004. A portable LIDAR system for rapid determination of forest canopy structure. Journal of Applied Ecology 41:755–767.

Pinheiro, J., D. Bates, S. DebRoy and D. Sarkar, and R Core Team. 2015. nlme: Linear and Nonlinear Mixed Effects Models.

Putz, F. E., G. G. Parker, and R. M. Archibald. 1984. mechanical abrasion and intercrown spacing. American Midland Naturalist 112:24–28.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria.

Reid, J. P., S. A. Schnitzer, and J. S. Powers. 2015. Short and long-term soil moisture effects of liana removal in a seasonally moist tropical forest. PLoS ONE 10:e0141891.

Sánchez-Azofeifa, G. A., M. Kalacska, M. M. do Espírito-Santo, G. W. Fernandes, and S. A. Schnitzer. 2009. Tropical dry forest succession and the contribution of lianas to wood area index (WAI). Forest Ecology and Management 258:941–948.

Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. The American Naturalist 166:262–276.

Schnitzer, S. A. 2015. Increasing liana abundance in neotropical forests: causes and consequences. Pages 451–464 *in* S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford.

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17:223–230.

Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology Letters 14:397–406.

Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849–857.

Schnitzer, S. A., P. B. Reich, B. Bergner, and W. P. Carson. 2002. Herbivore and pathogen damage on grassland and woodland plants: a test of the herbivore uncertainty principle. Ecology Letters 5:531–539.

Schnitzer, S. A., M. P. E. Parren, and F. Bongers. 2004. Recruitment of lianas into logging gaps and the effects of preharvest climber cutting in a lowland forest in Cameroon. Forest Ecology and Management 190:87–98.

Schnitzer, S. A., et al. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. PLoS ONE 7:e52114.

Schnitzer, S. A., G. M. F. van der Heijden, J. Mascaro, and W. P. Carson. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. Ecology 95:3008–3017.

Schnitzer, S. A., S. A. Mangan, and S. P. Hubbell. 2015. The lianas of Barro Colorado Island, Panama. Pages 76–90 *in* S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford.

Schnitzer, S. A., M. E. Kuzee, and F. Bongers. 2005. Disentangling above-and below-ground competition between lianas and trees in a tropical forest. Journal of Ecology 93:1115–1125.

Toledo-Aceves, T. 2015. Above- and belowground competition between lianas and trees. Pages 147–163 *in* S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford.

Van der Heijden, G. M., S. A. Schnitzer, J. S. Powers, and O. L. Phillips. 2013. Liana impacts on carbon cycling, storage and sequestration in tropical forests. Biotropica 45:682–692.

Van der Heijden, G. M. F., J. S. Powers, and S. A. Schnitzer. 2015. Lianas reduce carbon accumulation and storage in tropical forests. Proceedings of the National Academy of Sciences 112:13267–13271.

Welles, J. M., and J. M. Norman. 1991. Instrument for indirect measurement of canopy architecture. Agronomy Journal 83:818–825.

Wright, S. J., O. Calderón, A. Hernández, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-yr record from Panama. Ecology 85:484–489.

Yorke, S. R., S. A. Schnitzer, J. Mascaro, S. G. Letcher, and W. P. Carson. 2013. Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. Biotropica 45:317–324.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects modelling for nested data. Pages 101–142 Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

Reports