

Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees

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Citation: Tobin, M. F., A. J. Wright, S. A. Mangan, and S. A. Schnitzer. 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere* 3(2):20. <http://dx.doi.org/10.1890/ES11-00322.1>

Abstract. Lianas (woody vines) reduce growth and survival of host trees in both temperate and tropical forests; however, the relative strength of liana-tree competition in comparison to tree-tree competition remains unexplored. When controlling for biomass, lianas may have greater competitive effects than trees because the unique morphology of lianas allows them to reach the forest canopy at relatively small stem diameters and deploy a substantial crown above their host. We tested the hypothesis that lianas have a greater negative effect on canopy trees than do trees of similar biomass with a liana- and tree sapling-cutting experiment in a seasonal tropical moist forest in Panama. The response of canopy trees to the cutting treatments was characterized as the change in their daily water use by measuring their sap velocity before and after cutting. We compared the responses of canopy trees around which a similar biomass of either lianas or tree saplings had been cut to control trees with no cutting. Liana cutting increased canopy-tree sap velocity by ~8% from before to after cutting relative to control trees during the dry season. In contrast, canopy-tree sap velocity did not respond to tree cutting, probably because trees with biomass similar to lianas were confined to the forest understory. We observed a similar pattern of sap velocity changes during the wet season, but treatment differences were not significant. Our results demonstrate that release from liana competition, but not tree competition, resulted in increased water transport in canopy trees, and suggests that relative to their biomass, lianas have greater competitive effects on canopy tree performance than do competing trees.

Key words: Barro Colorado; competition; liana cutting; Panama; plant-plant interactions; sap velocity; tropical forests.

Received 11 November 2011; revised 9 January 2012; accepted 24 January 2012; **published** 21 February 2012. Corresponding Editor: C. Lepczyk.

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INTRODUCTION

Lianas have a major influence on community and ecosystem processes in tropical forests throughout the world (Schnitzer and Bongers 2002, 2011). Lianas have been shown to reduce tree recruitment, regeneration, and diversity (Schnitzer and Carson 2010), growth (Clark and Clark 1990, Grauel and Putz 2004, Ingwell et al. 2010), reproductive output (Stevens 1987, Wright

et al. 2005), and survival (Putz 1984a, Phillips et al. 2005, Ingwell et al. 2010). Lianas may alter forest tree species composition by infesting slow growing species more frequently than fast growing species (Putz 1984b, Clark and Clark 1990, Schnitzer et al. 2000, van der Heijden and Phillips 2008, Schnitzer et al. 2011). By altering forest composition in favor of fast growing tree species with lower wood density, lianas may lower the carbon storage capacity of tropical

forests (van der Heijden and Phillips 2008). Furthermore, the abundance and biomass of lianas in neotropical forests appear to be increasing, and thus the effects of lianas on forest processes are also likely increasing (reviewed by Schnitzer and Bongers 2011, Schnitzer et al. 2011).

Lianas likely compete with canopy trees for light. Lianas have much higher leaf area relative to stem cross-sectional area than trees (Putz 1983, Gerwing and Farias 2000), and they deploy their crown above the canopy of their host tree, thereby dramatically reducing light availability to leaves of the host tree (Avalos et al. 2007). Liana infestation also reduces the total leaf area maintained by canopy trees, and the reduction in tree leaf mass is approximately proportional to the mass of the leaves added to the crown by lianas (Kira and Ogawa 1971).

Lianas may also compete with canopy trees for soil moisture, particularly in tropical forests that experience seasonal drought where liana abundance can be high (Schnitzer 2005, DeWalt et al. 2010). However, the few studies that directly tested competition for soil moisture between lianas and canopy trees produced mixed results, with lianas competing for soil moisture with *Senna multijuga* (Pérez-Salicrup and Barker 2000), but apparently not competing with *Swietenia macrophylla* (Barker and Pérez-Salicrup 2000). Thus, the extent of spatial and temporal partitioning of soil water resources between lianas and trees remains unclear, but because lianas continue to grow and take up below-ground resources even during seasonal drought (Andrade et al. 2005, Schnitzer 2005), the potential for competition for soil moisture during this period is high. Lianas apparently use water from shallow soil horizons early in the dry season and then deeper horizons as the dry season progresses (Andrade et al. 2005). Some small trees follow a similar pattern, while other small trees and large canopy trees appear to rely on shallow soil horizons for water throughout the dry season (Meinzer et al. 1999).

Numerous correlative studies have shown that tree performance decreases with increasing levels of liana infestation (e.g., Clark and Clark 1990, Ingwell et al. 2010). Correlative studies, however, do not exclude the possibility that an environmental factor both reduces canopy tree perfor-

mance and results in higher liana density or that lianas more densely infest canopy trees with lower performance (Stevens 1987). Liana-cutting experiments solve this cause and effect problem, and liana-cutting experiments have demonstrated the negative impact of lianas on canopy tree performance (e.g., Pérez-Salicrup and Barker 2000, Grauel and Putz 2004, Schnitzer and Carson 2010). However, cutting vegetation of any type could elicit a physiological or growth response to reduced competition (Schnitzer and Carson 2010). To assess the unique competitive impact of the liana growth form on canopy trees, liana cutting must be compared directly with cutting treatments of other woody plants, primarily trees. Of the numerous liana-cutting experiments (e.g., Barker and Pérez-Salicrup 2000, Pérez-Salicrup and Barker 2000, Gerwing 2001, Grauel and Putz 2004, Campanello et al. 2007, Peña-Claros et al. 2008, Schnitzer and Carson 2010), none have explicitly included a cutting treatment to compare the competitive effect of lianas to that of trees. The relative effect of liana and tree competition is a critical issue because as lianas increase in abundance and biomass relative to trees in tropical forests (Schnitzer and Bongers 2011), lianas will likely have a much greater effect on canopy trees than would be predicted by their biomass.

We tested the hypothesis that lianas have a greater competitive impact on canopy trees than do trees. The unique morphology of lianas that allows them to reach the canopy and deploy a substantial crown with less investment in support tissue should result in a greater competitive impact on canopy trees than a similar biomass of competing trees. We addressed our hypothesis by monitoring the change in daily water use of canopy trees using measurements of their sap velocity before and after cutting a similar total biomass of either lianas or tree saplings. By standardizing the amount of biomass cut, we were able to assess the effect of morphological differences between woody growth forms on their competitive impact. The experiment was conducted twice: once at the end of the dry season, when soil moisture availability was at its yearly low, and again at the end of the wet season, when soil moisture availability was high. Because the supply of water to leaves by the vascular system is linked to carbon dioxide

uptake for photosynthetic fixation, changes in sap velocity and thus water use can serve as a measure of changes in tree metabolism.

METHODS

We conducted this study in the Barro Colorado Nature Monument, a 5400-ha area in central Panama that includes Barro Colorado Island and five adjacent mainland peninsulas. Our cutting experiments were carried out on Gigante Peninsula in semi-deciduous secondary tropical moist forest, approximately 40–60 years in age. The long-term mean annual rainfall of the area is ~2600 mm, with a pronounced dry season from mid-December to mid-April (Windsor 1990).

Experimental design

We conducted two separate liana- and tree sapling-cutting experiments: the first at the end of the dry season (beginning 11 April 2008), and the second near the end of the wet season (beginning 6 December 2008). For each experiment, we monitored four canopy trees at each of four sites (16 trees total). We selected sites where there were four canopy trees of similar size that were far enough apart to minimize competition for resources, while still allowing 15 m extension wires to connect sap flow sensors to the central data logger. To accomplish this, we located target canopy trees that were spatially distributed at the corners of an approximate square, where the diagonal joining corners was 24 m to 30 m. Target canopy trees were chosen so that two of them were surrounded by a substantial number of lianas and the other two were surrounded by a substantial number of tree saplings, and thus all four had the potential for strong competitive interactions with a similar biomass of either lianas or tree saplings. Because it was not possible to find canopy trees of the same species that met all of our other criteria, the target canopy trees varied in species identity within and across sites (Appendix A).

To quantify the biomass of vegetation around each target canopy tree, we measured the diameter of the main stem for all woody plants with a diameter ≥ 0.5 cm that were rooted within 4 m of the target canopy tree. The diameters of tree saplings and understory trees were measured at 1.3 m height, whereas liana diameters

were measured as recommended by Gerwing et al. (2006) and Schnitzer et al. (2008), generally 1.3 m from the rooting point. We then estimated the oven-dry above ground biomass (AGB) in kilograms of lianas or saplings and understory trees surrounding the target canopy trees using the equation $AGB = \exp[\alpha + \beta \ln(D)]$, where D was the diameter expressed in centimeters and $\alpha = -1.484$ and $\beta = 2.657$ for lianas (Schnitzer et al. 2006), and $\alpha = -2.134$ and $\beta = 2.530$ for saplings and understory trees (Brown 1997).

After an initial measurement period to characterize sap velocity of target canopy trees on sunny days (see *Sap velocity* below), we cut either lianas or tree saplings from within 4 m of two of the four target canopy trees at each site. The cut lianas and tree saplings were selected such that we cut a similar AGB of each growth form and maximized the AGB cut at each site. The diameter of individual lianas and tree saplings (< 12 cm DBH) that were cut had similar ranges during both the dry season (0.5–9.3 cm and 0.5–11.7 cm, respectively) and wet season experiments (0.5–6.2 cm and 0.5–10.5 cm, respectively). Because the total AGB of lianas and tree saplings within 4 m of treatment target trees at a site were not always similar, we did not always cut all lianas and tree saplings at each site so as to standardize the amount of AGB cut between growth forms. For lianas, we cut 97–100% of the total number of liana individuals within 4 m of target trees, which equaled 83–100% of the total liana AGB, except for one site in the dry season and two in the wet season at which approximately 50% of AGB was cut (60–93% of liana individuals). For trees, we cut 89–100% of the total number of individual tree saplings within 4 m of target trees, which constituted 78–100% of the total tree sapling AGB, except for one site during the wet season where 73% of individual tree saplings and 35% of total tree sapling AGB were cut because liana AGB was limiting. At one site during the wet season experiment, we mistakenly cut 100% more AGB of tree saplings than lianas. Even with this additional biomass cut, we observed no effect of cutting tree saplings and therefore retained the site in the analysis.

Sap velocity

We measured sap velocity in target canopy

trees using a heat pulse technique based on pioneering work by Marshall (1958) and further developed and described in Burgess et al. (2001a, b). Sensors consisted of three probes inserted radially into the xylem and aligned vertically with the bole: a central heater probe with equidistant thermocouple temperature probes placed 6 mm above and below it. We constructed the thermocouple probes by positioning two copper-constantin (36 AWG or 0.127 mm diameter wire) thermocouple junctions surrounded by heat transfer compound and an insulative sleeve inside a 40-mm 18-gauge (1.3 mm outer diameter) stainless steel tube, such that the thermocouples were 5 mm and 20 mm from the tip. The tip of the steel tube was sealed with solder and 10 mm of the tube base was embedded in epoxy, which also housed the connections of thermocouple wires to the extension wires. We constructed heater probes similarly, using a tightly coiled 15-cm length of nichrome wire (36 AWG) as a 19- Ω line heater inside the steel tube. The thermocouple probes were connected via 15 m wires to a 64-channel multiplexer (Model AM 16/32A, Campbell Scientific, Logan, Utah, USA) connected to a datalogger (Model CR 1000, Campbell Scientific). The heater probes were connected in parallel to a 12 V deep-cycle lead-acid battery by a relay controlled by the datalogger.

We installed the sensors in target canopy trees at approximately 1.5 m height or slightly higher when necessary to avoid buttresses. After removing a 4 cm by 4 cm square of bark, we drilled three 1.3-mm diameter holes at 6 mm spacing to a depth of 30 mm using a drill guide to ensure parallel and precisely spaced holes. We inserted probes into the holes and then thoroughly insulated them with reflective foil bubble insulation.

We calculated sap velocity from the heat pulse velocity determined from temperature changes at the upper and lower thermocouple probes following a pulse of heat released by the heater probe every 30 minutes using equations from Burgess et al. (2001a). The thermal diffusivity values used to calculate heat pulse velocity were estimated from equation 8 of Kluitenberg and Ham (2004) using values derived from measurements taken during periods of zero sap flow. Thermal diffusivity decreased throughout the

beginning of the wet season (Appendix B), so monthly estimates were used to calculate heat pulse velocity. We corrected heat pulse velocity for xylem wounding resulting from probe installation using the correction coefficients presented by Burgess et al. (2001a), assuming a 2-mm diameter wound suggested by dye staining patterns in other tropical trees (M. Tobin, *personal observation*). Corrected heat pulse velocity was used to calculate sap velocity according to equation 7 of Burgess et al. (2001a).

We measured the density and water content of sapwood for each target canopy tree to permit calculation of sap velocity from heat pulse velocity described above. We used an increment borer to remove a sapwood core at the height of the sap velocity sensor. Two 10-mm sections centered at 10 mm and 25 mm depth (sap velocity measurement depths) were immediately removed from the core and placed in pre-weighed microcentrifuge tubes. After measuring fresh mass of core sections, we determined their volume by water displacement. Cores were then oven-dried at 100°C and weighed to obtain dry mass. We calculated water content by dividing fresh mass minus dry mass by the dry mass, and calculated density as dry mass divided by fresh volume.

Soil matric potential

We characterized changes in soil moisture availability during the dry season experiment and between dry and wet season experiments by measuring soil matric potential using the filter paper technique (Deka et al. 1995, Scanlon et al. 2002). At each site, we collected a soil sample at eight depths (0.1–1.2 m) from a central location using a soil auger. In the lab, each soil sample was quickly sieved (2 mm), sealed in a 473 ml glass mason jar with a stack of three filter papers (Whatman no. 42) placed in the middle of the sample, and allowed to equilibrate at room temperature for 7 days in a thermally insulated container. We determined gravimetric water content of the center filter paper from masses measured before and after drying at 105°C for 24 h. We calculated soil matric potential from gravimetric water content using a generalized calibration equation for Whatman no. 42 filter paper (Scanlon et al. 2002).

Data analysis

We compared the percent change in mean sap velocity from before to after liana or tree cutting during both dry and wet seasons. We calculated the percent change in sap velocity using means of three or four individual day means of consecutive sunny days. We calculated these means for the four days immediately before cutting treatments, the three or four days beginning one day after the cutting treatment was completed, and for several additional periods throughout the experiments. Individual day means included measurements taken from 07:00 to 19:00. Both dry and wet season experiments had a single control tree excluded from the percent change analysis due to a deciduous target tree and a faulty sensor, respectively. An additional control target tree that lost its leaves during the wet season experiment was excluded from the second and third set of sap velocity means for that experiment. Soil moisture availability was low during the dry season experiment (Table 1), and may have begun to limit transpiration for some canopy trees. To control for differences in water status of target canopy trees and its effect on sap velocity during the dry season, we created an index of individual canopy tree water stress by calculating the percent change in mean sap velocity from one day before to the day after a rainfall event during the period before the cutting treatment.

We analyzed short-term response in percent change in sap velocity during the dry season using a mixed-model analysis of covariance (ANCOVA), and during the wet season using a mixed-model ANOVA. We analyzed longer-term

response in percent change in sap velocity using repeated-measures analyses. In all models, we included growth form (target canopy tree surrounded by either lianas or tree saplings) and treatment (cut or control) as fixed effects, and site as a random effect. For the analyses of the dry season experiment, we included the index of canopy tree water stress as a covariate. Within the growth form \times treatment interaction term, we examined whether liana or tree cutting differentially influenced sap velocity of target canopy trees using a priori contrasts. We analyzed soil water potential using an ANOVA with depth, season and their interaction as fixed effects. Statistical analyses were performed with SAS 9.1 (SAS Institute, Cary, North Carolina, USA).

RESULTS

During the dry season, cutting lianas resulted in a greater short-term increase in sap velocity than cutting tree saplings, as indicated by a significant growth form by treatment interaction (growth form: $F_{1,7} = 8.42$, $P = 0.0229$; treatment: $F_{1,7} = 0.92$, $P = 0.3701$; growth form \times treatment: $F_{1,7} = 6.42$, $P = 0.0391$; Fig. 1A). Cutting lianas increased canopy-tree sap velocity by $\sim 8\%$ relative to liana control trees ($t = 2.37$, $P = 0.0497$) and relative to tree sapling control trees ($t = 2.62$, $P = 0.0343$; Fig. 1A). In contrast, cutting tree saplings did not change canopy-tree sap velocity relative to sapling control trees ($t = 1.03$, $P = 0.3389$) or liana control trees ($t = 1.41$, $P = 0.2018$; Fig. 1A). The index of individual canopy-tree water stress included as a covariate was negatively related to short-term changes in sap velocity ($R = -0.82$, $t = -5.10$, $P = 0.0002$). Thus, target canopy trees with higher values for the water stress index exhibited greater decreases in sap velocity, likely due to increasing canopy-tree water stress over this period. In the longer-term analysis of changes in sap velocity over ~ 3 months following the cutting treatment, we found that the effect of cutting lianas was significant only for the first two time points (Fig. 2A). The lack of a growth form \times treatment interaction ($F_{1,7} = 0.90$, $P = 0.3733$; Appendix C) over the longer term reflected the increased variability in sap velocity changes that may be related to divergent responses of the target canopy trees to the onset of wet season rains

Table 1. Mean (SE) of soil matric potential (Ψ_m) for soil samples collected at the four study sites at multiple depths during the dry and wet season experiments (21 April 2008 and 9 December 2008, respectively).

Depth (m)	Soil Ψ_m (MPa)	
	Dry season	Wet season
0.1	-1.96 (0.20)	-0.01 (0.004)
0.2	-2.08 (0.29)	-0.02 (0.008)
0.3	-1.80 (0.29)	-0.03 (0.014)
0.4	-2.24 (0.31)	-0.08 (0.043)
0.6	-2.38 (0.15)	-0.10 (0.042)
0.8	-2.33 (0.25)	-0.17 (0.085)
1.0	-2.28 (0.35)	-0.09 (0.037)
1.2	-1.88 (0.14)	-0.12 (0.084)

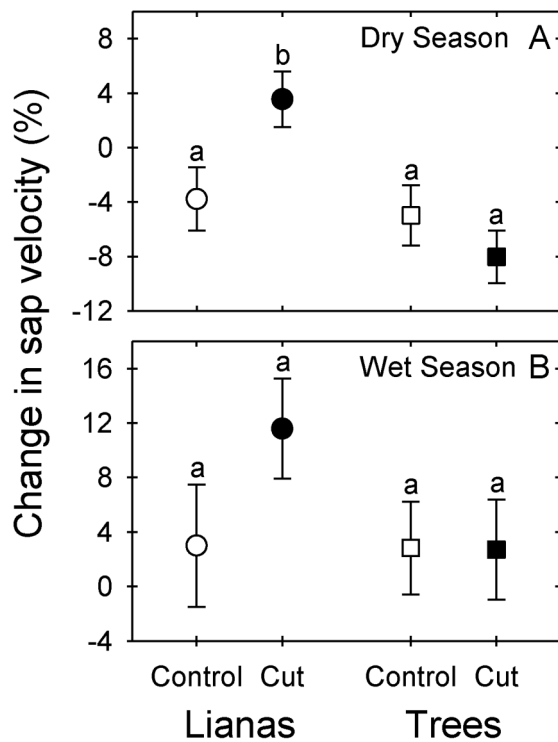


Fig. 1. Percent change in mean sap velocity of canopy trees from before to immediately after cutting a similar biomass of competing lianas or trees around treatment canopy trees for dry season (A) and wet season (B) experiments. Sap velocity values are adjusted means of percent change (\pm SE) of four canopy trees except for dry season liana control trees ($n = 3$) and wet season tree control trees ($n = 3$). Points not labeled with the same letter were significantly different from each other.

and concomitant increase in soil matric potential (Fig. 2C).

In the second experiment, conducted at the end of the wet season when soil moisture availability was high throughout the sampled profile (season: $F_{1,57} = 474.03$, $P < 0.0001$; depth: $F_{1,57} = 1.24$, $P = 0.2711$; season \times depth: $F_{1,57} = 0.04$, $P = 0.8414$; Table 1), we observed a pattern in short-term changes in sap velocity similar to the dry season experiment (Fig. 1B), but differences among treatments were not significant (growth form: $F_{1,7} = 1.30$, $P = 0.2924$; treatment: $F_{1,7} = 1.00$, $P = 0.3508$; growth form \times treatment: $F_{1,7} = 1.21$, $P = 0.3085$). Differences among treatments were not significant for the longer-term analysis for the wet season experiment (Fig. 2B; Appendix C).

DISCUSSION

Our findings indicate that lianas have a greater competitive effect on canopy trees during the dry season than do trees of similar biomass. The sap velocity of canopy trees increased rapidly following release from competition with lianas in the dry season, a period with relatively low soil moisture availability and high evapotranspirative demand. In contrast, cutting tree saplings did not affect canopy-tree sap velocity during the same period. We observed these increases in sap velocity following liana cutting despite not controlling for species of treatment or control target canopy trees, suggesting that the response may be common among secondary-growth tropical trees. The lack of a significant liana-cutting effect following the first substantial rainfall events at the end of the dry season may be due to increased variability in sap velocity changes related to divergent responses of individual target canopy trees to the onset of rains.

Increased canopy-tree sap velocity in response to cutting lianas, but not tree saplings, likely arises from the divergent morphologies of lianas and trees. Lianas in small diameter classes often reach the forest canopy, allowing them to position their leaves on top of supporting trees. In the Barro Colorado Nature Monument forests, for example, Kurzel et al. (2006) found that lianas with diameters >2.0 cm had an 80% chance of being in the forest canopy, and nearly all lianas >3.0 cm in diameter were in the forest canopy. Lianas also have four to five times the leaf mass per stem diameter than do trees (Gerwing and Farias 2000). Thus, even small diameter lianas can have well-developed crowns deployed above the host tree canopy, resulting in competition for both above- and below-ground resources. In contrast, trees of comparable size are confined to the shaded forest understory, and thus have a relatively minor competitive effect on canopy trees for light or soil resources.

The rapid increase in sap velocity of canopy trees after cutting lianas is likely due, in part, to the reduced shading of canopy trees by competing lianas. Increased irradiation of canopy tree leaves due to wilting of liana leaves following cutting would result in greater evaporative demand (Nobel 1983), and would contribute to greater transpiration and sap velocity. The

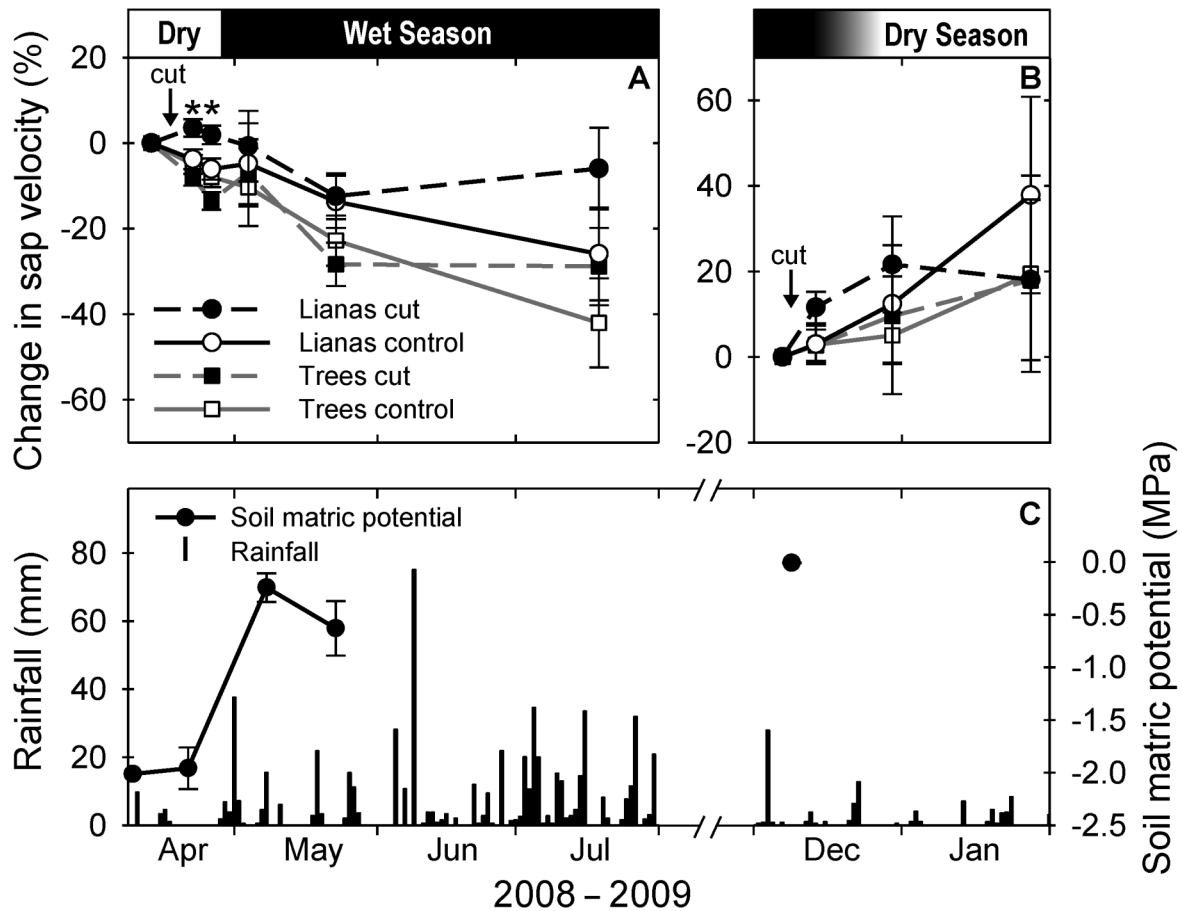


Fig. 2. Percent change in mean sap velocity of canopy trees from before to several months after cutting a similar biomass of competing lianas or trees around treatment canopy trees for dry season (A) and wet season (B) experiments, and daily rainfall and soil matric potential at 0.1 m depth (C) over the same periods. Dates labeled with an asterisk had greater increases in sap velocity for liana treatment trees than liana or tree control trees. Sap velocity points are adjusted means of percent change (\pm SE) of four canopy trees except for dry season liana control trees ($n=3$) and wet season tree control trees ($n=3$) and wet season both control trees ($n=3$) for final two dates. Soil matric potential points are means (\pm SE) of four sites except the first date ($n=1$).

observed increase in sap velocity also suggests that canopy trees released from liana competition will increase photosynthetic carbon uptake once leaves and branches acclimate to higher irradiation (Kursar and Coley 1999, Lemoine et al. 2002, Guo et al. 2006).

Reduced below-ground competition for soil moisture may also contribute to an increase in sap velocity of canopy trees following liana cutting. Cutting lianas effectively stops the removal of water from the soil by liana root systems, thereby slowing a decline in soil moisture in the vicinity of the host tree. Reduced

below-ground liana competition may be particularly important during seasonal drought when declining soil moisture availability may limit canopy tree uptake, because lianas continue to grow and take up below-ground resources during this period (Andrade et al. 2005, Schnitzer 2005). For example, in a seasonal forest in Bolivia, Pérez-Salicrup and Barker (2000) reported that cutting lianas at the beginning of the dry season resulted in unchanging pre-dawn water potential for canopy trees throughout the dry season, whereas pre-dawn water potential for canopy trees with lianas present declined during

the same period. During our dry season experiment, we expected sap velocity to increase with increasing soil moisture availability at the beginning of the wet season if low soil moisture availability had been limiting canopy tree transpiration. While sap velocity on sunny days increased substantially for three of 15 canopy trees (11%, 33%, and 128%) after the six days of rain (57.5 mm total) that ended the dry season, four canopy trees decreased substantially over the same period (−14%, −18%, −37%, and −24%). The lack of a consistent increase in sap velocity of canopy trees after the onset of the rainy season suggests that competition for soil moisture was not the only factor limiting canopy tree water use.

Our results may provide a physiological explanation for the increased growth of canopy trees following liana cutting observed in many studies (e.g., Pérez-Salicrup and Barker 2000, Gerwing 2001, Grauel and Putz 2004, Campanello et al. 2007, Schnitzer and Carson 2010). The increase in sap velocity of canopy trees we observed in response to liana cutting during the dry season suggests that lianas have the potential to reduce canopy tree growth. Since water transport to the canopy is strongly linked to whole-tree carbon uptake (Catovsky et al. 2002), canopy trees competing with lianas may be at a disadvantage in terms of carbon gain. Reduction in carbon gain due to competition with lianas could lead to reduced canopy-tree growth rates, especially for canopy trees with heavy infestations.

There is now strong evidence that lianas are increasing in abundance and biomass relative to trees in tropical forests (reviewed by Schnitzer and Bongers 2011, Schnitzer et al. 2011). The unique morphology of lianas allows them to compete for resources with canopy trees at a biomass at which trees do not measurably compete. Thus, as lianas increase relative to trees, the effects of lianas on tropical forest functioning and dynamics will also likely increase even though they comprise a relatively small fraction of the total forest biomass.

ACKNOWLEDGMENTS

We thank Tom Kursar and Phyllis Coley for use of laboratory space and equipment, Vanessa Boukili and Lou Santiago for technical advice on sap flow system

construction, and Kristen Becklund for assistance with probe assembly. Evelyn Sánchez, Al Domeyko and Gemma Rutten provided valuable assistance in the field, and David Brassfield assisted with tree identification. Smithsonian Tropical Research Institute provided logistical support and the rainfall dataset (Terrestrial-Environmental Science Program). Funding was provided by the University of Wisconsin-Milwaukee Research Growth Initiative and Graduate School, and the National Science Foundation (NSF-DEB 0613666 and NSF-DEB 0845071).

LITERATURE CITED

- Andrade, J. L., F. C. Meinzer, G. Goldstein, and S. A. Schnitzer. 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* 19:282–289.
- Avalos, G., S. S. Mulkey, K. Kitajima, and S. J. Wright. 2007. Colonization strategies of two liana species in a tropical dry forest canopy. *Biotropica* 39:393–399.
- Barker, M. G., and D. Pérez-Salicrup. 2000. Comparative water relations of mature mahogany (*Swietenia macrophylla*) trees with and without lianas in a subhumid, seasonally dry forest in Bolivia. *Tree Physiology* 20:1167–1174.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests. *FAO Forestry Papers*. Volume 134. FAO, Rome, Italy.
- Burgess, S. S. O., M. A. Adams, N. C. Turner, C. R. Beverly, C. K. Ong, A. A. H. Khan, and T. M. Bleby. 2001a. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology* 21:589–598.
- Burgess, S. S. O., M. A. Adams, N. C. Turner, C. R. Beverly, C. K. Ong, A. A. H. Khan, and T. M. Bleby. 2001b. Correction: an improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology* 21:1157.
- Campanello, P. I., J. Garibaldi, M. Gatti, and G. Goldstein. 2007. Lianas in a subtropical Atlantic forest: host preference and tree growth. *Forest Ecology and Management* 242:250–259.
- Catovsky, S., N. M. Holbrook, and F. A. Bazzaz. 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. *Canadian Journal of Forest Research* 32:295–309.
- Clark, D. B., and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemi-epiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6:321–331.
- Cleveland, W. S., E. Grosse, and W. M. Shyu. 1992. Local regression models. Pages 309–376 in J. M. Chambers and T. J. Hastie, editors. *Statistical models in S*. Wadsworth & Brooks, Pacific Grove, California, USA.

- Deka, R. N., M. Wairiu, P. W. Mtakwa, C. E. Mullins, E. M. Veenendaal, and J. Townend. 1995. Use and accuracy of the filter-paper technique for measurement of soil matrix potential. *European Journal of Soil Science* 46:233–238.
- DeWalt, S. J. et al. 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42:309–317.
- Gerwing, J. J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *Journal of Applied Ecology* 38:1264–1276.
- Gerwing, J. J. and D. L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* 16:327–335.
- Gerwing, J. J., et al. 2006. A standard protocol for liana censuses. *Biotropica* 38:256–261.
- 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.
- Guo, X. R., K. F. Cao, and Z. F. Xu. 2006. Acclimation to irradiance in seedlings of three tropical rain forest *Garcinia* species after simulated gap formation. *Photosynthetica* 44:193–201.
- Ingwell, L. L., S. J. Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- Kira, T., and H. Ogawa. 1971. Assessment of primary production in tropical and equatorial forests. Pages 309–321 in P. Duvigneaud, editor. *Productivity of forest ecosystems*. UNESCO, Paris, France.
- Kluitenberg, G. J., and J. M. Ham. 2004. Improved theory for calculating sap flow with the heat pulse method. *Agricultural and Forest Meteorology* 126:169–173.
- Kursar, T. A., and P. D. Coley. 1999. Contrasting modes of light acclimation in two species of the rainforest understory. *Oecologia* 121:489–498.
- Kurzel, B. P., S. A. Schnitzer, and W. P. Carson. 2006. Predicting liana crown location from stem diameter in three Panamanian lowland forests. *Biotropica* 38:262–266.
- Lemoine, D., S. Jacquemin, and A. Granier. 2002. Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. *Annals of Forest Science* 59:761–766.
- Marshall, D. C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiology* 33:385–396.
- Meinzer, F. C., J. L. Andrade, G. Goldstein, N. M. Holbrook, J. Cavellier, and S. J. Wright. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301.
- Nobel, P. S. 1983. *Biophysical plant physiology and ecology*. W.H. Freeman, New York, New York, USA.
- Peña-Claros, M., T. S. Fredericksen, A. Alarco, G. M. Blate, U. Choque, C. Leano, J. C. Licona, B. Mostacedo, W. Pariona, Z. Villegas, and F. E. Putz. 2008. Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management* 256:1458–1467.
- Pérez-Salicrup, D. R., and M. G. Barker. 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124:469–475.
- Phillips, O. L., R. Vásquez Martínez, A. Monteagudo Mendoza, T. R. Baker, and P. Núñez Vargas. 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology* 86:1250–1258.
- Putz, F. E. 1983. Liana biomass and leaf area of a “Tierra Firme” forest in the Rio Negro Basin, Venezuela. *Biotropica* 15:185–189.
- Putz, F. E. 1984a. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- Putz, F. E. 1984b. How trees avoid and shed lianas. *Biotropica* 16:19–23.
- Scanlon, B. R., B. J. Andraski, and J. Bilskie. 2002. Miscellaneous methods for measuring matrix or water potential. Pages 643–670 in J. H. Dane and G. C. Topp, editors. *Methods of soil analysis, Part 4: Physical methods*. Soil Science Society of America, Madison, Wisconsin, USA.
- Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262–276.
- 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., F. Bongers, and S. J. Wright. 2011. Community and ecosystem ramifications of increasing lianas in neotropical forests. *Plant Signaling & Behavior* 6:598–600.
- 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., J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88:655–666.
- Schnitzer, S. A., S. J. DeWalt, and J. Chave. 2006. Censusing and measuring lianas: a quantitative

- comparison of the common methods. *Biotropica* 38:581–591.
- Schnitzer, S. A., S. Rustishauser, and S. Aguilar. 2008. Supplemental protocol for liana censuses. *Forest Ecology and Management* 255:1044–1049.
- Stevens, G. C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68:77–81.
- van der Heijden, G. M. F., and O. L. Phillips. 2008. What controls liana success in Neotropical forests? *Global Ecology and Biogeography* 17:372–383.
- Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, D.C., USA.
- Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21:307–315.

SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Species and diameter at breast height (DBH) of canopy trees monitored for sap velocity changes by site, growth form (target canopy tree surrounded by either lianas or tree saplings) and treatment during each experiment.

Site	Growth form	Treatment	Dry season		Wet season	
			Species	DBH (cm)	Species	DBH (cm)
1	liana	control	<i>Cordia bicolor</i>	25.4	<i>Lonchocarpus latifolius</i>	31.3
1	liana	cut	<i>Lonchocarpus latifolius</i>	23.5	<i>Luehea seemannii</i>	32.8
1	tree	control	<i>Gustavia superba</i>	18.1	<i>Miconia argentea</i>	32.2
1	tree	cut	<i>Alchornea costaricensis</i>	40.9	<i>Luehea seemannii</i>	30.4
2	liana	control	<i>Tetragastris panamensis</i>	29.4	<i>Casearia sylvestris</i>	19.6
2	liana	cut	<i>Protium tenuifolium</i>	40.9	<i>Cordia bicolor</i>	23.6
2	tree	control	<i>Guarea grandifolia</i>	40.5	<i>Protium tenuifolium</i>	20.8
2	tree	cut	<i>Trichilia tuberculata</i>	30.0	<i>Inga cocleensis</i>	32.4
3	liana	control	<i>Inga punctata</i>	32.1	<i>Cordia bicolor</i>	35.6
3	liana	cut	<i>Protium tenuifolium</i>	34.2	<i>Enterolobium schomburgkii</i>	44.2
3	tree	control	<i>Tetragastris panamensis</i>	28.3	<i>Zanthoxylum panamense</i>	27.4
3	tree	cut	<i>Tetragastris panamensis</i>	30.7	<i>Cordia alliodora</i>	28.0
4	liana	control	<i>Alseis blackiana</i>	24.9	<i>Chrysophyllum argenteum</i>	22.1
4	liana	cut	<i>Prioria copaifera</i>	31.1	<i>Heisteria concinna</i>	24.6
4	tree	control	<i>Virola sebifera</i>	16.1	<i>Xylopia macrantha</i>	18.1
4	tree	cut	<i>Tetragastris panamensis</i>	27.0	<i>Alseis blackiana</i>	21.4

APPENDIX B

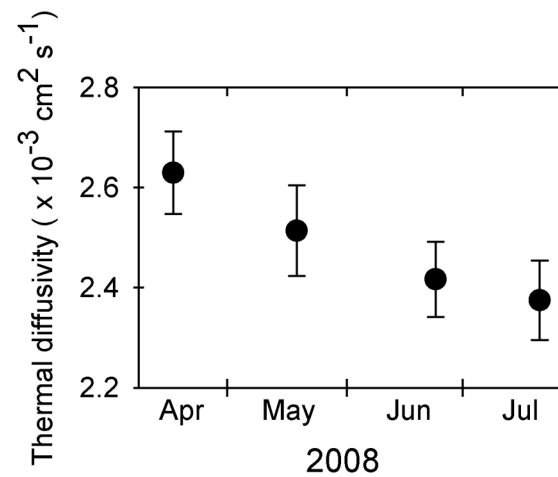


Fig. B1. Thermal diffusivity (k) of wood surrounding sap velocity probes installed in boles of canopy trees ($n = 16$) during a 95-day period from the end of dry season into the wet season. Analyzed as a linear mixed effects model with date as a continuous fixed effect and tree as a random effect, the linear decrease in k ($F_{1,47} = 43.8467$, $P < 0.0001$) with time led to a 10% drop over the period measured. Thermal diffusivity was calculated using equation 8 from Kluitenberg and Ham (2004) with values derived from measurements taken during periods of zero sap flow that resulted from rainy conditions for several hours preceding sunrise. The time from onset of the heat pulse to maximum temperature at a thermocouple temperature probe needed for this calculation was estimated from a local regression model (Cleveland et al. 1992) fit to the relationship between temperature increase and time since heat pulse over the first 200 s. For each sensor, k was the mean of values calculated for downstream and upstream thermocouple temperature probes.

APPENDIX C

Table C1. Repeated-measures analyses of change in sap velocity of canopy trees over time after implementing a treatment of cutting a similar biomass of competing lianas or trees.

Effect	Dry season experiment			Wet season experiment		
	df	F^\dagger	P	df	F^\dagger	P
Life form	1, 7	5.90	0.0444	1, 7	0.46	0.4213
Treatment	1, 7	0.96	0.3600	1, 7	<0.01	0.9910
Growth form \times Treatment	1, 7	0.90	0.3733	1, 7	<0.01	0.9465
Site	3, 7	2.38	0.1554	3, 7	0.21	0.8861
Water stress	1, 7	0.79	0.4032
Time	4, 28	11.38	<0.0001	2, 14	3.53	0.0537
Time \times Growth form	4, 28	0.93	0.4605	2, 14	0.10	0.9067
Time \times Treatment	4, 28	1.47	0.2385	2, 14	0.93	0.4187
Time \times Growth form \times Treatment	4, 28	0.20	0.9386	2, 14	0.63	0.5471
Time \times Site	12, 28	1.82	0.0947	6, 14	0.68	0.6685
Time \times Water stress	4, 28	3.91	0.0120

† Significance tests are based on higher-terms-included (SAS type III) adjusted sums of squares.