

Liana Impacts on Carbon Cycling, Storage and Sequestration in Tropical Forests

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ABSTRACT

Mature tropical forests sequester large quantities of atmospheric CO₂, which they store as plant biomass. These forests are changing however, including an increase in liana abundance and biomass over recent decades in Neotropical forests. We ask here how this increase in lianas might impact the tropical forest carbon cycle and their capacity for carbon storage and sequestration. Lianas reduce tree growth, survival, and leaf productivity; however, lianas also invest significantly in leaf production, and the increase in lianas could conceivably offset liana-induced reductions in tree canopy productivity with no adverse effects to the forest-level canopy productivity. By contrast, lianas decrease the total ecosystem uptake of carbon by reducing tree biomass productivity. Lianas themselves invest little in woody biomass, and store and sequester only a small proportion of the biomass in tropical forests. As lianas increase they may effectively displace trees, but the greater liana carbon stocks are unlikely to compensate for liana-induced losses in net carbon sequestration and storage by trees. A potentially important additional consideration is the impact of lianas on the tree community. By competing more intensely with shade-tolerant, more densely wooded trees than with fast-growing, light-wooded trees, lianas may shift tree composition toward faster-growing species, which store relatively little carbon, and thereby further reduce the carbon storage capacity of tropical forests. Overall, current evidence indicates that the increase in lianas will negatively impact the carbon balance of tropical forests, with potentially far-reaching consequences for global atmospheric CO₂ levels and associated climate change.

Abstract in Spanish is available in the online version of this article

Key words: carbon balance; carbon cycle; carbon sequestration; lianas; tree growth; tree mortality; tropical forests.

TROPICAL FORESTS WORLDWIDE CONSTITUTE THE LARGEST POOL OF TERRESTRIAL BIOMASS CARBON STOCKS, contribute more than half of the planet's terrestrial biodiversity and a third of its terrestrial global net primary productivity (Beer *et al.* 2010, Pan *et al.* 2011). Consequently, any modification to the productivity and dynamics in these forests may have global consequences, including increases in the concentration of atmospheric greenhouse gases and depletion of the world's biodiversity. Recent evidence indicates that tropical forests biomass, composition, and structure are now changing, presumably due to a combination of higher atmospheric CO₂ concentrations, changes in climatic conditions, and intensification of human interferences, such as logging and hunting (*e.g.*, Lewis *et al.* 2009a, Phillips *et al.* 2009). These changes include an increase in the abundance and biomass of lianas in tropical forests (Phillips *et al.* 2002, Wright *et al.* 2004, Ingwell *et al.* 2010, Schnitzer & Bongers 2011).

Lianas (woody vines) are structural parasites and have overcome the constraint of being self-supporting. They therefore depend on other plants, mainly trees, to support their biomass as they climb up into the canopy. The climbing habit of lianas and herbaceous vines has evolved many times during the

course of plant evolution, with more than 130 plant families including one or more climbing species (Gentry 1991). The majority of lianas are restricted to tropical forests, where they can contribute up to 35 percent of the total number of woody plant species (Schnitzer *et al.* 2012) and up to 45 percent of woody stems present (Putz 1983, Gentry 1991, DeWalt & Chave 2004).

Supporting lianas is not without risks for their host trees. Lianas often damage the trees on which they rely for support, leading to stem deformations and breakage of tree branches and stems (Putz 1991, 1995). Once they have reached the canopy, lianas can form a layer of dense foliage over the tree crown, thereby severely reducing the light intensity in the underlying tree crowns (Putz 1995, Avalos *et al.* 1999, 2007). In addition, lianas appear to have well-developed root systems (Holbrook & Putz 1996, Restom & Nepstad 2004, Cai *et al.* 2007) and extremely efficient vascular systems (Ewers & Fisher 1989, Ewers *et al.* 1990, 1991, Gartner *et al.* 1990, Carlquist 1991, Fisher & Ewers 1995, Restom & Nepstad 2001), and therefore may compete for water and nutrients with both their hosts and neighboring, non-host trees (Whigham 1984, Dillenburg *et al.* 1993a,b, 1995, Pérez-Saliciup & Barker 2000, Schnitzer 2005, Toledo-Aceves & Swaine 2008). Thus, lianas are strong competitors with their hosts for a combination of light, water, and nutrients.

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Competition and mechanical effects of lianas may affect many dynamic processes in tropical forests. There is now overwhelming evidence that lianas severely reduce tree growth (Putz 1984b, Clark & Clark 1990, Dillenburg *et al.* 1993a, 1995, Gerwing 2001, Grauel & Putz 2004, Schnitzer *et al.* 2005, Campanello *et al.* 2007, Chen *et al.* 2008, Toledo-Aceves & Swaine 2008, Grogan & Landis 2009, van der Heijden & Phillips 2009, Ingwell *et al.* 2010, Schnitzer & Carson 2010) and increase tree mortality due to direct competition for resources or by the increased risk of wind- and rain-related breakage and tree-fall (Putz 1984b, Phillips *et al.* 2005, Grogan & Landis 2009, Ingwell *et al.* 2010). Lianas can also reduce tree fruit production (Stevens 1987, Wright *et al.* 2005, Kainer *et al.* 2006, 2007, Fonseca *et al.* 2009, Nabe-Nielsen *et al.* 2009, Klimas *et al.* 2012). Furthermore, lianas appear to compete far more intensely than do trees of equivalent biomass (Tobin *et al.* 2012), suggesting that increase liana abundance and biomass will have serious consequences for tropical forest dynamics, including forest-level carbon cycling, sequestration and storage.

Over recent few decades lianas have been increasing in abundance and biomass relative to trees, most notably in Neotropical forests (Phillips *et al.* 2002, Wright *et al.* 2004, Wright & Calderon 2006, Ingwell *et al.* 2010, Schnitzer & Bongers 2011, Schnitzer *et al.* 2012), though information from Africa and Asia is limited by lack of long-term datasets (Caballé & Martin 2001, Ewango 2010). Although the drivers of this increase in liana dominance in the Neotropics still remain unknown, several mechanisms have been suggested (reviewed by Schnitzer & Bongers 2011), including increased atmospheric CO₂ concentrations (Granados & Körner 2002, Phillips *et al.* 2002, Hättenschwiller & Körner 2003, Mohan *et al.* 2006, Zotz *et al.* 2006), changing climatic conditions, and seasonal droughts (Schnitzer 2005), increases in natural disturbances (Phillips & Gentry 1994, Phillips *et al.* 2004) and changes in forest land use (Laurance *et al.* 2001, Wright *et al.* 2007). None of these drivers are necessarily mutually exclusive and all are expected to intensify over the coming decades. Because lianas have the potential to reduce tree growth by as much as 84 percent (van der Heijden & Phillips 2009), and lianas can increase tree mortality risks, by two- to threefold (Phillips *et al.* 2005, Ingwell *et al.* 2010), increasing liana abundance and biomass are likely to influence the carbon cycle and balance of tropical forests.

In this review, we discuss the role of lianas in tropical forest carbon dynamics and carbon balance. We detail how lianas impact carbon cycling, carbon uptake, and the carbon storage capacity of tropical forests. We also examine the extent to which increasing liana abundance and biomass compensate for any liana-induced reductions in ecosystem carbon sequestration and storage. Our goal is to provide a comprehensive assessment of the potential role of lianas in tropical forest carbon dynamics, which can help predict future impacts of lianas on tropical forest carbon balance.

CONTRIBUTION OF LIANAS TO THE CARBON CYCLE

The tropical forest biome is characterized by high productivity and tropical forests contribute approximately one-third of the

global terrestrial productivity (Beer *et al.* 2010). Considerable effort has been put into quantifying the different components of the internal carbon cycling of tropical forests to be able to understand their impact on the global carbon balance (Malhi & Grace 2000, Cavaleri *et al.* 2006, 2008, Aragão *et al.* 2009, Girardin *et al.* 2010, Robertson *et al.* 2010, Malhi 2012). Tropical forest canopies absorb atmospheric CO₂ via photosynthesis (gross primary productivity [GPP]) and release CO₂ into the atmosphere due to autotrophic respiration of leaves, wood, and roots and heterotrophic respiration due to decomposition processes. Approximately 30–40 percent of tropical forest GPP is used to produce plant structural biomass and organic compounds (net primary productivity [NPP]) (Malhi 2012). Eventually, these plant components will be transferred to the soil in the form of leaf, wood, and root litter. From the soil, carbon is eventually released through decomposition and respiration by heterotrophic organisms.

Lianas contribute to the different components of the carbon cycle of tropical forests, though remarkably few studies have quantified their exact contribution. In this section, we focus on the aboveground carbon cycle, where the majority of the research has been conducted, and discuss the contribution of lianas to aboveground net primary productivity (ANPP). By focusing specifically on ANPP, we will also indirectly cover information on the contribution of lianas to ecosystem autotrophic respiration (Cavaleri *et al.* 2006, 2008, Robertson *et al.* 2010, Fig. 1).

LIANA CONTRIBUTIONS TO ABOVEGROUND NET PRIMARY PRODUCTIVITY.—The main components of ANPP of tropical forests consist of the production of the woody stems, branches, and canopy components (twigs, leaves, flowers, fruit), plus a small contribution of the production of volatile organic compounds (Clark *et al.* 2001). Stem productivity of tropical forests is typically measured as the annual woody stem diameter increment based on repeated tree censuses. Aboveground biomass accumulation is then estimated from these repeated growth measurements. However, similar measurements for lianas are lacking. So far just one published study, in southeast Peru, has specifically focused on estimating liana biomass growth over time (van der Heijden & Phillips 2009). They estimated that liana biomass growth was 0.09 Mg C/ha/yr (average of two 1-ha plots, TAM-05 & 06), whereas tree biomass growth in those same two plots averaged 2.70 Mg C/ha/yr (Aragão *et al.* 2009). Thus, they reported that lianas contribute only a very small proportion (3.3%) of the total stem production in these plots. Branch production is often not measured in many studies (Aragão *et al.* 2009, Girardin *et al.* 2010) and therefore the separate contribution of lianas to this component currently remains unknown. As lianas invest relatively little in woody components (Putz 1983), their contribution to branch productivity is likely to be small.

Tropical forest canopy productivity consists of the formation and growth of leaves, twigs, flowers, and fruits, and is typically estimated to be equal to the rate of litterfall (*e.g.*, Malhi 2012). Indeed, litterfall is one of the most frequently measured components of ANPP. Leaf litterfall is typically the largest fraction of total litterfall (Malhi 2012). Studies from sites around the world

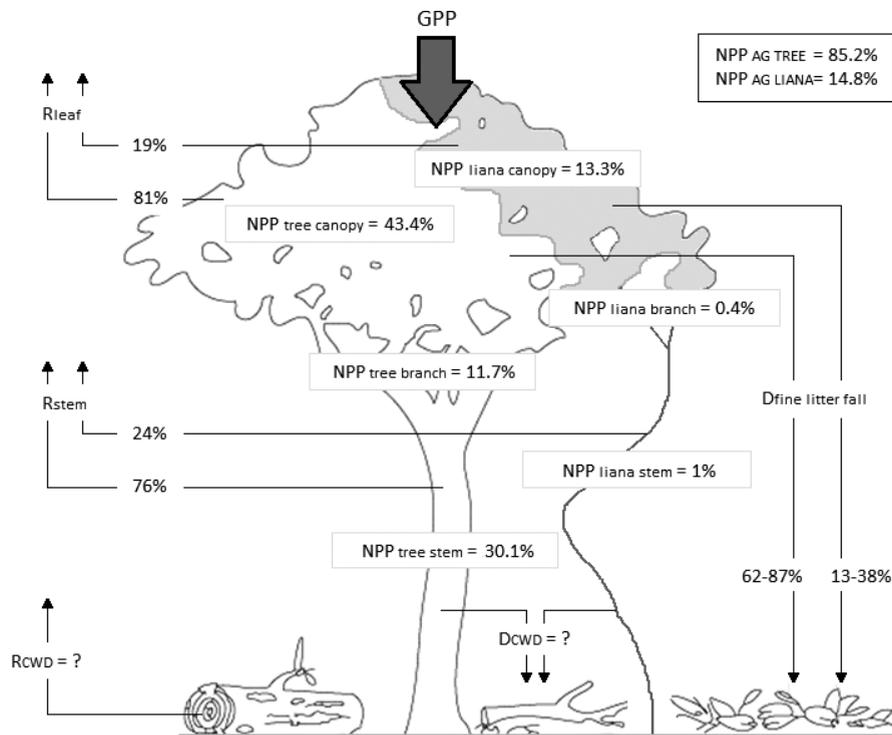


FIGURE 1. Proportional contribution of lianas to the individual components of the aboveground part of the carbon cycle of tropical forests. GPP, gross primary productivity; NPP, net primary productivity; NPP_{AG} , aboveground NPP; NPP_{canopy} , canopy NPP (Table 1); NPP_{stem} , aboveground stem wood NPP (trees: Aragão *et al.* 2009; lianas: van der Heijden & Phillips 2009), NPP_{branch} , branch turnover NPP (40% of NPP_{stem} ; cf. Girardin *et al.* 2010); $D_{litterfall}$, canopy litterfall (Table 1); D_{CWD} , wood mortality; R_{leaf} – leaf dark respiration (Cavaleri *et al.* 2008); R_{stem} , aboveground woody respiration (Cavaleri *et al.* 2006); R_{CWD} , coarse woody debris respiration. Question marks indicate that the proportional contribution of lianas to the component of the carbon cycle is currently unknown. The proportional contribution of lianas to ANPP is calculated based upon the average values for the different ANPP components for two plots (TAM-05 and TAM-06) in Tambopata, Peru (Aragão *et al.* 2009), an average contribution of lianas to $NPP_{liana\ canopy}$ of 23.5 percent and an $NPP_{liana\ stem}$ based upon van der Heijden & Phillips 2009 (see text).

have indicated that lianas can contribute to 11–38 percent of the total leaf litter production (Table 1). Liana leaf productivity is high because lianas allocate relatively less resources to a self-supporting stem, and thus more resources can be allocated to leaf productivity of the canopy (Putz 1983, Gehring *et al.* 2004, Gerwing 2004, Cai *et al.* 2007, Selaya *et al.* 2007) (Fig. 1). To date, however, the extent that lianas contribute to forest-level fruit and flower production is unknown for nearly all tropical forests.

There is limited information on the contribution of lianas to ANPP. In a tropical forest in southeast Peru (Tambopata), detailed measurements for most components of ANPP are available for both trees and lianas, which provide a unique estimate of the proportional contribution of lianas on ANPP for this forest (Fig. 1). Aragão *et al.* (2009) estimated ANPP in this forest to be 8.85 Mg C/ha/yr. This estimate is based on a total (lianas and trees) canopy productivity of 5.1 Mg C/ha/yr of litterfall, tree stem productivity of 2.7 Mg C/ha/yr, and tree branch productivity of 1.05 Mg C/ha/yr, but does not include liana stem and branch productivity. We therefore added stem (0.09 Mg C/ha/yr, van der Heijden & Phillips 2009) and branch (0.036 Mg C/ha/yr, assumed to be 40% of stem production;

cf. Girardin *et al.* 2010) productivity of lianas to this estimate of ANPP, which increased the total ANPP to 8.98 Mg C/ha/yr for this forest. The contribution of lianas to the litterfall in Tambopata was not known, so we assumed that liana litterfall contributed 23.5 percent of the total litterfall (the mean of the studies represented in Table 1). Based on these figures, lianas contribute to 1.32 Mg C/ha/yr or 14.8 percent of the total ANPP (Fig. 1).

The leaf area index of a forest is likely to correlate with its ANPP (Asner *et al.* 2003) and five studies from sites world-wide have quantified leaf area index of lianas in relation to that of trees (Table 1). The contribution of liana leaves to the forest leaf area ranged from as low as nine percent to as high as 31 percent (Table 1), suggesting that lianas also contribute to approximately nine to 31 percent of the ANPP in these sites. Lianas comprise a relatively small percentage of the forest biomass: 1.9 percent in Costa Rica (Clark *et al.* 2008) and Malaysia (Kato *et al.* 1978), 4.1 in Venezuela (Putz 1983), and 4.7 percent in Thailand (Ogawa *et al.* 1965). Thus, lianas contribute disproportionately to forest-level canopy productivity, compared to forest-level stem and branch production, and compared to forest biomass.

TABLE 1. Contribution of trees and lianas to Leaf Area Index (m^2/m^2) and annual leaf litterfall ($Mg\ C/ha^1$) in tropical forests.

Country	Forest type	Trees		Lianas		References
		m^2/m^2	%	m^2/m^2	%	
Leaf Area Index		m^2/m^2	%	m^2/m^2	%	
Costa Rica	Tropical wet forest	5.3	88	0.7	12	Clark <i>et al.</i> 2008,
Brazil	Tropical seasonal forest			1.3		Gerwing & Farias 2000,
Venezuela	Tropical wet forest	5.2	81	1.2	19	Jordan & Uhl 1978, Putz 1983,
Thailand	Tropical seasonal forest	7.4	69	3.3	31	Ogawa <i>et al.</i> 1965,
Malaysia	Tropical wet forest	7.3	91	0.7	9	Kato <i>et al.</i> 1978,
Litterfall		$Mg\ C/ha^1$	%	$Mg\ C/ha^1$	%	
Panama	Tropical seasonal forest	5.2–7.8	83–87	0.9–1.6	11–17	Wright <i>et al.</i> 2004,*
Brazil	Tropical seasonal forest	5.4	81	2.3	19	Da Hora <i>et al.</i> 2008,
Gabon	Tropical seasonal forest	3.9	62	2.3	38	Hladik 1974,
Australia	Subtropical forest	4.7	76	1.5	24	Hegarty 1991,
Malaysia	Tropical wet forest	5.7	87	0.8	13	Burghouts <i>et al.</i> 1994,
India	Tropical seasonal forest	5.6–6.9	62–71	2.8–3.4	29–38	Pragasam & Parthasarathy 2005,†

*Values indicate the range within a time series from 1986–2002.

†Values for two different plots in the same location.

EFFECT OF INCREASING LIANAS ON FOREST CARBON CYCLING.—The increases in liana densities observed in the last few decades (Phillips *et al.* 2002, Wright *et al.* 2004, Wright & Calderon 2006) have likely increased the proportional contribution of lianas to all components of ANPP due to a combination of: (1) the increasing direct contribution of lianas and (2) the liana-induced decrease in the contribution of trees. Increasing liana density can reduce woody tree biomass through reduced tree growth, greater mechanical damage, and higher mortality. The liana-induced loss of tree biomass is unlikely to be offset by increases in liana biomass (*e.g.*, van der Heijden & Phillips 2009). Increasing liana density therefore should lead to an overall decrease in forest-level woody biomass productivity.

By contrast, the effects of increasing lianas on forest-level canopy productivity are less clear. Trees that support a higher biomass of liana leaves appear to have a lower biomass of tree leaves, with lianas replacing host tree leaf biomass on a one-to-one basis (Ogawa *et al.* 1965, Kira & Ogawa 1971). In addition, since individual tree fruiting success in tropical forests is closely related to the light received by their canopy (*e.g.*, Phillips 1993), infestation with lianas can reduce or even completely halt host fruit production (Stevens 1987, Wright *et al.* 2005, Kainer *et al.* 2006, 2007, Fonseca *et al.* 2009, Nabe-Nielsen *et al.* 2009, Klimas *et al.* 2012). The loss of tree flower and fruit production may be offset, in terms of forest productivity, to some degree by the increased contribution of lianas to flower and fruit production (Wright & Calderon 2006). Increases in lianas might therefore reduce the overall contribution of trees to forest-level canopy productivity, but the effect on total forest-level canopy productivity is not known.

Lianas on Barro Colorado Island (BCI) have been increasing (Ingwell *et al.* 2010, Schnitzer *et al.* 2012) and this has led to a considerable proportional increase in liana leaf, flower, and fruit production relative to trees from 1986–2002 (Wright *et al.* 2004, Wright & Calderon 2006). Both liana and tree leaf production on

BCI increased over this period, leading to an increase in forest-wide canopy leaf production (Wright *et al.* 2004). Similarly, flower production of both lianas and trees increased, though that of lianas has increased nearly three-times faster than that of trees (Wright & Calderon 2006). Thus, both the relative productivity of lianas as well as the forest-level canopy production has increased on BCI, implying that factors beyond the increase in lianas might be affecting canopy productivity. Any liana impacts on the canopy productivity appear to be masked at the forest scale by an overall increase in leaf productivity and fecundity of trees, presumably due to a combination of elevated atmospheric CO_2 concentrations (Norby *et al.* 2005) and changing climatic conditions, possibly including increased solar radiation (Wright & Calderon 2006). Because of these wider changes in forest metabolism, additional research will be necessary to disentangle the effects of lianas from other factors impacting forest-level canopy productivity.

LIANA-INDUCED EFFECTS ON CARBON BALANCE

Tropical forests currently store 285 ± 64 Pg C in aboveground biomass worldwide (Feldpausch *et al.* 2012), which is over 30 percent of the earth's terrestrial carbon stock (*e.g.*, Cao & Woodward 2002). The exchanges of carbon between this long-term pool of carbon and the atmosphere dictate the carbon balance of tropical forests. Although the carbon balance is part of the larger carbon cycle of tropical forests, it warrants a separate discussion because it relates specifically to whether net fluxes into this carbon pool equal net fluxes out of this carbon pool. Any differences in those fluxes provide valuable information on whether tropical forests act as a carbon sink, *i.e.*, carbon stocks increase over time, or source, *i.e.*, carbon stocks decrease over time.

Aboveground carbon stocks of tropical forests change over time due to the difference between carbon gains by growth and carbon losses due to branch loss, mortality, and subsequent

branch and stem decomposition. The amount of carbon stored in tropical forests can also be altered by changes in species composition. Directional changes in species composition toward more fast-growing tree species with low wood densities, which store less carbon, will lead to a decrease in the carbon storage capacity of tropical forests, while changes toward more high wood density species, which store more carbon, will increase it. Currently, carbon stocks in tropical forests worldwide are increasing by ~ 1.2 Pg C/yr, equivalent to ~ 0.49 Mg/ha (Lewis *et al.* 2009b, Pan *et al.* 2011), indicating that these forests contribute to 50 percent of the global terrestrial carbon sink (Denman *et al.* 2007). In relative terms the net change per hectare in mean carbon stocks is low ($<0.3\%$ per ha per year), but the absolute impacts are large due to the scaling effects of the large geographical extent of tropical forests, their high productivity, and the large size of their trees.

Several observational studies have indicated that tree biomass of forests with a high biomass of lianas is considerably lower than that of forests with lower liana abundance, with their carbon storage capacity reduced by up to 50 percent (Chave *et al.* 2001, Laurance *et al.* 2001, Malhi *et al.* 2006). This liana-induced reduction in carbon stocks is likely caused by a combination of liana-induced: (1) reductions in tree growth; (2) increases in tree mortality; and (3) shifts in tree species composition due to different susceptibilities of trees to liana infestation and competition. In the next section, we will review these three distinct processes by which lianas impact on carbon balance, and assess how increasing liana abundance and biomass might influence the carbon balance of tropical forests in the future.

CARBON SEQUESTRATION.—By reducing tree survival and growth, lianas constrain the net carbon gain, *i.e.*, difference of carbon gains and losses, of tropical forests. While the negative effects of lianas on individual tree growth are now well-known, so far only one study has attempted to estimate the total effect of liana-induced reduction in tree growth on stand-level carbon sequestration. van der Heijden and Phillips (2009) evaluated the effect of lianas on tree growth while accounting for competition for light, potential competition for nutrients and water with neighboring trees, and wood density, by combining all these factors in a multi-species model. The model predicted tree growth in the presence of lianas (as measured) and in a scenario in which none of the trees were competing with lianas (by setting the liana competition component in the model to zero). The predicted growth rates were used to calculate the increment in aboveground biomass per plot for each of the scenarios (*i.e.*, with and without lianas), with the difference between the scenarios being a forest-level estimate of the effect of lianas (Fig. 2). Their results suggested that the decrease in tree growth due to lianas reduced mean aboveground tree biomass increment by 0.51 Mg dry weight/ha/yr. Since approximately 50 percent of the woody tissue of trees is composed of carbon, this effect translates to a reduction of 0.25 Mg C/ha/yr, which is equivalent to a relative reduction in 10 percent of tree carbon increment in this forest. Adding also the effects of

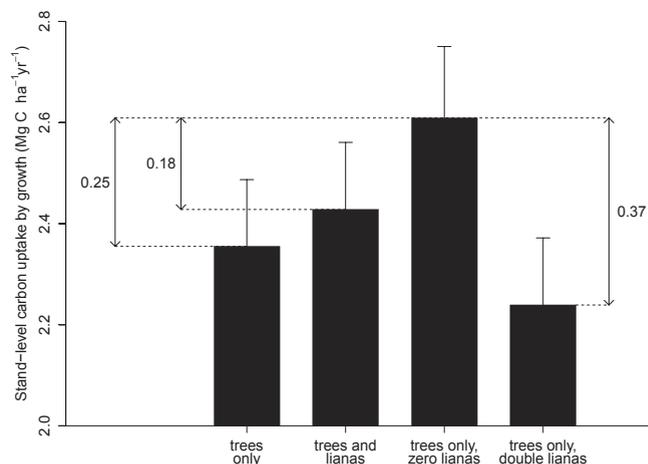


FIGURE 2. Mean predicted stand-level aboveground carbon uptake rates (Mg C/ha/yr) for trees only (leftmost bar), carbon uptake for the combination of trees and lianas (including both the competitive effect of lianas on trees and their contribution to carbon uptake; bar second from left), trees competing without lianas (bar third from left), and trees competing with double the observed liana infestation (right-most bar). Arrows and values indicate the difference in carbon uptake (Mg C/ha/yr) between the different scenarios (adapted from van der Heijden & Phillips 2009). The results are based upon a multi-species model predicting the effect of lianas on individual tree growth taking functional traits and individual growing conditions into account, and include all dicot trees ≥ 10 cm diameter occurring in five different 1-ha plots in Tambopata, Peru, measured in the first census (2003) and which were still alive in the second census (2006). The median growth rates of individual trees per scenario were converted to biomass estimates and summed for all trees occurring in a single plot. The bars indicate the mean (\pm SE) of the five plots. Carbon content was assumed to be 50 percent of biomass, both for trees and for lianas. For more information see van der Heijden and Phillips (2009).

lianas on tree mortality to these estimates of liana-induced reduction in carbon uptake, the focus of the multi-species model developed by van der Heijden and Phillips (2009), would increase the estimated effect of lianas on the net forest-level carbon uptake.

A study by Schnitzer *et al.* (unpubl. data) has experimentally quantified the effect of lianas on both the loss of tree growth and the increase in tree mortality in treefall gaps. After 8 yr, the cumulative aboveground biomass increment of the liana-free gaps was, on average, 0.16 Mg/ha higher than that of the control gaps (controlling for gap size and initial tree biomass). An estimated 84 percent of this increase in carbon was due to a greater tree growth in the gaps where lianas were removed, whereas the remaining 16 percent was attributed to the decrease in tree mortality. Based on these average effects, the authors estimated that the effect of lianas in gaps alone reduces forest carbon uptake by nearly 10 percent of the total net carbon gain. Expanding this liana-removal approach to include both gap and non-gap forest sites would substantially increase the estimate of liana-induced carbon reduction in tropical forests.

CHANGES IN TREE SPECIES COMPOSITION.—Trees differ in their susceptibility to lianas, potentially because some tree species are able to dislodge lianas or escape liana infestation altogether (Putz 1984b, a, Clark & Clark 1990, Balfour & Bond 1993, Campbell & Newbery 1993, Schnitzer *et al.* 2000, Pérez-Salicrup *et al.* 2001, Alvira *et al.* 2004, van der Heijden *et al.* 2008, Ingwell *et al.* 2010). In particular, fast-growing and light-wooded tree species tend to have lower levels of liana infestation, whereas dense-wooded, shade-tolerant tree species, which store the vast majority of forest carbon, have much higher liana infestation rates and suffer a proportionately greater reduction in liana-induced growth, survival, and recruitment (Putz 1984a, Clark & Clark 1990, Schnitzer *et al.* 2000, van der Heijden *et al.* 2008, van der Heijden & Phillips 2009, Ingwell *et al.* 2010, Schnitzer & Carson 2010). Fast-growing trees have wood densities that are, on average, 15 percent lower than shade-tolerant trees that suffer high liana infestations (van der Heijden *et al.* 2008).

By imposing a much stronger effect on slower-growing shade-tolerant tree species than on fast growing trees, lianas might alter the outcome of competition among tree species (Schnitzer *et al.* 2000, Schnitzer & Carson 2010). The differential effect of lianas has been shown in a liana-removal study in Panama, which tested whether lianas comparatively affected recruitment and diversity of shade-tolerant trees more than that of pioneer trees (Schnitzer & Carson 2010). Eight years after lianas had been removed from treefall gaps, shade-tolerant tree diameter growth, density, and diversity had increased considerably compared with control gaps, whereas pioneer trees remained relatively unaffected. These results indicate that by suppressing the growth and recruitment of shade-tolerant tree species, lianas may alter the floristic composition of tropical forests by replacing dense wooded, shade-tolerant tree species by liana and tree species with lower density wood.

There is accumulating evidence that the tree composition of tropical forests is changing in locations far from obvious, direct anthropogenic impacts – a process that may, in part, be due to lianas. In Tambopata, Peru, stand-level mean wood density has decreased since the early 1980s, indicating an overall relative increase of more fast-growing tree species (Fig. 3). In addition, a large cluster of plots in central Amazonia (18 1-ha plots over a 300 km² area) indicates an increase in the basal area or density of many genera of fast-growing trees, whereas there is no such increase in slower-growing trees (Laurance *et al.* 2004). The changes in floristic composition may be due to a rise in atmospheric CO₂ concentration, which may benefit faster-growing species more than shade-tolerant species (Phillips & Gentry 1994, Körner 1998, Laurance *et al.* 2004, Phillips *et al.* 2004). The directional changes in tree species composition toward fast-growing trees with low-density wood might also be driven, in part, by the negative effects of lianas.

EFFECTS OF INCREASING LIANA ABUNDANCE ON CARBON BALANCE.—Increases in liana stem density and biomass in tropical forests will likely exacerbate liana effects on forest-level tree growth and mortality, as the liana loads carried by trees increase. Using what we

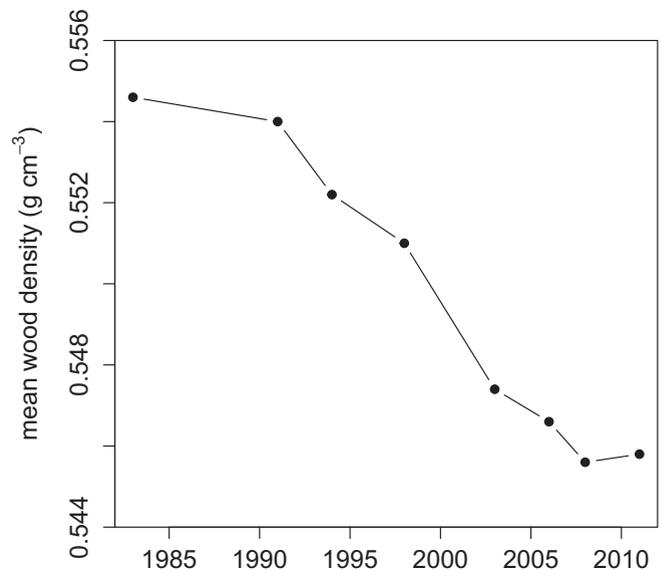


FIGURE 3. Mean wood density (± 0.02 SE) of trees across five 1-ha plots in Tambopata, Peru, from 1983 to 2011. Mean wood density across the five plots decreased over time ($P < 0.01$: Kendall's tau) – a 2 percent reduction (data extracted from Lopez-Gonzalez *et al.* 2011, 2012). The average trend was similar to that of four of the plots, which each significantly decreased in wood density by 2–3 percent. The wood density of one plot did not change over the period.

know about liana impacts and current forest structural and dynamical trends, we can now develop a simple first estimate of the likely impact of lianas over the first quarter of the 21st century. The relative basal area of large lianas has doubled over two decades in many western Amazonian locations (Phillips *et al.* 2002). van der Heijden and Phillips (2009) used a tree growth model to suggest that if this rate of lianas increase were to continue, stand-level reduction in carbon gains could decrease from 0.25 Mg C/ha/yr to 0.37 Mg C/ha/yr by 2025. This projected reduction would be equivalent to 25 percent of the current total average net carbon uptake of tropical forests (0.49 Mg C/ha/yr; Lewis *et al.* 2009b). This estimate is likely conservative because the model omits tree mortality (van der Heijden & Phillips 2009), and increasing liana abundance and biomass will likely lead to higher tree mortality rates (Ingwell *et al.* 2010). Hence, increases in liana density and biomass have the potential to severely reduce the carbon sink function of tropical forests.

Increased liana abundance and biomass may also significantly decrease carbon stocks of tropical forests by decreasing the proportion of trees with high wood density. A study simulating the effect of several biodiversity scenarios on the carbon storage capacity for a 50 ha forest in BCI showed that a liana-induced loss of slower-growing tree taxa could reduce the carbon storage capacity by trees of this forest by as much as 34 percent (Bunker *et al.* 2005). If the increase in liana abundance and biomass persists, and the 34 percent liana-induced reduction in carbon storage is representative of the wider tropics, the eventual potential liana-driven

reduction in carbon stored in tropical forest trees could conceivably reach as much as 36 Pg C in Amazonia and 97 Pg C worldwide.

COMPENSATORY EFFECTS OF LIANAS.—Liana growth and their potential increase in biomass stocks will compensate, to some extent, for the liana-induced reduction in tree biomass storage and sequestration. Few studies have attempted to quantify the compensation of lianas for the liana-induced decreases in tree biomass increment and stocks. Liana biomass growth has been estimated to compensate for 0.07 Mg ha/yr, equivalent to 30 percent, of the liana-induced reduction in carbon uptake by tree growth in an old-growth forest in Peru (van der Heijden & Phillips 2009). In a fragmentation study in Brazil, the compensatory effect of lianas was smaller: increases in liana biomass in forest edges only compensated for 8 percent of the tree biomass lost 10–17 years after fragmentation (Laurance *et al.* 1997).

Lianas displace far more carbon than they contribute because they have a relatively low amount of structural tissue and have porous stems. Instead of allocating carbon to a self-supporting trunk and an anchoring root system, lianas can invest the resources otherwise necessary for support tissue into height growth, increased leaf area, and stem and presumably root elongation without large investment in woody support tissue (Putz 1983, Gehring *et al.* 2004, Gerwing 2004, Schnitzer 2005, Cai *et al.* 2007, Selaya *et al.* 2007). For example, on the BCI 50 ha plot, lianas contribute 25 percent of woody stems (lianas and trees >1 cm diameter), 35 percent of woody species, but less than 3 percent of basal area (Schnitzer *et al.* 2012). In addition, lianas are dynamic components of tropical forests, with turnover rates as much as three times faster than those of trees (Phillips *et al.* 2005), so they have short woody biomass residence times. Carbon sequestered due to liana biomass growth will therefore be released back into the atmosphere much sooner than carbon taken up by trees. Increasing liana abundance and biomass in tropical forests is therefore likely to only offset a small portion of the reduction in tree carbon sequestration and storage caused by the increase in competitive effects of lianas.

CONCLUSIONS AND FUTURE DIRECTIONS

Lianas are currently responsible for around 15 percent of the ANPP in tropical forests. As liana leaves replace tree leaves on an approximately one-to-one basis, their contribution to forest-level canopy productivity most likely at least offsets the liana-induced reduction in tree canopy productivity. By contrast, lianas appear to be reducing carbon sequestration and carbon storage in tropical forests by: (1) reducing tree growth and survival; (2) causing a shift in tree species composition toward faster growing species with low-density wood; and (3) replacing carbon-dense trees with lianas, which sequester and store far less carbon than the trees they replace. Increasing liana abundance and biomass will exacerbate these effects of lianas in tropical forests and are therefore projected to accentuate losses in carbon sequestration and storage in these forests. While the recent whole-forest trend

has been toward increased biomass in tropical Amazonia and Africa, possibly driven by carbon dioxide fertilization, the effects of increasing lianas are one of several highly plausible mechanisms by which the tropical forest biomass sink may be reduced or reversed, with significant consequences for global atmospheric CO₂ levels and hence climate change.

BIOGEOGRAPHY.—Thus far, the observation that lianas are increasing has been a Neotropical phenomenon, with the very limited evidence from other tropical regions inconsistent with the observed pattern in the Americas (Schnitzer & Bongers 2011). This may indicate that the magnitude of change in the responsible driver(s) for the increase in lianas may vary across continents. Additional research in Africa and Asia is necessary to determine whether the increase in lianas is indeed just a Neotropical occurrence or is, in fact, happening worldwide.

A large variation in the abundance and biomass of lianas exists both within the Neotropics as well as across the continents. It has been difficult to identify key environmental variables that drive both Neotropical as well as pan-tropical differences in liana success, though the availability of host trees and their characteristics (van der Heijden & Phillips 2008) and rainfall seasonality (Schnitzer 2005, DeWalt *et al.* 2010) have been suggested. Multivariate data-rich biogeographical studies will be needed to pinpoint what factors drive pantropical variation in liana success, and therefore make it possible to identify the mechanisms responsible for liana increases.

BELOWGROUND PROCESSES.—Currently, information on the effect of lianas on belowground NPP and carbon sequestration and storage is completely lacking. To be able to accurately determine the total effect of lianas on the total (*i.e.*, above- and below-ground) carbon cycle and balance, studies which focus specifically on quantifying liana effects on belowground processes are urgently needed.

LIANA REMOVAL STUDIES.—Large scale experimental liana removal studies are needed to: (1) accurately quantify the current total effect of lianas on forest carbon sequestration and storage; (2) assess whether lianas indeed alter species composition on a large enough scale to affect the carbon storage capacity of tropical forests; (3) investigate the impacts of lianas on net primary productivity; and (4) to confirm and refine the findings of observational studies in case they were affected by confounding variables. These experiments should provide details of the functioning of the internal carbon cycle and carbon balance of tropical forests when liana impacts are completely removed, with insights likely beyond those that can be offered by observational studies alone. In addition, they may provide better indications of how increasing lianas will affect tropical forest productivity and their carbon balance.

One such large scale experiment is currently running in Panama, where the fate of more than 10,000 trees and 7500 lianas (≥ 1 cm) in eight 80 × 80 m control plots and more than 10,000 trees (≥ 1 cm) in eight 80 × 80 m liana-removal plots is followed

(S. Schnitzer, J. Powers, G. van der Heijden, and others). The goal of this experiment is to quantify the effects of lianas on tree and forest-level carbon dynamics, soil nutrient dynamics, and tree community composition. Additional experiments of this kind in other tropical forests will allow researchers to accurately quantify the effects of lianas in tropical forests as a whole. Such studies will provide the data necessary to be able to include the effects of lianas in vegetation models, and help predict the effects of increasing liana abundance and biomass on carbon sequestration and storage in tropical forests.

VEGETATION MODELS.—At present, lianas and liana-induced effects are not taken into account in any of the vegetation models on the carbon cycle and carbon balance of tropical forests. Because of the multitude of liana-induced effects on tropical forest carbon dynamics, we argue it will be necessary to include lianas as a functional type, and to account for liana-induced effects on tropical forests in these models to be able to provide better predictions of tropical forest behaviour this century. To further assist the incorporation of lianas into global vegetation models, more research should be dedicated to discovering the mechanisms responsible for the increase in liana abundance and biomass, as well as additional studies quantifying the effects of lianas on the carbon cycle and carbon balance of tropical forests.

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LITERATURE CITED

- ALVIRA, D., F. E. PUTZ, AND T. S. FREDERICKSEN. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. *For. Ecol. Manage.* 190: 73–86.
- ARAGÃO, L. E. O. C., Y. MALHI, D. J. METCALFE, J. SILVA ESPEJO, E. JIMENEZ, D. NAVARRETE, S. ALMEIDA, A. C. L. COSTA, N. SALINAS, O. L. PHILLIPS, L. O. ANDERSON, E. ALVAREZ, T. R. BAKER, P. H. GONCALVES, J. HUMAN OVALLE, M. MAMANI SOLORZANO, P. MEIR, A. MONTEAGUDO, S. PATIÑO, M. C. PENUELA, A. PRIETO, C. A. QUESADA, A. ROZAS DAVILA, A. RUDAS, J. A. SILVA, AND R. VASQUEZ. 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* 12: 2759–2778.
- ASNER, G. P., J. M. O. SCURLOCK, AND J. A. HICKE. 2003. Global synthesis of leaf area index observations: Implications for ecological and remote sensing studies. *Global Ecol. Biogeogr.* 12: 191–205.
- AVALOS, G., S. S. MULKEY, AND K. KITAJIMA. 1999. Leaf optical properties of trees and lianas in the outer canopy of a tropical dry forest. *Biotropica* 31: 517–520.
- 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.
- BALFOUR, D. A., AND W. J. BOND. 1993. Factors limiting climber distribution and abundance in a southern African forest. *J. Ecol.* 81: 91–100.
- BEER, C., M. REICHSTEIN, E. TOMELLERI, P. CIAIS, M. JUNG, N. CARVALHAIS, C. RÖDENBECK, M. A. ARAIN, D. D. BALDOCCHI, G. B. BONAN, A. BONDEAU, A. CESCATTI, G. LASSLOP, A. LINDROTH, M. R. LOMAS, S. LUYSSAERT, H. MARGOLIS, K. W. OLESON, O. ROUPSARD, E. VEENENDAAL, N. VIOUY, C. B. WILLIAMS, F. I. WOODWARD, AND D. PAPALE. 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science* 329: 834–838.
- BUNKER, D. E., F. DECLERK, J. C. BRADFORD, R. K. COLWELL, I. PERFECTO, O. L. PHILLIPS, M. SANKARAN, AND S. NAEEM. 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* 310: 1029–1031.
- BURGHOUTS, T. B. A., E. T. F. CAMPBELL, AND P. T. KOLDERMAN. 1994. Effects of tree species heterogeneity on leaf fall in primary and logged dipterocarp forest in the Ulu Segama Forest Reserve, Sabah, Malaysia. *J. Trop. Ecol.* 10: 1–26.
- CABALLÉ, G., AND A. MARTIN. 2001. Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecol.* 152: 167–173.
- CAI, Z.-Q., L. POORTER, K.-F. CAO, AND F. BONGERS. 2007. Seedling growth strategies in *Bauhinia* species: Comparing lianas and trees. *Ann. Bot.* 100: 831–838.
- CAMPANELLO, P. I., J. F. GARIBALDI, M. G. GATTI, AND G. GOLDSTEIN. 2007. Lianas in a subtropical Atlantic Forest: Host preference and tree growth. *For. Ecol. Manage.* 242: 250–259.
- CAMPBELL, E. J. F., AND D. M. NEWBERY. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *J. Trop. Ecol.* 9: 469–490.
- CAO, M., AND F. I. WOODWARD. 2002. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biol.* 4: 185–198.
- CARLQUIST, S. 1991. Anatomy of vine and liana stems: A review and synthesis. In F. E. Putz, and H. A. Mooney (Eds.). *Biology of vines*, pp. 53–72. Cambridge University Press, New York.
- CAVALERI, M. A., S. F. OBERBAUER, AND M. G. RYAN. 2006. Wood CO₂ efflux in a primary tropical rain forest. *Global Change Biol.* 12: 1–17.
- CAVALERI, M. A., S. F. OBERBAUER, AND M. G. RYAN. 2008. Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell Environ.* 31: 473–483.
- CHAVE, J., B. RIERA, AND M.-A. DUBOIS, 2001. Estimation of biomass in a neotropical forest of French Guiana: Spatial and temporal variability. *J. Trop. Ecol.* 17: 79–96.
- CHEN, Y.-J., F. BONGERS, K.-F. CAO, AND Z.-Q. CAI. 2008. Above- and below-ground competition in high and low irradiance: Tree seedling responses to a competing liana *Byttneria grandifolia*. *J. Trop. Ecol.* 24: 517–524.
- CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, AND J. NI. 2001. Measuring the net primary productivity in forests: Concepts and field methods. *Ecol. Appl.* 11: 356–370.
- 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. *J. Trop. Ecol.* 6: 321–331.
- CLARK, D. B., P. C. OLIVAS, S. F. OBERBAUER, D. A. CLARK, AND M. G. RYAN. 2008. First direct landscape scale measurement of tropical forest leaf

- area index, a key driver of global primary productivity. *Ecol. Lett.* 11: 163–172.
- Da HORA, R. C., O. PRIMAVESI, AND J. J. SOARES. 2008. Contribuição das folhas de lianas na produção de serapilheira em uma fragmento de floresta estacional semidecidual em São Carlos, SP. *Rev. Brasil. Bot.* 31: 277–285.
- DENMAN, K. L., G. BRASSEUR, A. CHIDTAISONG, P. CIAIS, P. M. COX, R. E. DICKINSON, D. HAUGLUSTAIN, C. HEINZE, E. A. HOLLAND, D. JACOB, U. LOHMANN, S. RAMACHANDRAN, P. L. DA SILVA DIAS, S. C. WOLFSY, AND X. ZHANG. 2007. Couplings between changes in the climate system and biochemistry. In S. Solomon, D. Qin, M. Manning, M. Marquis, K. Avery, M. M. B. Tignor, H. L. Miller, and Z. Chen (Eds.). *Climate change 2007: The physical science basis*, pp. 499–587. Cambridge University Press, Cambridge, UK.
- DEWALT, S. J., AND J. CHAVE. 2004. Structure and biomass of four lowland neotropical forests. *Biotropica* 36: 7–19.
- DEWALT, S. J., S. A. SCHNITZER, J. CHAVE, F. BONGERS, R. J. BURNHAM, Z.-Q. CAI, G. CHUYONG, D. B. CLARK, C. E. N. EWANGO, J. J. GERWING, E. GORTAIRE, T. B. HART, G. IBARRA-MANRIQUEZ, K. ICKES, D. KENFACK, M. J. MACÍÁ, J.-R. MAKANA, M. MARTINEZ-RAMOS, J. MASCARO, S. MOSES, H. C. MULLER-LANDAU, M. P. E. PARREN, N. PARTHASARATHY, D. R. PÉREZ-SALICRU, F. E. PUTZ, AND H. ROMERO-SALTOS, AND D. W. THOMAS. 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42: 309–317.
- DILLENBURG, L. R., A. H. TERAMURA, I. N. FORSETH, AND D. F. WHIGHAM. 1995. Photosynthetic and biomass allocation responses of *Liquidambar styraciflua* (Hamamelidaceae) to vine competition. *Am. J. Bot.* 82: 454–461.
- DILLENBURG, L. R., D. F. WHIGHAM, A. H. TERAMURA, AND I. N. FORSETH. 1993a. Effect of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93: 48–54.
- DILLENBURG, L. R., D. F. WHIGHAM, A. H. TERAMURA, AND I. N. FORSETH. 1993b. Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *Am. J. Bot.* 80: 244–252.
- EWANGO, C. E. N. 2010. The liana assemblage of a Congolian rainforest. Diversity, structure and function. PhD Dissertation. Wageningen University, Wageningen, The Netherlands.
- EWERS, F. W., AND J. B. FISHER. 1989. Variation in vessel length and diameter in stems of six tropical and subtropical Lianas. *Am. J. Bot.* 76: 1452–1459.
- EWERS, F. W., J. B. FISHER, AND S. T. CHIU. 1990. A survey of vessel diameter in stems of tropical lianas and other growth forms. *Oecologia* 84: 544–552.
- EWERS, F. W., J. B. FISHER, AND K. FICHTNER. 1991. Water flux and xylem structure in vines. In F. E. Putz, and H. A. Mooney (Eds.). *Biology of vines*, pp. 127–160. Cambridge University Press, Cambridge, UK.
- FELDPASCH, T. R., J. LLOYD, S. L. LEWIS, R. J. W. BRIENEN, E. GLOOR, A. MONTEAGUDO MENDOZA, G. LOPEZ-GONZALEZ, L. BANIN, K. ABU SALIM, L. E. O. C. ARAGAÓ, A. ARAUJO MURAKAMI, E. J. M. M. ARETS, L. ARROYO, G. AYMARD, T. R. BAKER, O. BANKI, N. J. BERRY, N. CARDOZO, J. CHAVE, J. A. COMISKEY, E. A. DAVILA, A. A. DE OLIVEIRA, A. DIFIORE, G. DJAGBLETEY, T. DOMINGUES, T. J. ERWIN, P. M. FEARNSIDE, M. B. FRANÇA, M. A. FREITAS, N. HIGUCHI, E. N. HONORIO CONRADO, Y. IIDA, E. JIMENEZ, A. R. KASSIM, T. J. KILLEEN, W. F. LAURENCE, J. C. LOVETT, Y. MALHI, B. S. MARIMON, B. H. MARIMON-JUNIOR, E. LENZA, A. R. MARSHALL, C. MENDOZA, D. J. METCALFE, E. T. A. MITCHARD, B. W. NELSON, R. NILUS, E. M. NOGUEIRA, A. PARADA, K. S.-H. PEH, A. PENA CRUZ, M. C. PENEUELA, N. C. A. PITMAN, A. PRIETO, C. A. QUESADA, F. RAMIREZ, H. RAMIREZ-ANGULO, J. M. REITSMA, A. RUDAS, G. SAIZ, R. P. SALOMAO, M. SCHWARZ, J. E. SILVA-ESPEJO, M. SILVEIRA, B. SONKE, J. STROPP, H. E. TAEDOUNG, S. TAN, H. TER STEEGE, J. W. TERBORGH, M. TORELLO-RAVENTOS, G. M. F. van der HEIJDEN, R. VASQUEZ, E. VILANOVA, V. VOS, L. WHITE, S. WILCOCK, H. WOELL, AND O. L. PHILLIPS. 2012. Integrating height into tropical biomass estimates. *Biogeosciences* 9: 3381–3403.
- FISHER, J. B., AND F. W. EWERS. 1995. Vessel dimensions in liana and tree species of *Gnetum* (Gnetales). *Am. J. Bot.* 82: 1350–1357.
- FONSECA, M. G., E. VIDAL, AND F. A. MAES DOS SANTOS. 2009. Intraspecific variation in the fruiting of an Amazonian timber tree: Implications for management. *Biotropica* 41: 179–185.
- GARTNER, B. L., S. H. BULLOCK, H. A. MOONEY, V. B. BROWN, AND J. L. WHITEBECK. 1990. Water transport properties of vine and tree stems in a tropical deciduous forest. *Am. J. Bot.* 77: 742–749.
- GERHING, C., S. PARK, AND M. DENICH. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *For. Ecol. Manage.* 195: 96–83.
- GENTRY, A. H. 1991. Distribution and evolution of climbing plants. In F. E. Putz, and H. A. Mooney (Eds.). *Biology of vines*, pp. 3–49. Cambridge University Press, Cambridge.
- GERWING, J. J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *J. Appl. Ecol.* 38: 1264–1276.
- GERWING, J. J. 2004. Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *For. Ecol. Manage.* 190: 57–72.
- 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 rainforest. *J. Trop. Ecol.* 16: 327–335.
- GIRARDIN, C. A. J., Y. MALHI, L. E. O. C. ARAGAÓ, M. MAMANI, W. HUARACA HUASCO, L. DURAND, K. J. FEELEY, J. RAPR, J. E. SILVA-ESPEJO, M. R. SILMAN, N. SALINAS, AND R. J. WHITTAKER. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biol.* 16: 3176–3192.
- GRANADOS, J., AND C. KÖRNER. 2002. In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biol.* 8: 1109–1117.
- GRAUEL, W. T., AND F. E. PUTZ. 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *For. Ecol. Manage.* 190: 99–108.
- GROGAN, J., AND R. M. LANDIS. 2009. Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. *J. Appl. Ecol.* 46: 1283–1291.
- HÄTTENSWILLER, S., AND C. KÖRNER. 2003. Does elevated CO₂ facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? *Funct. Ecol.* 17: 778–785.
- HEGARTY, E. E. 1991. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *J. Trop. Ecol.* 7: 201–214.
- van der HEIJDEN, G. M. F., J. R. HEALEY, AND O. L. PHILLIPS. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. *J. Veg. Sci.* 19: 747–756.
- van der HEIJDEN, G. M. F., AND O. L. PHILLIPS. 2008. What controls liana success in Neotropical forests? *Global Ecol. Biogeogr.* 17: 372–383.
- van der HEIJDEN, G. M. F., AND O. L. PHILLIPS. 2009. Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences* 6: 2217–2226.
- HLADIK, A. 1974. Phenology of leaf production in rain forest of Gabon: Distribution and composition of food for folivores. *C. R. Acad. Sci.* 278: 2527–2530.
- HOLBROOK, N. M., AND F. E. PUTZ. 1996. Physiology of tropical vines and hemiepiphytes: Plants that climb up and plants that climb down. In S. S. Mulkey, R. L. Chazdon, and A. P. Smith (Eds.). *Tropical forest plant ecophysiology*, pp. 363–394. Springer, New York.
- 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. *J. Ecol.* 98: 879–887.
- JORDAN, C. F., AND C. UHL. 1978. Biomass of a ‘terra firme’ forest of the Amazon Basin. *Oecol. Plant.* 13: 387–400.

- KAINER, K. A., L. H. O. WADT, D. A. P. GOMES-SILVA, AND M. CAPANU. 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. *J. Trop. Ecol.* 22: 147–154.
- KAINER, K. A., L. H. O. WADT, AND C. L. STAUDHAMMER. 2007. Explaining variation in Brazil nut fruit production. *For. Ecol. Manage.* 250: 244–255.
- KATO, R., Y. TADAKI, AND H. OGAWA. 1978. Plant biomass and growth increment studies in Pasoh Forest. *Malay. Nat. J.* 30: 211–224.
- KIRA, T., AND H. OGAWA. 1971. Assessment of primary production in tropical and equatorial forests. In P. Duvigneaud (Ed.). *Productivity of forest ecosystems*, pp. 309–321. UNESCO, Paris, France.
- KLIMAS, C. A., K. A. KAINER, L. H. O. WADT, C. L. STAUDHAMMER, V. RIGAMONTE-AZEVEDO, M. FREIRE CORREIA, AND L. M. DA SILVA LIMA. 2012. Control of Carapa guianensis phenology and seed production at multiple scales: A five year study exploring the influences of tree attributes, habitat heterogeneity and climate cues. *J. Trop. Ecol.* 28: 105–118.
- KÖRNER, C. 1998. Tropical forests in a CO₂-rich world. *Clim. Change* 39: 297–315.
- LAURANCE, W. F., S. G. LAURANCE, L. V. FERREIRA, J. M. RANKIN-DE MERONA, C. GASCON, AND T. E. LOVEJOY. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278: 1117–1118.
- LAURANCE, W. F., A. A. OLIVEIRA, S. G. LAURANCE, C. R. , H. E. M. NASCIMENTO, A. C. SANCHEZ-THORIN, T. E. LOVEJOY, A. ANDRADE, S. D'ANGELO, J. E. RIBEIRO, AND C. W. DICK. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428: 171–175.
- LAURANCE, W. F., D. PÉREZ-SALICRUP, P. DELEMÓNICA, P. M. FEARNSIDE, S. D'ANGELO, A. JEROZOLINSKI, L. POHL, AND T. E. LOVEJOY. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82: 105–116.
- LEWIS, S. L., J. LLOYD, S. SITCH, E. T. A. MITCHARD, AND W. F. LAURANCE. 2009a. Changing ecology of tropical forests: Evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.* 40: 529–549.
- LEWIS, S. L., G. LOPEZ-GONZALEZ, B. SONKE, K. AFFUM-BAFFOE, T. R. BAKER, L. O. OJO, O. L. PHILLIPS, J. M. REITSMA, L. WHITE, J. A. COMISKEY, M.-N. DJUIKOUO KAMDEM, C. E. N. EWANGO, T. R. FELDPAUSCH, A. C. HAMILTON, M. GLOOR, T. B. HART, A. HLADIK, J. LLOYD, J. C. LOVETT, J.-R. MAKANA, Y. MALHI, F. M. MBAGO, H. J. NDANGALASI, J. PEACOCK, K. S.-H. PEH, T. C. H. SUNDERLAND, M. D. SWAINE, J. TAPLIN, D. TAYLOR, S. C. THOMAS, R. VOTERE, AND H. WOLL. 2009b. Increasing carbon storage in intact African tropical forests. *Nature* 457: 1003–1007.
- LOPEZ-GONZALEZ, G., S. L. LEWIS, M. BURKITT, AND O. L. PHILLIPS. 2011. Forestplots.net: A web application and research tool to manage and analyse tropical forest plot data. *J. Veg. Sci.* 22: 610–613.
- LOPEZ-GONZALEZ, G., S. L. LEWIS, O. L. PHILLIPS, AND M. BURKITT. 2012. Forest Plots Database - www.forestplots.net. Date of extraction 12/09/2012.
- MALHI, Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. *J. Ecol.* 100: 65–75.
- MALHI, Y., AND J. GRACE. 2000. Tropical forests and atmospheric carbon dioxide. *Trends Ecol. Evol.* 15: 332–337.
- MALHI, Y., D. WOOD, T. R. BAKER, J. WRIGHT, O. L. PHILLIPS, T. COCHRANE, P. MEIR, J. CHAVE, S. ALMEIDA, L. ARROYO, N. HIGUCHI, T. J. KILLEEN, S. G. LAURANCE, W. F. LAURANCE, S. L. LEWIS, A. MONTEAGUDO, D. A. NEILL, P. NÚÑEZ VARGAS, N. C. A. PITMAN, C. A. QUESADA, R. SLALOMAO, J. N. M. SILVA, A. TORRES LEZAMA, J. W. TERBORGH, R. VÁSQUEZ MARTÍNEZ, AND B. VINCETI. 2006. The regional variation of above-ground live biomass in old-growth Amazonian forests. *Global Change Biol.* 12: 1107–1138.
- MOHAN, J. E., L. H. ZISKA, W. H. SCHLESINGER, R. B. THOMAS, R. C. SICHER, K. GEORGE, AND J. S. CLARK. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO₂. *PNAS* 103: 9086–9089.
- NABE-NIELSEN, J., J. KOLLMAN, AND M. PEÑA-CLAROS. 2009. Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *For. Ecol. Manage.* 257: 987–993.
- NORBY, R., E. H. DELUCIA, B. GIELEN, C. CALFAPLETRA, C. P. GIARDINA, J. S. KING, J. LEDFORD, H. R. MCCARTHY, D. J. P. MOORE, R. CEULEMANS, P. DE ANGELIS, A. C. FINZI, D. F. KARNOSKY, M. E. KUBISKE, K. S. PREGITZER, G. SCARASCIA-MUGNOZZA, W. H. SCHLESINGER, AND R. OREN. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *PNAS* 102: 18052–18056.
- OGAWA, H., K. YODA, K. OGINO, AND T. KIRA. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand II: Plant biomass. *Nat. Life Southeast Asia* 4: 49–80.
- PAN, Y., R. A. BIRDSEY, J. FANG, R. A. HOUGHTON, P. E. KAUPPI, W. A. KURZ, O. L. PHILLIPS, A. Z. SHVIDENKO, S. L. LEWIS, J. G. CANADELL, P. CIAIS, R. B. JACKSON, S. W. PACALA, A. D. MCGUIRE, S. PIAO, A. RAUTIAINEN, S. SITCH, AND D. HAYES. 2011. A large and persistent sink in the world's forests. *Science* 333: 988–993.
- PÉREZ-SALICRUP, D., 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.
- PÉREZ-SALICRUP, D., V. L. SORK, AND F. E. PUTZ. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33: 34–47.
- PHILLIPS, O. L. 1993. The potential for harvesting fruits in tropical rainforests: New data from Amazonian Peru. *Biodivers. Conserv.* 2: 18–38.
- PHILLIPS, O. L., L. E. O. C. ARAGAO, S. L. LEWIS, J. B. FISHER, J. LLOYD, G. LOPEZ-GONZALEZ, Y. MALHI, A. MONTEAGUDO MENDOZA, J. PEACOCK, C. A. QUESADA, G. M. F. van der HEIJDEN, S. ALMEIDA, I. AMARAL, L. ARROYO, G. AYMARD, T. R. BAKER, O. BANKI, L. BLANC, D. BONAL, P. BRANDO, J. CHAVE, A. C. ALVES DE OLIVEIRA, N. DAVILA CARDOZO, C. I. CZIMCZIK, T. R. FELDPAUSCH, M. APARECIDA FREITAS, M. GLOOR, N. HIGUCHI, E. JIMENEZ, G. LLOYD, P. MEIR, C. MENDOZA, A. MOREL, D. A. NEILL, D. C. NEPSTAD, S. PATIÑO, M. C. PENUELA, A. PRIETO, F. RAMIREZ, M. SCHWARZ, J. N. M. SILVA, M. SILVEIRA, A. S. THOMAS, H. ter STEEGE, J. STROPF, R. VASQUEZ, P. ZELAZOWSKI, E. ALVAREZ DAVILA, S. ANDELMAND, A. ANDRADE, K.-J. CHAO, T. ERWIN, A. DI FIORE, E. N. HONORIO CONRADO, H. C. KEELING, T. J. KILLEEN, W. F. LAURANCE, A. PENNA CRUZ, N. C. A. PITMAN, P. NÚÑEZ VARGAS, H. RAMIREZ-ANGULO, A. RUDAS, R. SALAMAQ, N. SILVA, J. W. TERBORGH, AND A. TORRES LEZAMA. 2009. Drought sensitivity of the Amazon Rainforest. *Science* 323: 1344–1347.
- PHILLIPS, O. L., T. R. BAKER, L. ARROYO, N. HIGUCHI, T. KILLEEN, W. F. LAURANCE, S. L. LEWIS, J. LLOYD, J. TERBORGH, R. VÁSQUEZ MARTÍNEZ, M. ALEXIADES, S. ALMEIDA, S. BROWN, J. CHAVE, J. A. COMISKEY, C. I. CZIMCZIK, A. DI FIORE, T. ERWIN, C. KUEBLER, S. G. LAURANCE, H. E. M. NASCIMENTO, J. OLIVIER, W. PALACIOS, S. PATIÑO, N. PITMAN, C. A. QUESADA, M. SALDIAS, A. TORRES LEZAMA, AND B. VINCETI. 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359: 381–407.
- PHILLIPS, O. L., AND A. H. GENTRY. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954–958.
- PHILLIPS, O. L., R. VÁSQUEZ MARTÍNEZ, L. ARROYO, T. R. BAKER, T. KILLEEN, S. L. LEWIS, Y. MALHI, A. M. MENDOZA, D. NEILL, P. N. VARGAS, M. ALEXIADES, C. CERÓN, A. D. FLORA, T. ERWIN, A. JARDIM, W. PALACIOS, M. SALDIAS, AND B. VINCETI. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- 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.
- PRAGASON, L., AND N. PARTHASARATHY. 2005. Litter production in tropical dry evergreen forests of south India in relation to season, plant life-forms and physiognomic groups. *Curr. Sci. India* 88: 1255.
- 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. How trees avoid and shed lianas. *Biotropica* 16: 19–23.
- PUTZ, F. E. 1984b. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.

- PUTZ, F. E. 1991. Silvicultural effects of lianas. In F. E. Putz, and H. A. Mooney (Eds.). *Biology of vines*, pp. 493–501. Cambridge University Press, Cambridge, UK.
- PUTZ, F. E. 1995. Vines in treetops: Consequences of mechanical dependence. In M. D. Lowman, and N. M. Nadkarni (Eds.). *Forest canopies*, pp. 311–324. Academic Press Limited, London, UK.
- RESTOM, T. G., AND D. C. NESTAD. 2001. Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant Soil* 236: 155–163.
- RESTOM, T. G., AND D. C. NESTAD. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *For. Ecol. Manage.* 190: 190–118.
- ROBERTSON, A. L., Y. MALHI, F. FARFAN-AMEZQUITA, L. E. O. C. ARAGÃO, J. SILVA ESPEJO, AND M. A. ROBERTSON. 2010. Stem respiration in tropical forests along an elevational gradient in the Amazon and Andes. *Global Change Biol.* 16: 3193–3204.
- SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *Am. Nat.* 166: 262–276.
- SCHNITZER, S. A., AND F. BONGERS. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecol. Lett.* 14: 397–406.
- SCHNITZER, S. A., AND W. P. CARSON. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol. Lett.* 13: 849–857.
- SCHNITZER, S. A., J. W. DALLING, AND W. P. CARSON. 2000. The impact of liana on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *J. Ecol.* 88: 655–666.
- SCHNITZER, S. A., M. E. KUZEE, AND F. BONGERS. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *J. Ecol.* 93: 1115–1125.
- SCHNITZER, S. A., S. A. MANGAN, J. W. DALLING, C. A. BALDECK, S. P. HUBBELL, A. LEDO, H. C. MULLER-LANDAU, M. F. TOBIN, S. AGUILAR, D. BRASSFIELD, A. HERNANDEZ, S. LAO, R. PEREZ, O. VALDEZ, AND S. R. YORKE. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7: e52114.
- SELAYA, N. G., N. P. R. ANTEN, R. J. OOMEN, M. MATTHIES, AND M. J. A. WERGER. 2007. Above-ground biomass investments and light interception of tropical forest trees and lianas early in succession. *Ann. Bot.* 99: 141–151.
- STEVENS, G. C. 1987. Lianas as structural parasites: The *Bursera simaruba* example. *Ecology* 68: 77–81.
- 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: 20.
- TOLEDO-ACEVES, T., AND M. D. SWAINE. 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecol.* 196: 233–244.
- WHIGHAM, D. F. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (Sweetgum). *Can. J. For. Res.* 14: 37–39.
- WRIGHT, S. J., AND O. CALDERON. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* 9: 35–44.
- WRIGHT, S. J., O. CALDERÓN, A. HERNÁNDEZ, AND S. PATON. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85: 484–489.
- WRIGHT, S. J., A. HERNANDEZ, AND R. CONDIT. 2007. The bushmeat harvest alters seedling banks by favouring lianas, large seeds and seed dispersed by bats, birds, and wind. *Biotropica* 39: 363–371.
- 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. *J. Trop. Ecol.* 21: 307–315.
- ZOTZ, G., N. CUENI, AND C. KÖRNER. 2006. *In-situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO₂. *Funct. Ecol.* 20: 763–769.