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Disentangling Above- And Below-Ground Competition Between Lianas and Trees in a Tropical Forest

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Summary

1. Light is thought to be the most limiting resource in tropical forests, and thus above-ground competition is commonly accepted as the mechanism that structures these communities. In many tropical forests, trees compete not only with other trees, but also with lianas, which compete aggressively for below-ground resources and thus may limit tree growth and regeneration.
2. Using a replicated experiment, we tested the relative strengths of above- and below-ground competition from lianas on tree saplings in a disturbed forest in Côte d'Ivoire with a heterogeneous canopy and relatively high light penetration. We planted seedlings of three tree species and subjected them to below-ground competition with lianas (BGC), above- and below-ground competition with lianas (ABGC), or a liana-free control treatment. After 2 years, we harvested the saplings and compared the amount of above-ground biomass and its relative allocation among the three experimental treatments and different tree species.
3. Lianas competed intensely with saplings in this tropical forest, substantially limiting sapling growth. Saplings grown in the ABGC and BGC treatments had only 18.5% and 16.8% of the above-ground dry biomass of those grown in the liana-free control treatment.
4. Sapling biomass did not differ significantly among the ABGC and BGC treatments, suggesting that below-ground competition was the driving force behind liana vs. tree competition in this forest. Above-ground competition with lianas, however, did affect the allocation of biomass in saplings, resulting in shorter, thicker stems and a poorly developed crown.
5. Collectively, our findings suggest that below-ground competition with lianas plays a substantial role in limiting the growth of saplings in disturbed and secondary tropical forests, and above-ground effects may be due to a combination of above-ground competition and mechanical stress.
6. Disentangling above- and below-ground competition between lianas and trees is critical for a comprehensive understanding of the dynamics of naturally regenerating tropical forests, as well as formulating successful management plans for sustainable timber harvest.

Introduction

Competition for shared resources is one of the main processes that structures plant and animal communities and maintains species diversity (e.g. [Connell 1961](#); [Tilman 1982](#); [Weiner 1986](#); [Grace & Tilman 1990](#)). In closed-canopy plant communities, such as forests, competition is thought to be primarily for light, with species differing in their capacity for shade tolerance (e.g. [Kitajima 1994](#); [Bongers & Sterck 1998](#); [Bloor & Grubb 2003](#); [Poorter *et al.* 2004a](#); but see [Pearson 1929](#); [Toumey 1929](#); [Casper & Jackson 1997](#); [Ostertag 1998](#); [Coomes & Grubb 2000](#); [Lewis & Tanner 2000](#); [Barberis & Tanner 2005](#)). Indeed, the emphasis on canopy gaps as one of the phenomena that structure and maintain species diversity in forests is a result of this viewpoint (e.g. [Denslow 1987](#); [Hubbell *et al.* 1999](#); [Brokaw & Busing 2000](#); [Schnitzer & Carson 2000, 2001](#)). Canopy gaps are acknowledged as sites of intense plant recruitment and regeneration and as being responsible for the maintenance of some plant diversity ([Popma & Bongers 1988](#); [Denslow 1995](#); [Schnitzer *et al.* 2000, 2004](#)), even

though gaps alone have failed to explain the diversity of shade-tolerant tree species (e.g. [Hubbell et al. 1999](#); [Schnitzer & Carson 2000, 2001](#)).

Although the importance of below-ground competition has a long history (e.g. [Pearson 1929](#); [Toumey 1929](#)), most contemporary studies have implicitly assumed that the vigorous plant growth in such high-light areas as canopy gaps and regenerating secondary forests is the result of competition for light, with very little attention having been paid by researchers to below-ground resources (e.g. [Denslow 1987](#); [Hubbell et al. 1999](#); [Schnitzer et al. 2000](#); but see [Ostertag 1998](#); [Barberis & Tanner 2005](#)). Competition for below-ground resources in canopy gaps and secondary forests, however, may be intense and experiments have revealed that below-ground competition in high-light conditions may limit the recruitment and growth of plants, particularly in tropical forests that are nutrient poor or have seasonal droughts ([Becker et al. 1988](#); [Sanford 1989, 1990](#); [Gerhardt 1996](#); [Ostertag 1998](#); [Coomes & Grubb 2000](#); [Lewis & Tanner 2000](#); [Barberis & Tanner 2005](#)). For example, in the seasonal forest on Barro Colorado Island, Panama, [Barberis & Tanner \(2005\)](#) reported that trenching increased seedling growth in gaps, possibly because of increased nutrient availability during the wet season and increased soil water availability during the dry season (see also [Gerhardt 1996](#); [Lewis & Tanner 2000](#)). In contrast, in the wet forest at La Selva Biological Station, Costa Rica, [Ostertag \(1998\)](#) found that below-ground competition in gaps played a relatively small role in seedling competition, possibly because of the year-round rainfall and relatively fertile soils (see also [Denslow et al. 1998](#)).

Lianas (woody climbers), an abundant and taxonomically diverse growth form in tropical forests, may compete particularly intensely with trees, especially in canopy gaps and secondary forests ([Gentry 1991](#); [Schnitzer & Bongers 2002](#); [Schnitzer 2005](#)). Many canopy gaps become colonized by lianas very soon after gap formation ([Putz 1984](#); [Schnitzer & Carson 2001](#); [Schnitzer et al. 2004](#)), resulting in severely reduced tree growth rates, sometimes to the point where the gap becomes stalled at a low canopy height for many years ([Schnitzer et al. 2000](#)). Lianas, which are significantly more abundant in young secondary forests (≤ 40 years-old) than in older forests (≥ 100 years-old; [Dewalt et al. 2000](#); [Kuzee & Bongers 2005](#)) may reduce tree recruitment, growth rates, fecundity and survival, as well as alter the successional trajectories of gap-phase regeneration ([Stevens 1987](#); [Clark & Clark 1990](#); [Pérez-Salicrup & Barker 2000](#); [Schnitzer et al. 2000](#)).

Lianas have well-developed root and vascular systems and thus may compete effectively with trees for below-ground resources when light is abundant ([Schnitzer 2005](#)). For example, in a seasonal tropical forest in Bolivia, [Pérez-Salicrup & Barker \(2000\)](#) reported that the pre-dawn water potential of the host tree *Senna multijuga* became significantly less negative within 1 day of cutting lianas from around the tree, suggesting strong root competition for water between lianas and this tree species (but see [Barker & Pérez-Salicrup 2000](#)). In a competition experiment between sweetgum trees (*Liquidambar styraciflua*) and two species of temperate lianas in an experimental garden in North America, [Dillenburg et al. \(1993a, 1993b, 1995\)](#) demonstrated that below-ground competition from lianas reduced rates of tree growth, whereas above-ground competition was not a significant factor. However, under natural conditions in tropical forests, direct tests of the relative effects of above- and below-ground competition from lianas on tree growth are lacking. Furthermore, because liana abundance appears to be increasing in neotropical forests ([Phillips et al. 2002](#); [Wright et al. 2004](#)) and the rate of disturbance is also increasing ([Phillips & Gentry 1994](#); [Laurance et al. 2004](#)), establishing the mechanisms by which lianas compete with regenerating trees following disturbance is particularly important.

We tested the relative strengths of above- and below-ground competition from lianas on three tree species in a disturbed tropical forest in Côte d'Ivoire. We hypothesized that below-ground, rather than above-ground, competition with lianas limits tree sapling growth in this relatively high-light but heterogeneous environment. In a total of 30 randomly selected sites, we planted saplings of three tree species with either below-ground competition with lianas (BGC), both above- and below-ground competition with lianas (ABGC), or no

competition (control). We quantified the biomass and related morphometric measurements of the saplings after 2 years.

This design allowed us to predict that if competition by lianas under heterogeneous, high-light conditions is solely for above-ground resources, then sapling biomass will be significantly lower in the ABGC treatment than in the other two treatments, which will not differ significantly. Conversely, if competition is solely for below-ground resources, then sapling biomass will not differ significantly between BGC and ABGC, but both will have significantly less biomass than the control. If above- and below-ground resources are both independently limiting, then the treatments should differ in an additive or multiplicative fashion, with sapling size ranked: control > BGC > ABGC. Finally, if neither above- nor below-ground resources were limiting, then we would expect to see no significant difference among any of the three treatments.

Methods

study site

We conducted this experiment in a 39 000 ha tract of lowland tropical forest in the south-west region of Côte d'Ivoire (< 50 m a.s.l.; 4°50' N, 6°25' W). The forest was established as a reserve in 1973 and consists of a matrix of mature and secondary forests as well as plantations ([SODEFOR 1995](#)). Mean annual rainfall in this region ranges from 1800 to 2000 mm, with a dry season from December to April and a less pronounced dry spell in October and November. However, the forest receives some rain in most months and remains mostly evergreen throughout the year ([Chatelain et al. 2004](#)). The soils in this region are ferralsols derived from migmatite and are moderately well drained and poorly to moderately fertile ([Papon 1973](#)).

study species

We selected three target tree species, each of which was relatively common in the forest reserve but differed in shade tolerance ([Poorter et al. 2004b](#)). *Khaya anthotheca* is a slow growing canopy species and is the most shade tolerant of the three species, whereas *Terminalia superba* is an intermediate shade-tolerant canopy species that is found in both the intact forest and in canopy gaps and *Ceiba pentandra* is a fast growing, relatively high-light demanding emergent species, typically found in open high-light areas. Seedlings were initially grown in plant-bags in a large shade-house, and we transplanted all species into the field with a small amount of nursery soil (to avoid damaging the fine roots) within a 2-day period, when seedlings of *K. anthotheca* and *C. pentandra* were both 5 months old and *T. superba* were 3 months old. Although the plants were all small seedlings at the start of the experiment, most of the target individuals had reached a height in excess of 2 m after 2 years, and we therefore refer to them as saplings rather than seedlings.

experimental design

We selected a 2.5-ha area located within the forest reserve in which none of the large canopy trees had been cut, but the understory, including sapling-sized trees and climbers, had been recently cleared. We randomly placed thirty 9 × 12 m plots, with each plot located at least 10 m from any other plot or the edge of the understory-free area (although the distance between the nearest plot or edge was typically much greater than 10 m). Within each of the 30 plots, we randomly planted 12 saplings, four of each of three target tree species in a 3 × 4 grid (360 individuals in total). Each individual was separated from its nearest neighbour by 3 m and was at least 1.5 m from the edge of the plot.

Rather than planting lianas in the plots, we allowed lianas to regenerate following the initial understory clearing. Lianas typically regenerate rapidly and copiously from seed and by resprouting after being cut or suffering damage from treefalls ([Putz 1984](#); [Schnitzer et al. 2004](#)), and thus tree vs. liana competition following a disturbance, either natural or human-induced, is a common phenomenon ([Schnitzer & Bongers 2002](#)). Because

lianas were cut prior to planting the saplings, however, the intensity of competition in this study was probably less than that found in natural gap conditions (e.g. [Schnitzer et al. 2000](#)).

We randomly selected 10 replicate plots to receive one of each of the three treatments. For the control plots, we maintained a liana-free understory by carefully cutting the regenerating lianas above the soil surface each month throughout the study period. We did not manipulate the lianas in the above- and below-ground competition treatment (ABGC), allowing natural competition to occur. Unlike sapling-sapling competition, in which the removal of a competing sapling affects both above- and below-ground competition with other saplings, young lianas could be unwound from their host sapling each month, without damaging the liana root system, resulting in below ground only competition (the BGC treatment).

This experimental design allowed us to measure directly the growth of saplings with different competitive regimes, as well as avoiding the unpredictable artifacts associated with the trenching experiments that are commonly used to separate above- and below-ground competition (see [McLellan et al. 1995](#); [Casper & Jackson 1997](#); [Coomes & Grubb 2000](#); [Lewis & Tanner 2000](#)). Although we did not examine the contribution of above-ground competition directly, comparing the BGC and ABGC treatments allowed us to assess its relative contribution.

light and liana measurements

We measured the light quantity in each plot to test whether the amount of light was similar among the various treatments. Six months after planting the saplings, we measured the percentage of light transmittance of diffuse photosynthetic photon flux density (PPFD) using LI-190 quantum sensors (LI-COR, Lincoln, Nebraska, USA) directly above each of the 360 saplings. Simultaneously, we took reference readings in a large forest opening located nearby, in order to calculate the percentage of total available light incident on each of the saplings. Light readings were taken for three consecutive days, three times per day, at 09.00, 12.00 and 15.00, and we used the average of nine measurements per individual.

The relative percentage of light above each sapling was, on average, high (23.9% of full sun \pm 20.6 SD) and was similar to that of a large treefall gap or a regenerating secondary forest that is still developing a full canopy ([Bongers et al. 2001](#)). Light quantity was highly variable among the plots ($P < 0.001$), ranging from 2 to 100% of full sun; however, it did not differ significantly among the treatments ($P = 0.38$). We estimated the amount of above-ground competition between lianas and saplings by counting the number of lianas in the crown of each of the 30 saplings harvested from the ABGC treatment (see below). We also visually estimated the percentage of the sapling canopy covered by lianas, from 0 to 100%, using 10 categories of 10%.

To ensure that there were no obvious differences in the density of lianas between the BGC and ABGC treatments, we calculated the amount of liana biomass in each of these treatments. Specifically, we measured the length of all of the lianas that were rooted within 3 m of each of the target trees, the maximum distance at which we assumed that lianas and relatively small saplings would potentially compete. In a companion study, we had calculated the average amount of biomass per cm length of stem at varying diameters for each of the species of liana that we encountered in the study ($n > 6$ per species; Kuzee & Bongers, unpublished data). We used these species-specific biomass equations to estimate the above-ground liana biomass competing with each target tree without having to disturb the lianas. We found no significant difference in mean estimated liana biomass within 3 m of saplings in the ABGC and BGC plots ($5.1 \text{ g} \pm 0.9 \text{ SE}$ and $6.1 \text{ g} \pm 0.8$, respectively).

data quantification and statistical analysis

Two years after planting the saplings, we quantified the height, stem diameter, number of branches, tree slenderness (height/diameter), number of leaves (or leaflets) and mortality of all of the saplings in all of the treatments. We measured stem diameter 10 cm above the soil surface to ensure consistency in measurement

among the species and treatments. To quantify sapling biomass, we harvested the above-ground portion of 90 randomly selected individuals, 10 of each of the three species from each of the three treatments. Immediately after harvest, we weighed separately the stem (the main bole without the branches), branch and leaf biomass of each selected sapling. We also calculated the stem mass ratio (SMR), branch mass ratio (BMR) and leaf mass ratio (LMR) for each individual. The mass ratios, which we calculated as the amount of biomass of each plant organ divided by the total amount of above-ground biomass for that plant, allowed us to test whether above- or below-ground competition from lianas altered above-ground biomass allocation patterns for each of the tree species.

We analysed these data using a type III sum of squares analysis of variance (anova), with species, treatment and the interaction term as the independent variables, and the sapling biomass, morphometric measurements and the mass ratios as the dependent variables ([SAS Institute 2000](#)). In the case of significant differences in the models, we used Tukey HSD tests to determine which of the variables differed significantly from the others ([SAS Institute 2000](#)). To account for multiple tests on the correlated morphometric response variables, we used sequential Bonferroni corrections to adjust the α level ([Rice 1990](#)). Prior to the analyses, we log-transformed the biomass and morphometric data and arcsin square-root transformed the stem-, branch- and leaf-mass ratio data so that they were normally distributed ([Sokal & Rohlf 1995](#)). To compare sapling mortality among the treatments and species, we used a proportional hazards survival model ([SAS Institute 2000](#)), which is recommended for comparing the type of mortality data collected in this study ([Fox 1993](#)).

Results

After 2 years, competition with lianas significantly limited the biomass gain in the saplings. In the treatments where lianas were present, saplings had, on average, five times less biomass than in the control treatment ([Fig. 1a](#), [Table 1](#)). The response to competition from lianas was nearly identical for all three of the tree species ([Fig. 1b–d](#)).

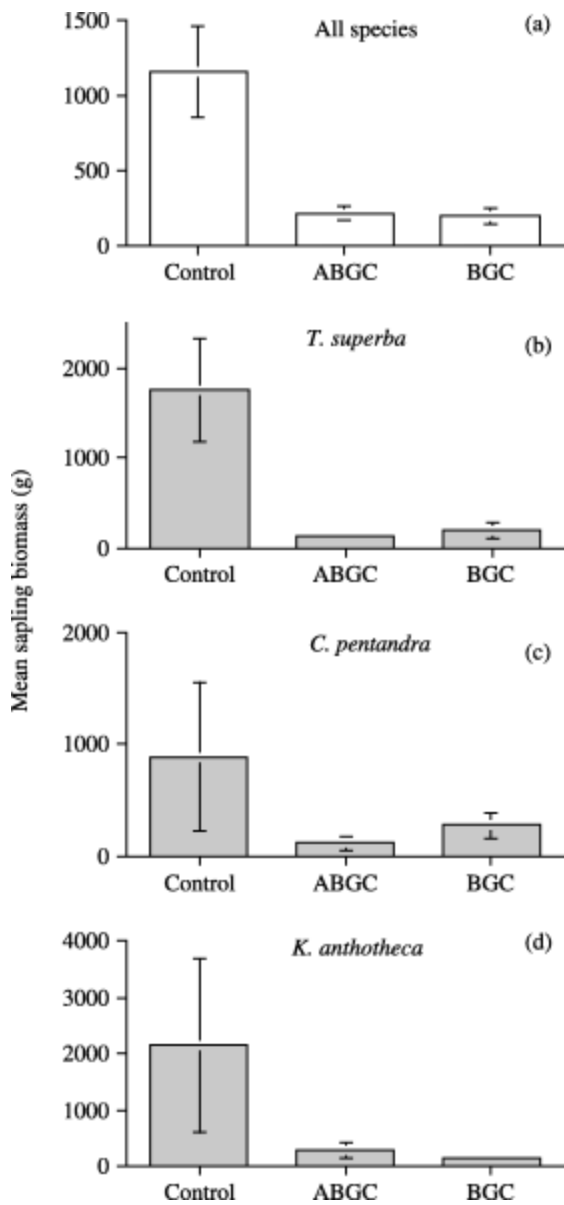


Figure 1 Mean above-ground dry biomass of three sapling species grown for 2 years in a disturbed forest in Côte d’Ivoire under three experimental competition treatments: without competition from lianas (Control), with both above- and below-ground competition from lianas (ABGC), and with only below-ground competition from lianas (BGC). Data are presented for: (a) the three species combined ($n = 30$ per treatment); (b) *T. superba*; (c) *C. pentandra*; and (d) *K. anthotheca* ($n = 10$ per species). In all cases, saplings without competition from lianas had significantly more biomass than saplings grown under either competition treatments, there were no significant differences among the three species (Table 1). Data were log transformed for analysis; non-transformed data are presented. Error bars represent ± 1 standard error (SE).

Table 1. anova of sapling above-ground biomass for each of the three species exposed to the three competition treatments. Treatment, species and the interaction term were the independent variables. The interaction term was not significant in any of the tests. Biomass data were normalized using log transformation. Sequential Bonferroni corrections were used to account for multiple tests. Significant *P*-values are listed in bold

Source	Competition treatment		<i>P</i>
	d.f.	<i>F</i>	
Total biomass	2	4.94	0.009
Stem biomass	2	2.55	0.08

Branch biomass	2	8.06	0.0009
Leaf biomass	2	51.01	< 0.0001
Source	Tree species		<i>P</i>
	d.f.	<i>F</i>	
Total biomass	2	0.79	0.07
Stem biomass	2	3.47	0.04
Branch biomass	2	0.56	0.57
Leaf biomass	2	6.60	0.002

Most (83%) of the harvested saplings from the ABGC plots had lianas in their crowns, covering an average of 21% (± 3.4 SE) of their canopies. If above-ground competition had played a dominant role, then we should have found significantly more sapling biomass in the BGC plots, compared with the ABGC plots. In both treatments, however, total above-ground sapling biomass was essentially the same (214 ± 48 SE vs. 195 ± 53 , respectively; [Fig. 1a](#)). This trend was consistent among each of the three tree species ([Fig. 1b–d](#)) and for each of the above-ground plant organs: stem, branches and leaves ([Fig. 2](#), [Table 1](#)). These findings support the hypothesis that it is below-ground competition with lianas that limits sapling growth in heterogeneous, high-light environments, which are common in young secondary forests, in disturbed forests, and in treefall gaps.

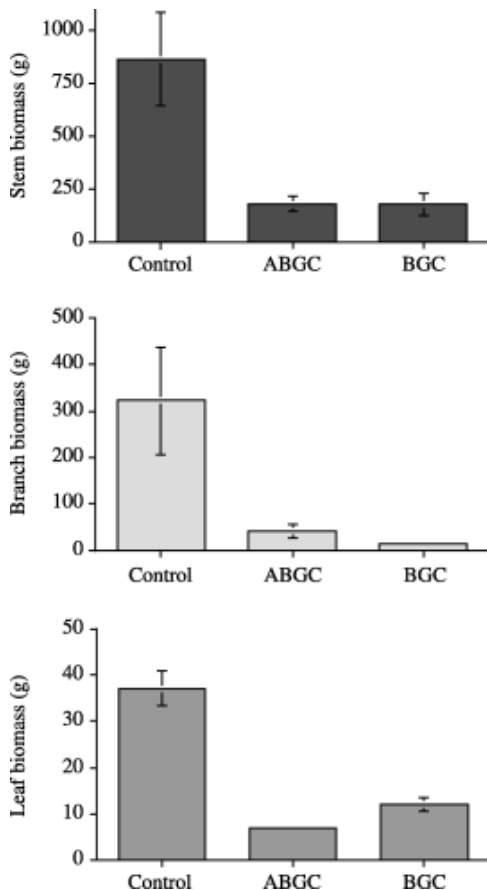


Figure 2 Mean stem, branch and leaf biomass for three sapling species combined grown under the three competition treatments. Competition from lianas significantly reduced branch and leaf biomass but mean stem biomass did not significantly differ among the treatments ([Table 1](#)). Data were log transformed to normalize them for analysis; non-transformed data are presented. Error bars represent ± 1 SE.

The relative allocation of above-ground biomass into the various plant organs differed significantly among the treatments. For all three species combined, the stem mass ratio (SMR), which is the proportion of stem biomass to total above-ground biomass, was significantly lower in the control treatment than in either treatment where lianas were present (Fig. 3, Table 2), and the leaf mass ratio (LMR) was lowest where above-ground competition from lianas was present (the ABGC treatment). Branch mass ratio (BMR) was highest in the control treatment and lowest in the BGC treatment, and the ABGC treatment did not differ from either of the other two. The sapling species differed significantly only in SMR (Table 2), with the intermediate shade-tolerant species (*T. superba*) having significantly lower SMR than the other two species. Collectively, these results suggest that competition with lianas causes saplings to invest a higher proportion of their above-ground biomass into stem construction, and that above-ground competition with lianas displaces leaf biomass.

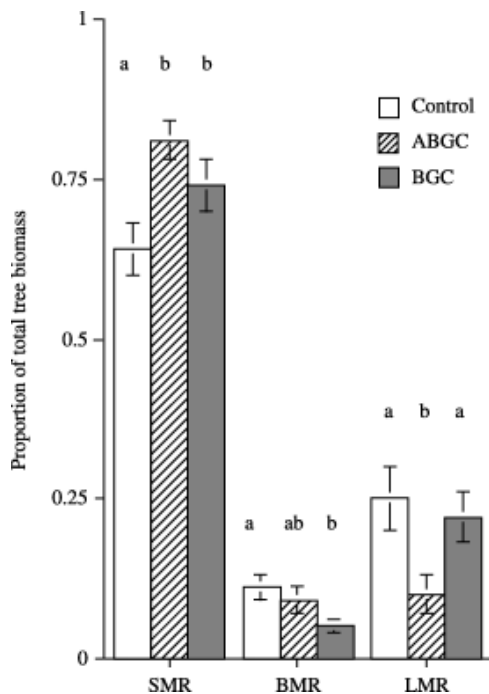


Figure 3 Mean stem mass ratio (SMR), branch mass ratio (BMR) and leaf mass ratio (LMR) of all three sapling species combined grown under the three competition treatments ($n = 30$ per treatment). Different letters indicate significantly different results. Data were arcsin transformed for analysis; non-transformed data are presented. Error bars represent ± 1 SE.

Table 2. anova of sapling stem mass ratio (SMR), branch mass ratio (BMR) and leaf mass ratio (LMR) for each of the three species exposed to the three competition treatments. Treatment, species and the interaction term were the independent variables. The interaction term was not significant in any of the tests. Data were normalized using arcsin transformation. Sequential Bonferroni corrections were used to account for multiple tests. Significant P -values are listed in bold

Source	Competition treatment		P
	d.f.	F	
SMR	2	8.90	0.0003
BMR	2	3.81	0.03
LMR	2	3.97	0.02
Source	Tree species		
	d.f.	F	P
SMR	2	11.73	< 0.0001
BMR	2	3.24	0.05

LMR	2	2.65	0.08
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Morphometric measurements also demonstrated that saplings responded to above-ground competition from lianas by changing their relative allocation of above-ground biomass. For instance, saplings were shorter and thicker when above-ground competition was present, which is exemplified by sapling slenderness (height/diameter ratio), which was more than 50% greater in the absence of above-ground competition with lianas (Fig. 4, Table 3). This relationship was driven mostly by the significantly larger stem diameter in the ABGC treatment than in the control and BGC treatments, as sapling height did not differ significantly among the treatments (Fig. 4, Table 3). This relationship was also driven by the strong response of *Terminalia*, which was significantly more slender than the other two species (Table 3). However, there was not a significant species–treatment interaction for this analysis ($P = 0.77$), indicating that all species responded similarly to the treatments. The number of branches and leaves were marginally greater in the control compared with the ABGC treatments, with the BGC treatment positioned intermediately in both cases (Fig. 4). These differences, however, were not significant after we applied the sequential Bonferroni correction. Nevertheless, taken together these findings suggest that above-ground competition with lianas causes saplings to be shorter in stature with a thicker trunk, and with fewer branches and leaves.

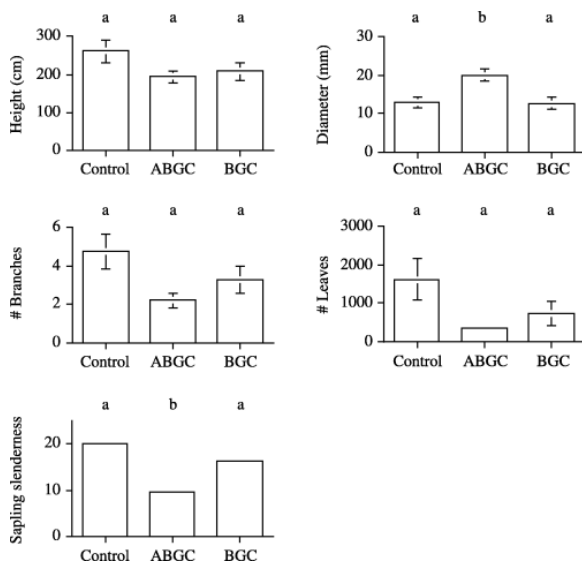


Figure 4 Mean stem height, diameter, number of branches, number of leaves and slenderness (height/diameter ratio) of saplings grown under the three competition treatments ($n = 30$ per treatment for stem height, no. of branches and no. of leaves; for stem diameter and slenderness, $n = 15, 29$ and 20 for the Control, ABGC and BGC treatments, respectively). Different letters indicate significantly different results. Data were log transformed to normalize the data; however, non-transformed data are presented. Error bars represent ± 1 SE.

Table 3. anova of sapling morphological attributes for each of the three species exposed to the three competition treatments. Treatment, species and the interaction term were the independent variables. The interaction term was not significant in any of the tests. Data were normalized using log transformation. Sequential Bonferroni corrections were used to account for multiple tests. Stem slenderness is defined as the height/diameter ratio. Significant P -values are listed in bold

	Competition treatment		
Source	d.f.	F	P
Stem slenderness	2	4.73	0.01
Height	2	1.03	0.36
Diameter	2	5.37	0.007

No. of branches	2	3.13	0.05
No. of leaves	2	2.43	0.09
	Tree species		
Stem slenderness	2	7.88	0.001
Height	2	3.67	0.03
Diameter	2	2.44	0.09
No. of branches	2	18.11	< 0.0001
No. of leaves	2	2.01	0.14

Mean percentage mortality of the saplings was low and not significantly different among the treatments ($P = 0.43$, $\chi^2 = 1.67$, d.f. = 2). It is worth noting that sapling mortality was the lowest for the control treatment (1.7 individuals \pm 0.5 SE), compared with the ABGC and BGC treatments (3.0 \pm 0.7 and 2.7 \pm 0.6, respectively), although the lack of statistical differences prevents us from concluding that lianas were responsible. Mortality differed significantly among the tree species ($P = 0.006$, $\chi^2 = 10.06$, d.f. = 2), with the pioneer species (*C. pentandra*) suffering the highest mortality (4.3 \pm 0.9%), the intermediate shade-tolerant species (*T. superba*) having the lowest mortality (0.6 \pm 0.5%), and the shade-tolerant species (*K. anotheca*) falling in between (2.4% \pm 1.3). We did not determine the exact cause of mortality for any of the three species.

Discussion

above- vs. below-ground competition with lianas

Our findings support the hypothesis that below-ground competition with lianas limits tree sapling growth in disturbed environments. Below-ground competition with lianas reduced the above-ground biomass of saplings by nearly fivefold compared with saplings growing without competition, a result that was consistent among the three tree species and for all of the above-ground plant organs. In contrast, the additional presence of above-ground competition with lianas had no noticeable impact on the amount of biomass for any of the three tree species. Our findings are consistent with other studies suggesting that lianas reduce sapling growth via below-ground competition for shared resources ([Dillenburg et al. 1993a, 1993b](#); [Gerhardt 1996](#); [Pérez-Salicrup & Barker 2000](#)). Furthermore, our findings may explain why the blanket cutting of lianas can increase tree growth at the experimental plot level, and still be independent of the number of lianas found in the crown of any given tree (e.g. [Grauel & Putz 2004](#)). Because the lianas in this study were small individuals, originating as sprouts from previously cut stems or recruited from seed, our study demonstrates that even a small degree of below-ground competition can limit sapling growth. In treefall gaps and young secondary forests, where lianas are in high abundance ([Putz 1984](#); [Dewalt et al. 2000](#); [Schnitzer et al. 2000, 2004](#); [Tabanez & Viana 2000](#)), below-ground competition is probably extremely intense.

A potential alternative explanation for our findings might be that the lianas did not cover enough of the sapling crown to adequately compete for light in the ABGC treatment. We believe that this explanation is unlikely. Lianas occupied an average of 21% of the canopy of each of the harvested trees in the ABGC plots, with only five of the 30 trees having no lianas in their canopy. Although we did not detect a difference in biomass between the saplings of the ABGC and BGC treatments, above-ground competition with lianas was strong enough to cause a significant decrease in sapling leaf mass ratio, an increase in stem thickness, and a significant decrease in stem slenderness in all species. The significant decrease in leaf mass ratio (LMR) in the treatment that included above-ground competition with lianas ([Fig. 3](#)) may be due to a direct displacement of tree leaves by liana leaves, a conclusion that is consistent with observations by [Ogawa et al. \(1965\)](#). Additionally, saplings experiencing above-ground competition were half as slender as the controls. Thus, above-ground competition with lianas was a factor in this study, resulting in saplings that were short, thick in stature, and with a poorly developed crown,

presumably because of the added weight of lianas on the saplings as well as a combination of mechanical stress or damage and the casting of dense shade.

Currently, a consensus for the relative importance of above- vs. below-ground competition in forests has not been reached. Some studies have reported strong evidence for below-ground competition ([Dillenburg et al. 1993b](#); [Dillenburg et al. 1995](#); [Lewis & Tanner 2000](#); [Pérez-Salicrup & Barker 2000](#); [Barberis & Tanner 2005](#)), while other studies reported the opposite result ([Denslow et al. 1990](#); [Ostertag 1998](#); [Barker & Pérez-Salicrup 2000](#)). The disparate findings among these studies may be explained by the relative availability of above- vs. below-ground resources ([Coomes & Grubb 2000](#); [Lewis & Tanner 2000](#); [Barberis & Tanner 2005](#)). For example, at La Selva Biological Station, Costa Rica, where the soil is relatively wet and nutrient rich and the understory is relatively dark, [Ostertag \(1998\)](#) found no effect from the exclusion of roots on the above-ground relative growth rate of the seedling *Hampea appendiculata* in either treefall gaps or the understory (see also [Denslow et al. 1990, 1998](#)). In contrast, in a trenching experiment in a nutrient-poor tropical wet forest in Brazil, [Lewis & Tanner \(2000\)](#) demonstrated that below-ground competition for nutrients limited seedling growth and increased mortality in both high- and low-light environments. In an extremely nutrient-poor caatinga in Amazonia, [Coomes & Grubb \(1998\)](#) reported that below-ground competition for nutrients was more important than competition for light. In tropical moist forests that are not extremely nutrient poor, such as the one used in this study, water, rather than nutrients, may be the most limiting resource ([Fisher et al. 1991](#); [Gerhardt 1996](#); [Pérez-Salicrup & Barker 2000](#)). In our case, water may have been particularly limiting during the dry season, increasing the strength of below-ground competition during this period.

The strong role of below-ground competition from lianas in this and other studies (e.g. [Dillenburg et al. 1993a, 1993b](#); [Gerhardt 1996](#); [Pérez-Salicrup & Barker 2000](#)) may have been due, in part, to the relatively high light conditions. The forest light regime in this study was highly variable, with mean light availability resembling that of a large gap or a young secondary forest. Under these conditions, competition from lianas may be predominantly for below-ground resources. As canopy gaps and secondary forests regenerate and develop a closed canopy, light will probably become limiting and then the predominant form of competition may switch from mostly below ground to above ground.

The contrasting findings among studies on above- vs. below-ground competition may also be explained by the differential responses of trees to competition from lianas. Tree species may respond differently to competition from lianas depending on their tolerance to shade and water availability ([Pérez-Salicrup 2001](#)). For example, water potential in adult *Senna multijuga* trees increased immediately after the lianas were cut from around the base of the tree ([Pérez-Salicrup & Barker 2000](#)). Using similar methods, however, [Barker & Pérez-Salicrup \(2000\)](#) found no effect of lianas on the water potential of adult mahogany trees (*Swietenia macrophylla*). Several studies have also noted the ability of pioneer trees to grow well in the presence of lianas, whereas shade-tolerant trees appear to suffer far more competition from lianas ([Putz 1984](#); [Clark & Clark 1990](#); [Schnitzer et al. 2000](#)). In our study, however, we did not find a species-specific response of saplings to above- vs. below-ground competition from lianas. The three disparate tree species differed in their rates of mortality and biomass allocation, as was expected, but these differences did not vary with any of the three treatments (i.e. there were no significant treatment by species interactions).

how lianas compete for resources

Competition for below-ground resources with lianas may be particularly intense because of their ability to efficiently forage for water and nutrients (see [Schnitzer 2005](#)). Lianas as a group have exceptionally well-developed root systems, which allow them to rapidly take up water from the soil ([Fichtner & Schulze 1990](#); [Restom & Nepstad 2004](#)). Lianas also have extremely large vessel elements, which allow them to transport water efficiently to their crown ([Ewers et al. 1991](#)). The ability of lianas to compete for below-ground resources

may be particularly intense during seasonal droughts, when water is in limited supply ([Schnitzer 2005](#)). For example, using deuterium isotopes to determine the depth in the soil at which woody plants accessed water throughout the dry season on Barro Colorado Island in Panama, [Andrade et al. \(2005\)](#) found that lianas consistently tapped water from deeper sources as the dry season progressed, whereas many tree species in this forest did not or could not access water deep in the soil ([Meinzer et al. 1999](#)). In a tropical forest in Panama, [Schnitzer \(2005\)](#) demonstrated that lianas were able to grow significantly more than trees during the dry season relative to their growth in the wet season, suggesting that lianas compete effectively for water even when it is in low supply. Consequently, lianas may be particularly aggressive competitors in seasonal tropical forests due to their ability to effectively forage for below-ground resources.

Lianas are often in high abundance and diversity in the high-light conditions of secondary forests and treefall gaps ([Putz 1984](#); [Dewalt et al. 2000](#); [Schnitzer & Carson 2001](#)), where they can proliferate to the point of forming extremely dense tangles, thus stalling tree regeneration for many years ([Schnitzer et al. 2000](#); [Tabanez & Viana 2000](#)). Previously, we ([Schnitzer et al. 2000](#)) had attributed the recruitment of lianas into gaps to the availability of light and the effects of lianas on regenerating saplings to the pre-emption of light and the mechanical stress that lianas impose on trees. Although these conclusions are probably true to some degree, the findings of this study, combined with others from tropical moist and dry forests (e.g. [Stevens 1987](#); [Pérez-Salicrup & Barker 2000](#)), suggest that lianas also limit the regeneration of trees via below-ground competition.

management implications

The finding that below-ground competition in relatively high-light environments is an important form of competition between saplings and lianas has profound implications for forest management. Lianas may be, as [Putz \(1991\)](#) claimed, 'among the most serious obstacles to timber management, from the Solomon Islands ([Neil 1984](#)) to West Virginia ([Trimble & Tryon 1974](#))'. Indeed, lianas are a well-known nuisance for many types of forest management, including reforestation, enrichment planting and the establishment of tree plantations. Lianas can reduce the value of timber trees by suppressing their growth and regeneration and causing trunk malformations ([Pinard & Putz 1994](#); [Vidal et al. 1997](#); [Gerwing 2001](#); [Schnitzer et al. 2004](#)). Management of lianas is now widespread, and many authors have argued for pre-harvest liana cutting in managed stands to reduce the competitive effects of lianas after logging, a process that costs millions of dollars annually worldwide ([Putz et al. 1984](#); [Vidal et al. 1997](#); [Gerwing 2001](#); [Parren & Bongers 2001](#); [Pérez-Salicrup et al. 2001](#)). Recently, a number of studies on controlling lianas in managed forests have advocated the strategy of cutting only the lianas growing into the crown of economically important trees, while ignoring the lianas located elsewhere in the forest (see [Schnitzer & Bongers 2002](#)). Because below-ground competition appears to be a key interaction between trees and lianas, cutting only the lianas that are growing in the crown of a given tree does not guarantee release from competition, which will be realized only when the lianas competing below ground are also severed. A reasonable approach for reducing below-ground competition with lianas may be the method used by [Pérez-Salicrup & Barker \(2000\)](#), i.e. cutting all of the lianas directly below the crown of the target tree with the rationale that the rhizosphere of a tree is directly related to the dimensions of its crown ([Sanford & Cuevas 1996](#)). This strategy may reduce competition from lianas for both above- and below-ground resources while remaining economically feasible.

Conclusions

The majority of studies on the effects of competition by lianas on trees have focused almost exclusively on light, ignoring below-ground competition. However, the vigorous regeneration of lianas in the high-light environments of disturbed forests, secondary forests and treefall gaps may result in intense competition for below-ground resources. Our study demonstrates that in high-light environments lianas compete with saplings for below-ground resources, severely limiting sapling growth. Above-ground competition with lianas did not appear to

reduce sapling growth, although mechanical stress and shading from lianas caused saplings to allocate biomass towards a relatively thick, short stem and away from leaf biomass. Because lianas commonly compete with trees in tropical forests, especially in treefall gaps and secondary forests, teasing apart the nature of this competition is critical for a comprehensive understanding of the regeneration and dynamics of tropical forests.

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References

- Andrade, J.L., Meinzer, R., Goldstein, G. & Schnitzer, S.A. (2005) Water uptake and transport in lianas of a seasonally dry tropical forest. *Trees: Structure and Function*, 19, 282– 289.
- Barberis, I.M. & Tanner, E.V.J. (2005) Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. *Ecology*, 86, 667– 674.
- Barker, M.G. & Pérez-Salicrup, D.R. (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.
- Becker, P., Rabenold, P.E., Idol, J.R. & Smith, A.P. (1988) Water potential gradient for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology*, 4, 173– 184.
- Bloor, J.M.G. & Grubb, P.J. (2003) Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology*, 91, 77– 85.
- Bongers, F. & Sterck, F.J. (1998) Architecture and development of rainforest trees: responses to light variation. *Dynamics of Tropical Communities* (eds D.M. Newbery, H.H.T. Prins & N. Brown), pp. 125– 162. Blackwell Science, Oxford.
- Bongers, F., van der Meer, P.J. & Thery, M. (2001) Scales of ambient light variation. *Nouragues: Dynamics and Plant Animal Relations in a Neotropical Rain Forest* (eds F. Bongers, P. Charles-Dominique, P.M. Forget & M. Thery), pp. 19– 29. Kluwer Academic, Dordrecht.
- Brokaw, N. & Busing, R.T. (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution*, 15, 183– 188.
- Casper, B.B. & Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, 28, 545– 570.
- Chatelain, C., Dao, H., Gautier, L. & Spichiger, R. (2004) Forest cover changes in West Africa Côte d'Ivoire and Upper Guinea. *Biodiversity of West African Forests: an Ecological Atlas of Woody Plant Species* (eds L. Poorter, F. Bongers, F.N. Kouamé & W. Hawthorne), pp. 15– 32. CABI Publishing, Wallingford.
- Clark, D.B. & Clark, D.A. (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology*, 6, 321– 331.
- Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42, 710– 723.
- Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, 70, 171– 207.
- Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, 18, 431– 451.
- Denslow, J.S. (1995) Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications*, 5, 962– 968.

- Denslow, J.S., Ellison, A.M. & Sanford, R.E. (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, 86, 597– 609.
- Denslow, J.S., Schulz, J.C., Vitousek, P.M. & Strain, B.R. (1990) Growth responses of tropical shrubs to treefall gap environments. *Ecology*, 71, 165– 179.
- Dewalt, S.J., Schnitzer, S.A. & Denslow, J.S. (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology*, 16, 1– 9.
- Dillenburg, L.R., Teramura, A.H., Forseth, I.N. & Whigham, D.F. (1995) Photosynthetic and biomass allocation responses of *Liquidambar styraciflua* (Hamamelidaceae) to vine competition. *American Journal of Botany*, 82, 454– 461.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H. & Forseth, I.N. (1993a) Effects 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., Whigham, D.F., Teramura, A.H. & Forseth, I.N. (1993b) Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *American Journal of Botany*, 80, 244– 252.
- Ewers, F.W., Fisher, J.B. & Fichtner, K. (1991) Water flux and xylem structure in vines. *The Biology of Vines* (eds F.E. Putz & H.A. Mooney), pp. 127– 160. Cambridge University Press, Cambridge.
- Fichtner, K. & Schulze, E.D. (1990) Xylem water flow in tropical vines as measured by a steady state heating method. *Oecologia*, 82, 350– 361.
- Fisher, B.L., Howe, H.F. & Wright, S.J. (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. *Oecologia*, 86, 292– 297.
- Fox, G.A. (1993) Failure-time analysis: emergence, flowering, survivorship, and other waiting times. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 253– 289. Chapman & Hall, New York.
- Gentry, A.H. (1991) The distribution and evolution of climbing plants. *The Biology of Vines* (eds F.E. Putz & H.A. Mooney), pp. 3– 49. Cambridge University Press, Cambridge.
- Gerhardt, K. (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, 82, 33– 48.
- Gerwing, J.J. (2001) Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in eastern Amazon. *Journal of Applied Ecology*, 38, 1264– 1276.
- Grace, J.B. & Tilman, D. (1990) Perspectives on Plant Competition. Academic Press, San Diego.
- Grauel, W.T. & Putz, F.E. (2004) Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *Forest Ecology and Management*, 190, 99– 108.
- Hubbell, S.P., Foster, R.B., O'Brian, S.T., Harms, K.E., Condit, R., Wechsler, B. *et al.* (1999) Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554– 557.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98, 419– 428.
- Kuzee, M.E. & Bongers, F. (2005) Climber abundance, diversity and colonization in degraded forests of different ages in Côte d'Ivoire. *Forest Climbers of West Africa: Diversity, Ecology and Management* (eds F. Bongers, M.P.E. Parren & D. Traoré), pp. 67– 84. CABI Publishing, Wallingford.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C. *et al.* (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171– 175.
- Lewis, S.L. & Tanner, E.V.J. (2000) Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology*, 81, 2525– 2538.
- McLellan, A.J., Fitter, A.H. & Law, R. (1995) On decaying roots, mycorrhizal colonization and the design of removal experiments. *Journal of Ecology*, 83, 225– 230.
- Meinzer, F.C., Andrade, J.L., Goldstien, G., Holbrook, N.M., Cavellier, J. & Wright, S.J. (1999) Partitioning of soil water among canopy trees in a seasonal dry tropical forest. *Oecologia*, 121, 293– 301.
- Neil, P.E. (1984) Climber problems in Solomon Islands forestry. *Commonwealth Forestry Review*, 63, 27– 34.

- Ogawa, H., Yoda, K., Ogino, K. & Kira, T. (1965) Comparative ecological studies of three main types of forest vegetation in Thailand. 2. Plant biomass. *Nature and Life in Southeast Asia*, 4, 49– 80.
- Ostertag, R. (1998) Belowground effects of canopy gaps in a tropical wet forest. *Ecology*, 79, 1294– 1304.
- Papon, A. (1973) Geologie et Mineralisations de Sud-Ouest de la Côte d'Ivoire, Synthèse Des Travaux de L'Operation SASCA, 1962– 1968. SODEMI, Abidjan.
- Parren, M.P.E. & Bongers, F. (2001) Does climber cutting reduce felling damage in southern Cameroon? *Forest Ecology and Management*, 141, 175– 188.
- Pearson, G.A. (1929) The other side of the light question. *Journal of Forestry*, 27, 807– 812.
- Pérez-Salicrup, D.R. (2001) Effect of liana cutting on tree regeneration in a liana forest in Amazonian Brazil. *Ecology*, 82, 389– 396.
- Pérez-Salicrup, D.R. & Barker, M.G. (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.R., Claros, A., Guzman, R., Licona, J.C., Ledezma, F., Pinard, M.A. *et al.* (2001) Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia. *Biotropica*, 33, 324– 329.
- Phillips, O.L. & Gentry, A.H. (1994) Increasing turnover through time in tropical forests. *Science*, 263, 954– 957.
- Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L. *et al.* (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, 418, 770– 774.
- Pinard, M.A. & Putz, F.E. (1994) Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: biomechanical facilitation in vine succession. *Journal of Tropical Forest Science*, 6, 302– 309.
- Poorter, L., Bongers, F., Kouamé, F.N. & Hawthorne, W.D. (2004b) Biodiversity of West African Forests: An Ecological Atlas of Woody Plant Species. CABI Publishing, Wallingford.
- Poorter, L., Bongers, F., Sterck, F.J. & Wöll. H. (2004a) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, 84, 602– 608.
- Popma, J. & Bongers, F. (1988) The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia*, 75, 625– 632.
- Putz, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 65, 1713– 1724.
- Putz, F.E. (1991) Silvicultural effects of lianas. *The Biology of Vines* (eds F.E. Putz & H.A. Mooney), pp. 493– 501. Cambridge University Press, Cambridge.
- Putz, F.E., Lee, H.S. & Goh, R. (1984) Effects of post-felling silvicultural treatments on woody vines in Sarawak. *Malaysian Forester*, 47, 214– 226.
- Restom, T.G. & Nepstad, D.C. (2004) Seedling growth dynamics of a deeply-rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management*, 190, 109– 118.
- Rice, W.R. (1990) A concensus combined *P*-value test and the family-wide significance of component tests. *Biometrics*, 46, 303– 308.
- Sanford, R.L. (1989) Fine root biomass under a tropical forest light gap opening in Costa Rica. *Journal of Tropical Ecology*, 5, 251– 256.
- Sanford, R.L. (1990) Fine root biomass under light gap openings in an Amazon rain forest. *Oecologia*, 83, 541– 545.
- Sanford, R.L. & Cuevas, E. (1996) Root growth and rhizosphere interactions in tropical forests. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 268– 300. Chapman & Hall, New York.
- SAS Institute (2000) JMP Statistics and Graphics Guide, Version 4. SAS Institute, Cary, North Carolina.
- Schnitzer, S.A. (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, 166, 262– 276.
- Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, 17, 223– 230.
- Schnitzer, S.A. & Carson, W.P. (2000) Have we missed the forest because of the trees? *Trends in Ecology and Evolution*, 15, 375– 376.

- Schnitzer, S.A. & Carson, W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, 82, 913– 919.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (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., Parren, M.P.E. & Bongers, F. (2004) Recruitment of lianas into logging gaps and the effects of pre-harvesting climber cutting. *Forest Ecology and Management*, 190, 87– 98.
- SODEFOR (1995) Plan d'Aménagement de la Forêt Classée de Monogaga 1995–2004. Société de Développement des Forêts, Ministère de l'Agriculture et des Ressources Animales, Abidjan, Cote d'Ivoire.
- Sokal, R.R. & Rohlf, F.J. (1995) Biometry. W.H. Freeman, New York.
- Stevens, G.C. (1987) Lianas as structural parasites: the *Bursera simarouba* example. *Ecology*, 68, 77– 81.
- Tabanez, A.A.J. & Viana, V.M. (2000) Patch structure within Brazilian Atlantic forest fragments and implications for conservation. *Biotropica, Special Issue*, 32, 925– 933.
- Tilman, D. (1982) Resource Competition and Community Structure. Monographs in Population Biology. Princeton University Press, Princeton.
- Toumey, J.W. (1929) The vegetation of the forest floor; light vs. soil moisture. *Proceedings of the International Congress of Plant Science 1926*, 1, 575– 590.
- Trimble, G.R. & Tryon, E.H. (1974) Grapevines, a serious obstacle to timber production on good hardwood sites in Appalachia. *Northern Logger and Timber Processor*, 23, 22– 23.
- Vidal, E., Johns, J., Gerwing, J., Barreto, P. & Uhl, C. (1997) Vine management for reduced-impact logging in eastern Amazonia. *Forest Ecology and Management*, 98, 105– 114.
- Weiner, J. (1986) How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology*, 67, 1425– 1427.
- Wright, S.J., Calderón, O., Hernandez, A. & Paton, S. (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Barro Colorado Island, Panama. *Ecology*, 85, 484– 489.