

Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting

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Summary

1. Lianas or woody vines can be detrimental to the trees that support them. Research on liana cutting for tropical timber management has demonstrated positive yet costly benefits, but liana cutting to enhance commercial outputs of nontimber forest products has not been examined. We implemented a controlled experiment to quantify the effects of cutting lianas on Brazil nut *Bertholletia excelsa* Bonpl. fecundity.

2. We conducted our 10-year experiment in a Brazilian extractive reserve where local harvesters collect fruits from this Amazonian canopy-emergent species as part of their forest-based livelihood system. We cut 454 lianas with a total basal area of 2.41 m² from 78 of 138 host trees ≥ 50 cm diameter at breast height.

3. Treated trees were significantly better producers 3 ½ years after liana cutting, and these differences increased dramatically in subsequent years, with consistent proportionally higher production in treated versus untreated individuals.

4. The number of lianas rooted within 5 m of the host tree significantly explained production levels, suggesting both above- and below-ground liana–host tree competition. Once host crowns were liana-free, branch regrowth was highly visible, particularly in heavily infested trees, and crown reassessments suggested that liana cutting improved crown form. Additionally, liana cutting may induce some nonproducing trees to become producers and may circumvent mortality of trees heavily infested with lianas (> 75% crown covered).

5. Liana removal can be implemented easily when harvesting Brazil nut fruits. Only lianas associated with *B. excelsa* trees should be cut to conserve liana ecosystem functions.

6. *Synthesis and applications.* We quantified effects of liana cutting on Brazil nut host tree fecundity and provided estimates of increased commercial yields. Our long-term (10-year) study permits understanding of biological variation and informs related management decisions. Findings suggest that liana cutting reduces above- and below-ground competition with individual trees, ultimately allowing mature host crowns to recover such that 9–10 years after liana cutting, treated trees produced on average three times more fruits than untreated trees. Application of liana cutting to other tropical species would likely boost fruit and seed production, increase host tree fecundity and potentially enhance future recruitment.

Key-words: above-ground competition, below-ground competition, *Bertholletia excelsa*, fecundity, fruit production, liana load, nontimber forest product, tropical forest, vine

Introduction

Although present in forests across the globe, lianas (or woody vines) attain their greatest abundance and diversity in the tropics (Gentry 1991). Their key role in tropical

forest structure and maintenance is unquestioned. Although estimated to represent less than 5% of above-ground tropical forest biomass (Putz 1983), they constitute upwards of 40% of leaf area (Hegarty & Caballé 1991). Lianas also provide critical pathways for arboreal residents and are key food sources for local fauna (Emmons & Gentry 1983). In recent decades, however,

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liana abundance and biomass have escalated, increasingly dominating tropical forest ecosystems (Schnitzer & Bongers 2011). Evidence for this change is particularly persuasive from neotropical forests (Phillips *et al.* 2002), compelling some researchers to use the term 'infestation' to indicate the negative and often highly aggressive dominance by this vascular plant group (Ingwell *et al.* 2010). Explanatory research suggests that lianas benefit from landscape and planetary increases in forest disturbance (DeWalt, Schnitzer & Denslow 2000), fragmentation (Laurance *et al.* 2001) and CO₂ concentrations (Condon, Sasek & Strain 1992), although van der Heijden & Phillips (2008) contend that host tree characteristics and availability may be more important determinants of liana success in Neotropical forests.

Lianas clearly are detrimental to the trees that support them (Schnitzer & Bongers 2002). They can increase host tree mortality, while negatively affecting host tree growth rates (Clark & Clark 1990; Ingwell *et al.* 2010) and fecundity (Stevens 1987; Nabe-Nielsen, Kollmann & Peña-Claros 2009). Lianas can rapidly take over treefall and/or logging gaps, inhibiting tree regeneration and potentially dominating species composition for over a decade (Putz 1984; Schnitzer, Dalling & Carson 2000). These negative tree–liana relationships have precipitated experimental treatments to examine the effects of liana cutting on host tree growth and water interactions (Dillenburg *et al.* 1993; Pérez-Salicrup & Barker 2000) and advanced tree regeneration (Campanello *et al.* 2012). What effect would liana cutting have on host tree fecundity? Within 2 years following liana removal, *Bursera simaruba* L. fecundity in a deciduous forest of Costa Rica improved (Stevens 1987), although robust, inferential conclusions were limited due to a small ($n = 5$) sample size and short study period.

Liana cutting treatments also have been applied to enhance commercial benefits of tropical timber management (Vidal *et al.* 1997). Preharvest liana cutting is considered essential to reduce canopy connectivity and thus minimize the size of logging disturbances, reduce future crop tree damage (Fox 1968; Appanah & Putz 1984) and secure worker safety (Amaral *et al.* 1998). Liana cutting also reduces postlogging liana infestations (Alvira, Putz & Fredericksen 2004), increases residual tree growth and enhances postlogging tree regeneration (Gerwing & Vidal 2002; Grauel & Putz 2004). To our knowledge, however, application of liana cutting to enhance commercial outputs of nontimber forest products (NTFP) has not been examined.

We tested the silvicultural recommendation that lianas should be cut from Brazil nut trees *Bertholletia excelsa* Bonpl. (Kainer *et al.* 2006). This NTFP is a cornerstone of the Amazonian extractive economy, with combined Bolivian, Brazilian and Peruvian 2010 exports greater than US\$123 million (UN Comtrade 2010). Virtually, all Brazil nuts are collected from old-growth Amazonian forests almost exclusively by local harvesters, some of whom implement liana cutting, considering it a 'best management

practice' that improves yield. In addition to this local knowledge, previous research has demonstrated that Brazil nut trees with >25% of the crown covered by lianas produce fewer fruits (Kainer *et al.* 2006). Nonetheless, empirical evidence and quantification of a liana cutting effect on this important NTFP are lacking. We implemented a controlled experiment to quantify the effects of liana cutting on *B. excelsa* host tree fecundity. Additionally, we monitored trees for a lengthy timeframe (10 years) to permit an understanding of long-term biological variation and facilitate exploration of our hypothesis that expected fruit production increases in liana-cut trees would be attributed to reduced competition with lianas above- and below-ground coupled with host tree crown recovery.

Materials and methods

STUDY SPECIES AND SITE

Throughout the Amazon basin, *B. excelsa* is found in nonflooded (*terra firme*) forests (Prance 1990) in areas where annual rainfall ranges from 1400 to 2800 mm year⁻¹ and an annual water balance deficit exists for 2–7 months (Diniz & Bastos 1974). At maturity, it is a very large, canopy-emergent tree [40.9 ± 0.7 m ($\bar{x} \pm SD$) in height] and can live for centuries (Vieira *et al.* 2005), providing a physical support for lianas to attain upper canopy heights without significant structural investments. The large, indehiscent, approximately round fruits (10–16 cm) reach maturity and synchronically fall on average 14 months after successful pollination (Maués 2002). The 10–25 large (*c.* 4 × 2 cm) seeds remain inside the woody fruits upon falling until extraction by seed predators/dispersers, almost exclusively agoutis *Dasyprocta* sp. or humans.

Data were collected within Extractive Reserve Chico Mendes, located in the state of Acre, Brazil, within a landscape of gently undulating topography. The Reserve maintains 92% forest cover (SEMA 2010) and is dominated by open tropical forest with bamboo and/or palms, with a small area classified as dense tropical forest (FUNTAC 2008). The region has a pronounced dry season from June to August, and average annual rainfall is between 1770 and 1880 mm (ZEE 2000). The liana cutting experiment was conducted in an unlogged 420-ha extractivist landholding in the south-eastern portion of the Reserve (Colocação Rio de Janeiro in Seringal Filipinas) (see Wadt, Kainer & Gomes-Silva 2005 for map). A 2001–2002 inventory of all *B. excelsa* individuals ≥10 cm diameter at breast height (DBH; measured at 1.3 m above-ground level) revealed a population density of 1.35 trees ha⁻¹ and an average diameter of 86.1 ± 45.0 cm DBH (Wadt, Kainer & Gomes-Silva 2005). Of 145 trees < 50 cm inventoried, only 20% had initiated fruit production, while 96% of 404 trees ≥ 50 cm DBH were reproductive (Wadt, Kainer & Gomes-Silva 2005). Of this latter subset, almost all had dominant or co-dominant crown positions, while liana load was highly variable: 39% had no lianas, 32% had light liana loads (≤25% crown covered), 20% had moderate to heavy liana loads (25–75% crown covered), and 10% had very heavy liana loads (>75% crown covered) (Wadt, Kainer & Gomes-Silva 2005). Finally, a preliminary 5-year analysis (2002–2006) of fruit production of a subset of these trees ≥50 cm DBH revealed considerable

production variation among trees in the population [$(66 \pm 98$ fruits per tree per year ($\bar{x} \pm SD$))] and within *B. excelsa* individuals ($CV_i = 0.95$), contrasting with extremely low population-level, annual production variation ($CV_p = 0.20$) (Kainer, Wadt & Staudhammer 2007).

SAMPLE POPULATION AND FIELD MEASUREMENTS

From this previous inventory, 140 reproductively mature *B. excelsa* adults (50–194 cm DBH) were selected for further study; in the first year of the study, one tree died and a pasture was cleared immediately adjacent to another, leaving 138 study trees. To obtain representation of tree sizes, a stratified sample was selected across 10 DBH classes (nine 10-cm DBH classes and one of trees ≥ 150 cm DBH), roughly in proportion to the population. In addition, we also randomly selected trees to include representatives within each of four liana load categories: (1) no lianas in crown; (2) $\leq 25\%$ crown covered; (3) 25–75% crown covered; and (4) $>75\%$ crown covered. The focus of this study was liana cutting; therefore, this stratification scheme sampled trees with $>25\%$ liana load at a higher rate than that of the population. Tree geospatial location confirmed that sample trees were well distributed spatially across the study landscape, and a field check ensured no overlap between individual tree crowns and fruitfall areas. To further explore liana loads on each sample tree, liana number, basal area, origin ($\leq 5, 10, 15$ or 20 m from the host tree) and family-level taxonomy were assessed (see Kainer *et al.* 2006 for more details), revealing a total of 594 lianas representing 24 botanical families. Mean number and basal area of lianas tree⁻¹ ($\bar{x} \pm SD$) were 4.26 ± 0.43 and 0.0235 ± 0.0027 m², respectively. Most lianas originated within 5 (64.8%) or 10 m (an additional 25.4%) of host trees.

Three crown attributes of each sample tree were assessed in 2001–2002: (1) crown position was categorized as (a) dominant (full overhead and side light), (b) co-dominant (full overhead light) and (c) intermediate (some overhead or side light) or (d) suppressed (no direct light); (2) crown cross-sectional area was measured; and (3) crown form was categorized as: (a) good, (b) tolerable, (c) poor or (d) very poor. Crown form was reassessed in 2005 and again in 2012. For 10 consecutive years (2002–2012), fruit production of each individual tree was measured after fruitfall in February. Numbers of fruits harvested from the ground, however, do not reflect absolute counts of total fruit production per tree. The very few fruits remaining in the crowns contribute a small error, plus continuous removal by scatterhoarding *Dasyprocta* sp. constitutes a second potential error. Fruitfall and fruit removal from 20 nearby *B. excelsa* trees were monitored biweekly over 70 days, approximately matching the synchronous fruitfall period; only 5.2% of fruits were removed by animals or remained in the crown (L.H.O. Wadt, unpublished data). We did not adjust fruit counts for these potential sources of error, assuming them to be small and consistent over our sample.

Tree DBH was also assessed annually. Initial DBH in the 2001–2002 inventory was directly measured with a diameter tape. Through 2008, these trees were monitored with dendrometer bands, and annual band increments were added to the initial DBH measurement to obtain annual DBH. From 2010 to 2012, DBH was again measured with a diameter tape in a clearly pre-marked location to guarantee measurement consistency. In 2009, DBH was estimated using a linear regression of the observed and incremental measures in the other years.

LIANA CUTTING TREATMENT

Lianas were cut from 78 of the 138 trees (treated trees) during the dry season in July 2002, stratifying such that the distribution by liana load was roughly the same for treated and untreated trees. Each liana was cut in two places: near the ground (ground cut) and at c. 2 m from ground level (aerial cut). Any liana resprouts or new lianas associated with these treated trees over the study period were cut so that host trees persisted as liana-free.

LIANA CUTTING TREATMENT ANALYSIS

We used repeated-measures analysis of variance methods to analyse the effects of liana cutting treatment on the annual number of fruits produced. In our liana cutting treatment and analyses, we only included trees with liana loads originally classified as $>0\%$ to ensure that treated and untreated trees were subject to the same liana loading pressures. Thus, 23 liana-free trees of our 138 study trees were excluded from this analysis, leaving 115 trees with liana loads $>0\%$. By the end of the study, 14 of these trees were no longer present in the data set: five were excluded from measurement after 3–7 years because of sampling difficulties and adjacent land clearing activities; another nine trees died after 3–9 years of measurement. Crown cross-sectional area was not used in the model because it is strongly correlated with DBH ($r = 0.53$, $P < 0.0001$). Predictive differences between these two variables were very small, and because DBH is a more common field measurement, we preferentially retained it to facilitate data interpretation. Few trees had crowns classified as ‘very poor’, so we combined this class with those classified as ‘poor’ resulting in only three crown form classes: good, tolerable and poor. Similarly, because few trees exhibited liana loads $>75\%$, only two classes of liana load were defined in analyses: $\leq 25\%$ and $>25\%$. A previous study showed a quadratic relationship between DBH and fruit production (Wadt, Kainer & Gomes-Silva 2005), and thus both annually assessed DBH and DBH² were tested in model development. Although there were significant correlations between total liana basal area and total liana numbers with liana load in the tree crown (Spearman’s $r = 0.539$ and 0.456 , respectively), inclusion of all three of these liana variables in the fruit production model lowered model AIC and presented no evidence of multi-collinearity. Finally, we initially examined liana basal area and number of lianas associated with each host tree at three possible distances ($\leq 5, 10$ or 20 m), but only retained basal area and number of lianas ≤ 5 m because this distance best predicted fruit production.

Subsequently, production models were first constructed with three continuous tree variables (annual DBH, number and basal area of lianas within 5 m) and five class variables (initial crown form, crown position, liana load, liana cutting treatment and year of measurement). We used a log transformation to stabilize the variance and meet statistical assumptions necessary for model testing. The statistical software, SAS, was utilized for all analyses (version 9.2, SAS Institute, Cary, North Carolina, USA). Fruiting data were both spatially and temporally correlated, because fruit production data were collected annually and trees were located in a contiguous forest area. To ensure correct formation of error covariance matrices and proper statistical tests, individual trees were treated as random effects, repeatedly measured each year, with a compound symmetric variance–covariance structure best describing the relationship between measurements taken on the

Table 1. Best-fit model to explain annual Brazil nut fruit production

Effects	Num d.f.	Den d.f.	F value	<i>P</i> > <i>F</i>
Initial liana load	1	102	5.51	0.0209
Year	10	989	2.88	0.0015
Annual DBH	1	116	5.61	0.0195
Annual DBH ²	1	118	3.98	0.0484
Annual DBH*Year	10	988	2.08	0.0234
Liana cutting treatment	1	107	5.61	0.0196
Liana cut*Year	10	979	2.53	0.0052
Initial crown form	2	106	7.71	0.0007
Liana cut*Initial crown form	2	106	3.13	0.0477
Initial crown form*Year	20	979	1.4	0.1114
Liana cut*Initial crown form*Year	20	978	1.92	0.0086
Number of lianas within 5 m	1	102	0.73	0.3963
Number of lianas within 5 m*Year	10	975	1.98	0.0319
Basal area of lianas within 5 m	1	100	0.12	0.7312
Basal area of lianas within 5 m*Initial crown form	2	100	6.36	0.0025

same tree over time. In other words, measurements from the same tree did show significant correlations; however, those correlations were not more similar in adjacent measurement periods (Littel *et al.* 2006). UTM easting and northing was included so that tree spatial location could be incorporated into the error covariance matrix. Variograms were first constructed to reveal possible patterns of spatial dependency, and several candidate models of spatial covariance were tested in the mixed model (Schabenberger & Pierce 2001). No spatial correlation structure was significant, indicating that production of adjacent trees was not more similar than that of those located farther apart.

All two- and three-way interactions with year were included in initial models. Model parameters were found via maximum likelihood, and error covariance structures were tested. Model results were compared using Akaike Information Criteria (AIC; Akaike 1973) and by visual examination to test normality and homoscedastic model residuals. Those variables that did not improve (lower) AIC were dropped sequentially (Burnham & Anderson 2002). Conventional model building methods of sequentially dropping nonsignificant interactions ($P < 0.05$) and covariates based on P -values revealed almost identical results; we report results using the AIC method.

Results

We cut 454 lianas total from 78 treated Brazil nut trees. Lianas did not completely fall from the crowns to the base of the liberated host trees until 1 year postcutting. At that time, only 9 of 454 (1.98%) of the aerial-cut portion of the lianas had resprouted, contrasted with 169 of 454 (37.22%) of the ground-cut liana portion.

Ten years after study inception, 2012 production of treated trees was 77% higher than controls. This result was corroborated by our best-fit model (lowest AIC), which considered additional covariates and clearly demonstrated that liana cutting improved fruit production of Brazil nut trees ($P = 0.0196$, Table 1). This effect, however, varied over years and by initial crown form class as evidenced by the three-way interaction of these variables ($P = 0.0086$, Table 1). Trees with good initial crown forms consistently produced the most fruit, followed by those classified as tolerable then poor, though the magnitude of this effect varied by year and with cutting treatment. While treated and untreated trees produced statistically equal numbers of fruits from 2002 to 2005, from 2006 on, trees receiving the liana cutting treatment were significantly better producers (except in 2010) (Fig. 1). Further related evidence revealed that prior to 2006, the number of lianas rooted within 5 m of the host tree significantly explained levels of Brazil nut production – greater liana numbers proximate to host trees resulted in fewer fruits (Fig. 2). From 2006 on, however, liana numbers (counted at study inception) no longer explained fruit production. Basal area of these same lianas also significantly affected production, but this varied by initial crown form ($P = 0.0025$, Table 1; Fig. 3). Although trees with good crown forms on average had higher production, as the basal area of lianas within 5 m of the host tree increased, this trend was highly uncertain and statistically insignificant (Fig. 3). Trees with crowns in the tolerable category, however, clearly had significantly lower production with increased near-tree (5 m) liana basal area, whereas trees with the poorest crown forms demonstrated consistently low fruit production, regardless of initial near-tree liana basal area (Fig. 3). A third liana variable, initial liana

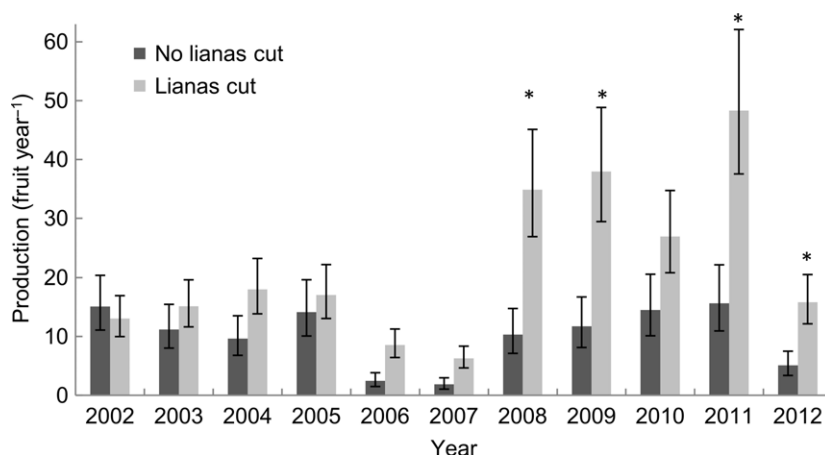


Fig. 1. Least square mean predicted values of annual production by year and liana cutting treatment. *Production differences ($P < 0.05$) between treated and untreated trees within any given year.

Fig. 2. Least square mean predicted values of annual production by year and number of lianas within 5 m. Prior to 2006, production increased significantly ($P \leq 0.05$) as number of lianas within 5 m increased; afterwards, this trend is not significant.

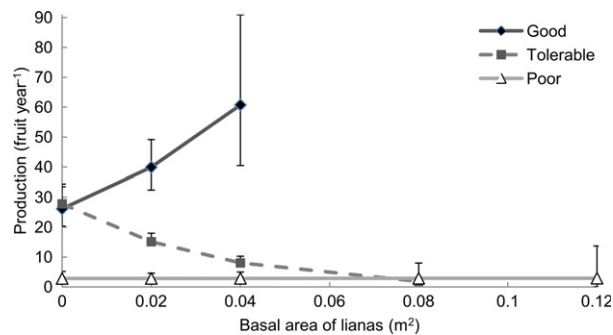
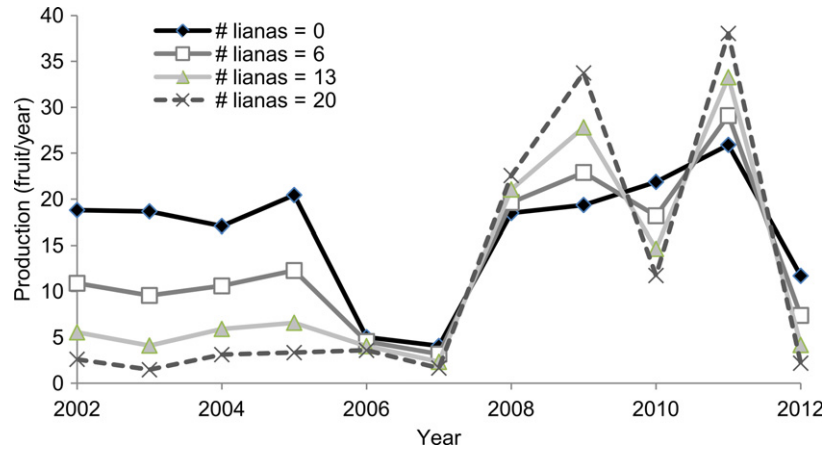


Fig. 3. Least square mean predicted values of annual average production by basal area of lianas within 5 m and initial crown form class. At $P \leq 0.05$, trees with good crown form had no significant tree production–liana basal area relation. Trees in the tolerable category, however, had a significant production decrease as basal area increased, and there was no such significant relationship in trees with poor crown forms.

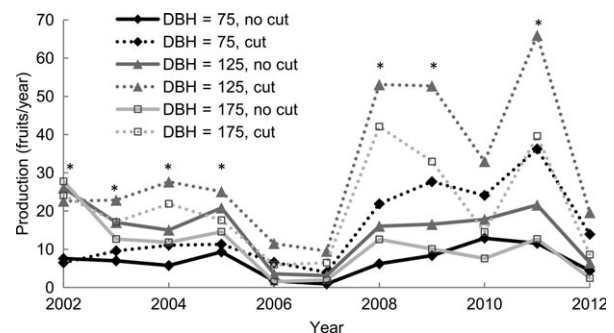


Fig. 4. Least square mean predicted values of annual production by diameter and year, separated by liana cutting treatment. *Production differences ($P \leq 0.05$) between DBH=125 and DBH=75. Within each of the three DBH sizes, there were no significant differences in production between trees cut and not cut.

loads in Brazil nut crowns, revealed a significant simple effect on fruit production ($P = 0.0209$, Table 1); trees with < 25% of their crowns covered produced significantly more fruits than those with >25% coverage.

Finally, tree girth also explained Brazil nut fruit production. Both annually assessed DBH and DBH² had explanatory significance, while the effect of the former varied by year (Table 1). Trees 100–150-cm DBH tended to produce significantly more fruits than those <75-cm DBH in most years. While this difference became even more pronounced after 2007 in treated versus untreated trees, there was no significant interaction of liana cutting treatment by DBH value at $P \leq 0.05$ (Fig. 4).

Discussion

LIANA CUTTING ENHANCES HOST TREE FECUNDITY

In the last 2 years of our study (2011, the highest production year, and 2012, one of the lowest), Brazil nut trees with vines cut (treated trees) produced on average three times as many fruits as trees without vines cut (untreated or control trees). Whereas untreated trees had approxi-

mately the same average production 2002–2006 versus 2007–2012, treated trees produced on average twice as many fruits in this latter timeframe. This parallels Stevens (1987) who reported an average 2½ times production increase on a limited sample of five *B. simaruba* trees 2 years after liana removal.

The positive host tree fecundity effects of liana cutting did not occur immediately. A statistically significant effect of the July 2002 liana cutting was not apparent until February 2006 (Fig. 1). Additionally, liana cutting may induce some nonproducing trees within a population to become producers. Our proportion of trees that produced zero fruits fell from a high average of 20% for the first two study years (2002–2003) to an average of 6.4% in the last five (2008–2012). Because Brazil nut fruits take 14 months to mature, only fruits counted in or after 2004 were entirely formed after liana cutting. During the first four study years, treated trees with higher liana numbers produced far fewer fruits than trees with low liana numbers; however, once the cutting treatment eliminated below- and above-ground liana competition and crowns began to recover, liana numbers initially associated with treated trees became irrelevant (Fig. 2). Production differences between treatments increased dramatically after

2005, with consistent proportionally higher production in treated versus untreated individuals in all years except 2010 (Fig. 1).

POSSIBLE PROCESSES BEHIND FECUNDITY INCREASES

Reduction of below-ground competition

Although sparse, some evidence exists to implicate lianas in below-ground competition with host trees. Based on liana resprouting, below-ground liana competition ceased entirely only *c.* 3 years after the cutting treatment (July 2005). Pérez-Salicrup & Barker (2000) reported an immediate effect when cutting lianas from 10- to 20-cm DBH *Senna multijuga* (Rich.) Irwin and Barneby trees at dry season inception in a lowland tropical dry forest. One day postcutting, treated trees had significantly less negative predawn and mid-day water potentials than control trees, demonstrating liana–host tree competition for water. In contrast, Barker & Pérez-Salicrup (2000) found no such liana cutting effect on larger (mean DBH *c.* 41 cm) *Swietenia macrophylla* King trees in a similarly dry tropical forest. They concluded that water was not a limiting factor for either host trees or lianas in this case, because both enjoy conservative water relations or each had spatially separate root systems to access sufficient and different water sources. Dillenburg *et al.* (1993) also found no change in host predawn leaf water potentials after cutting vines from *Liquidambar styraciflua* L. saplings in a temperate site with high available soil moisture capacity. Thus, whether below-ground competition for water and nutrients has a negative effect on host parameters appears contingent on diverse site factors and species attributes.

Lianas have wider and larger vessels than trees, with less allocation of stem tissue per unit of leaf area supplied with water and nutrients (Tyree & Ewers 1996; Paul & Yavitt 2011), providing lianas with a competitive advantage over arboreal neighbours to obtain below-ground resources. In our study, years of high rainfall (Staudhammer, Wadt & Kainer 2013) resulted in dramatically greater production differences between treated and untreated trees (2008, 2009 and 2011) than in drought years (2006, 2007 and 2012) (Fig. 1). This suggests that when water is limited and liana–tree competition for this resource is greater, lianas may be more competitive. Lianas have been shown to consistently tap deeper sources of water as the dry season progresses (Andrade *et al.* 2005), whereas larger canopy trees tend to rely primarily on water from the upper soil profile where nutrients are most abundant (Meinzer *et al.* 1999). Nonetheless, the oversized liana water column may enhance nutrient uptake under certain conditions. Reduced leaf nitrogen concentration in tree saplings under competition with vines was attributed to combined effects of reduced host sapling growth and vine-sapling competition for soil N (Dillenburg *et al.* 1993).

We found that the greater the number of lianas rooted within 5 m of the host tree, the fewer Brazil nut fruits produced. This relationship, however, cannot be attributed unambiguously to below-ground competition because these same proximate lianas accounted for almost 70% of those reaching host crowns (Kainer *et al.* 2006). To disentangle above- and below-ground liana competition, Schnitzer, Kuzee & Bongers (2005) conducted a controlled experiment and concluded that below-ground dynamics drove liana–host tree competition. All host tree saplings had five times less biomass of those grown liana-free, regardless of whether liana competition was solely removed below-ground or both below- and above-ground. Nonetheless, host tree and liana root morphological variation and unknowns about root architecture complicate more in-depth understanding of below-ground liana–host tree relationships.

Reduction in above-ground competition

Liana loads in host tree crowns significantly and parsimoniously explained Brazil nut fruit production (Table 1); when lianas covered >25% of host crowns, Brazil nut trees produced fewer fruits. Lianas bear their leaves near or above those in host tree crowns, intercepting light and reducing solar radiation available to host leaves (Clark & Clark 1990). Their removal results in greater canopy openness (Grauel & Putz 2004) and light transmittance (Gerwing 2001). Almost immediately after cutting, liana leaves hosted in Brazil nut tree canopies began to wilt, rapidly affecting the host tree canopy light environment. It took *c.* 1 year, however, for the substantial liana biomass to decompose and fall to the forest floor, fully liberating the host canopy. Smaller diameter trees are unlikely to obtain a similar photosynthetic boost from this competition reduction as larger trees, given that Brazil nut tree crown area is highly positively correlated with DBH (Kainer, Wadt & Staudhammer 2007) – the larger the tree, the larger the crown area released. Although production differences by tree diameter were evident from study commencement, by 2007, these differences became even more pronounced for treated trees (Fig. 4), suggesting another mechanism, also related to host crowns, at work over time.

Crown recovery over time

Initial tree crown form (a categorical scoring of good, tolerable or poor) explained fruit production, but this varied by year and liana cutting treatment (Table 1). Up until 2007, crowns with good forms produced better than all others, and throughout the study period, fruit production of these trees was unaffected by liana cutting. From 2007 onward, however, trees initially scored with good or tolerable crown forms produced equally as well, suggesting that these tolerable crowns were recovering following liana removal. In the field, we observed that once host

crowns were liana-free, branch regrowth was highly visible, particularly in trees that were originally heavily infested. Crown form reassessments of these trees in 2012 suggested that liana cutting improved crown form (Fig. 5). Fresh shoots had emerged, and slowly, new branches were formed to support flowers and eventually fruits.

Population-level benefits

While our study focused on individual trees, liana removal benefits and subsequent crown recovery could lead to population-level improvements in fruit production over time through decreased mortality and increased growth in girth. Our data weakly suggest that liana cutting may prevent mortality of trees heavily infested with lianas (>75% crown covered) (Fig. 5). Ingwell *et al.* (2010) found that such heavily infested trees in Panama had twice the probability of mortality (42 vs. 21%) as their less-infested counterparts over a 10-year period. Liana presence (>25% of host crown covered) in reproductively mature Brazil nut adults also significantly impedes basal area growth (Staudhammer, Wadt & Kainer 2013). Others have quantified significant increases in annual circumference or DBH growth rates of other tropical host species following liana cutting (Peréz-Salicrup & Barker 2000; Grauel & Putz 2004).

PUTTING LIANA CUTTING INTO PRACTICE

Long-term studies such as ours permit understanding of biological variation and change over time, which, in turn, facilitates more robust management applications. We are not the first to suggest that liberating Brazil nut trees of lianas improves fruit production. Producers themselves and government and nongovernmental organizations have promoted this 'best management practice' (Cardó 2000; Wadt *et al.* 2005). Indeed, liana cutting was the most widespread Brazil nut management practice shared by

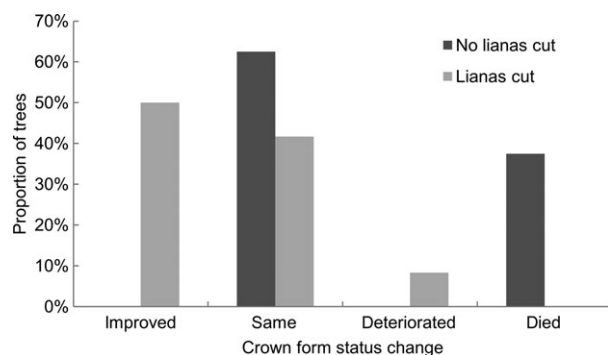


Fig. 5. Proportion of heavily liana-infested trees (> 75% crown covered) with their respective change in crown form status 10 years after liana cutting. Low sample numbers in this liana load category ($N = 8$ and 12 for treated and untreated trees, respectively) prohibited statistical testing.

producers in the tri-border region of Bolivia, Peru and Brazil (Duchelle, Kainer & Wadt 2014). Liana removal may become even more important given the expected regional increases in drought occurrence and severity (Lewis *et al.* 2011), and the potentially linked increases in liana dominance (Phillips *et al.* 2002; Schnitzer & Bongers 2011). Liana cutting should be applied only to individuals associated with target host trees, whether randomly distributed as in our study or in high-density groves (Peres & Baider 1997), addressing important economic interests while also allowing conservation of liana ecosystem functions (Paul & Yavitt 2011).

Liana removal can be implemented with relative ease. One producer who cut lianas from 40 Brazil nut trees not previously treated only failed to cut 10 of 256 (<4%) lianas, most of which were rooted >10 m from the tree host, a distance less likely to invoke below-ground competition and where <7% of lianas that reach Brazil nut host crowns surfaced (Kainer *et al.* 2006). Additionally, the actual cutting of lianas and repeated treatments as necessary takes only a few minutes. It is the travel time to each individual tree that is time-consuming. Thus, incorporating liana cutting into routine annual fruit harvests would reduce the time invested in this silvicultural activity to near zero, rendering application to other commercial NTFPs (e.g. *Carapa guianensis* Aublet.) worth testing. This contrasts with prelogging liana removal, where research documents clear silvicultural benefits of liana removal, but also high costs (Vidal *et al.* 1997; Pérez-Salicrup *et al.* 2001).

Finally, the monetary benefits of this silvicultural treatment can be substantial. That treated Brazil nut trees produced on average three times as much fruit as untreated trees suggest a potential threefold increase in NTFP income. It is therefore no surprise that that over 90% of harvesters interviewed ($N = 77$) in Extractive Reserve Chico Mendes already cut lianas (Duchelle, Kainer & Wadt 2014). When considering a subset of these families shown to average USD \$765 in gross annual Brazil nut income ($N = 47$, Duchelle *et al.* 2011), a threefold increase in yield would represent USD \$500 of the \$765 total. Given that Brazil nut prices have quadrupled in the last two decades, reaching US\$1.18 per kilogram in Acre in 2011 (Wadt & Kainer 2012), the silvicultural recommendation to cut lianas from Brazil nut trees can translate a positive ecological response into a substantial economic one.

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References

- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Proceedings of the Second International Symposium on Information Theory* (eds B.N. Prentov & F.F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.
- Alvira, D., Putz, F.E. & Fredericksen, T.S. (2004) Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. *Forest Ecology and Management*, **190**, 73–86.
- Amaral, P., Veríssimo, A., Barreto, P. & Vidal, E. (1998) *Floresta Para Sempre: Um Manual Para a Produção de Madeira na Amazônia*. World Wildlife Fund/IMAZON/USAID, Belém, Pará, Brazil.
- Andrade, J.L., Meinzer, F.C., Goldstein, G. & Schnitzer, S.A. (2005) Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees*, **19**, 282–289.
- Appanah, S. & Putz, F.E. (1984) Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester*, **47**, 335–342.
- Barker, M.G. & Pérez-Salícup, 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.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretical Approach*, 2nd edn. Springer-Verlag, New York.
- Campanello, P.I., Villagra, M., Garibaldi, J.F., Ritter, L.J., Araujo, J.J. & Goldstein, G. (2012) Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. *Forest Ecology and Management*, **284**, 213–221.
- Cardó, A.A. (2000) *Manejando Bien Tu Castañal*. Asociación para la Conservación de la Cuenca Amazónica (ACCA), Puerto Maldonado, Peru.
- 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.
- Condon, M.A., Sasek, T.W. & Strain, B.R. (1992) Allocation patterns in two tropical vines in response to increased atmospheric CO₂. *Functional Ecology*, **6**, 680–685.
- DeWalt, S.J., Schnitzer, S.A. & Denslow, J.S. (2000) Density and diversity of lianas along a seasonal tropical forest chronosequence in central Panama. *Journal of Tropical Ecology*, **16**, 1–19.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H. & Forseth, I.N. (1993) Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *American Journal of Botany*, **80**, 244–252.
- Diniz, T.D.de.A.S. & Bastos, T.X. (1974) *Contribuição ao conhecimento do clima típico da castanha do Brasil*. Boletim Técnico, **64**, pp. 59–71. Instituto de Pesquisas e Experimentação Agropecuárias do Norte. Brazilian Agricultural Research Corp. (Embrapa).
- Duchelle, A.E., Kainer, K.A. & Wadt, L.H.O. (2014) Is certification associated with better forest management and socioeconomic benefits? A comparative analysis of three certification schemes applied to Brazil nuts in Western Amazonia. *Society & Natural Resources*, **27**, 121–139.
- Duchelle, A.E., Cronkleton, P., Kainer, K.A., Guanacoma, G. & Gezan, S. (2011) Resource theft in tropical forest communities: Implications for non-timber management, livelihoods, and conservation. *Ecology and Society*, **16**. [online] URL: <http://www.ecologyandsociety.org/vol16/iss1/art4/>.
- Emmons, L.H. & Gentry, A.H. (1983) Tropical forest structure and the distribution of gliding and prehensile tailed vertebrates. *The American Naturalist*, **121**, 513–524.
- Fox, J.E.D. (1968) Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *Malaysian Forester*, **31**, 326–347.
- FUNTAC (Fundação de Tecnologia do Estado do Acre) (2008) *Atlas do Estado do Acre*. FUNTAC, Rio Branco, Acre, Brazil.
- 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.
- Gerwing, J.J. (2001) Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *Journal of Applied Ecology*, **38**, 1264–1276.
- Gerwing, J.J. & Vidal, E. (2002) Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonian forest. *Conservation Biology*, **16**, 544–548.
- 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.
- Hegarty, E.E. & Caballé, G. (1991) Distribution and abundance of vines in forest communities. *The Biology of Vines* (eds F.E. Putz & H.A. Mooney), pp. 313–335. Cambridge University Press, Cambridge.
- van der Heijden, G.M.F. & Phillips, O.L. (2008) What controls liana success in Neotropical forests? *Global Ecology and Biogeography*, **17**, 372–383.
- Ingwell, L.L., Wright, S.J., Becklund, K.K., Hubbell, S.P. & Schnitzer, S.A. (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology*, **98**, 879–887.
- Kainer, K.A., Wadt, L.H.O. & Staudhammer, C.L. (2007) Explaining variation in Brazil nut fruit production. *Forest Ecology and Management*, **250**, 244–255.
- Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D.A.P. & Capanu, M. (2006) Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology*, **22**, 147–154.
- Laurance, W.F., Pérez-Salícup, D., Delamônica, P., Fearnside, P.M., D'Ángelo, S., Jerzowski, A., Pohl, L. & Lovejoy, T. (2001) Rain forest fragmentation and the structure of the Amazonian liana communities. *Ecology*, **32**, 105–116.
- Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M.F. & Nepstad, D. (2011) The 2010 Amazon drought. *Science*, **331**, 554.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. (2006) *SAS for Mixed Models*, 2nd edn. SAS Institute Inc., Cary, North Carolina.
- Maués, M.M. (2002) Reproductive phenology and pollination of the Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. Lecythidaceae) in Eastern Amazonia. *Pollinating Bees: The Conservation Link Between Agriculture and Nature* (eds P. Kevan & V.L. Imperatriz Fonseca), pp. 245–254. Ministry of the Environment, Brasília, Brazil.
- Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J. & Wright, S.J. (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia*, **121**, 293–301.
- Nabe-Nielsen, J., Kollmann, J. & Peña-Claros, M. (2009) Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *Forest Ecology and Management*, **257**, 987–993.
- Paul, G.S. & Yavitt, J.B. (2011) Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. *Botanical Review*, **77**, 11–30.
- Peres, C.A. & Baider, C. (1997) Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in south-eastern Amazonia. *Journal of Tropical Ecology*, **13**, 595–616.
- Pérez-Salícup, 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-Salícup, D.R., Guzmán, R., Licona, J.C., Ledezma, F., Pinard, M.A. & Putz, F.E. (2001) Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia. *Biotropica*, **33**, 324–329.
- Phillips, O.L., Vásquez Martínez, R., 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.
- Prance, G.T. (1990) *Bertholletia. Lecythidaceae-Part II: The Zygomorphic-flowered New World Genera* (eds S.A. Mori & G.T. Prance), pp. 114–118. New York Botanical Garden, Bronx, New York.
- 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. (1984) How trees avoid and shed lianas. *Biotropica*, **16**, 19–23.
- Schabenberger, O. & Pierce, F.J. (2001) *Contemporary Statistical Models for the Plant and Soil Sciences*. CRC Press, Boca Raton, Florida.
- Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology & Evolution*, **17**, 223–230.
- Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters*, **14**, 397–406.
- 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., Kuzee, M.E. & Bongers, F. (2005) Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, **93**, 115–1125.

- SEMA (Secretaria de Estado de Meio Ambiente do Governo do Estado do Acre). (2010) *Diagnóstico socioeconômico e cadastro da Reserva Extrativista Chico Mendes – Plano Resex sustentável*. ICMBIO, Rio Branco, Brazil.
- Staudhammer, C.L., Wadt, L.H.O. & Kainer, K.A. (2013) Tradeoffs in basal area growth and reproduction shift over the lifetime of a long-lived tropical species. *Oecologia*, **173**, 45–57.
- Stevens, G.C. (1987) Lianas as structural parasites: the *Bursera simaruba* example. *Ecology*, **68**, 77–81.
- Tyree, M.T. & Ewers, F.W. (1996) Hydraulic architecture of woody tropical plants. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 217–243. Chapman & Hall, New York.
- UN Comtrade (United Nations Commodity Trade Statistics Database) (2010) UN Comtrade Commodities page <http://comtrade.un.org/>. Accessed 1 May 2013.
- Vidal, E., Johns, J., Gerwing, J.J., Barreto, P. & Uhl, C. (1997) Vine management for reduced-impact logging in eastern Amazonia. *Forest Ecology and Management*, **98**, 105–114.
- Vieira, S., Trumbore, S., Camargo, P.B., Selhorst, D., Chambers, J.Q. & Higuchi, N. (2005) Slow growth rates of Amazonian trees: consequences for carbon cycling. *Proceedings of the National Academy of Sciences*, **102**, 18502–18507.
- Wadt, L.H.O. & Kainer, K.A. (2012) Domestication and breeding of the Brazil nut tree. *Domestication and breeding: Amazonian species* (eds A. Borém, M.T.G. Lopes, C. Clement & H. Noda), pp 297–317. Universidade Federal de Viçosa, Minas Gerais, Brazil.
- Wadt, L.H.O., Kainer, K.A. & Gomes-Silva, D.A.P. (2005) Population structure and nut yield of a *Bertholletia excelsa* stand in Southwestern Amazonia. *Forest Ecology and Management*, **211**, 371–384.
- Wadt, L.H.O., Kainer, K.A., Cartaxo, C., Nunes, G.M., Leite, F.M., Souza, J.M., Gomes-Silva, D.A.P. & Sousa, M.M. (2005) *Manejo da castanha (Bertholletia excelsa) para produção de Castanha-do-Brasil*. Documento Técnico - Seprof 03. Governo do Estado do Acre, Rio Branco, Brazil.
- ZEE (Zoneamento Ecológico-Econômico do Acre), (2000) *Recursos Naturais e Meio Ambiente*. Vol. I. Secretaria de Estado de Ciência, Tecnologia e Meio Ambiente, Rio Branco, Acre, Brazil.

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