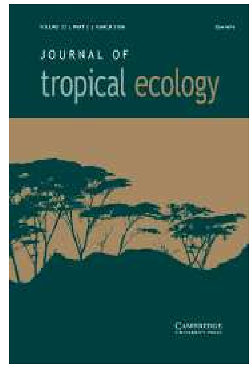

Liana loads and their association with Bertholletia excelsa fruit and nut production, diameter growth and crown attributes

Karen A. Kainer, Lúcia H. O. Wadt, Daisy A. P. Gomes-Silva and Marinela Capanu

Journal of Tropical Ecology / Volume 22 / Issue 02 / March 2006, pp 147 - 154
DOI: 10.1017/S0266467405002981, Published online: 01 February 2006

Journal of Tropical Ecology (2006) **22**:147–154. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467405002981 Printed in the United Kingdom

Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes

Karen A. Kainer*†[1], Lúcia H. O. Wadt‡, Daisy A. P. Gomes-Silva§ and Marinela Capanu#

* School of Forest Resources and Conservation (SFRC), University of Florida, Gainesville, FL 32611, USA
† Tropical Conservation and Development Program, Center for Latin American Studies, University of Florida, Gainesville, FL 32611, USA
‡ Centro de Pesquisa Agroflorestal do Acre (Embrapa Acre), Caixa Postal 321, Rio Branco, Acre, Brazil 69908-970
§ Fellow, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Rio Branco, Acre, Brazil
# Department of Statistics, University of Florida, Gainesville, FL 32611, USA
(*Accepted 1 August 2005*)

Abstract: We investigated the association between lianas and *Bertholletia excelsa* (Brazil nut), a long-lived, emergent tree of significant ecological and economic importance in Amazonia. Our objectives were: (1) to determine the relationship between crown liana load and liana number, basal area, and origin in relation to the *B. excelsa* host; and (2) to determine the relationship between liana load and *B. excelsa* fruit and nut production, diameter growth, and crown form, position and area. One hundred and forty trees (≥ 50 cm dbh) were selected with representatives of 10 diameter classes and four liana load categories. To quantify fruit and nut production, fruit counts and nut fresh weights per tree were measured in 2002 and 2003, and annual diameter growth was quantified using dendrometer bands. Trees with lianas produced significantly fewer fruits and had reduced nut fresh weights than liana-free trees. Trees with the most extensive liana loads (> 75% crown coverage) were 10.2 times more likely to have crown forms categorized as less than half-crowns or few branches than trees with reduced liana loads. No statistically significant relationship was found between liana load and tree diameter growth. Results suggest that liana cutting might increase *B. excelsa* fecundity and commercial nut yields.

Key Words: Amazon, Brazil nut, competition, non-timber forest products, tropical forest, vines

INTRODUCTION

Lianas are abundant in almost all tropical forests (Gentry 1991) and require structural support from a host tree for their long-term survival. Using a variety of climbing strategies, these woody vines exploit trees to access potentially scarce light resources (Hegarty 1991, Putz 1984a, Schnitzer & Bongers 2002). Lianas are important in maintaining tropical forest structure (Putz & Mooney 1991), contribute significantly to the overall density and diversity of tropical forests (Gentry & Dodson 1987, Schnitzer & Carson 2001), and are responsible for a large portion of forest transpiration and carbon sequestration (Schnitzer & Bongers 2002).

For the host, lianas often have a negative impact on tree growth (Clark & Clark 1990, Dillenburg *et al*. 1993, Pérez-Salicrup & Barker 2000), regeneration (Grauel & Putz 2004) and fecundity (Stevens 1987). While these studies emphasize above-ground competitive processes (with the exception of Dillenburg *et al*. 1993 and Pérez-Salicrup & Barker 2000), Schnitzer & Bongers (2002) comment that below-ground competition may be critically important and merits greater study. There is also a growing body of literature that focuses on evaluating the effects of liana cutting as a silvicultural treatment for improving timber management (Alvira *et al*. 2004, Gerwing 2001, Grauel & Putz 2004, Putz 1984b), recognizing the negative economic impacts of liana-tree associations.

The association between lianas and the Brazil nut tree *Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae) may also have economic impacts given the high commercial value of Brazil nuts. Long-lived canopy dominants, such as *B. excelsa*, are more commonly infested by lianas than shorter-lived species found in the lower forest strata (Clark & Clark 1990). As lianas seek light and establish themselves in the crowns of these emergents, the resulting competition is likely to reduce *B. excelsa* fecundity and

[1]Corresponding author, at SFRC. Email: kkainer@latam.ufl.edu

lower commercial Brazil nut yields. In addition, traditional ecological knowledge expressed by local extractivists corroborates this hypothesis, and some extractivists maintain their trees liana-free. Still, this assumed relationship has not been commonly quantified, nor has the broader Brazil nut–liana relationship been described.

We investigated the association between *B. excelsa* and crown liana loads in a relatively pristine, unlogged forest located in Extractive Reserve Chico Mendes in the Western Brazilian Amazon. Our objectives were twofold: (1) to determine the relationship between crown liana load and liana number, basal area, and origin in relation to the *B. excelsa* host; and (2) to determine the relationship between crown liana load and *B. excelsa* fruit and nut production, diameter growth, and crown form, position and area. In accordance with extractivist experience and the one known study that quantified negative impacts of vines on tree fecundity (Stevens 1987), we hypothesize that Brazil nut trees with heavy liana loads produce fewer fruits and nuts than those free or relatively free of lianas. We also expect *B. excelsa* trees with heavy liana loads to demonstrate slower growth, poorer crown form, and reduced crown area than their liana-free neighbours.

STUDY SPECIES

Bertholletia excelsa is distributed throughout much of the *terra firme* forests in the Amazon basin. Individual trees may or may not be totally deciduous, with floral buds emerging on axillary spikes at the apex of recent leaf flushes produced toward the end of the dry season (Maués 2002, Mori & Prance 1990). Fruits reach maturity 14 mo after successful pollination, resulting in a hard, large round fruit (10–16 cm) that falls during the rainy season (January and February in our study region). The 8–26 large (∼3.5–5 × 2 cm) seeds remain inside this woody fruit until extraction by humans or other seed predators/dispersers, notably agoutis (*Dasyprocta* spp.). Individual trees show considerable year-to-year variation in fruit production, though production of the entire population is fairly constant between years (Zuidema 2003).

STUDY SITE

Field studies were carried out within Extractive Reserve (RESEX) Chico Mendes, a conservation unit located 10–11° south of the equator within the eastern portion of the state of Acre, Brazil. The study region has gently undulating topography, and the dominant vegetation is classified as humid, moist tropical forests (Holdridge 1978), with a pronounced 3-mo dry season from June to August. Annual rainfall in the region ranges from 1600–2000 mm, 95% of which falls between September and May (IMAC 1991). Average temperature is approximately 25°C (ZEE 2000), and brief intrusions of frigid air from the south are common during the dry season, with temperatures frequently dropping to 12°C. Soils of the region are classified under the Brazilian system as Argissolos (ZEE 2000), roughly equivalent to Ultisols under the U.S. Soil Taxonomy system.

Within RESEX Chico Mendes, research was conducted at a 420-ha extractivist landholding (*colocação*) in the south-eastern portion of the reserve – Colocação Rio de Janeiro in Seringal Filipinas. A previous inventory of 568 *B. excelsa* trees ≥ 10 cm dbh in this study area revealed a population density of 1.35 trees ha^{-1}, average tree diameters of 86.1 ± 45.0 cm (ranging from 10.0–207.0 cm dbh), with almost all Brazil nut tree crown positions scored as dominant or co-dominant (Wadt *et al.* 2005). Critical for the current study, 39% of the reproductively mature adults (≥ 50 cm dbh) had no lianas, 32% had few lianas (≤ 25% crown covered), 20% had moderate to heavy liana loads (25–75% crown covered), and 10% had very heavy vine loads (> 75% crown covered) (Wadt *et al.* 2005).

METHODS

Field measurements

From the previous inventory, 140 of 404 reproductively mature *B. excelsa* adults (≥ 50 cm dbh) were selected for study. To obtain a representative sample of both tree diameters and liana loads, all 404 trees were initially placed into diameter classes. Study trees were then randomly selected to include representatives within each diameter class and four crown liana load categories, previously determined as follows: (1) no lianas in crown; (2) ≤ 25% crown covered; (3) 25–75% crown covered; and (4) > 75% crown covered. Finally, based on GPS points collected in the field, the geospatial location of the 140 selected trees was plotted, confirming fairly representative spatial distribution of the sample across the study landscape.

Liana parameters. To further explore liana loads on each of the 140 trees, liana number, basal area, origin in relation to the Brazil nut host, and family-level taxonomy were assessed. Liana origin was determined by establishing concentric radii at distances of 5, 10, 15 and 20 m from the trunk of each of the 140 trees, assigning each liana to its corresponding ring. In a few cases, it was difficult to determine whether lianas were genetically separate individuals since multiple liana stem segments (ramets) often rooted to the ground. Following Putz (1984c) and Schnitzer & Carson (2001), we considered any liana that had established roots to be a separate individual. Liana stem circumference was measured at the base of the vine, followed by calculation of basal area. Finally, specimens for all species encountered were identified to family by local field identification specialists (*mateiros*) from the herbarium at the Federal University of Acre (UFAC) and Embrapa Acre (Brazilian Agricultural Research Institute).

Tree parameters. Fruit and nut production of the 140 trees were determined in February 2002 and 2003, following fruit fall. Fruit production was quantified as the number of fruits collected and counted at that time. Total fresh weight of nuts was estimated from these fruits (or a subsample if number of fruits > 50), quantifying nut production. We considered nut fresh weights to be a better indicator of the commercial value of production given its common usage, while number of fruits is independent of moisture content, providing a more robust ecological indicator of fecundity.

To monitor tree diameter growth, dendrometer bands were installed in November 2001 on a subsample of 60 trees that represented the various diameter classes and liana loads. After allowing 3 mo for band adjustment, diameter growth was determined for two consecutive 12-mo periods, beginning in February 2002.

Crown attributes (form, relative canopy position, and cross-sectional area) of each of the 140 trees were assessed. To evaluate crown form, trees were placed into one of five categories (Synnott 1979): (1) complete circle, (2) irregular circle, (3) half-crown, (4) less than half-crown and (5) one or a few branches. Based on a modified Dawkins illumination index cited in Synnott (1979), crown position of each tree was categorized into one of the following: (1) dominant (full overhead and side light); (2) co-dominant (full overhead light), (3) intermediate (some overhead or side light); and (4) suppressed (no direct light). Crown cross-sectional area of each tree was determined by measuring maximum crown diameter and a second diameter at right angles to the axis of the maximum, followed by application of an ellipsoid formula.

Data analysis

Liana load was analysed as a univariate response variable. Multiple models were explored with various predictors and combinations thereof tested as explanatory variables (i.e. liana numbers, liana basal areas, and liana origins from the four radii). Since the crown liana load is an ordinal categorical variable, model testing was conducted using an ordinal multinomial model (Proc Genmod, using SAS code).

To analyse the fruit and nut production variables, we fitted log-linear models with negative binomial distributions (Proc Genmod). Fruit and nut production means by liana load were compared after adjusting for Type I errors using the Bonferroni method.

A mean annual growth variable was created to analyse diameter growth. It was square-root transformed to attain normality and analysed using a linear model (Proc GLM). For both production and the growth response variable, univariate linear models were tested using various predictors, including tree dbh, liana load, and crown position, form and area, and combinations thereof, and model validity was consistently checked through residual analysis. The residual plots suggested a quadratic relationship between mean fruit and nut production and diameter growth. We therefore introduced dbh^2 into the models, and since this variable showed a significant effect, it was retained in the analyses. In some analyses, the crown form variable was collapsed into three categories since using the original five resulted in very large standard errors. Specifically, the two categories reflecting complete and irregular circles were combined, and the two categories reflecting all trees with less than half-crowns were combined.

We analysed the association between crown vine load and crown form using an ordinal multinomial model (Proc Genmod) that incorporated the ordinal nature of the crown form response. For all statistical tests, we considered a P-value < 0.05 to be statistically significant, and the final models presented reflect only those predictors and combinations that were statistically significant at P < 0.05. All statistical analyses were accomplished with SAS, Version 8.2 (SAS Institute, Inc., Cary, North Carolina).

RESULTS

Liana loads and vine parameters

In independent univariate analyses, liana loads were explained by both number of lianas (P < 0.0001) and liana basal area (P < 0.0001) (Table 1). Ninety percent of the associated lianas originated within 10 m of the trees (Figure 1). Correspondingly, statistical analyses based on four concentric rings established at distances of 5, 10, 15 and 20 m from the trunk of each of the 140 trees, revealed that liana loads were best explained by

Table 1. Mean number of lianas and liana basal area (m^2) per Brazil nut tree for each liana load class. Mean values are reported with SE.

Liana load (% crown covered)	N	Number of lianas per tree (x ± SE)	Basal area (m^2) of lianas per tree (x ± SE)
0	23	–	–
≤ 25	58	2.16 ± 0.18	0.0112 ± 0.0014
25–75	37	4.14 ± 0.50	0.0283 ± 0.0038
> 75	20	8.80 ± 1.64	0.0522 ± 0.0109
Total	138	3.30 ± 0.36	0.0199 ± 0.0024

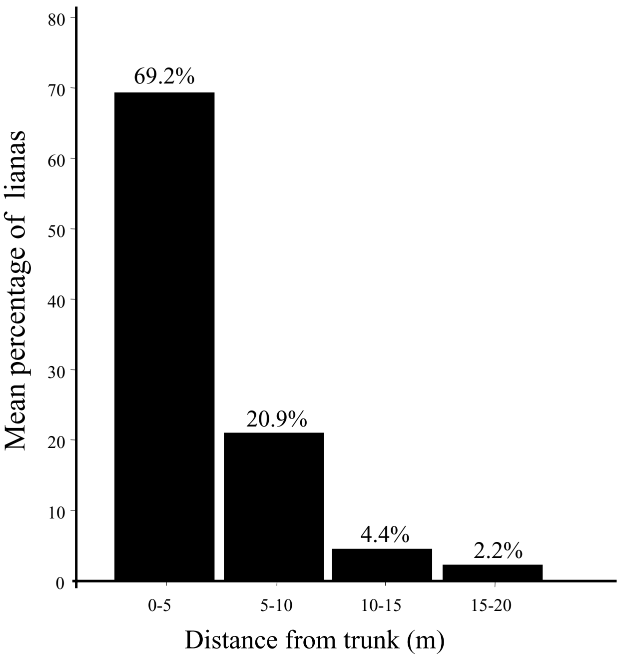

Figure 1. Mean percentage of lianas reaching *Bertholletia excelsa* crowns, originating at different distances from the host trunk.

Table 2. Best-fit log-linear model of the two production variables, *Bertholletia excelsa* fruit counts and nut fresh weight, showing the four predictors that proved statistically significant.

		Fruit counts		Nut fresh weight	
Source	Df	χ^2	P	χ^2	P
liana load	3	11.9	0.0078	12.3	0.0063
dbh	1	12.8	0.0003	12.2	0.0005
dbh × dbh	1	8.9	0.0029	8.1	0.0044
crown form	2	25.5	< 0.0001	27.6	< 0.0001

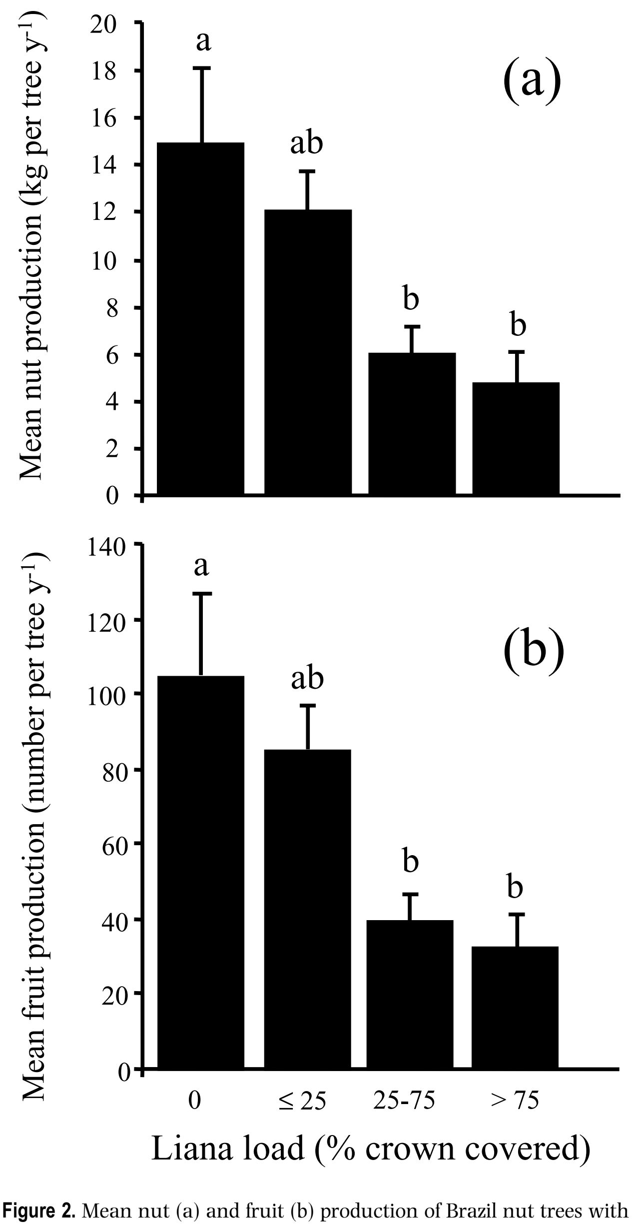

Figure 2. Mean nut (a) and fruit (b) production of Brazil nut trees with four different crown liana loads: (1) No lianas, n = 23; (2) ≤ 25% crown covered, n = 58; (3) 25–75% crown covered, n = 37; and (4) > 75% crown covered, n = 20. Letters indicate statistically significant differences at $P < 0.05$.

the number of lianas originating from the first and second rings ($P < 0.0001$), although liana numbers in the third ring were also significant ($P < 0.05$). Liana basal area results were similar, with first and second rings highly significant ($P < 0.0001$), and the third also significant ($P < 0.05$).

The average number and average basal area of lianas per Brazil nut tree was 3.3 ± 0.36 (range = 0–26) and 0.0199 ± 0.0024 m^2 (range = 0–0.2144 m^2), respectively. Of the 456 lianas observed, 439 were identified to family. While 24 different families were represented, almost half of the lianas were Bignoniaceae, and the majority of the other half represented by Caesalpiniaceae, Fabaceae, Combretaceae, Malpighiaceae, Menispermaceae and Dilleniaceae.

Liana loads and tree parameters

Fruit and nut production. For the entire Brazil nut population of 140 trees, the mean number of fruits collected per tree was 65.5 ± 7.3 and 72.0 ± 8.6 in 2002 and 2003, respectively. Mean nut production (nut fresh weights) was 9.70 ± 1.10 and 10.07 ± 1.18 kg per tree in 2002 and 2003, respectively. Variation between years was not statistically significant for either mean fruit or mean nut production ($P = 0.57$ and $P = 0.82$, respectively).

There were significant differences in fruit and nut production among Brazil nut trees, and this variation was explained by several variables (Table 2), including liana load (Figure 2). Comparison of the Bonferroni-adjusted least-square means revealed that trees with lianas produced significantly fewer fruits and less nut weights than trees free of lianas (Figure 2).

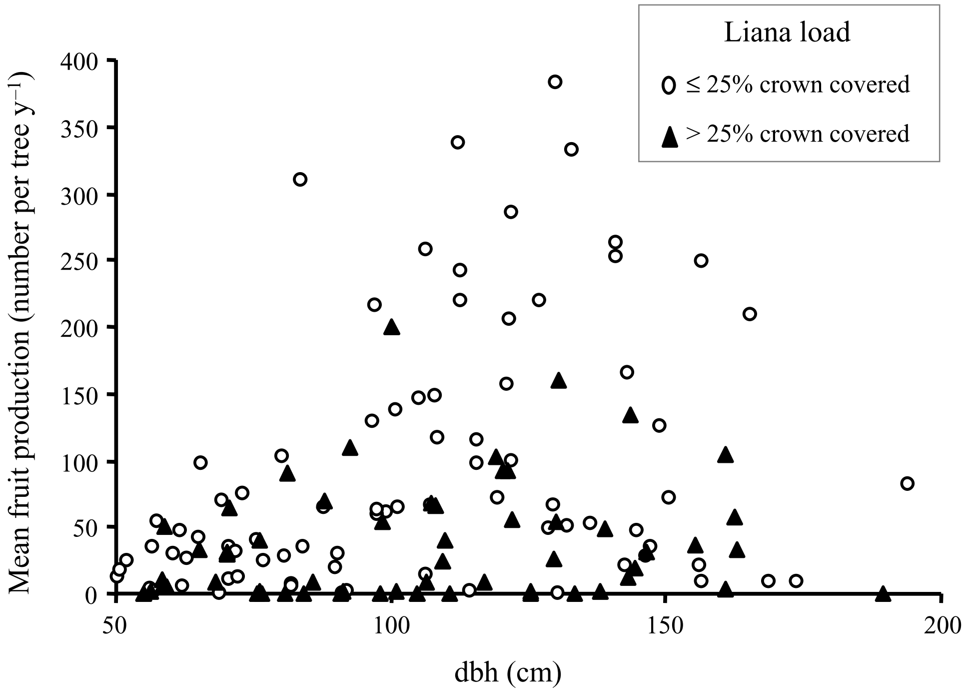

Figure 3. Mean number of fruits produced annually by *Bertholletia excelsa* trees at varying diameters, bearing different liana loads.

Table 3. Chi-square statistics and P-values of the Bonferroni-adjusted least-square means comparisons of the association between *Bertholletia excelsa* crown form and fruit and nut production. Statistics for nut results are in parentheses.

		Half-crown		Less than half-crown/Few branches	
Crown form	Complete/Irregular circle	χ^2	P	χ^2	P
Complete/Irregular circle	–	8.7 (10.8)	0.0186 (0.0066)	32.6 (25.4)	< 0.0001 (< 0.0001)
Half-crown				17.1 (13.7)	< 0.001 (0.0012)

A pattern of tree dbh and liana load effects on fruit production also emerged with trees peaking in production at approximately 125 cm dbh (Figure 3). Mean annual nut production in relation to tree dbh and liana load followed a similar pattern. A separate statistical analysis revealed that there was no significant correlation between dbh and liana load ($P = 0.08$).

In addition to liana load and dbh, the variation in production was also explained by crown form, which was the only crown variable measured that was statistically significant and therefore retained in the final model (Table 2). Comparisons of the Bonferroni-adjusted least-square means indicated that those trees with crown forms categorized as either complete or irregular circles produced significantly more fruits and nuts than trees with crown forms categorized as half-crowns, less than half-crowns or supporting few branches (Table 3). Least-squares mean comparisons also revealed that even trees with half-crowns were superior fruit and nut producers to those with less than half-crowns or only a few branches (Table 3)

Table 4. Annual diameter growth of *Bertholletia excelsa* by liana load.

Liana load (% crown covered)	Diameter growth (cm y^{-1}) N	Diameter growth (cm y^{-1}) x ± SE
No liana	19	0.43 ± 0.05
≤ 25	17	0.27 ± 0.07
25–75	9	0.33 ± 0.07
> 75	6	0.35 ± 0.12

Diameter growth. The impact of liana load on tree diameter growth was not as clear cut. Liana load showed no significant effect on diameter growth when all four liana load categories were included in the model ($P = 0.10$). In addition, those trees with no lianas present in the crown and those with the most (> 75% of the crown covered) demonstrated the best growth rates (Table 4). Because

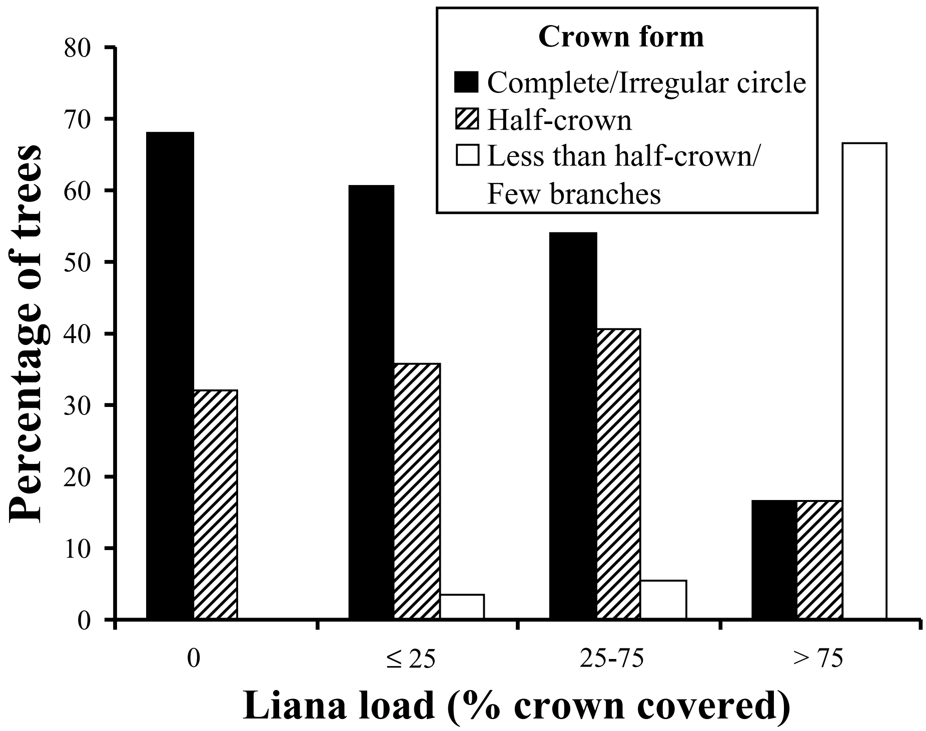

Figure 4. Percentage of *Bertholletia excelsa* trees with three kinds of crown forms within each of four liana load categories.

we had few trees with more than 25% of their crowns covered in lianas, we then collapsed the liana load data into two categories: with lianas and without lianas, and reran the model. Results of this analysis suggested that the presence of lianas in tree crowns might decrease diameter growth ($P = 0.06$).

Crown variables. Liana loads in Brazil nut tree crowns explained crown form variance ($P < 0.001$). Based on subsequent contrasts tested, trees with the most extensive liana loads (> 75%) were 10.2 times more likely to have crown forms categorized as less than half-crowns or few branches (versus half-crowns, irregular or complete circles) than trees with reduced liana loads (Figure 4) ($P < 0.001$). Liana load did not explain crown area variance ($P = 0.24$).

DISCUSSION

We tested the hypothesis that *Bertholletia excelsa* trees with heavy liana loads produce fewer fruits and nuts than those free or relatively free of lianas. Our results demonstrate that liana presence is associated with reduced Brazil nut fruit counts and diminished commercial nut production. Trees with crowns that were liana-free produced approximately three times more fruits than those with crowns more than 75% covered in lianas. During the 2-y timeframe of this study, only 12 of the 140 trees monitored failed to fruit in both 2002 and 2003, and 9 of those 12 had crown liana loads greater than 25%. To our knowledge, only Stevens (1987), in his landmark study of *Bursera simaruba* in Costa Rica, has previously demonstrated that liana-infested trees produce fewer fruits than those that are liana-free.

What are the mechanisms by which lianas reduce fruit counts? Stevens (1987) suggests that lianas impact host canopies by constricting growing twigs and branches and reducing fecundity. Clark & Clark (1990) add that lianas potentially affect tree growth and survival by reducing host leaf area. In our observations, the foliage of lianas invades the *B. excelsa* crown, covering leaves and branches to varying degrees. Once established, the liana competitors significantly reduce light availability to tree leaves (Grauel & Putz 2004) and in Brazil nut, can inhibit new leaf and inflorescence development that occurs at the onset of the rainy season. In those crown regions where liana loads are particularly heavy, tree leaf area and therefore transpiration can be greatly reduced, such that water and nutrient transport to that crown segment is limited. Secondary and primary branches may then break, resulting in crown deformation.

We found that liana loads are negatively correlated with *B. excelsa* crown form (Figure 4), perhaps through the process described above. Alvira *et al.* (2004) report similar results in their liana study of 80 commercial timber trees in Bolivian dry forests. We also expected Brazil nut trees with heavy liana loads to have smaller crowns than their liana-free conspecifics, assuming that branch breaking would account for a reduction in crown area. Our results did not support this hypothesis, and Alvira *et al.* (2004) report a very weak negative correlation ($P = 0.07$) between crown area and liana load. One possible explanation for this unexpected result is that when branches of liana-laden crowns break, lianas fall with them, and our snap-shot observations do not reflect this dynamic. By the time we quantified crown area and liana loads of heavily infested trees, some had likely already rid themselves of lianas and reduced their crowns, such that small crowns correlated with few lianas, confounding statistical results. One might conclude that in mature trees, crown form is a better indicator of historical liana-tree relations than crown area. Our data also linked crown form with fruit and nut production, demonstrating that Brazil nut trees with crown forms categorized as either complete or irregular circles were superior producers.

We expected to find a negative correlation between liana loads and *B. excelsa* diameter growth. Liana cutting experiments have consistently demonstrated that liberated trees outgrow control trees (Alvira *et al.* 2004, Gerwing 2001, Grauel & Putz 2004, Pérez-Salicrup & Barker 2000) and Vidal *et al.* (2002) reported statistical differences between trees growing with and without vines in the crown. In addition, Clark & Clark (1990) contrasted annual diameter growth with crown liana loads of five emergent tropical species across a spectrum of diameter classes. For three of these species, they reported that liana loads were strongly negatively correlated with diameter growth. In our study, we found only weak evidence that large ($\geq$ 50 cm dbh) Brazil nut trees without lianas may have better diameter growth than those with.

Liana parameters measured (number, basal area, origin and crown liana load) were independent of Brazil nut tree dbh, suggesting that tree diameter, and perhaps age, has no bearing on the lianas supported by any particular individual. While Clark & Clark (1990) found a positive correlation between diameter and liana load when analysing their Costa Rican data set on trees 10–70 cm dbh, they also reported that almost all trees in the 10–30 cm dbh class were liana-free. Our findings presented herein are based solely on larger reproductively mature trees ($\geq$ 50 cm dbh). A previous analysis of the larger population from which this 140-tree subset was derived included trees between 10 and 50 cm dbh, and demonstrated a significant positive correlation between crown liana load and dbh (Wadt *et al.* 2005).

In sum, our data suggest a process whereby lianas reduce crown area of the *B. excelsa* host, increasing breakage of small and large Brazil nut branches, ultimately resulting in quantifiably negative changes in crown form of individual trees. Lianas may also directly retard development of new Brazil nut leaves and inflorescences, though we did not research this possibility. Our data demonstrate that liana presence in the host crown dramatically reduces *B. excelsa* fruit and nut production, suggesting that the cutting of lianas associated with *B. excelsa* trees might increase fruit counts and commercial Brazil nut yields.

ACKNOWLEDGEMENTS

This research was supported by grants from FINEP/MCT/CNPq in Brazil, The William and Flora Hewlett Foundation in the USA, and the International Science Foundation Stockholm, Sweden through a grant to Dr Wadt. Embrapa Acre and the University of Florida's School of Forest Resources and Conservation and the Center for Latin American Studies wholly supported this research, and CNPT/IBAMA in Brazil gave permission to conduct the research in RESEX Chico Mendes. We also thank Paulo Rodrigues de Carvalho for his excellent assistance in the field. Our thanks to two anonymous reviewers and Edson Vidal, Jack Putz and Stefan Schnitzer who provided helpful comments on earlier drafts of the manuscript. Finally, we are most grateful to Valderi and Maria Alzenira for so graciously sharing their home and extractivist insights.

LITERATURE CITED

ALVIRA, D., PUTZ, F. E. & FREDERICKSEN, T. S. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolívia. *Forest Ecology and Management* 190:73–86.

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.

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.

GENTRY, A. H. 1991. The distribution and evolution of climbing plants. Pp. 3–52 in Putz, F. E. & Mooney, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

GENTRY, A. H. & DODSON, C. 1987. Contribution of non-trees to species richness of tropical rain forest. *Biotropica* 19:149–156.

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.

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. 1991. Vine-host interactions. Pp. 357–374 in Putz, F. E. & Mooney, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

HOLDRIDGE, L.R. 1978. *Ecología basada en zonas de vida*. Instituto Interamericano de Ciencias Agrícolas, San José, Costa Rica.

IMAC – INSTITUTO DE MEIO AMBIENTE DO ACRE. 1991. *Atlas geográfico ambiental do Acre*. IMAC, Rio Branco, Acre, Brazil.

MAUÉS, M. M. 2002. Reproductive phenology and pollination of the Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. Lecythidaceae) in Eastern Amazonia. Pp. 245–254 in Kevan, P. & Imperatriz Fonseca, V. L. (eds.). *Pollinating bees – the conservation link between agriculture and nature*. Ministry of the Environment, Brasilia.

MORI, S. A. & PRANCE, G. T. 1990. Taxonomy, ecology, and economic botany of the Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.: Lecythidaceae). *Advances in Economic Botany* 8:130–150.

PÉREZ-SALICRUP, D. & 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.

PUTZ, F. E. 1984a. How trees avoid and shed lianas. *Biotropica* 16:19–23.

PUTZ, F. E. 1984b. Effects of post-felling silvicultural treatments on woody vines in Sarawak. *Malaysian Forester* 47:214–226.

PUTZ, F. E. 1984c. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.

PUTZ, F. E. & MOONEY, H. A. (eds.). 1991. *The biology of vines*. Cambridge University Press, Cambridge. 526 pp.

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. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.

STEVENS, G. C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68:77–81.

SYNNOTT, T. J. 1979. *A manual of permanent sample plot procedures for tropical rainforests*. Tropical Forestry Papers No. 14. Commonwealth Forestry Institute, University of Oxford, Oxford.

VIDAL, E., VIANA, V. & BATISTA, J. L. F. 2002. Crescimento de floresta tropical três anos após colheita de madeira com e sem manejo florestal na Amazônia oriental. *Scientia Forestalis* 61:133–143.

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.

ZEE – ZONEAMENTO ECOLÓGICO-ECONÔMICO DO ACRE. 2000. *Recursos Naturais e Meio Ambiente*, Volume I. Secretaria de Estado de Ciência, Tecnologia e Meio Ambiente, Rio Branco, Acre, Brazil.

ZUIDEMA, P. A. 2003. *Demography and management of the nut tree* (Bertholletia excelsa). PROMAB Scientific Series 6, PROMAB, Riberalta, Bolivia.