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Explaining variation in Brazil nut fruit production
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Abstract

Brazil nut is widely recognized as the cornerstone of the Amazonian extractive economy. Tight linkages between Brazil nut production, regional income, and intact mature forests have thrust this species into focus as a key component of Amazonian conservation and income generation strategies. Nonetheless, a comprehensive synthesis of factors explaining Brazil nut fruit production variation is lacking. We aimed to address this knowledge gap, asking: (1) What are the rates and annual variation of Bertholletia excelsa fruit production at individual and population levels? (2) What factors explain B. excelsa production variation, focusing on spatial and temporal variables, diameter at breast height (dbh), crown attributes, liana loads, and soil attributes? and (3) Does liana cutting affect fruit production?

Our model explained 73% of the variability in fruit production by 140 trees over 5 years. Dbh alone explained >50%, and trees in the middle diameter range (100 cm ≤ dbh ≤ 150 cm) produced best. Top-producing trees were loosely grouped spatially. Cation exchange capacity and P also explained production variation. The liana load variable was only weakly significant for explaining production variation, and there were no direct significant effects of liana cutting. Cutting, however, did improve crown forms—another highly significant model variable. This, coupled with a weakly significant interaction of liana cutting by year, suggests that liana cutting could improve production over time.

In any given year, approximately 25% of the trees produced 72% of the total population production. Annual variation of fruit production at the individual level was relatively high, and at the population level was extremely low, with annual production departing from average only in a year of delayed and reduced rainfall. These results coupled with low synchronicity of fruiting, confirm long-term observations of harvesters that Brazil nut populations exhibit relatively constant fruit production.

Results suggest that fruit productivity at the individual tree level could be increased, possibly through experimental liana cutting and/or P amendments. At the population level, Brazil nut collectors could potentially increase efficiency by concentrating collection efforts on consistently high producers and possible production “hotspots”.

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1. Introduction

Brazil nut (Bertholletia excelsa Humb. and Bonpl.) is widely recognized as the cornerstone species of the Amazonian extractive economy, and is the only internationally traded nut collected almost entirely from natural populations in mature forests (Clay, 1997). Historically, collection and processing have been centered in eastern Amazonia where it has been commercially exploited since the mid-1600s (de Souza, 1963). Over the last three decades, however, large-scale collection has shifted westward to the tri-border region of Brazil, Bolivia, and Peru (Peres et al., 2003) where commercial harvest and marketing represent a major income source for rural and peri-urban collectors and processors (Stoian, 2005). Because of this central importance of Brazil nut to the regional economy, household income shortfalls across this entire supply chain were attributed most frequently to insufficient Brazil nut production in any given locality or year (Stoian, 2005). This socioeconomic link between Brazil nut production and income can also have clear consequences for conservation as documented in Peru, where Brazil nut income alone was insufficient to thwart deforestation by small producers who concurrently participated in more environmentally destructive income-generating activities like cattle ranching and intensive
agriculture (Escobar and Aldana, 2003). Indeed, these tight linkages between Brazil nut production, regional income, and intact mature forests have thrust this species into focus as a key component of Amazonian conservation and income generation strategies (Clay, 1997; Ortiz, 2002). Nonetheless, a comprehensive synthesis of factors explaining Brazil nut fruit production variation is lacking. Indeed, there is a paucity of quantitative information on fruit production and sources of production variation of most tropical non-timber forest product (NTFP) fruits, nuts, and seeds of commercial interest. This is surprising given that NTFPs are considered an important component of developing country economies and tropical forest conservation strategies (Freese, 1997; Alexiades and Shanley, 2004). The main aim of our study is to address this knowledge gap in production variation using Brazil nut as a model species, while providing scientific insights to the larger ecological question of fruit production variation.

1.1. Fruit production variation

Variation in fruit and seed production in forest trees has been attributed to exogenous and endogenous factors. Climate is a major contributor to crop size variation, leading to a resource matching hypothesis that annual seed production patterns “match” annual rainfall distribution and/or some key seasonal temperature variable. Koenig and Knops (2000) reviewed 443 data sets of multiple northern hemisphere species within three families, and found that annual rainfall and temperature variation were important, and identified latitudinal patterns linked to climate. Kelly and Sork (2002) came to similar conclusions in their global analysis of 570 data sets. Seedfall variation of 108 tropical species — a forest type poorly represented in all previous analyses — corroborated these latitudinal patterns; while production variation was substantial for these tropical species, it was significantly smaller than for higher latitudes (Wright et al., 2005).

Nonetheless, most polycarpic woody plants adhere to alternating supra-annual schedules of low and high production years (Herrera et al., 1998; Koenig and Knops, 2000; Kelly and Sork, 2002). This provides strong evidence that rainfall and temperature, which are more normally distributed and much less variable than production (Koenig and Knops, 2000), are not the only determinants of fruit production variation. Disease, herbivory, or adverse weather such as high winds or storms, particularly during key phenological events such as pollination or fruit development, can reduce flowering or seed set (Stephenson, 1981). Liana presence has been shown to reduce fruit production of trees (Stevens, 1987; Kainer et al., 2006), and proximate disturbances such as fire also have been implicated (Layne and Abrahamson, 2004). Controlled experiments in monoculture orchards (Ponder and Jones, 2001), agroforestry systems (Jones et al., 1995), and natural forests (Vaughton, 1991) clearly demonstrate the importance of nutrient and light availability as explanatory variables of production variation.

Endogenous factors such as life cycle rhythms play a central role in fruiting. Reproduction is a function of accumulated resources, and is positively correlated to total tree height (Layne and Abrahamson, 2004) and diameter (Ares and Brauer, 2004). Successful reproduction in 1 year, however, is often followed (or “switched”) at the expense of vegetative growth (Harper and White, 1974; Kelly and Sork, 2002).

Fruiting variation has strong implications for fauna dependent on fruit and seed resources for their caloric and nutritional values. In general, woody plants produce more expensive fruits than herbaceous plants (Sutherland, 1986), and the expected return for this costly expenditure is dispersal. Scatterhoarding (burial of one or a few seeds at many widely scattered sites), a dispersal method typically restricted to trees producing large nutritious nuts (Jansen, 2003), has several advantages for the plant: facilitation of transportation away from the source plant, nut burial for seed protection and improved germination, and caching in microenvironments more favorable for seedling establishment (Vander Wall, 2001). In return, these cached food supplies are available to scatterhoarders for periods of scarcity, such as tropical dry seasons or temperate zone winters (Jansen, 2003). Cached seeds not reclaimed by scatterhoarders (e.g., forgotten or due to predator mortality) are well positioned for germination.

1.2. Management significance of production variation

For tree fruits with high economic value, maximum levels of fruiting and minimal annual variation can be central to commercial success. In these cases, plant breeding and selection programs, resource amendments (nutrients, water), and other controls to direct resource partitioning to fruits and minimize production variation are commonly practiced within domesticated populations (Acquaah, 2002). Very little research, however, has focused on understanding or manipulating fruit production of natural populations of species with commercial and/or subsistence import, such as Brazil nut and other NTFPs (Ticktin, 2004). For example, most Brazil nut collectors in our study region cut lianas, stating that this practice increases nut yield (personal observations, KK and LW), but to our knowledge, effects of liana cutting have not been quantified. Understanding demographic parameters, including fruit production, also is essential for fostering population persistence, and such ecological knowledge coupled with management interventions could enhance fruit production levels for meeting both economic and demographic goals. Such interventions advocated include: reducing localized resource competition, including measures such as liana cutting, tree girdling, and/or felling; enrichment planting; tending or favoring new recruits; alternating geographic areas of harvest; setting harvest quotas; and recruitment monitoring (Peters, 1996; Peres et al., 2003; Ticktin, 2004).

Using Brazil nut (Bertholletia excelsa Humb. and Bonpl.) as a model species, we aim to contribute to scientific understanding of fruit production variation and provide ecological information that could contribute to improved management of natural populations of commercially important NTFPs. Production variation of tropical species in general is poorly documented (Herrera et al., 1998; Kelly and Sork, 2002; although see Wright et al., 2005), and very few studies have
explored manipulation of natural populations for enhancing production. We focused on three research questions: (1) What are the rates and annual variation of *B. excelsa* fruit production at individual and population levels? (2) What factors explain *B. excelsa* production variation, focusing on spatial and temporal variables, diameter at breast height (dbh), crown attributes, liana loads, and soil attributes? and (3) Does liana cutting affect fruit production?

2. Study species

At maturity, *B. excelsa* is a very large, emergent tree. Adults can be long-lived, with three individuals >45 cm dbh radio-carbon-dated as older than 650 years (Vieira et al., 2005). 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 (Mori and Prance, 1990; Maue´s, 2002). Individuals rely on out-crossing for seed development (O’Malley et al., 1988), and are pollinated principally by large bodied bees, especially Euglossinae, capable of lifting the hood of the zygomorphic flower (Prance, 1976; Nelson et al., 1985). The hard, large round fruit (10–16 cm) reaches maturity 14 months after successful pollination, falling during the rainy season (January and February in our study region). The 8–26 large (~3.5–5 cm × 2 cm) seeds (or nuts) remain inside this woody fruit until extraction by humans or other seed predators/dispersers; agoutis (*Dasyprocta* spp.) are the almost exclusive scatterhoarding dispersers. The nut reward is a nutritious food source packed with 14–17% protein and 65–70% oil (Prance and Mori, 1979).

3. Study site

Research was conducted in Extractive Reserve (RESEX) Chico Mendes, a conservation unit 10–11° south of the equator in the eastern region of the state of Acre, Brazil. The area has gently undulating topography; a pronounced dry season, dropping temperatures to 12°C, and brief intrusions of frigid southern air are common during the dry season, dropping temperatures to 12°C. Soils are classified under the Brazilian system as Argissolos (ZEE, 2000) or red-yellow podzolics. In our study region, those soils under the Solimões geological formation are influenced by volcanic material, likely ashes, deposited during soil genesis by Andean winds (Gama et al., 1992). Thus, while aluminium and its associated acidity dominate other weathered Amazonian podzolic soils, Solimões podzolics tend to be relatively new soils with higher silt content, nutrient stocks, and cation exchange capacity (Gama et al., 1992).

Research efforts were concentrated in a 420-ha extractivist landholding (colocação) in the southeastern portion of the reserve (Colocação Rio de Janeiro in Seringal Filipinas) (see Wadt et al., 2005 for study site map). The resident family collects Brazil nuts annually, but like others in the region (Ortiz, 2002), would not likely harvest from trees that typically produce less than 20 fruits. A 2001–2002 inventory of 568 *B. excelsa* trees ≥10 cm dbh in this landholding revealed a population density of 1.35 trees ha⁻¹ and average diameters of 86.1 ± 45.0 cm dbh (Wadt et al., 2005).

4. Methods

Study trees were selected by initially placing all 404 reproductively mature *B. excelsa* adults (≥50 cm dbh) from the previous inventory into 10 diameter classes, and then randomly selecting 140 trees to include representatives within each diameter class and four liana load categories: (1) no lianas in crown, (2) lianas present, but ≤25% crown covered, (3) 25–75% crown covered, and (4) >75% crown covered. Selected trees were then revisited in the field to exclude individuals with overlapping crowns or fruit fall areas. Finally, the geospatial location of the 140 selected trees was determined through GPS and plotted, confirming fairly representative spatial distribution of the sample across the study landscape.

4.1. Fruit counts

Production was measured in the last 15 days of February, after fruit fall, for 5 consecutive years (2002–2006). Fruit production was quantified as the number of fruits harvested from the ground by the research team. These count values do not reflect 100% total counts of fruit production per tree. A small count error is attributed to the very few fruits remaining in the crowns at the time of fruit collection. Scatterhoarding *Dasyprocta* spp. and other minor seed predators, however, are a larger source of error since they open and/or remove fallen fruits prior to the late-February counts. We used two methods to estimate this count discrepancy.

In September 2004, a period after premature fruit abortion had occurred and deciduous *B. excelsa* individuals were leafless, we surveyed our 140-tree study population. We counted absolute numbers of fruits on trees in which crowns were entirely visible (a minority of all trees) and fruits were not too numerous to impede accurate counts (~100 fruits, N = 19). When comparing these absolute crown counts with subsequent on-the-ground harvest from the same trees, we found a strong correlation (r = 0.89) between crown and ground counts. On average, we collected only 62% of those fruits counted in the crown, suggesting a 38% predator removal rate. Since canopy counts were conducted after the exocarp had hardened, we assumed little to no macaw predation of immature canopy fruits as reported by Trewedi et al. (2004). A second method involved enumerating depressions with traces of the non-woody exocarp and/or mesocarp on the ground below each tree canopy. These depressions are created when the heavy fruits fall from the approximately 50 m tree canopy, and become visible when the predator removes the fruit from this microsite. Each depression count was sometimes augmented when additional predator-opened fruits clearly not associated with the depressions were encountered. Based on this method applied to the entire study population during ground counts, predators removed 7.9 and 6.1% of the total 2005 and 2006 production, respectively. Using
similar methods, Zuidema and Boot (2002) estimated that 7% of all production was not harvested by collectors in Bolivia.

Though far from error-free, we believe that crown counts more accurately reflect count discrepancies because of the possibly large error associated with depression counts given that predators could easily remove a substantial number of fruits that left no ground trace. Repeated fruit counts that consider daily or weekly fruit removal by predators are warranted for highly accurate estimates of absolute fruit production—a procedure that was not possible in our study. Nonetheless, for consistency, all subsequent discussion of fruit production rates reflect fruits counted on the ground without adjustments for these potential sources of error.

4.2. Tree and soil attributes

Crown attributes (crown form, cross-sectional area, and canopy position) were assessed for each of the 140 trees. Crown form categorizations was adapted from Synnott (1979), and included: (1) complete or irregular circle (perfect or good); (2) half-crown (tolerable); (3) less than half-crown (poor); and (4) one or a few branches (very poor). Each crown was originally evaluated in July 2001, and again in July 2005. Tree crown cross-sectional area was determined in July 2002 by measuring maximum crown diameter and a second diameter at right angles to the maximum axis, followed by application of an ellipsoid formula. Crown position was scored as: (1) dominant (full overhead and side light); (2) co-dominant (full overhead light); (3) intermediate (some overhead or side light); or (4) suppressed (no direct light).

In October 2002, leaves were collected from a random sample of 24 study crowns, controlling to include trees at different fruit production levels, dispersed locations on the 420-ha landscape and liana cutting treatment (described below). Leaves were dried at 105 °C for 72 h, ground with a Wiley mill, and passed through a 1 mm sieve. For P, K, Ca, and Mg, samples were digested in a 2:1 nitric-perchloric acid, with concentrations determined using the metavanadate colorimetry method and absorption spectrophotometry (P) or atomic absorption spectrophotometry (K, Ca, and Mg). Nitrogen was analyzed by the Kjeldahl method as modified by Mills and Jones (1996).

To determine soil properties, a composite of six soil cores were excavated beneath the crown of each of the 140 trees in July 2002. Samples were extracted below the litter layer at two depths: 0–10 and 10–20 cm. Two replicates of each composite were dried for 4 days at 65 °C, and passed through a 2 mm stainless steel sieve. Soil pH was measured at a 1:2.5 soil to water ratio. Extractable P and K were processed using a dilute double acid extraction (Mehlich-1), with concentrations determined colorimetrically using the molybdate blue method for P, and flame emission spectrophotometry for K. Exchangeable Ca and Mg were measured after extracting cations with a 1N KCl solution, with concentrations determined through atomic absorption spectrophotometry. To determine total potential acidity, H⁺ + Al³⁺ was extracted with a buffered solution of calcium acetate at pH 7, and then titrated with 0.1N NaOH. Cation exchange capacity (CEC) was calculated as the sum of this potential acidity plus base cations. Oxidizable organic carbon was determined on soils passed through a 1 mm screen, ground in a porcelain mortar, and then digested in a potassium dichromate acid medium with external heat. Organic matter was estimated by multiplying this value by 1.75. All soils analyses were conducted at the Soils Laboratory of Embrapa Acre, Brazil (EMBRAPA, 1997).

4.3. Liana cutting

Lianas were cut from 80 of the 140 trees in July 2002. Each liana was cut near the ground and at approximately 2 m from ground level. Since B. excelsa fruits take 14 months to mature, impacts would only be detectable with 2004 production data. Thus, fruit and nut production in 2002 and 2003 were clearly not associated with any liana cutting impacts, while data for 2004, 2005, and 2006 could potentially be affected by liana cutting.

4.4. Data analysis

We modelled fruit production as a function of the liana cutting treatment, with tree and soil attributes acting as covariates, using SAS software for all data analysis (Version 9.1). Since the number of possible predictor variables was large, a principal components analysis (PCA) was first performed with all quantitative explanatory variables to illuminate relationships and show redundancies (PROC PCA) (Appendix A). Two-way correlations between all variables, including the dependent variable, were calculated using PROC CORR to verify PCA results and reveal further relationships between annual fruit production and possible predictor variables.

A mixed model was constructed first with all quantitative tree variables (dbh and crown size), class variables (crown position, crown form class, liana load, and liana cutting treatment), and the group of soil variables determined from the PCA to have high explanatory power. Because fruit production data were collected annually for each of 5 years on 140 trees located in a contiguous forest area, data were both spatially and temporally correlated. A mixed effects approach, accounting for the repeated measures structure of the data ensured correct formation of the error covariance matrix and proper tests of significance. Year of measurement was treated as a repeated measurement, but not as a linear one, as it was known that fruit production by year did not follow a linear trend. Location (UTM easting and northing) was included so that spatial location of trees could be incorporated into the error covariance matrix. Variograms were constructed to reveal patterns of spatial dependency in the data (PROC VARIOGRAM), and several candidate models of spatial covariance (e.g., exponential, power, and Gaussian) were incorporated and tested in the mixed model (Schabenberger and Pierce, 2001). Because a previous study showed a quadratic relationship between dbh and fruit production (Wadt et al., 2005), dbh² was included in the model. Using PROC MIXED, model parameters were found via maximum likelihood, and several error covariance structures were tested.

Model results were compared using Akaike’s Information Criteria (AIC, Akaike, 1973), and by visual examination to test
normality and homoscedastic model residuals. Second- and third-order interactions, and later covariates, were included in the first iterations of the model, and those that did not improve (lower) AIC were dropped sequentially as recommended by Burnham and Anderson (2002). We also explored model building by conventional methods of sequentially dropping non-significant interactions and covariates based on P-values. In this case, we used a significance level of $\alpha = 0.10$ rather than the usual arbitrary 0.05 level (Johnson, 1999; Burnham and Anderson, 2002) to allow all possible significant effects to remain for the purpose of building the best explanatory model (Bancroft, 1968, p. 8). Since we found almost identical results using this second method, we only report results using the AIC method. Because a primary purpose of data analysis was to develop an explanatory model of fruit production with and without liana cutting treatments, the indicator variable for liana cutting was considered fundamental. As such, it was retained in the model without regard to its significance level (Neter et al., 1996, p. 354).

Using methods detailed in Kelly and Sork (2002), fruit production variability at the individual level ($x_{CV_i}$) was determined by calculating the mean of the coefficient of variation of fruits per tree of each tree over 5 years, and then calculating the mean of these individual tree coefficients of variation. Fruit production variation at the population level ($CV_p$) was measured by the coefficient of variation of the mean number of fruits per tree of each tree over 5 years. Following Snook et al. (2005), synchronicity of fruiting by the study population ($x_{PCC}$) was determined by calculating the Pearson correlation coefficient of all possible pairs of trees in the sample, and then calculating the mean of those correlation coefficients.

Finally, we also assessed relevant relationships not specifically tested in the mixed model. We computed Pearson’s correlation coefficients for relevant variable pairs, and to specifically test liana cutting effects on crown form, we modelled the change in crown form class controlling for initial crown form class.

5. Results

5.1. Fruit production rates

Without adjusting for the liana cutting treatment, mean number of $B. excelsa$ fruits produced per tree per year was 66.2 (S.D. = 98.5, $N = 681$). Of the 140 $B. excelsa$ trees studied, approximately 40% produced, on average, fewer than 20 fruits year$^{-1}$. Correspondingly, in any given year, approximately 25% of the trees (those that produced > 200 fruits year$^{-1}$) produced, on average, 72% of the total annual production.

5.2. Fruit production variation explained

The final mixed model explained 73% of the variability in number of fruits produced. The analysis incorporated significant spatial correlation into the error covariance structure with a power model and included significant random effects for dbh. Significant fixed effects were detected for year, dbh$^2$, crown form, liana load, and two soil attributes (Table 1).

<table>
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<tr>
<td>P</td>
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</table>

Table 1: Results of the final mixed model explaining fruit production variation

The calculated population variability ($CV_p$) was relatively low at 0.1974. Significant production variation within the study population was detected by year ($P < 0.01$) (Table 1), however, with Scheffe’s test revealing that 2006 was the only year departing from average (Fig. 1, column 1), producing almost 50% fewer fruits than the preceding 4 years.

The annual individual variation in number of fruits was high ($x_{CV_i} = 0.8894$), with the widest range represented by one tree that produced 140 fruits in 1 year and 801 in the subsequent. There were, however, individual trees that departed from that high variation. Eleven trees of the 140 studied were consistently among the best 5 producers in any given year, and 1 tree made this top-5 list every year. At the other extreme, 5 trees produced no fruits in any of the 5 years, and 14 others produced no fruits in 3 of 5 years and very few fruits ($\leq 17$) in the other 2. Significant correlations ($P < 0.001$) revealed that observations of fruit production in alternate years were more highly correlated than those of consecutive years, implying that the number of fruits produced by a tree in the second previous year was a better predictor of current fruit production than that of the immediately previous year. Further exploration revealed that 12% of the trees had a strong biannual production pattern over the 5-year period (years of high production followed by years of low), while 46% approximated this pattern, deviating from this
sequence in 1 year only. Overall synchronicity of fruiting (considering all possible pairs of all individuals and all years) by the study population was very low ($sPCC = 0.0565$).

5.2.2. Spatial variation
The spatial proximity of trees across the 420-ha landscape was relevant in explaining production variation. Although initial variograms of the data did not reveal any obvious spatial pattern, patterns could easily be masked by treatment effects. Variograms of the residuals for a mixed model that did not account for spatial dependencies showed asymptotically increasing variation between residuals as the distance between observations increased, which is indicative of significant spatial correlation. After introducing a spatial covariance matrix for better model fit, we found a significant relationship between fruit counts and tree proximity ($P < 0.0001$), and the 11 most consistently top-producing trees were grouped spatially (Fig. 2).

5.2.3. Variation by dbh
Fruit production was also explained by dbh ($P < 0.01$) (Table 1) in a quadratic manner (Fig. 3). Grouping trees into three 50-cm diameter classes revealed that those in the middle range (100 cm ≤ dbh < 150 cm) were consistently the best producers (Fig. 1, columns 2–4).

5.2.4. Variation by crown form
Crown form was important to explain variation in fruit production ($P < 0.05$) (Table 1). Scheffe's means comparisons revealed that trees with the best crown forms (complete or irregular circles) were significantly better fruit producers than those in all other crown form classes (Fig. 3).

5.2.5. Variation by liana load
The liana load variable may explain some of the production variance, although statistically this variable was not highly significant ($P < 0.10$) (Table 1). Of those trees that produced the least (0–20 fruits tree$^{-1}$), the majority had crowns that were more than 25% covered by lianas; in contrast, those that produced the most fruits (>200 fruits tree$^{-1}$) rarely had liana load levels of that magnitude.

The mixed model suggested an interaction effect of liana cutting treatment by year, although not highly significant statistically ($P < 0.10$) (Table 1). In 2005, those trees from which lianas were not cut produced more fruits than those that received the liana cutting treatment. In 2006, this rank changed, whereby those trees that received the liana cutting treatment were comparatively superior producers.

Significant changes in crown form over the 2001–2005 period were detected for some trees liberated from lianas, when initial 2001 crown form condition was considered ($P = 0.0003$). Specifically, changes were detected in trees with the poorest initial crown forms (few branches only) ($P < 0.0001$) (Fig. 4), indicating that those trees responded differently to liana cutting than trees with complete or irregular circles, or half-crowns ($P < 0.01$).

5.2.6. Variation by soil attributes
Of the soil variables subjected to a PCA (Table 2), potential acidity ($H^+ + Al^{3+}$) and CEC had nearly identical loadings—relationships corroborated with simple correlations. There were no differences in soil property values between sampling depths except for exchangeable Ca. Therefore, with the exception of Ca, all values were averaged by tree and collapsed into one depth (0–20 cm) for analysis in the mixed model.

CEC and levels of extractable P contributed to explaining fruit production variation (Table 1) ($P < 0.01$ and $<0.05$, respectively). CEC levels had a positive relationship with fruit production, while extractable P levels showed a weakly negative one.

Foliar nutrient concentrations were not included in the model because they were only assessed on a subsample of 24 study trees. Of those measured, only foliar P at 1.68 ± 0.49 g kg$^{-1}$ (t ± S.D.) was significantly correlated with number of fruits produced in 2002, the year in which foliar samples were collected ($r = 0.414, P = 0.045$). Similarly,
only P foliar levels were correlated with its corresponding (0–10 cm depth) P soil value \((r = 0.478, P < 0.05)\).

6. Discussion

Our model explained over 70% of the variation in Brazil nut fruit production over a 5-year period, identifying multiple factors implicated in regulating *B. excelsa* fruit production. This information could contribute to fostering population persistence and improving commercial yield of this increasingly managed species, while providing scientific insights into the larger ecological question of what causes fruit production variation. To the extent that fruit production of other NTFPs is regulated by the same factors, our study may indicate management directions for those species as well.

Based on our 140-tree data set observed over 5 years, *B. excelsa* produced 66 ± 98 fruits tree\(^{-1}\) year\(^{-1}\) (\(\bar{x} \pm\) S.D.). The only other published study that quantified fruit production reported much higher production levels and slightly lower variation at two sites (184 ± 122, \(N = 40\), over 5 years; 139 ± 104, \(N = 53\), over 3 years) (Zuidema and Boot, 2002). This study was similar in that it was also conducted in western Amazonia, in Bolivia; however, it was based on smaller sample sizes and included only reproductive individuals from which Brazil nut collectors typically harvest. The variation in production of this commercially-harvested Bolivian population would be, by definition, less than our sampled Brazilian population which included non-producing individuals that would not have been visited during a commercial harvest. Nonetheless, standard deviations from these three data sets suggest ample variation in production between individual trees in any given year, an observation shared by Brazil nut collectors and researchers (Viana et al., 1998; Ortiz, 2002). Indeed, overall production of our studied population is attributed to relatively few trees; 1/4 of the trees produced almost 3/4 of the annual production. Zuidema (2003) reported similar findings from Bolivia, noting that the majority of trees in the analyzed populations produced very few fruits.

6.2. Annual production variation

Annual variation of fruit production at the population level (CV\(_P = 0.20\)) was extremely low—far from Kelly’s (1994) criteria for mast fruiting of >1. It is also substantially lower than the median value of 1.10 for 108 tropical species, almost half of which were trees measured over 15 years (Wright et al., 2005). Indeed, none of their species had a CV\(_P < 0.20\). Perhaps a longer term *B. excelsa* data set (>5 years measured) would detect greater variation (Kelly, 1994; although see Kelly and Sork, 2002), but our low CV\(_P\) coupled with low synchronicity of fruiting \((x_{PCC} = 0.0565)\) and long-term observations of more or less continuous production by Brazil nut collectors, confirm that Brazil nut is not a masting species (sensu Janzen, 1976). Rather, *B. excelsa* fruit production variation follows a pattern predicted by Kelly and Sork (2002) and empirically tested by Wright et al. (2005): tropical species exhibit more constant fruit production than temperate species. A departure from average production of our studied population is attributed to relatively few trees; 1/4 of the trees produced almost 3/4 of the annual production. Zuidema (2003) also reported a significant drop in production than temperate species. A departure from average production of our studied population is attributed to relatively few trees; 1/4 of the trees produced almost 3/4 of the annual production. Zuidema (2003) also reported a significant drop in production that Brazil nut is not a masting species (sensu Janzen, 1976).

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No single pattern of annual fruit production was detected at
the individual level. Previously, Zuidema (2003) had reported
that Brazil nut individuals with high production in 1 year were
often preceded and followed by years with substantially lower
production. A little over 10% of our study trees exhibited such a
strong biannual pattern, but another 46% (almost half)
approximated it, deviating from this sequence in 1 year.
Resource switching, whereby plants move resources into and
away from reproduction in successive years (Norton and Kelly,
1988), is suggested by these results, but we present no data as to
where resources might be allocated (e.g., growth) in “off-
production” years. We also observed that 11 trees of the 140
studied were consistently among the best 5 producers in any
given year, and 1 tree made this top-5 list every year. Similarly,
Ortiz (2002) reported that Brazil nut collectors in Peru have
observed that highly productive \textit{B. excelsa} trees typically
produce better in relation to their local conspecifics,
independent of year. These results of consistently good or
poor reproductive performances of individual plants apparently
unrelated to site conditions or tree size (within reproductive
limits) suggest genotypic influences over production (Vander
Wall, 2001).

6.3. Explaining production variation

In addition to rainfall embedded in year, what factors
contributed to the significant temporal and spatial variation in
\textit{B. excelsa} nut production encountered in our study? The great
variation in annual production within \textit{B. excelsa} individuals
(CV\textsubscript{i} = 0.95) indicates that other explanatory variables at the
scale of the individual were important. Dbh was the most
critical variable, explaining >50% of fruit production variation
(partial $R^2 = 0.565$). Trees in the middle diameter range of our
study population (100 cm $\le$ dbh $< 150$ cm) were better pro-
ducers than both smaller and larger trees (Fig. 1, columns 2–4).
Most trees produce their best seed crop in middle age, which
may last from decades to centuries, followed by decline and
senescence (Harper and White, 1974). While \textit{B. excelsa}
diameter is not perfectly correlated with age (Vieira et al.,
2005), it seems reasonable to use dbh as a proxy for observing
tree development over time. The quadratic nature of the
relationship observed in our study (Fig. 3) contrasts to that of
Zuidema and Boot (2002), who reported a positive linear
relationship between dbh and production, although based on a
smaller and constrained sample. For \textit{Swietenia macrophylla},
Snook et al. (2005) also found that fruit production increased
with diameter, although they reported a pattern whereby
production continued to increase with increasing dbh,
apparently throughout tree life.

Crown attributes (area, position, and form) also played a role
in fruit production variation. Crown area was strongly
correlated with dbh ($r = 0.53$, $P < 0.0001$), and preliminary
model tests demonstrated that it was a slightly better predictor
of fruit production than diameter (similar to Zuidema, 2003),
although both variables explained fruit production well. We
retained dbh in the mixed model, however, because predictive
differences between dbh and crown area were very small, and to
facilitate data interpretation because dbh is a common field
measurement. Crown position or ability to access light
resources is clearly an important determinant of fruit
production, but since almost all \textit{B. excelsa} study trees had a
co-dominant or dominant canopy position, this variable fell out
of the model. While Zuidema (2003) states that trees below
canopy level do not seem to produce fruits, we observed six
trees (4%) that were in an intermediate canopy position and
produced fruits. Finally, crown form was an important
explanatory variable in our study (Table 1), such that better
fruit producers consistently had the best crown forms.

A previous analysis of the first 2 years of our data set (prior
to liana cutting), specifically testing liana load and fruit
production, clearly demonstrated an association between liana
presence and reduced Brazil nut fruit counts (Kainer et al.,
2006). Similarly, Stevens (1987) had demonstrated negative
impacts of lianas on \textit{Bursera simaruba} fecundity. Thus, we
expected positive fruit production effects from liana cutting.
Nonetheless, single variable effects from our current mixed
model did not support this expectation (Table 1). We did find
some evidence that effects of liana cutting on production were
changing, based on the weakly significant interaction effect of
liana cutting by year ($P < 0.10$). We also observed that liana
cutting improved crown form and/or circumvented mortality of
trees with very poor crown forms (Fig. 4). These observations
confirm that branch regrowth following liana liberation had
begun in some of our study trees, and that crown forms (a highly
significant explanatory variable of \textit{B. excelsa} fruit production)
of Brazil nut trees liberated of lianas could improve over time.
Both long-term liana consequences, such as branch modifica-
tion (Stevens, 1987), and short-term, such as light interception
(Grauel and Putz, 2004), have been speculated upon for
suppressing host tree fruit production. We conclude that liana
impacts (and liana cutting effects) are complex and may be
attributable to a series of events at multiple levels over time.

Soils and nutrient availability have been cited as important
factors in \textit{B. excelsa} fruit production (Viana et al., 1998;
Zuidema, 2003); however, these potential effects had not been
tested previously. In analyzing soil chemical characteristics,
only two variables were implicated in fruit production
(Table 1). Not surprisingly, CEC was positively associated
with increased production, and CEC in our study site was
higher compared to other Amazonian podzolics (Lathwell and
Grove, 1986). Base cation levels (Ca, Mg, and K) were
relatively high, and similar to another primary forest in the
region (McGrath et al., 2001), though not significant in our
model. Extractable P was implicated, but this statistical
significance may not be meaningful since it was slightly
negatively correlated with production, and coefficients of
variation for production in years prior to and after soil sampling
were very small (<0.1). Foliar P, however, a better indicator of
plant nutrient status than soil stocks, was fairly strongly
positively correlated with number of fruits produced. These
results are too limited to reveal how P is cycling through the
soil–plant system, but suggest that the relationship between P
and \textit{B. excelsa} fruit production merits further study. P is often
cited as limiting tropical forest productivity (Jordan, 1985;
Cuevas and Medina, 1988; McGrath et al., 2001), and is a key component of reproductive tissues (Marschner, 1995) such as fruits and nuts. Experimental studies of multiple apple varieties, revealed that addition of P in 1 year of production significantly increased flowering and fruit set in the subsequent year (Nielsen et al., 1990).

We did not directly evaluate predator and pollinator availability or genotypic variation—factors potentially important in B. excelsa fruit production. Discrepancies between number of fruits collected off the ground and absolute fruit numbers from crown and soil depression counts reveal strong interactions with the agouti predator/disperser. These interactions must affect fruit production as measured in our study, and possibly fruit production variation. Ortiz (2002) speculated that the principal determinant of low B. excelsa productivity is pollination deficiency, perhaps due to smoke from increasing forest fires or lower bee visitation in trees within forest fragments or isolated in converted pastures. While we did not study pollinator activity, our study site was located within a largely unfragmented conservation unit exposed to minimal smoke. Five trees in our sample exhibited individual characteristics of good producers (good dbh and crown form, no to few lianas), but produced no or few fruits (≤6) throughout the 5-year period, implicating at least some genetic influences (Vander Wall, 2001).

Finally, our data suggest a spatial pattern of production variation across the 420-ha landscape, with highly productive trees found in loose groups (Fig. 2). Ortiz (2002) reported the existence of Brazil nut “hot spots” of greater tree densities, and bigger and better producers. Reasons for these patterns remain speculative, but soils and genetic factors influenced by disperser activity are plausible explanations.

6.4. Management implications

The more or less continuous reproduction pattern of B. excelsa at the population level documented in our study has certainly contributed to the high commercial success of Brazil nut over the decades, and consequently, its importance for Amazonian conservation. Results from our study suggest several avenues that could further minimize production variation and maximize levels of fruiting. Brazil nut collectors and processors across the Amazon basin depend on B. excelsa fruit production as part of their cash income and food security, and processors across the Amazon basin depend on it for harvesting. Brazil nut harvest is based on a trail system originally blazed for collecting rubber. While Brazil nut collectors are very familiar with the large reproductive B. excelsa trees on and near these trails, there is limited preoccupation with systematically seeking and tending younger trees entering reproductive maturity, which could increase the harvest pool. Additionally, over time, this traditional trail system could preferentially concentrate harvesting from the largest trees (>150 cm dbh), whereas we found that those of intermediate diameters (100–150 cm dbh) are the most productive. Our study also shows that some trees (11 of 140) were consistently super-producers, while a full 40% produced fewer than 20 fruits year⁻¹ on average, a quantity that would not likely be collected given current harvest practices. To achieve maximum efficiency, harvesters could concentrate collection efforts on these consistently high producers that also seem to be spatially aggregated. These production “hot spots” might also be targeted for incorporating new trees into the harvest regime. Poor producers could be targeted for individual tree interventions highlighted above.

Differences in ground fruit counts, reported throughout our study as fruit production, versus our measured crown counts or fruit depressions, clearly indicate that many fruits are “lost” to predators, rather than human-harvested. While more intensive extraction would certainly increase commercial yield, caution should be exercised to not exceed a theoretically unsustainable harvest threshold as documented in populations very intensively harvested over decades (Peres et al., 2003). Overharvest could also adversely affect the broader forest community (such as agouti dynamics) and ecosystem functions (such as nutrient cycling) (Ticktin, 2004).

Finally, although we did not find any one pattern of annual fruit production at the individual tree level, harvesters could begin tracking production levels of individual trees over time, revealing patterns that might increase collection efficiency and predictability of crop yield. Indeed, many Brazil nut harvesters who have been collecting from the same trees for years, have developed a mental map of high production trees, and often can fairly accurately predict average individual tree production (Wadt et al., 2005). Tapping into this local knowledge and integrating it with science could enhance our understanding of B. excelsa autecology and augment Brazil nut productivity. It may also further our understanding of the complex interactions between Dasyprotidae spp., Homo sapiens, and B. excelsa, which are poorly documented in the literature. Understanding of production and production variation coupled with interventions to achieve management goals can hopefully further advance Amazonian forest conservation efforts in which Brazil nut is a keystone element.

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Appendix A. Principal component loadings and percent variation explained by quantitative tree, location, and soil variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Loadings</th>
<th>Variation Explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>CEC</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>Ca</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>Mg</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>K</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>P</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>DBH</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>Crown form</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
<tr>
<td>Vine load</td>
<td>0.93</td>
<td>90.14%</td>
</tr>
</tbody>
</table>

Appendix B. Final coefficients of the mixed model explaining fruit production

<table>
<thead>
<tr>
<th>Variable</th>
<th>Base coefficient</th>
<th>Additional coefficient for Severity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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</tr>
<tr>
<td>Year</td>
<td></td>
<td>20.09 17.55 17.49 17.49 0.00</td>
</tr>
<tr>
<td>DBh</td>
<td>3.0061</td>
<td></td>
</tr>
<tr>
<td>DMa</td>
<td>-0.0111</td>
<td></td>
</tr>
<tr>
<td>Crown form</td>
<td></td>
<td>52.62 31.24 17.98 0.00</td>
</tr>
<tr>
<td>Vine cutting</td>
<td>-16.59</td>
<td>23.42 25.97 12.23 36.16 0.00</td>
</tr>
<tr>
<td>No vine cutting</td>
<td>0.00</td>
<td>0.00 0.00 0.00 0.00 0.00</td>
</tr>
<tr>
<td>P</td>
<td>-6.478</td>
<td></td>
</tr>
<tr>
<td>CEC</td>
<td>7.617</td>
<td></td>
</tr>
</tbody>
</table>

References


UFAC (Univsersidade Federal do Acre), 2006. Group of Environmental Services and Studies, Natural Sciences Department, Federal University of Acre, Rio Branco, Acre, Brazil.


