

Tradeoffs in basal area growth and reproduction shift over the lifetime of a long-lived tropical species

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Abstract Understanding of the extent to which reproductive costs drive growth largely derives from reproductively mature temperate trees in masting and non-masting years. We modeled basal area increment (BAI) and explored current growth–reproduction tradeoffs and changes in such allocation over the life span of a long-lived, non-masting tropical tree. We integrated rainfall and soil variables with data from 190 *Bertholletia excelsa* trees of different diameter at breast height (DBH) sizes, crown characteristics, and liana loads, quantifying BAI and reproductive output over 4 and 6 years, respectively. While rainfall explains BAI in all models, regardless of DBH class or ontogenic stage, light (based on canopy position and crown form) is most critical in the juvenile ($5 \text{ cm} \leq \text{DBH} < 50 \text{ cm}$) phase. Suppressed trees are only present as juveniles and grow ten times slower ($1.45 \pm 2.73 \text{ m}^2 \text{ year}^{-1}$) than trees in dominant and co-dominant positions (13.25 ± 0.82 and $12.90 \pm 1.35 \text{ m}^2 \text{ year}^{-1}$, respectively). Additionally, few juvenile trees are reproductive, and those that are, demonstrate reduced

growth, as do reproductive trees in the next 50 to 100 cm DBH class, suggesting growth–reproduction tradeoffs. Upon reaching the canopy, however, and attaining a sizeable girth, this pattern gradually shifts to one where BAI and reproduction are influenced independently by variables such as liana load, crown size and soil properties. At this stage, BAI is largely unaffected by fruit production levels. Thus, while growth–reproduction tradeoffs clearly exist during early life stages, effects of reproductive allocation diminish as *B. excelsa* increases in size and maturity.

Keywords *Bertholletia excelsa* · Dendrometer bands · Fruit production · Non-masting · Tropical forest

Introduction

There is a generalized premise in plant ecology that the cost of reproduction plays such a fundamental role in the life history of a given individual that it influences not only reproductive patterns, but also growth trajectories, plant architecture, and physiological integration (Obeso 2002; Thomas 2011). A well-developed literature converges on the basic assumption that reproductive costs are a central driver of tree growth (Koenig and Knops 2000; Kelly and Sork 2002; Obeso 2002), such that growth–reproduction tradeoffs concurrently observed during a given season provide an organizing paradigm to explain life history evolution (Kelly 1994; Knops et al. 2007). More recent ecophysiological literature, however, points to the important role of biophysical and environmental variables in influencing tree growth and reproductive output over a tree's life span, suggesting that preferential resource diversion to reproductive structures at the expense of growth is overemphasized (Knops et al. 2007; Thomas

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2011). Indeed, Knops et al. (2007) concluded that observed negative correlations between radial growth and reproduction in *Quercus* species were not causal tradeoffs, but rather, both were independently influenced by the same environmental factors. Light, water, and nutrient availability, as well as competition for these resources by other organisms (Oliver and Larson 1996), partially explain both vegetative growth and reproductive output of any given individual.

Studies from the 1950s first report tradeoffs between reproductive output and both diameter and shoot growth (Thomas 2011), implying an internal competition for resources (Harper and White 1974). These early observations centered on conifer species, while more specific hypotheses for the presence or absence of growth–reproduction tradeoffs have been tested mostly on trees classified as masting species (Koenig et al. 1994; Herrera et al. 1998; Obeso 2002; Monks and Kelly 2006; Yasumura et al. 2006; Knops et al. 2007; Sánchez-Humanes and Sork 2011). Masting or mast seeding is an observed phenomenon in which certain plant populations synchronize production of massive seed quantities in some years, while producing small to no seed crops in other years (Janzen 1976). More subtle examination of the great variation in masting behavior led to the conclusion that important theoretical advances in our understanding of mechanisms behind reproductive output would come from quantifying synchrony (Kelly 1994; Kelly and Sork 2002) and examining reproductive costs (and potentially tradeoffs with growth) in species with less variable seed output (Kelly 1994). Would species that have fairly constant reproductive levels reveal different allocation patterns? However, to our knowledge, very few studies to date have specifically examined such tradeoffs using non-masting model systems. Furthermore, most growth–reproduction tradeoff studies have been conducted on temperate species (although see Newberry et al. 2006). This may be due to the historical scientific focus on temperate species in general, or perhaps because, as predicted by Kelly and Sork (2002) and empirically tested by Wright et al. (2005), tropical species exhibit more constant fruit production across years, with the notable exceptions of bamboo (Janzen 1976) and dipterocarp species (Janzen 1974). Complementary investigations using tropical species would provide fresh insights into the larger tradeoff debate, while also examining trees constrained by different levels and perhaps types of interacting abiotic and biotic factors, such as rainfall and liana loads.

Another empirical challenge to go beyond growth–reproduction tradeoffs in a given season has stemmed from the difficulty in following cohorts of trees through time. This is the most direct method for assessing age- and size-related tradeoffs and concurrent interactions with the

environment over the life span of any given species (Thomas 2011). In tropical forest ecosystems, non-pioneer woody species ascend to the canopy at different rates based on light levels, and may pass through multiple series of suppression and release events before attaining canopy heights (Brienen and Zuidema 2006). Subsequently, height growth increasingly becomes insignificant, radial growth continues, and reproduction is initiated upon reaching some threshold size (Obeso 2002). Additionally, potential growth–reproduction tradeoffs vary at different hierarchical levels (i.e., trunk, branch, shoot) and some degree of physiological shoot autonomy can mitigate the general costs of reproduction (Sánchez-Humanes and Sork 2011). In sum, resource allocation to growth and reproduction shift over the life cycle of the plant, and tradeoffs vary between developmental stages, plant parts, and among species.

In this study, we aim to shed light on the complex story of growth and reproduction by examining a model tropical species with relatively constant fruit production once reaching reproductive maturity (i.e., non-masting). We explore current basal area growth–reproduction tradeoffs and quantify how these relationships change over the species life span, and also include important biotic and abiotic variables in our analyses. Our underlying research questions are:

1. What factors influence growth over the life span of long-lived trees;
2. Are there tradeoffs in basal area growth and reproduction;
3. Do these change over tree ontogeny?

We explored these questions using data collected from 190 *Bertholletia excelsa* (brazil nut) trees of different diameter sizes and crown characteristics, following their basal area growth and fruit production over 4 and 6 years, respectively, while also measuring annual and monthly rainfall variation and additional site variables. While we were only able to follow tree cohorts through a short period of their life span, we rely on the key assumption that examination of behavior by diameter size class, though not foolproof, provides a reasonable alternative to explore changes over the species life span.

Materials and methods

Study site

Research was conducted in Extractive Reserve Chico Mendes located 10° to 11° south of the equator in the state of Acre, Brazil. The reserve maintains 96 % forest cover (Souza et al. 2006) 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 gently undulating topography and a pronounced dry season from June to August (IMAC 1991) when southern air masses can drop temperatures to 12 °C. Average annual rainfall is between 1,770 and 1,880 mm (Zoneamento Ecológico-Econômico do Acre 2000). Red-yellow podzolic soils are of the Solimões geological formation which is influenced by volcanic material deposited during soil genesis by Andean winds, resulting in soils that tend to be relatively young with higher silt content, nutrient stocks, and cation exchange capacity (Gama et al. 1992). Research was concentrated in an unlogged 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 map). A 2001–2002 inventory of all *B. excelsa* individuals ≥ 10 cm diameter at breast height (DBH; measured at 1.5 m above ground level) in old growth forest of this landholding revealed 568 trees, or a population density of 1.35 trees ha⁻¹, and an average diameter of 86.1 \pm 45.0 cm DBH (Wadt et al. 2005).

Study species

B. excelsa is found in non-flooded (terra firme) forests throughout the Amazon basin (Prance 1990), but is limited to areas where annual rainfall ranges from 1,400 to 2,800 mm year⁻¹ and a water balance deficit exists for 2 to 7 months each year (Diniz and Bastos 1974). At maturity, it is a very large, canopy-emergent tree that can be long-lived; one 233 cm DBH individual was radiocarbon dated as 440 \pm 60 years (Camargo et al. 1994) and two individuals of 129.5 and 101.0 cm DBH as 668 and 996 years, respectively (Vieira et al. 2005). *B. excelsa* is monoecious, self-incompatible and reproduces by outcrossing (O'Malley et al. 1988). The large, indehiscent, approximately round fruits (10–16 cm) (Prance 1990) reach maturity and synchronically fall (Tonini 2011) on average 14 months after successful pollination (Maués 2002). The 10–25 large ($\sim 4 \times 2$ cm) seeds per fruit are of high energetic cost (Sutherland 1986), and remain inside the woody fruits upon falling.

Reproductive status of *B. excelsa* trees is highly correlated with DBH. Of 364 trees examined in two Bolivian Amazon sites, only 3.5 % of individuals <40 cm DBH were reproductively mature Zuidema (2003). Our site-specific baseline characterization of 568 individuals determined that of 145 trees <50 cm DBH inventoried, only 20 % had initiated fruit production, while 96 % of those ≥ 50 cm DBH were reproductive (Wadt et al. 2005). Once reproductively mature, annual fruit production among trees is highly variable (Zuidema and Boot 2002; Kainer et al. 2007). A 5-year study of 140 reproductively

mature individuals (50–194 cm DBH) reported that they produced 66 \pm 98 fruits tree⁻¹ year⁻¹ ($\bar{x} \pm$ sd) (Kainer et al. 2007), while trees in the middle diameter range (100 cm \leq DBH < 150 cm) had the highest fruit production levels (98.2 \pm 126.3 fruits tree⁻¹ year⁻¹) ($\bar{x} \pm$ sd). In contrast, annual fruit production variation at the population (p) level was extremely low [coefficient of variation (CV)_p = 0.20] (Kainer et al. 2007). Growth in girth also has shown considerable variation both among and within diameter size classes, with annual diameter growth rates for 297 trees observed over a 3-year period peaking at >1.5 cm in the 30 to 60 cm DBH size classes (Zuidema and Boot 2002).

Data collection

Sample selection

The potential pool of 404 reproductively mature *B. excelsa* individuals (≥ 50 cm DBH—hereafter termed “adults”) identified in the 2001–2002 inventory were initially placed into ten diameter classes (nine 10-cm DBH classes and one class that grouped all trees ≥ 150 cm DBH). A 140 study tree sample was then randomly selected to include representatives within each diameter class and four initial liana load categories: (a) no lianas in crown, (b) ≤ 25 % crown covered, (c) 25–75 % crown covered, and (d) >75 % crown covered. The geospatial location of the 140 trees was plotted, confirming fairly representative spatial distribution of the sample across the study landscape. Similarly, a field check ensured that individuals with overlapping crowns or fruit fall areas were excluded from the adult sample. Selection of trees 5 cm \leq DBH < 50 cm was similar. We identified a pool of 155 individuals in the field, placed them into four DBH classes (<20, 20–30, 30–40, and 40–50 cm) and randomly selected 54 individuals to represent these size classes and their landscape-level spatial distribution. Hereafter, these trees are referred to as “juveniles” as they are far less likely to have attained reproductive maturity.

Basal area growth

Over a 4- and 3-year period, respectively, basal area growth measurements were taken quarterly on *B. excelsa* adults and juveniles to observe basal area increment (BAI) (or interchangeably, basal area growth) and capture growth patterns throughout rainy and dry seasons. Dendrometer bands were installed at ~ 1.5 m above ground level on all adults in October 2001, with first quarterly measurements recorded only in June 2002 to allow for an extended calibration period (~ 9 months). For juveniles (5 cm \leq DBH < 50 cm), bands were installed on the 54 trees in February

2003. The calibration period for these smaller trees was only one quarterly measurement cycle. Periodically, tree growth would supersede their bands, whereby a second band was installed prior to missing growth observations. During re-measurements, band integrity was inspected, and if compromised due to falling branches or faunal (monkeys and insects) activity, bands were re-installed and allowed to re-calibrate, resulting in some missing observations. Like others (Vieira et al. 2004), we did not make data corrections for seasonal variations in stem water content, assuming that averaged over the course of a year, water content changes will be zero. Finally, breast height of the two juvenile trees <10 cm DBH was marked with a permanent marker and calipers were utilized to ensure accurate measurement.

Fruit counts

Adult fruit production was measured in the last 15 days of February, after fruit fall, for 7 consecutive years (2002–2008). Numbers of fruits harvested from the ground, however, do not reflect 100 % absolute counts of total fruit production per tree. A small error can be attributed to the very few fruits remaining in the crowns. A second error is attributed to continuous removal by scatterhoarding agoutis (*Dasyprocta* spp.)—the almost exclusive fruit/seed dispersers capable of gnawing through the woody fruits. A recent study monitored fruitfall and fruit removal from 20 *B. excelsa* trees biweekly over 70 days, approximately matching the synchronous fruitfall period, and found that 5.2 % of fruits were removed by predators or remained in the crown (L. H. O. Wadt, unpublished data). In our study, we did not adjust fruit counts for these potential sources of error, assuming them to be small and consistent over our sample. Finally, for juveniles, the reproductive status of each individual was assessed as a binomial variable (fruits present or absent) because fruit production, when present, was minimal.

Crown attributes

Crown attributes (canopy position, cross-sectional area, and crown form) of each of the 140 adult trees were assessed during the initial inventory. 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). Tree crown cross-sectional area was determined by measuring maximum crown diameter and a second diameter at right angles to the maximum axis, followed by application of an ellipsoid formula. Crown form categorizations were adapted from Synnott (1979), and included: (1) complete or irregular circle (good), (2) half-crown

(tolerable), (3) less than half-crown (poor). This final crown attribute was also re-assessed in July 2005. For juvenile trees, only crown form and crown canopy position were similarly assessed and only once, when juveniles were encountered and added to the data set (over a period of ~3 years).

Liana loads

Previous analyses revealed a significantly lower level of *B. excelsa* fruit production when at least 25 % of adult Brazil nut crowns were covered by lianas (Kainer et al. 2006). Thus, for this study, the initial liana load variable was reduced from four (0, ≤25, 25–75, and >75 % covered) to two levels: (a) ≤25 % of crown covered, and (b) >25 % crown covered. Because liana presence can affect crown form (Kainer et al. 2007), we used crown form assessments of July 2005 (rather than initial 2001–2002 assessments) in our analyses to better reflect crown form status during the study period. Finally, juvenile trees were rarely associated with lianas, and thus when present, lianas were removed.

Rainfall and soil attributes

Localized climate data were unavailable for our remote study site over the entire research period; however, monthly rainfall was recorded consistently at the Federal University of Acre (Rio Branco, Acre, Brazil), located 107 km from the center of our study site. Since these two rainfall data sets were strongly correlated ($r = 0.89$ over 44 months), we utilized the more complete one.

To determine soil properties under adult trees, a composite of six soil cores was excavated near each of the 140 adult individuals in July 2002 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 determined 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 1 N KCl solution, with concentrations determined through atomic absorption spectrophotometry. To determine total potential acidity, $H^+ + Al^{3+}$ was extracted with a buffered solution of calcium acetate at pH 7, and then titrated with 0.1 N NaOH. Oxidizable organic C 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).

Data analysis

The statistical software, SAS, was utilized for all data analyses (version 9.2, SAS Institute). While many growth studies utilize cumulative growth observations, we based our analysis on annualized quarterly growth increments to better link growth observations to annual production and periodic rainfall data. Dendrometer readings taken at each i th period, which measure circumferential growth, were first converted into basal areas (B). Then, measurements were annualized into BAIs (BAI_i) by calculating:

$$BAI_i = \frac{B_i - B_{i-1}}{t_i - t_{i-1}} \times 365$$

where t_i is the time (in days) of the i th measurement.

Variable selection

Since the number of possible predictor variables was large, two-way correlations were calculated as a preliminary step to reduce the number of independent variables input into the models. These preliminary analyses revealed that very few variables were significantly correlated with growth; only rainfall in the previous 3 months ($r = 0.40$), DBH ($r = 0.10$), fruit production in year subsequent to growth ($r = 0.12$), the inverse of average fruit production ($r = 0.05$), soil C ($r = 0.05$) and soil P ($r = -0.06$) had absolute correlations ≥ 0.05 . Based on these observations, the transformed variable Inverse of average fruit production was included in the model. Other strong correlations among tree variables included crown size with DBH ($r = 0.56$) and also average fruit production ($r = 0.42$). Based on highly significant correlations obtained from soil nutrient measurements at depths of 0–10 and 10–20 cm, soil variables were averaged to create a single 0- to 20-cm-depth soil variable. Other significant correlations were obtained for $H^+ + Al^{3+}$ content with soil C (0.64), and Ca with the ratio of Ca + Mg (0.81) and the ratio of Ca + Mg over K (0.62). Thus, models were formulated with either DBH or crown size (but not both), and with subsets of soil variables.

Model construction

Data were both spatially and temporally correlated, because growth data were collected every 2 to 4 months, fruit production data were collected annually, and trees were located in a contiguous forest area. To ensure correct formation of the error covariance matrix and proper tests of significance, individual trees were treated as random

effects with date of measurement as the repeated measure, and both compound symmetric and autoregressive variance–covariance structures were investigated (Littell et al. 2006). In all cases, the compound-symmetric variance–covariance structure best described the relationship between measurements taken on the same tree over time. In other words, measurements from the same tree did show significant correlations; however, these correlations were not more similar in adjacent measurement periods. Location (universal transverse Mercator easting and northing) was included so that spatial location of trees could be incorporated into the error covariance matrix. Variograms were first constructed to reveal possible patterns of spatial dependency in the data using the SAS procedure 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). None of the models indicated a significant spatial correlation structure; that is, trees that were located closely in space were not more similar than those located farther apart.

As a first step, mixed models for annual basal area growth were separately formulated for adults (≥ 50 cm DBH) and juveniles (< 50 cm). While all 54 juveniles remained over the entire study period, four adult trees were removed from our sample early on, and thus adult analyses were based on 136 trees. Adult growth models were first constructed with continuous tree variables (initial DBH or crown size, fruit production) and class variables (crown position, crown form class, liana load, and liana-cutting treatment). Because a previous study showed a quadratic relationship between DBH and fruit production (Wadt et al. 2005), both DBH and DBH^2 were included in model development. To assess both longer- and shorter-term effects of fruit production on growth, we tested four fruit production values in the models. First, to reflect long-term tree productivity, we included Inverse average fruit production over the entire study period. Since fruit formation in *B. excelsa* occurs over a period of 14 months, we also examined: (1) fruit produced in the year prior to the growth measurement, (2) fruit produced in the current year of the growth measurement, and (3) fruit produced in the year subsequent to the growth measurement. Several rainfall measurements were calculated and tested in the models to reflect the delayed effect that rainfall may have on growth: rain in the month previous to growth, rain in the 3 months prior to growth, and rain in the rainy season (November up to and including April) prior to growth. Interactions between some variables were included in the first iterations of the model. Using the SAS procedure PROC MIXED, model parameters were found via maximum likelihood, and the 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. Those variables that did not improve (lower) AIC were dropped sequentially (Burnham and Anderson 2002). Subsets of soil variables were then added to the models and dropped sequentially in the same manner to estimate a final model for all adults. We also explored model building by conventional methods of sequentially dropping non-significant interactions and covariates based on *P*-values. Since we found almost identical results using this second method, we only report results using the AIC method.

Annual basal area growth for juveniles was modeled in a similar fashion although with slightly different variables. Fruit production was not continuous, but rather binomial (present or absent). Both soils and liana data were entirely excluded, because soil samples were only collected below adult trees and the liana load variable did not apply to this juvenile data set. Additionally, we did not measure crown size of juveniles.

Finally, to provide further insights into basal area growth over the entire *B. excelsa* life span, we combined juvenile and adult data sets. In this overall model, we were restricted to testing only those variables common to both data sets: initial DBH, crown form and position, fruit production as a binomial variable (present or absent), and rainfall measurements.

Further testing for adult growth and production tradeoffs

To more closely investigate the potential tradeoffs as trees of reproductive size increased in girth, growth models were also formulated for three size classes ($50 \leq \text{DBH} < 100$ cm, $100 \leq \text{DBH} < 150$ cm, $\text{DBH} \geq 150$ cm). Recognizing these diameter restrictions, these models did not test DBH as an explanatory variable, but rather the correlated variable crown size. Finally, we utilized the same repeated measures variance–covariance structures as in previous models.

Results

Basal area increment

Basal area growth rates of *B. excelsa* varied by DBH size class (Fig. 1). Juveniles ($5 \text{ cm} \leq \text{DBH} < 50$ cm) averaged $10.0 \pm 1.86 \text{ cm}^2 \text{ year}^{-1}$; the top 10 % had growth rates above $22.8 \text{ cm}^2 \text{ year}^{-1}$, and all of these individuals were larger than 35 cm DBH, had co-dominant or dominant canopy positions, and none had initiated fruit production. Adults (≥ 50 cm DBH) grew on average $12.5 \pm 1.6 \text{ cm}^2 \text{ year}^{-1}$, and more than half (eight of 14 trees) of the best growers (top 10 % at rates above $22.1 \text{ cm}^2 \text{ year}^{-1}$)

were in the 50 to 100-cm diameter class, produced on average fewer than 26 fruits year^{-1} , and all but one were co-dominant or dominant. Just as BAI changed over the life span of *B. excelsa*, the factors that explained growth also changed. Our best model of juvenile BAI included significant positive effects for rainfall in the previous 3 months, initial DBH, and better-quality crown form, and significant negative effects for those juveniles that had initiated fruit production (Table 1). For adults, rainfall in the previous 3 months also showed the far-and-away strongest positive relationship with adult BAI (Table 1). Furthermore, rainfall seasonality created a sinusoidal growth curve, with negative BAI recorded during the extreme drought year of 2005 (Fig. 2). Though marginally significant, initial tree DBH was also implicated as in juvenile growth, but with adults, this relationship was quadratic, suggesting an overall pattern in which basal area growth slowed as adults increased in girth (Table 1). The relationship between average fruit production over the study period and adult BAI was an inverse one, suggesting again that adult trees that produced few fruits grew faster than those that produced more. Furthermore, for adults, growth in one year was positively related to fruit production in the subsequent year. Additionally, adults with more extensive liana loads (>25 % crown covered) presented significantly slower growth. Finally, four soils variables were implicated in the adult model: two positively related to BAI (Ca and marginally, C) and two negatively related (P and Ca + Mg).

Our overall model of BAI that combined juvenile and adult data sets implicated comparable explanatory variables as in the separate models: rainfall in the previous 3 months, initial DBH and the binomial variable indicating fruit production (Table 2). This model similarly demonstrated less growth when trees were reproductively active. The significance of a cubic effect of DBH captured both the significant linear positive effect in the juvenile model, and the significant concave quadratic effect in the adult model. For smaller trees, increases in DBH led to significant increases in growth rates up to 50 cm DBH, followed by a flattening of rates with less certainty at the tail end of the curve (Fig. 3, solid line). Additionally, trees with crowns in dominant and co-dominant positions exhibited virtually the same growth rates (13.25 ± 0.82 and $12.90 \pm 1.35 \text{ m}^2 \text{ year}^{-1}$, respectively), intermediate trees grew at lower rates ($8.75 \pm 1.79 \text{ m}^2 \text{ year}^{-1}$), and suppressed trees grew slowest ($1.45 \pm 2.73 \text{ m}^2 \text{ year}^{-1}$). This varied by reproductive maturity (juvenile vs. adult) (Fig. 4), with trees moving into the dominant classes as they increased in girth (Fig. 1). Corroborating this finding, an alternate competing model which had similar AIC values to the one presented above, only included two highly significant ($P < 0.0001$) explanatory variables: rainfall in the previous 3 months and canopy position.

Fig. 1 Annual basal area growth rates (mean ± SE) of *Bertholletia excelsa* trees ($n = 190$) by diameter class and corresponding proportion of individuals in each class in four categories of canopy position. DBH Diameter at breast height

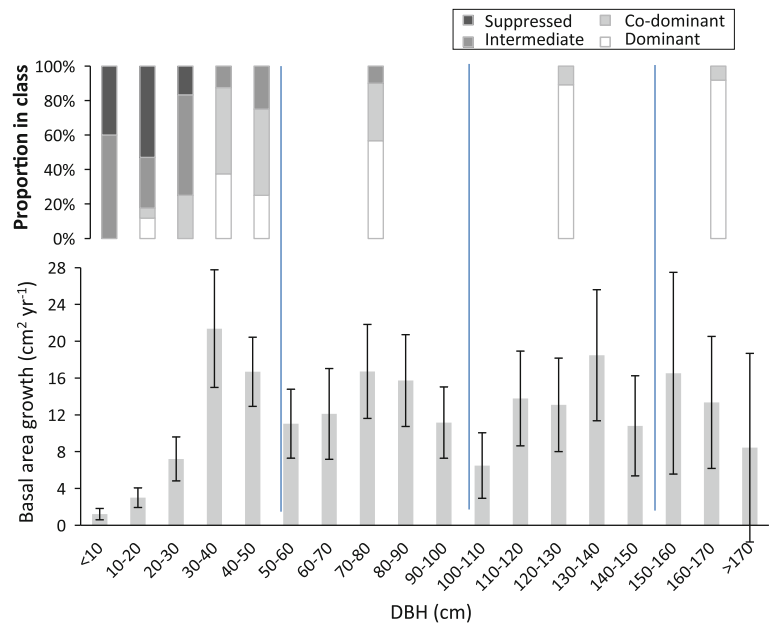


Table 1 Estimates of fixed effects, SE and P -values for the *Bertholletia excelsa* juvenile and adult models of basal area increment (BAI) ($\text{cm}^2 \text{ year}^{-1}$)

Effect	Juveniles ^a			Adults ^b		
	Estimate	SE	$P > t $	Estimate	SE	$P > t $
Intercept	-20.508	2.813	<0.0001	10.5623	6.8195	0.1240
Rainfall previous 3 months	0.02300	0.0015	<0.0001	0.02813	0.001326	<0.0001
Initial DBH	0.702	0.075	<0.0001	-0.2423	0.1286	0.0617
Initial DBH ²				0.001104	0.000578	0.0584
Fruit production initiated	-8.873	2.672	0.0029	0.0017		
Crown form (good vs. poor)	4.532	2.400	0.0682	0.0654		
Crown form (tolerable vs. poor)	-1.2939	3.054	0.6467	0.6868		
Average fruit production ($\text{no. tree}^{-1} \text{ year}^{-1}$)				13.2271	3.8542	0.0008
Fruiting in subsequent year				0.01217	0.004411	0.0059
Liana load >25 %				-2.6360	1.3583	0.0546
Soil Ca				8.6131	2.5416	0.0009
Soil P				-1.0058	0.3865	0.0104
Soil Ca + Mg				-2.3401	0.9353	0.0136
Soil C				3.7810	2.0886	0.0727

^a Juveniles include individuals of $5 \text{ cm} \leq \text{diameter at breast height (DBH)} < 50 \text{ cm}$ ($n = 54$)

^b Adults include individuals $\geq 50 \text{ cm DBH}$ ($n = 138$)

Relationship between adult BAI and fruit production by diameter class

Growth models formulated for each of three 50-cm size classes ($50 \leq \text{DBH} < 100 \text{ cm}$, $100 \leq \text{DBH} < 150 \text{ cm}$, $\text{DBH} \geq 150 \text{ cm}$) provided finer insights into growth dynamics as *B. excelsa* trees of reproductive size increased in girth (Table 3). As with all previous models examined, rainfall in the previous 3 months had the strongest

relationship with BAI. Also common across all size classes, basal area growth of trees in one year was positively associated with fruit production in the subsequent year. While Inverse of average fruit production was implicated in the adult-only growth model, this refined analysis further suggested that this relationship only applied to the smallest size class, whereby only the best adult growers in the 50 to 100-cm DBH class produced fewer fruits across all years. Liana loads and crown variables were not significant for

Fig. 2 Patterns of mean fruit production (*upper panel*) and basal area growth rates (*lower panel*) of *B. excelsa* adults ($n = 136$ individuals ≥ 50 cm DBH) closely follow monthly precipitation over a 5-year period

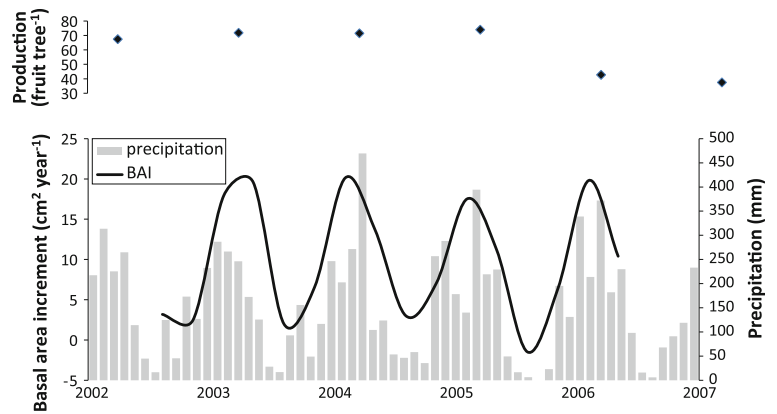


Table 2 Overall model of BAI with juvenile and adult *B. excelsa* data combined ($n = 192$). For abbreviations, see Table 1

Effect	Estimate	SE	df	t-value	P > t
Intercept	-19.202	3.613	185	-5.31	<0.0001
Rainfall previous 3 months	0.0279	0.001114	40	24.95	<0.0001
Initial DBH	0.9132	0.1938	185	4.71	<0.0001
Initial DBH ²	-0.00868	0.0020	185	-4.34	<0.0001
Initial DBH ³	0.000026	6.615×10^{-6}	185	3.86	0.0002
Fruit production present	-9.5824	3.5673	185	-2.69	0.0079

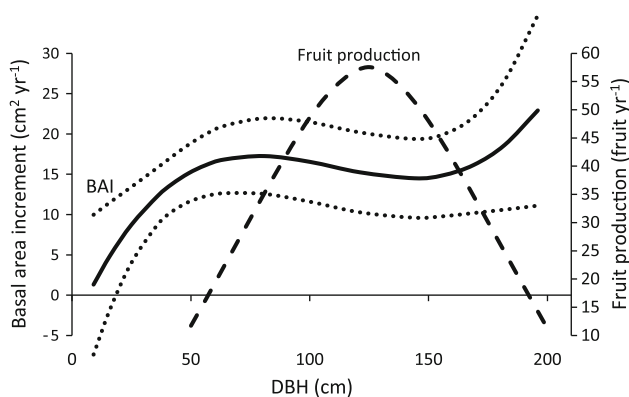


Fig. 3 Model of basal area increment (BAI; *continuous line* with 95 % confidence intervals) and annual fruit production (*dashed line*) of *B. excelsa* trees ($n = 190$) by tree diameter. DBH Diameter at breast height

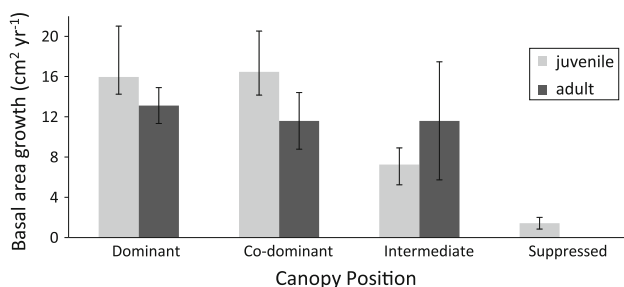


Fig. 4 Basal area growth rates (mean \pm SE) of juvenile ($n = 54$) and adult *B. excelsa* trees ($n = 136$)

any of the three size class growth models, while some soils variables were significant for the 50 to 100- and 100 to 150-cm DBH classes (Table 3, $P < 0.001$).

Discussion

Most studies examining the cost of reproduction focus on radial and/or crown growth of mature trees of masting species well established in temperate forest canopies (Herrera et al. 1998; Koenig and Knops 2000; Obeso 2002). To reach those canopy heights, light is considered the most important environmental driver, and an entirely different line of research has focused on competition, species' adaptations to shade, gap and overall forest dynamics to get to the top (Denslow et al. 1990; Clark and Clark 1992; King et al. 2005). Still other studies meticulously hone in on one key factor to understand tropical tree growth, such as rainfall (Brienen and Zuidema 2005) or light (Rüger et al. 2011a). There have been few growth analyses that have integrated diverse biotic and abiotic factors over the different development stages of any given species, perhaps because of the logistical difficulties in obtaining such data. We sought to capture the effects of rainfall, tree size, direct competition (via lianas), light availability (via canopy position), photosynthetic capacity (via crown form and size), soil chemical attributes, and most importantly, fruit production, on radial growth of a

Table 3 Estimates of fixed effects, SEs, and *P*-values for adult models of annual BAI (cm² year⁻¹) by diameter class (50 ≤ DBH < 100 cm, 100 ≤ DBH < 150 cm, DBH ≥ 150 cm). For abbreviations, see Table 1

Effect	50 ≤ DBH < 100 cm			100 ≤ DBH < 150 cm			DBH ≥ 150 cm		
	Estimate	SE	<i>P</i> > <i>t</i>	Estimate	SE	<i>P</i> > <i>t</i>	Estimate	SE	<i>P</i> > <i>t</i>
Intercept	1.9835	2.8576	0.4899	-13.074	3.9543	0.0016	-0.9335	3.44	0.7869
Rainfall previous 3 months	0.03367	0.001691	<0.0001	0.02268	0.002077	<0.0001	0.02722	0.005713	<0.0001
Average fruit production (no. tree ⁻¹ year ⁻¹)	11.4348	4.6717	0.0172						
Fruiting in subsequent year	0.02509	0.01089	0.0216	0.00899	0.004804	0.0619	0.07482	0.02884	0.0133
Soil P	-1.3465	0.5223	0.0125						
Soil C				7.9356	2.7632	0.0057			
Soil Ca				6.7103	1.5052	<0.0001			

long-lived dominant tropical species, *B. excelsa*. Although we only followed cohorts of trees over 6 years, our sample included individuals covering a range of diameters as a surrogate to capture growth–reproduction tradeoff dynamics over the life span of this large, long-lived canopy emergent species.

What factors influence growth over the life span of long-lived trees?

We observed variation in basal area growth rates over seasons as well as over the life span of *B. excelsa*. Annual rainfall patterns generated a sinusoidal growth curve with expected negative growth registered, as is common to tropical regions with precipitation-induced seasons (Pélissier and Pascal 2000). BAI patterns over the life span of *B. excelsa* revealed a sharp increase in growth rates of small-diameter juveniles with increasing DBH, followed by a flattening of growth at larger diameters (Fig. 3). What variables seemed to influence this comprehensive growth pattern? Among the environmental factors that influence tropical plants, light availability is likely to be the resource most frequently limiting growth, survival and reproduction (Chazdon et al. 1996). Our findings support this emphasis on light resources. Of all trees, BAI rates of individuals <20 cm DBH were the lowest; most of these trees were suppressed and almost all the rest had intermediate crown positions (Fig. 1). Subsequent increases in girth were accompanied by increases in BAI rates, as very small trees with small crowns transitioned to larger-sized individuals that could produce greater quantities of carbohydrates to support greater growth. Some of these small trees obtained dominant and co-dominant positions, while others had not yet obtained these favorable canopy levels. Based on tree ring analysis of six tropical tree species, Brienen and Zuidema (2006) observed that the largest variation with the passage of time from one 10-cm DBH class to the next was when trees were <20 cm DBH. At this stage, light

availability, represented by canopy position, is critical and either promotes or stagnates growth (Pélissier and Pascal 2000). Suppressed trees completely fell out of our data set for individuals ≥30 cm DBH, while trees with intermediate crown positions were no longer present above 100 cm DBH (Fig. 1). While we only measured radial growth, juveniles in these old-growth forests also are allocating significant biomass to reach the canopy, and even our 50 to 100-cm DBH reproductively mature adults continued to grow in height to attain co-dominance/dominance—the only canopy position categories of trees >100 cm (Fig. 1). BAI rates of these canopy trees flattened out with no significant growth differences between adult size classes (Fig. 3), presenting more constant growth rates over time than other long-lived Amazonian species (Brienen and Zuidema 2006). In fact, BAI rates of canopy trees >100 cm in this study were more constant than those of tropical species in general; Clark and Clark (1996) reported decreasing BAI rates with increasing diameter for very large trees of five emergent species in Costa Rica. Nonetheless, trees in senescence tend to grow more slowly (Rüger et al. 2011b), a conclusion that coincides with our field observations of individuals just prior to mortality.

Upon reaching the canopy and attaining sizeable girth, light limitations cede importance to other variables. For example, adult *B. excelsa* trees with more than 25 % of their crown covered with lianas grew slower in basal area than those with less, since lianas compete directly with trees for both above- and below-ground resources (Schnitzer and Bongers 2002). Consistent with other tropical tree growth studies (Vieira et al. 2004), soil properties and hydrological regime were also implicated in explaining adult *B. excelsa* growth rates. Indeed, rainfall (more precisely, rainfall in the 3 months prior to diameter growth measurements) was the only and strongest measured variable implicated in all our *B. excelsa* growth models, regardless of ontogenetic stage. In sum, with the exclusion of water availability, our models suggest that as *B. excelsa*

trees increase in basal area over their life span, growth limitations shift from the predominating influence of light to other abiotic and biotic variables. We now turn to the influence of reproduction, which becomes an increasingly important cost in resource allocation budgets as trees mature (Obeso 2002).

Do basal area growth–reproduction tradeoffs change over tree ontogeny?

Trees generally show a long period of pre-reproductive growth (Thomas 2011), and *B. excelsa* is no exception. Of our 54 juvenile trees (<50 cm DBH), only nine had initiated fruit production, and all but one of these were in the 40- to 50-cm DBH class. Some of these juveniles could be over 100 years old, given that Brienen and Zuidema (2006) estimated that the mean age of 12 *B. excelsa* trees at 60 cm DBH was 166.4 years. At this stage, resources are allocated to radial and height growth over reproduction, and our basal area growth model of this juvenile class demonstrates that those few trees producing fruits present slower BAI rates (Table 1). Our BAI model for 50 to 100-cm DBH trees implicates the same trend and growth–reproduction tradeoff (Table 3). Although investment in growth does not necessarily imply a causal tradeoff with reproduction (Knops et al. 2007), in this size class, BAI rates begin to flatten out with increases in girth, height growth continues depending on canopy position, and fruit production is on the increase (Fig. 3).

Trees in the 100 to 150-cm DBH range present a different growth and reproduction pattern. Fruit production peaks (Fig. 3), yet no fruit production variable is implicated in explaining basal area growth of trees in this size class; solely rainfall and soil variables have explanatory significance (Table 3). BAI rates are no different between very high and very low producers (Table 4). These large trees dominate with robust girth, supporting tall stems that rise to or above the canopy (Fig. 1). They seem to have the structural potential to both produce well and grow, and our data demonstrate no tradeoffs between BAI and reproduction, suggesting that these two traits may be independently influenced at this stage by other abiotic (i.e., rainfall and nutrient availability) and biotic (e.g., genetic makeup, lianas) factors. Knops et al. (2007) similarly rejected the growth–reproduction tradeoff hypothesis for their masting oak populations studied over a 13-year period, and also suggested that environmental factors influenced both fitness traits. Still closer examination of fruit production within this 100 to 150-cm DBH size class reveals that reproduction rates do differ significantly by crown size. Trees that produce very high numbers of fruits (>300 fruits tree⁻¹ year⁻¹) have enormous crowns that are almost twice as expansive as those that produce ~3 fruits tree⁻¹ year⁻¹

(Table 4). Crown size indicates photosynthetic capacity and potential carbohydrate production, and serves as an obligatory structural support for fruit production. However, we did not monitor branch growth, and thus cannot assess carbohydrate production at these lower modular levels against the potentially competing growth and reproduction sinks at play in the crowns of these trees over their life spans—dynamics explored by Sánchez-Humanes and Sork (2011) who demonstrated allocation nuances to vegetative and reproductive structures at such lower hierarchical canopy levels in a masting oak species. Still, in our study species, it is clear that previous resource allocation to *B. excelsa* branches and shoots to create large crown structures contributed to enhanced reproduction, but not necessarily radial growth (Table 4).

Our largest trees (150–200 cm DBH) follow a fairly similar pattern. Though the sample size for this class is small ($n = 14$), basal area growth in any given year is significantly positively related to fruiting in the subsequent year (Table 3), suggesting that trees are perhaps building structure in anticipation of fruit formation; BAI and fruit production go hand in hand at this stage. Thus, while environmental conditions (i.e., water availability via rainfall) continue to influence tree performance, we conclude that individuals in this size class that are in good health and with sound genetics continue to grow and produce well, while we speculate that the opposite holds for those in senescence. Senescence is a particularly plausible state for some in this size class, given that our tree sample includes trees with the largest possible diameters and possibly the oldest trees within our population. Thomas (2011) suggests that negative reproductive effects on growth increase with tree ontogeny, likely contributing to age-related declines, perhaps the final growth–reproduction tradeoff. Our empirical growth data on these largest *B. excelsa* trees, however, do not necessarily suggest a decline in radial growth (Figs. 1, 3), but rather, in reproductive output (Kainer et al. 2007).

Theoretical implications for understanding tradeoffs

This study contributes to our theoretical understanding of growth–reproduction tradeoffs by filling a gap in our understanding of long-lived non-masting tropical trees over their life spans. Our results indicate that the hypothesis that current growth is sacrificed for reproduction does not hold over tree life span. While these tradeoffs clearly exist during early life stages, the effects of reproductive allocation are not as important for *B. excelsa* as it increases in size and maturity. Trees present a lengthy period of growth prior to reproduction; evolutionarily, growth can be viewed as the means to achieve reproductive success (Thomas 2011). This growth-only stage is characterized by

Table 4 Average production, basal area growth, diameter at breast height (DBH) and crown size (mean \pm SE) of *B. excelsa* individuals in the best producer size class ($100 \leq \text{DBH} < 150$ cm) by production class

Production class	Number of trees	Production (fruits year ⁻¹)	Growth (cm ² year ⁻¹)	DBH (cm)	Crown size (m ²)
1. Very high	12	302.6 \pm 12.6 a	20.4 \pm 3.1 a	119.9 \pm 3.8 a	1,739.5 \pm 134.5 a
2. High	15	111.7 \pm 11.2 b	15.9 \pm 2.8 a	122.2 \pm 3.4 a	1,337.5 \pm 120.3 ab
3. Medium	12	66.6 \pm 12.6 c	12.5 \pm 3.0 a	118.5 \pm 3.8 a	1,258.8 \pm 134.5 b
4. Low	9	22.6 \pm 14.5 cd	17.0 \pm 3.5 a	138.5 \pm 4.4 b	1,209.8 \pm 155.3 b
5. Very low	12	3.1 \pm 12.6 de	21.1 \pm 3.2 a	116.6 \pm 3.8 a	979.8 \pm 140.4 b

Values in a column with the *same letter* are not significantly different based on a test of means at $P < 0.05$, except for the crown size column in which: (1) high vs. medium fruits, and (2) very high vs. medium and low fruits are significantly different at $P < 0.10$

Very high 182–508 average fruits, *high* 88–142 average fruits, *medium* 52–79 average fruits, *low* 10–35 average fruits, *very low* 0–9 average fruits

limitations in light capture (Poorter and Kitajima 2007) as evidenced by the significant influences of initial DBH and crown form on *B. excelsa* juvenile growth as well as the predominance of the smallest juveniles in the suppressed and intermediate canopy position categories. Once attaining a size significant enough to support reproduction, however, preferential allocation of resources to reproduction begins. Trees that initiate fruiting demonstrate reduced basal area growth rates, suggesting a tradeoff between current growth and reproduction. Trees in the 50 to 100-cm DBH size class also present a tradeoff between radial growth and fruiting in the current year, with BAI rates decreasing and fruit production increasing with increases in girth. With the increased passage of time and tree maturity, however, this tradeoff phase slowly shifts to one where growth in girth and reproduction act fairly independently. Both fitness traits are fundamentally influenced by environmental factors, although not necessarily in the same way. With *B. excelsa*, water availability was a consistent explanatory variable for basal area growth across all diameter classes. Similarly, year-to-year variability (a surrogate for environmental influences) was also a strong predictor of reproductive output in these same adults (Kainer et al. 2007). The key environmental variable of light is no longer a limiting factor once this canopy emergent species reaches dominant and co-dominant positions. Canopy position does not explain either adult radial growth (this paper) or fruit production (Kainer et al. 2007), while soil nutrient availability is implicated in both. Biotic factors also differentially influence growth and production. In examining our model species, measured variables that significantly explained fruit production such as crown size (a strong correlate to DBH) and form (Kainer et al. 2007), were not significant explanatory variables for adult basal area growth. In contrast, liana load seemed to have explanatory importance for both. Examining these biotic and abiotic influences coupled with allocation patterns over the life span of other species is necessary, because their relative importance varies as a function of

species (Thomas 2011). Many factors beyond simplistic one-on-one tradeoffs explain variation in growth and fruit production, and further research would shed new light on this important relationship.

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