Population Structure and Fruit Production of Carapa guianensis (Andiroba) in Amazonian Floodplain Forests Implications for Community-Based Management

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Population Structure and Fruit Production of *Carapa guianensis* (Andiroba) in Amazonian Floodplain Forests: Implications for Community-Based Management

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Abstract

Andiroba (*Carapa guianensis*) is a multiple-use tree species that plays a crucial socioeconomic role across thousands of Amazonian traditional and indigenous communities. In the floodplain forests of the Amazon estuary, we partnered with local forest managers to investigate *C. guianensis* ecological parameters, addressing seed production rates, tree density, and size class structure across a range of environmental conditions and forest use history. *C. guianensis* population structure was measured in three forest types: *baixio*, *restinga*, and *terra preta*, differentiated by tidal influence, species dominance and composition, and edaphic conditions. We found significant differences across forest types, whereby seedling and sapling densities were higher in terra preta and adult densities were higher in baixio. Adult densities were 28.7, 23.0, and 19.5 trees/ ha, and seedling densities were 22.9, 105, and 151 trees/ha in baixio, restinga, and terra preta forest types, respectively. Seed production rates varied significantly across forest types, year, size class, crown form, and crown illumination. There were higher numbers of viable seeds in terra preta versus baixio (5.5 kg and 2.6 seeds/tree/year, respectively) as well as more trees with better crown forms, more light, and larger diameter sizes. Long-term patterns of community timber management intensity by forest type significantly influenced both population structure and population-level seed production. Nonetheless, assessment of seed production for the total population suggests that the local community was collecting less than 1% of the viable *C. guianensis* seeds produced annually within community forest lands. This study illustrates the potential of management to impact the sustainability of an important multiple use species and shows the impact that community conservation planning and action can have on future natural resource availability.

Sustainable use of tropical forests is advocated as a strategy that reconciles biodiversity conservation, poverty alleviation, and economic development (Bawa & Seidler, 1998; Dickinson, Dickinson, & Putz, 1996; Pearce, Putz, & Vanclay, 2003). The Brazilian government has designated millions of hectares as sustainable use areas and public production forests (Bauch, Sills, Rodriguez, McGinley, & Cubbage, 2009); yet, sound ecological understanding to guide sustainable harvest of economically valuable species is often lacking. Moreover, it is estimated that more than a third of the tree species harvested in the Brazilian Amazon also have nontimber

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uses (Herrero-Jáuregui et al., 2013). *Carapa guianensis* (Meliaceae; Brazilian name = *andiroba*), valued for both its high quality timber and seed oil, is a model species for such a sustainable-use approach. Medicinal oil extracted from *C. guianensis* seeds constitutes one of the Amazonia's most widely used natural remedies (Shanley & Londres, 2011). Market demand for both locally extracted seeds and oil has been created by pharmaceutical and cosmetic companies, while *C. guianensis* populations have experienced increasing logging pressure, coincident with declining mahogany populations (Grogan et al., 2010). Research on *C. guianensis* population biology is available to guide sustainable management (e.g., Henriques & Sousa, 1989; Klimas, Kainer, & Wadt, 2007; Klimas, Kainer, Wadt, et al., 2012; Plowden, 2004; Sist et al., 2014), but most studies have had small sample sizes, and none have been conducted in the diverse forest types encountered in floodplain (*várzea*) forests of the Amazon estuary.

To design sustainable management systems for timber and nontimber forest products (NTFPs), species structure and production potential need to be assessed on a population level and across forest types to provide insight into population dynamics such as recruitment history, shade tolerance, and regeneration potential (Hartshorn, 1980; Peters, 1996). Moreover, in intensively used forests across centuries—as is the case in most Amazonian floodplain forests (Little, 2001)—tree population structures reflect land-use legacies that condition current management (Anderson, 1990).

Much of the effort toward sustainable forest management has focused on industrial-scale timber harvests (see Verssimo, Cochrane, & Souza, 2002). Less has been done to understand the ecology, management, and production potential of key forest resources within a community context, even though local communities in developing countries own or manage approximately 31% of the world's forests (Rights and Resources Initiative, 2012). Within a sustainable-use reserve in the floodplain forests (várzea) of the Amazon estuary, we partnered with a local forest-dwelling community to explore *C. guianensis* ecology. We asked (a) what are the density and size class structure of *C. guianensis* within the floodplain forests across the range of environmental conditions and forest use history? (b) What are *C. guianensis* seed production rates, and what main factors explain observed production variation? Herein, we present an initial assessment of *C. guianensis* management potential within the context of a sustainable-use reserve.

Study Species

C. guianensis Aubl. (Meliaceae) is a canopy tree species, attaining 30 to 50 m height at maturity. It occurs across the Amazon basin, and in Central America, and the Caribbean islands (Kenfack, 2011; Pennington, 1981; Plowden, 2004). Although it grows at elevations up to 1,400 m above sea level (MASL) and on dry sites (Klimas et al., 2007; Sampaio, 2000), *C. guianensis* thrives in wet lowlands (McHargue & Hartshorn, 1983; Pennington, 1981; Plowden, 2004). Its fruit is a four-valved woody capsule, 9 to 13 cm in diameter, with each valve containing one to four seeds, 4 to 5 cm in diameter (Kenfack, 2011; Pennington, 1981; Sampaio, 2000). Seed dispersal varies by environment; in flooded forests, the buoyant seeds are commonly water dispersed, while in *terra firme* forests, scatter-hoarding rodents disperse the nutrient-rich seeds (McHargue & Hartshorn, 1983). In Eastern Amazonia, flowering occurs from August to October and fruit fall between March and August (Leão & Carvalho, 1998). The species shows high phenotypic plasticity (Leite, 1997); and in some regions of Amazonia, multiple species of *Carapa* are lumped under the common name andiroba. Nonetheless, in our study area, previous botanical collections (Londres, 2004) and observed seedling morphology confirmed the presence of the single species, *C. guianensis* (Fisch, Ferraz, & Rodrigues, 1995).

Study Site

Our study was conducted in the 64,000 ha Itatupã-Baquiá Sustainable Development Reserve (SDR) in Gurupá County, Pará State, Brazil. Várzea forests cover most of this region, which has a long history of forest use by riverine communities (Little, 2001). While the 2005 SDR designation granted greater land and resource tenure security, it also precipitated a greater need to develop livelihood systems based on sustainable production. The reserve focal community of São João do Jaburu is located on a large island in the mouth of the Amazon River. Average annual rainfall is approximately 2.5 m (Projeto Radar da Amazônia [RADAM], 1974), with a pronounced dry season from July to November, and an estuary flood pulse linked to daily inundations and annual flooding (Wittmann, Junk, & Piedade, 2004). Elevation is less than 5 MASL, and even modest topographic variation has a pronounced effect on the flooding regime (amplitude and duration), causing formation of several forest types (Kalliola, Salo, Puhakka, & Rajasilta, 1991; Wittmann et al., 2004).

Superimposed on the geophysical variation among forest types are patterns of forest use history (primarily timber and NTFP extraction), which also vary by forest type and proximity to rivers and residences. In contrast to most terra firme areas, where logging is recent and impacts are easily quantified (e.g., stumps and canopy gaps are still visible), the long history of várzea management often can only be partially reconstructed through resident interactions. For example, using interviews and participatory mapping exercises (Londres, 2009), residents in our study

area unanimously indicated that logging had been more intensive in forest types nearest to the main river. Such combined anthropogenic and environmental gradients are the norm in the Amazon estuary region.

Socioeconomic Framework

Following the end of the second and short lived boom of the Amazonian rubber economy (precipitated by World War II) in the 1950s, rubber barons left the area and the *caboclo* population, dispersed along riversides, continued their adaptive livelihood strategies—which included fishing, hunting, small-scale farming, and extraction of NTFPs such as *C. guianensis* and *Virola surinamensis* for seed harvest, as well as an assortment of resins (Hiraoka, 1995; Little, 2001). Logging activities across the estuary region expanded from 1950s onward, when the first veneer mills were established with foreign capital; *V. surinamensis* and *C. guianensis* were the most exploited species destined for the export market (Barros & Uhl, 1995). In the 1970s, palm heart exploitation from *Euterpe oleracea* represented another economic boom in the Amazon estuary, and hundreds of canning factories established in the region in the 1990s (Pollak, Mattos, & Uhl, 1995). The açaí fruit (*E. oleracea*) economy emerged in the 1970s in response to regional population growth and urban expansion. Since the mid-1990s, açaí fruit has reached national and international markets (Brondízio, Safar, & Siqueira, 2002). Because of poor drainage and daily floods, agricultural and cattle production is limited within várzea forests (Little, 2001).

During our study period of 2007–2008, the main economic activities of the riverine populations centered on açaí fruits, açaí palm heart, and timber extraction of mainly *V. surinamensis, C. guianensis, Platymiscium filipes, Cedrela spp.,* and *Mora paraensis*. The remaining productive and subsistence activities extended to collection of NTFPs (such as fiber, fruits, firewood, seeds, honey), fishing, hunting, gardening, and raising of small animals. Shifting cultivation was restricted by the várzea flooding regimes and conducted as a traditional agroforestry system, whereby annual crops were planted with perennial crops, mostly fruiting trees. However, not all families regularly engaged in these small agricultural systems; only 64% of community families participated in this activity in 2004 (Londres, 2004).

Timber exploitation in the community was conducted at low intensities and without the use of heavy machinery: Trees were felled with a chainsaw, and logs dragged manually to and transported via streams. As such, trees growing in proximity to the river were more intensively exploited due to easy access. In the early 2000s, timber within the community was harvested at an average intensity of 4 m^3/ha/year (Carlos Augusto Ramos, personal communication, May 25, 2017).

Traditional Uses of C. guianensis Seeds

In the Amazonia estuary region where Sao João do Jaburu is embedded, the tradition of *C. guianensis* oil extraction for medicinal and market purposes has occurred for generations. While the rubber economy dominated, women extracted *C. guianensis* oil in high quantities (~50l per family per year) for local use (medicine, repellent, and soap) and as a commodity sold to the soap industry (Londres, 2004). Although they had their land titled, community members were aware of the fact that their current resource use patterns, particularly those based on tree felling for timber and palm heart, had negative impacts on the ecology and productivity of the forest ecosystems on which their livelihoods depended. Consequently, they sought to more effectively plan their forest management activities. In this process, the potential commercialization of NTFPs arose as a promising alternative to timber and palm heart extraction that could improve livelihoods, while generating fewer negative impacts on the forest. In that context, *C. guianensis* seed oil garnered great community attention due to increasing market demand in the region. With external nongovernmental organization support, in 2003, the community's women's association prepared a *C. guianensis* oil sustainable management plan (Londres, 2004).

As a way of adapting management techniques to local traditions and finding ways to optimize *C. guianensis* seed collection, this group of women monitored weekly collection quantities and patterns (Londres, 2004). Of total seeds collected, 61% were collected in the river (by canoes) and 39% on land (below trees). This research revealed that seed collection performed on land yielded 3 times more seeds than collected in the river and that the former was almost always synergistically related to other important productive activities (i.e., hunting, açaí harvests). Despite the fact that only women produced *C. guianensis* oil, whole families participated in seed collection, with 32% of the total collected by children. By 2004, almost one ton of seeds were collected by the women's group, which yielded 200l of oil produced and sold to a pharmaceutical industry. While this contract was only in force for 4 years (2002–2005), the community subsequently established a contract with a cosmetics company, for *C. guianensis* seeds along with other forest seeds such as *V. surinamensis* and *Astrocaryum murumuru*.

Method

Forest-Type Mapping

Forest types were identified through a participatory mapping process that combined satellite image analysis with traditional ecological knowledge. The community jointly classified different forest types and identified spatial

Table 1. Description of Four Main Forest Types at São João do Jaburu, Gurupá, Pará, Brazil.

Forest type	Inundation pattern	Location of forest zone with respect to the river	Harvest history
Baixio	Influenced by both tide and rainy season. During the rainy season (January–July), inundation occurs daily with the tide, two times a day and 3 hr of length each time	30–1,500 m from the sides of the river, drained by a dense stream system	Intensively harvested for timber
Restinga	Influenced by both tide and rainy season. During the peak of the rainy season (February–April), inundation occurs with spring tides (full and new moon), on average 5 days a month, twice a day for 2–3 hr duration each event	At riverside	Intensively harvested for timber
Igapó	Influenced by both tide and rainy season. Permanently flooded 9 months a year (November–July), water level varying with tide	80–3,000 m from the sides of the river	Intensively harvested for timber and palm heart
Terra Preta	Influenced by rainy season only. Seasonally flooded during the peak of the rainy season (February–April). No direct tidal influence	Starts 500 m upstream from main stem of Jaburu river	Lightly harvested for timber, intensively harvested for palm heart

patterns of species distribution and resource extraction. These community-generated maps were subsequently used to formulate a stratified sampling design for forest inventories and ecological studies. Although mapping and quantitative inventories included all species of economic importance, the community prioritized *C. guianensis* on which to conduct the detailed ecological studies presented herein. The participatory mapping process identified four forest types in São João do Jaburu—*baixio*, *restinga*, *igapó*, and *terra preta* (a local term with no relation to so-called "black earth" soils), differentiated by tidal influence, species dominance and composition, and edaphic conditions (Table 1). Local extractivists reported harvesting *C. guianensis* for timber more intensively in baixio and restinga forest types over the past four decades. While *C. guianensis* was also logged in terra preta, this forest type was less intensively exploited because of its distant location from the river.

Population Structure

Forest inventories were conducted from December 2005 to September 2006, providing the following estimates of *C. guianensis* (and other economic species) populations in each forest type: (a) stem density and size class distribution and (b) individual tree characteristics relevant to fruit production. Using the forest-type map, random sampling locations were selected to provide spatially independent and well-distributed replicates of forest types across the várzea landscape. Six 1-ha (500×20 m^2) plots were

installed within each forest type, totaling 24 ha inventoried. The following data were collected for each *C. guianensis* individual ≥ 10 cm dbh (diameter at breast height; measured 1.4 m above ground level): (a) dbh; (b) estimated commercial height (height to the first major branch); (c) liana load: $\leq 10\%$ of crown covered; 10% to 60% of crown covered; or $>60\%$ of crown covered; (d) crown illumination: no direct light, some overhead or side light, or full overhead light; (e) crown form: perfect—complete circle and no physical damage (major limbs broken), good—some damage but at least half-crown present, or poor—less than half-crown present; and (f) canopy position (lower, midstory, or upper).

Since *C. guianensis* did not occur in the igapó forest type in the initial inventory, we revisited only the 18 1-ha plots in baixio, restinga, and terra preta forests from May to July 2008 to gather information about individuals >50 cm height and <10 cm dbh. While all individuals with $2 \leq$ dbh <10 cm dbh were measured in all 18 plots, seedlings <2 cm dbh and >50 cm height were measured in 10 nested 7×25 m^2 subplots within each plot. For each individual, we recorded the six tree-level variables and noted whether it occurred in a forest gap, building forest phase, or mature forest phase (Clark & Clark, 1992).

Fruit and Seed Counts

Floodplain forests of the Amazon estuary region are subject to daily high tides that penetrate the forest and carry seeds downriver. Therefore, to estimate fruit production,

we used two sampling regimes in all three forest types: (1) an extensive sample of the population of trees ≥10 cm dbh (*n* = 507 trees) with monthly crown observations of fruit production; and (2) a smaller intensive sample (*n* = 49) of fenced-off individuals in which seed counts were conducted biweekly from January to September of 2007 and 2008.

Extensive sample. In January and February 2007, we installed 21 line transects stratified by forest type (seven per forest type where *C. guianensis* occurred). For each transect, the starting point and angle of orientation were randomly selected, subject to the constraint that transects remained entirely within a single forest type. We first estimated population densities in each size class (10–30, 30–45, 45–60, 60–90, and ≥ 90 cm dbh) and forest type from the forest structure inventory data and determined a sampling rate for each. We searched for *C. guianensis* trees ≥10 cm dbh within a 100 m strip on each side of the line transect, creating a strip plot 200 m wide. For each size class, every *i*th tree encountered was included in the extensive sample pool, with *i* determined from the estimated population densities by size class and forest type (details in Appendix A). This method of selection produced an unbiased and well-distributed minimum sample of 40 trees per size class and forest type (*n* = 507 trees in total) and allowed us to develop a model of individual tree production that gave precise estimates by size class. Estimated population densities by size class found in the forest structure inventory data were used to scale production estimates up to population levels.

For each of the 507 trees in the extensive sample, we assessed the six tree-level variables and conducted monthly monitoring from March to September 2007 and from January to September 2008 to estimate fruit production in two steps. First, we counted all fruits in the visible portion of the crown with binoculars, and then we estimated the proportion of the visible crown to arrive at the extrapolated estimate of the total number of fruits in the entire crown (Gullison, Panfil, Strouse, & Hubbell, 1996; Snook, Cámara-Cabrales, & Kelty, 2005).

Intensive sample. To verify extensive sample estimates, another sample of 49 trees was randomly selected and monitored from January to September of 2007 and 2008. Six trees were monitored in each of the three size classes (10–30, 30–45, and 45–60 cm dbh) for all forest types and two additional classes (60–90 and ≥90 cm dbh) for terra preta forest type only. The ground below the crowns of the 49 selected fruiting adults was cleared of underbrush and fenced using nylon fishing nets. Nets were secured below ground at close intervals to prevent seed escape and exclude seed predators (mostly rodents) from consuming fallen seeds. Each sample tree was monitored biweekly to count seed production and maintain fencing. Assessing trees in the intensive sample by both biweekly seed counts on the ground and by monthly fruit counts in the crown allowed us to parameterize a model for relating visual estimates from the small, intensive sample to those of the large, extensive sample.

Data Analyses

Population Structure

Histograms of tree dbh were constructed by forest type to visually assess differences in population structures. Because size-class distributions do not meet assumptions of normality and homoscedasticity required by most parametric statistical methods, differences by forest type were tested through nonparametric methods using the Statistical Analysis System (SAS) procedure PROC LIFETEST. Wilcoxon and log-rank statistics were calculated to compare the frequency distributions of individuals ≥2 cm dbh, with forest type as an explanatory variable. To assess differences in seedling densities (<2 cm dbh) across forest types, we utilized Poisson regression via the SAS procedure PROC GLIMMIX. This properly accounted for the nonnormal, strictly nonnegative nature of the count data inherent in describing densities. To assess differences in the distribution of trees ≥10 cm dbh in relation to crown form, crown liana load, crown illumination, forest phase, and canopy position by forest type, univariate χ^2 tests of independence were performed for each of these classification variables.

Seed Production

Using the intensive sample (49 fenced trees), we estimated a predictive equation for relating fruit counts in the crown (fruits/tree) to seed counts on the ground (kg viable seed/tree). Seeds that were mature and not damaged by larvae or mammal predation were considered viable. The total number of viable seed/tree/year for trees within the intensive sample was highly correlated to the maximum number of fruits observed in the crown ($r = .6$; $p < .0001$), but the strength of this correlation differed by year because annual crown counts for both intensive and extensive monitoring started in different months (March for 2007 vs. January for 2008). Using the SAS procedure PROC MIXED, we estimated total seed production on the ground separately in each year (kg viable seed/tree/year) as a function of maximum number of fruits in the crown, forest type, and the six tree-level variables. To ensure that model assumptions were met, the response variable was log-transformed. Nonsignificant variables were dropped sequentially (based on *p* values), and model results were compared using Akaike's information criteria (Akaike, 1973). The final annual predictive models included only the

maximum number of fruits in the crown (Table A1). Modeling assumptions were verified through residual analyses.

Using the predictive model for each year, we then estimated the seed production for each tree in the extensive sample (507 trees). Because the seed production model was derived from productive trees only, we excluded non-producing trees from the predictive extrapolation and assumed zero production for the predicted extensive data set. The production data from the intensive sample and the predicted production from the extensive sample were then used to estimate a mixed model to relate seed production to tree and environmental variables. Using a log-transformation to meet model assumptions, we modeled viable seeds as a function of year, forest type, the six tree-level variables, and their two-way interactions. We employed the same model selection criteria used for the intensive sample. Where effects were significant ($p < .05$), we performed pairwise comparison tests between levels of the effect, maintaining an overall significance level of $\alpha = .05$ with Scheffe's multiple comparison test.

Forest-type average production by dbh class was estimated by first generating least square means at the average value of the population independent variables in each forest type and size class. Total production in each forest type was then extrapolated using the estimated population tree density and the area of each forest type within community lands.

Results

Population Structure

Density of *C. guianensis* individuals $\geq 10\,cm$ dbh was highest in baixio, with 28.7 ($\pm 10.3\,SE$) trees/ha, followed by restinga and terra preta forest types (23.0 ± 4.2 and 19.5 ± 5.8 trees/ha, respectively). The average basal area, on the other hand, was highest in terra preta, with 3.18 ($\pm 0.67\,SE$) m^2/ha, versus that of baixio and restinga (2.17 ± 0.42 and 1.93 ± 0.42 m^2/ha, respectively). The forest types differed in diameter distributions (log-rank and Wilcoxon tests: $p < .001$); terra preta differed strongly from both forest types ($p < .001$), with a weaker difference between baixio and restinga ($p = .042$). In addition, seedling densities (dbh $< 2\,cm$) estimated via Poisson regression differed dramatically. In baixio, we found 22.9 seedlings/ha, which was significantly lower than the other forest types ($p < .001$); densities in restinga, in turn, were significantly lower than terra preta (105 vs. 151 seedlings/ha; $p = .035$). Considering individuals $\geq 2\,cm$ dbh, restinga and baixio tended to have a greater proportion of small trees (2–20 cm dbh) versus large trees (20–40 and $\geq 40\,cm$ dbh) than terra preta (Figure 1). Finally, in baixio and restinga, we found a lack of individuals $> 50\,cm$ dbh (0.3 and 0 trees/ha, respectively), while in terra preta, we found 2.8 trees/ha in this class.
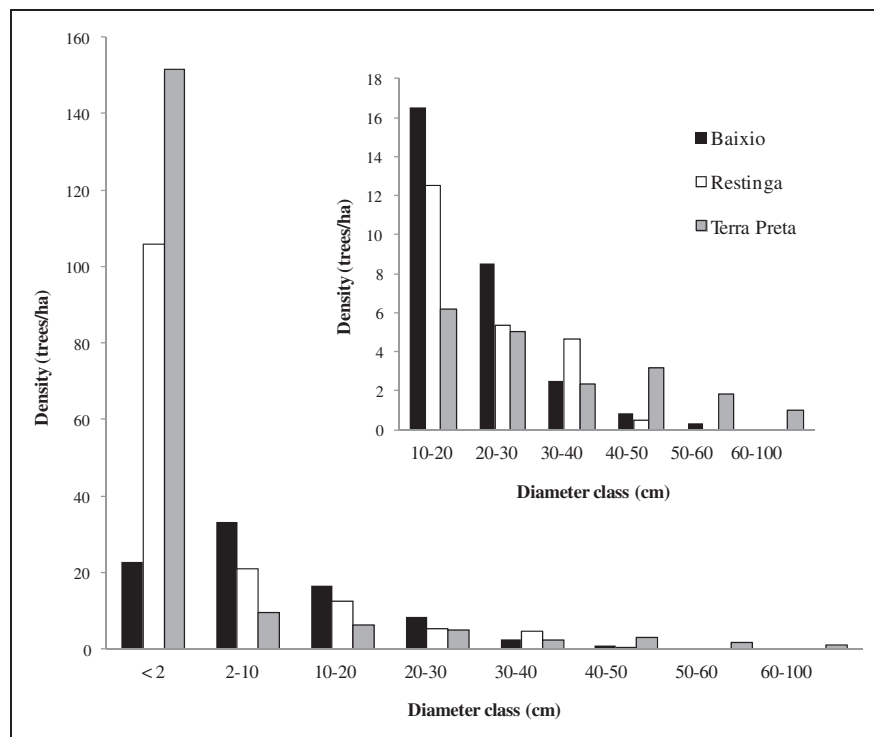

Figure 1. Size class distribution of 1,105 *C. guianensis* trees, by forest type. The inset figure represents the same data but enhances visual differences between the larger diameter classes by forest type.

Seed Production

The estimated mixed model for the 507 extensive sample trees indicated that multiple variables explained *C. guianensis* seed production: forest type, dbh, crown form, crown illumination, year, and interactions (Table 2). Tree dbh was the strongest predictor of seed production with year of production also strong, but for both, the effect of dbh depended on forest type. The model demonstrated good fit with the majority of the sample population, but residuals showed some lack of fit for trees that produced zero fruits (23% of the sample trees in either one or both years).

Production rates. Based on 2-year measurements of our 556-tree sample across three forest types, we estimate that 2.6 (±0.4), 4.1 (±0.4), and 5.5 (±0.4) kg of viable seeds/tree/year were produced in baixio, restinga, and terra preta, respectively; individual tree production varied widely, with a range of 0 to 192.5 kg of viable seeds/tree/year (Table 3).

At least 10% of all trees produced no fruits in any given year, while only 3% of the trees sampled did not produce in either year (Table 3). However, all these consistent nonproducers were relatively small individuals (<30 cm dbh). Despite extremely high maximum observed production, only 0.6% and 2.6% of the trees sampled produced >50 kg of viable seeds in 2007 and 2008, respectively.

Variation by year and by forest type. *C. guianensis* seed production at the population-level mean dbh was higher in 2008 than 2007 (Figure 2). The average individual seed production adjusted for the diameter distribution for each forest type revealed that in 2007, restinga presented significantly higher mean individual seed production rates when compared to baixio and terra preta ($p = .012$ and .002, respectively), which were not significantly different. However, in 2008, mean individual seed production in terra preta was significantly greater than in baixio ($p = .028$) but not significantly more than in restinga.

Table 2. Fixed Effects Estimates and Their Respective Standard Errors, Degrees of Freedom (*df*), *t* Values, and *p* Values for the Final Model of Log (Total kg of Viable Seed Production/Tree/Year) for the Extensive Sample.

Effect	Estimate	Standard error	df	t Value	Pr > |t|
Intercept	−.228	.150	496	1.52	.1286
Forest type: Restinga vs. Baixio	−.140	.174	496	0.81	.4202
Forest type: Terra preta vs. Baixio	−.423	.168	496	−2.52	.012
DBH	−.050	.006	496	8.02	<.0001
DBH^2	−.0003	.0001	496	−4.64	<.0001
Crown form: Good vs. perfect	−.125	.102	496	−1.22	.2216
Crown form: Poor vs. perfect	−.178	.047	496	−3.79	.0002
Illumination: Some vs. full	−.411	.168	496	−2.45	.0148
Illumination: No direct vs. full	−.171	.051	496	−3.38	.0008
Year: 2008 vs. 2007	−.832	.069	504	12.01	<.0001
Forest type × Year: Restinga vs. Baixio, 2008 vs. 2007	−.543	.111	504	−4.9	<.0001
Forest type × Year: Terra preta vs. Baixio, 2008 vs. 2007	−.351	.105	504	−3.35	.0009
DBH × Forest type: Restinga vs. Baixio	.011	.005	496	2.28	.0231
DBH × Forest type: Terra preta vs. Baixio	.020	.005	496	4.23	<.0001

Note. DBH = diameter at breast height.

Table 3. Mean (± Standard Error) Values of Viable Seed Production per *C. guianensis* Tree by Forest Type and Percentage of Nonproducer Trees.

Forest type	Viable seeds (kg)[a]	Viable seeds 2007 year (kg)[a]	Viable seeds 2008 year (kg)[a]	Nonproducers 2007 (%)	Nonproducers 2008 (%)	Consistent non producers (%)
Baixio	2.6 ± 0.4	1.8 ± 0.4	3.6 ± 0.4	18	15	7
Restinga	4.1 ± 0.4	3.4 ± 0.4	4.9 ± 0.4	5	15	2
Terra Preta	5.5 ± 0.4	3.3 ± 0.4	8.8 ± 0.4	15	3	1
All				13	10	3

[a]Average production of each forest type based on average dbh in population structure sample.
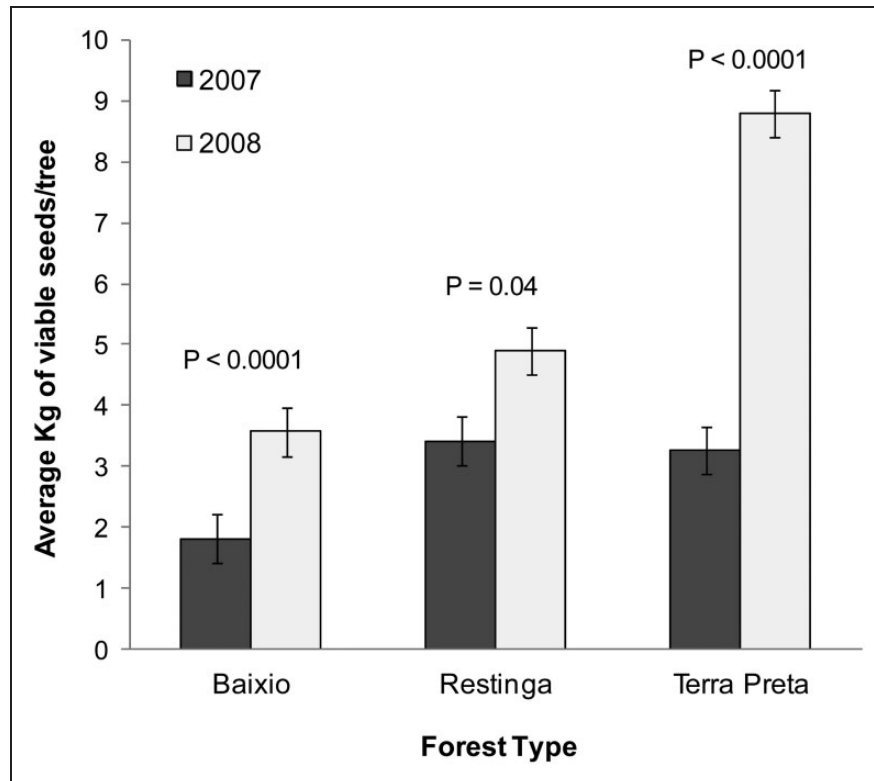
Figure 2. Mean (± standard error) *C. guianensis* individual seed production by forest type and year. Estimates were adjusted to represent the average dbh of *C. guianensis* populations at each forest type (based on inventory data).

Variation by dbh and by forest type at the individual level. Seed production increased as dbh increased, with a quadratic effect indicating a peak in production at 82.6 cm dbh, after which production declined with larger dbh (Figure 3). This pattern, however, was driven by observations in terra preta only, as this was the only forest type where trees >60 cm dbh were encountered in our transect samples. All size classes ≥10 cm dbh sampled produced fruits, suggesting that *C. guianensis* can be reproductively mature at small sizes. However, even though our data did not illustrate a clear threshold of minimum production size, nearly a quarter of the trees in the 10 to 19.9 cm dbh size class did not produce fruit in either year, and in any given year, approximately half of these same-sized trees produced. In contrast, all trees >30 cm dbh produced fruit in at least 1 year, with 95% producing in both years (Table A2). Trees 40 to 60 cm dbh in terra preta had significantly lower mean production than in baixio and restinga (Figure 3).

Variation by crown illumination and form. Individual trees exposed to full overhead light produced 18% more seeds than those exposed to partial overhead light ($p < .001$), and 40% more than trees receiving only diffuse or side light ($p < .05$). Although not significant, trees with perfect crowns produced 20% more seeds than trees with good crowns, and significantly, 34% more than those with poor crowns ($p < .001$).

Total population seed production. In São João do Jaburu, total production was estimated at 852,303 kg of viable seeds/year or an average of 90.3 kg of viable seeds/ha (Table 4). This estimate is based on the density of *C. guianensis* adult trees in each forest type, the area of each forest type (ha) on community lands, and the average seed production/tree/year.

Discussion

Population Structure

C. guianensis tree densities found in all three várzea forest types were much higher than those reported for terra firme forests (Klimas et al., 2007; Klimas, Kainer, Wadt, et al., 2012), particularly reports from the eastern Amazon (Cloutier, Kanashiro, Ciampi, & Schoen, 2007; Plowden, 2004; Table A3). Higher *C. guianensis* densities in floodplain (várzea) versus upland (terra firme) forests mirrors the broader pattern of lower tree diversity and greater species dominance in várzea forests (Anderson, 1991; Prance, 1979).

We found relatively high seedling and sapling densities in all forest types except baixio, including a high proportion in low light conditions. This reverse-J population structure is characteristic of shade-tolerant canopy tree species and signals that recruitment is constant and probably sufficient for population maintenance (Peters, 1996).
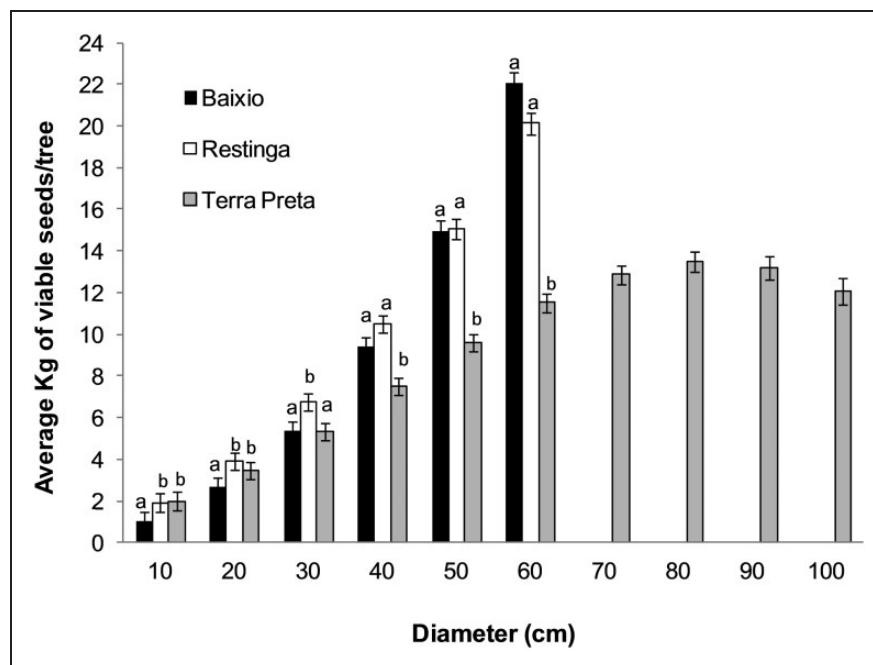
Figure 3. Estimated mean (± standard error) *C. guianensis* individual seed production by dbh and by forest type. The letters represent significant differences in seed production among forest types at α = .05 (Scheffe's multiple comparison test).

Table 4. *C. guianensis* Estimated Total Population Seed Production by Forest Type and by Year.

Forest type	Density[a] (trees/ha)	Area (ha)	Estimated number of trees >10 cm dbh	Mean production[a] (kg viable seeds/tree)	Estimated seed production per hectare (kg viable seeds/ha)	Estimated population production (kg of viable seeds)
Baixio	28.7	4,190	120,250	2.6	74.6	312,650
Restinga	23.0	1,758	40,441	4.1	94.3	165,807
Terra Preta	19.5	3,486	67,972	5.5	107.3	373,846
Total		9,434			90.3	852,303

[a]Individuals ≥ 10 cm dbh.

Seed Production

While mean *C. guianensis* seed production rates reported from monitoring of small samples (5–103 trees) range from 0.2 to 80.2 kg of seeds/tree/year (Klimas, Kainer, & Wadt, 2012; McHargue & Hartshorn, 1983; Plowden, 2004; Ranklin, 1978), our substantially larger sample (*n* = 556) revealed averages ranging from 2.6 to 5.5 kg of viable seeds/tree/year—consistent with the average of 5.8 kg of viable seeds/tree/year in terra firme forest in the eastern Amazon (Sist et al., 2014). Production variation close to two orders of magnitude among individuals in our várzea study area suggests that larger samples are required for reliable population-level production estimates.

We found on average, a 2-fold difference in *C. guianensis* individual seed production from 1 year to another.

While this pattern is consistent with Sist et al. (2014) and with the suggestion of McHargue and Hartshorn (1983) that *C. guianensis* produces good seed crops every other year, our data were limited to 2 years. Our results are also consistent with Klimas, Kainer, Wadt, et al. (2012), who found large variation in annual seed production, with production nine times greater in "high" versus "low" production years.

In all three forest types studied, *C. guianensis* can be reproductively mature at 10 cm dbh. Both the strong correlation between *C. guianensis* individual seed production and dbh observed in our study, and the quadratic curve between nut production and dbh found in the lightly logged terra preta are consistent with other production studies of *C. guianensis* (Klimas, Kainer, Wadt, et al., 2012) and *Bertholletia excelsa* (Kainer, Wadt, &

Staudhammer, 2007). We also found a significant and positive relationship between crown illumination and seed production. Trees that received more sunlight tended to produce more fruits. On the other hand, liana infestation was not significant in our model, whereas other studies have found lianas to negatively affect fruit production (Kainer, Wadt, Gomes-Silva, & Capanu, 2006; Kainer et al., 2007; Klimas, Kainer, Wadt, et al., 2012; Stevens, 1987). Relatively few trees in our population, however, presented heavy liana loads, and those that did were mostly large trees expected to have the highest production rates.

Although forest type was a significant variable in explaining seed production in our model, the patterns of variation observed at the population level were not consistent between years. Moreover, the patterns were likely influenced by different logging histories among forest types. Terra preta was the forest type with the overall highest mean seed production per tree (i.e., production calculated at average dbh; Table 3). However, this results from the differences in population structures: Terra preta had the highest proportion of trees >45 cm dbh, the size classes with the highest production rates. When looking at differences in seed production of comparable size classes by forest type, terra preta displayed substantially lower individual production rates for adult trees >40 cm dbh (Figure 3). These findings imply that the near absence of large trees (presumably a legacy of logging activities or perhaps environmental limitations) compromised total seed production in baixio and restinga; that is, with comparable diameter distributions, these two forest types would probably display the highest mean seed production rates on a per hectare basis.

Implications for Conservation and Management

C. guianensis seed harvest levels and oil production targets must be compatible with population-level seed production by forest type. According to a detailed study in the same community (Londres, 2004), all families together harvested 949 kg of viable seeds in 1 year; that is, 0.1% of the total estimated annual seed production within community forest lands (Table 4). This disparity between production and harvest levels strongly suggests that seed harvests could increase substantially without negative impacts on regeneration. Indeed, harvest scenarios from a *C. guianensis* population model (Klimas, Cropper, et al., 2012) indicated that removal of 10% of total seed production proved ecologically sustainable and economically viable (Klimas, Kainer, & Wadt, 2012). Our data provide an opportunity to create *C. guianensis* management plans and test different seed harvesting scenarios designed to improve the livelihood of this community and others with similar *C. guianensis* population structure.

While difficult to untangle differences in population structures among forest types with a long and varied timber harvest history, our evidence suggests that the intensive timber harvests in baixio and restinga affected current population structure and thereby seed production potential on a per area basis. The size classes at which *C. guianensis* seed production was highest overlap almost entirely with commercial sizes for timber harvests (historically ≥45 cm and currently ≥50 cm dbh). Community accounts that large trees were once common in baixio and restinga coupled with extant scattered large trees in these forest types suggest that present day size class distribution are land-use legacies rather than reflections of environmental constraints on adult size. Since this size class had the highest level of seed production, previous logging in baixio and restinga might have reduced fruit production substantially in these forest types. On the other hand, this might indicate that the environment of these forest types may not favor survival of large trees due to some unmeasured factor, such as soil stability. Although the unlogged terra preta site displayed the lowest production rates at the individual level, average production per hectare was higher, due to higher densities of large trees.

In the context of community livelihoods, careful consideration of trade-offs and interactions between timber and seed production is needed (see Klimas, Kainer, & Wadt, 2012). Historically, *C. guianensis* timber was much easier to sell than seed oil, even though the price community members received for logs paled in comparison to potential earnings from seed production (Londres, 2009; Shanley & Londres, 2011). Improved market access and social organization show potential to allow residents better economic returns from *C. guianensis*. Indeed, in 2016, the community traded 11 tons of *V. surinamensis* and 330 kg of *C. guianensis* seeds to a cosmetics company (Nilza Miranda, personal communication May 28, 2017). This study presents an opportunity to improve natural resource management and conservation through better understanding of production trends and drivers for an important nontimber forest species.

Appendix A. Extensive Sample Procedures

Transect length was variable, as the goal for this sample was to obtain a representative spatial distribution of monitoring trees, not to generate population density estimates. To achieve relatively even spatial coverage of the forest-type strata and approximately equal representation of stems in each size class, sampling criteria were developed for each forest type. For example, for the *restinga* forest type, size class proportions identified in the inventory data indicated a reverse *J* size class distribution, that is, there were many trees in the 10 to 29.9 cm dbh size

class, fewer trees in the 30 to 44.9 cm dbh size class, and very few trees ≥45 cm dbh. Thus, every eighth tree in the smallest size class was selected; every third tree of the medium size class was selected; and all trees in the largest size class were selected. The diameter classes sampled were 10 to 29.9, 30 to 44.9, and 45 to 59.9 cm dbh for *baixio* and *restinga* forest types; *terra preta* forest type included additional classes for individuals 60 to 89.9 cm and ≥90 cm, since logging had not eliminated these classes, as it had in *baixio* and *restinga*. For the entire extensive sample, we selected a minimum of 40 trees (and a maximum of 60) in each diameter class for each forest type.

Appendix A1. Parameter Estimates and Their Respective Standard Errors (*SE*), Degrees of Freedom (*df*), *t* Values, and *p* Values for Models of ln(Total kg of Viable Seed Production/Tree/Year). Separate Models Are Given 2007 and 2008 Based on the Intensive Sample Data.

Year	Effect	Estimate	*SE*	*df*	*t* Value	*Pr > |t|*
2007	Intercept	1.194	.205	43	5.82	<.001
	max_fruits[a]	0.051	.012	43	4.27	<.001
2008	Intercept	0.823	.271	47	3.04	.004
	max_fruits[a]	0.047	.008	47	5.69	<.001

[a]Maximum number of fruits estimated from crown counts observations.

Appendix A2. Proportion of Nonproducing Trees by Size Class, São João do Jaburu, Gurupá, Pará, Brazil.

Size class(cm dbh)	Nonproducers 2007 (%)	Nonproducers 2008 (%)	Consistent nonproducers (%)
10–20	42	61	23
20–30	19	5	1
≥30	5	0	0

Appendix A3. Summary of *C. guianensis* Densities at Different Study Sites.

C. guianensis density	Forest type	Region	Source
28.9, 23.0 and 19.5[a]	Floodplain forests (*baixio*, *restinga* and *terra preta* forest types, respectively)	Amazon estuary	Londres *et al.* (this study)
25.7 and 14.6[a]	Occasionally inundated and in terra firme, respectively	Western Amazonia	Klimas *et al.* (2007)
6.7 and 5.6[a]	Occasionally inundated and in terra firme, respectively	Eastern Amazonia	Plowden (2004)
62[a]	Occasionally inundated	Costa Rica	McHargue and Hartshorn (1983)
2.5[b]	Terra firme	Eastern Amazonia	Cloutier *et al.* (2007)

[a]Trees > 10 cm dbh ha^{-1}.
[b]Trees > 30 cm dbh ha^{-1}.

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