Population structure of *Carapa guianensis* in two forest types in the southwestern Brazilian Amazon

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Abstract

Carapa guianensis Aublet. is a tropical tree with strong multiple-use characteristics, and is valued for both the high quality oil extracted from its seeds and as a timber resource. This study compares the population structure of this economically important rainforest tree in two contrasting forest types: occasionally inundated and *terra firme* forests. Main study objectives were (a) to assess the density, spatial distribution, and size class structure of *C. guianensis* in these two forest types and (b) to use patterns of abundance, distribution and demographic structure to help infer key demographic stages or ecological variables that merit special focus for management. Four 400 m × 400 m plots, two in each forest type, were established to determine distribution and density patterns of *C. guianensis* ≥10 cm diameter at breast height (dbh) at the landscape level, and 32 10 m × 10 m subplots were randomly nested within each of the larger plots to measure individuals <10 cm dbh. Larger individuals (≥10 cm dbh) were found at higher densities in occasionally inundated forest than in *terra firme* forest: 25.7 trees ha^{-1} and 14.6 trees ha^{-1}, respectively. Mean density of *C. guianensis* individuals <10 cm dbh was also higher in occasionally inundated forests, but variation of regeneration density among the subplots was high. Spatial distribution methods revealed a tendency toward clumping in both forest types, and both had similar size class structures, suggesting that both environments are suitable for *C. guianensis*. This new finding illustrates the potential for *C. guianensis* management in *terra firme* forests. High densities and clumped distributions in both forest types are also indices favorable for sustainable species management. Finally, several ecological variables (tree density and reproductive potential) were sufficiently different between *terra firme* and occasionally inundated forests to recommend stratification by forest type when conducting further studies on key ecological and management variables of *C. guianensis*.
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1. Introduction

The Amazon basin contains over half of the world's remaining tropical rainforest, and is facing unprecedented changes that will have major impacts on biodiversity, regional hydrology and the global carbon cycle (Nepstad et al., 2001; Fearnside, 2005). Humans play a significant role in these changes, often as part of a struggle to improve their standard of living (Schmink, 1994; Wood, 2002). Use of forest resources is frequently necessary for improving the social and economic living conditions of forest residents (reviewed in Ticktin, 2004) and may add to the perceived value of standing tropical forest

(Arnold and Pérez, 2001). Logging and non-timber forest product (NTFP) extraction, however, incurs associated environmental costs (Peters, 1996; Nepstad et al., 1999; Peres et al., 2003). Effective forest management can mitigate these costs, particularly when based on an understanding of the ecological parameters under which sustainable harvest can exist (Putz et al., 2000). In contrast, management activities that ignore the regeneration and growth requirements of the species under exploitation have little chance of long-term success (Hartshorn, 1995; Peters, 1996).

While there is still considerable scientific debate over whether natural resource extraction can be sustained over the long term and how to accomplish this (Nepstad et al., 1999; Peres et al., 2003; Pearce et al., 2003; Fearnside, 2005), the debate is hindered by the lack of demographic information for most tropical species (Gullison et al., 1996; Zuidema, 2003). To

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sustain, or even increase the abundance of an extracted product, detailed knowledge of species life history and demographic behavior is essential (Sunderland and Drasnfield, 2002). Peters (1996) specifies four key ecological parameters for guiding sustainable management of any given species: life cycle characteristics, multiplicity of uses and types of resources produced, abundance in different forest types, and size-class distribution of populations. Patterns of abundance, distribution and demographic structure can be used to help infer key demographic stages or ecological variables that merit special focus when implementing a management scheme (Bruna and Ribeiro, 2005). Since these variables can differ by habitat type (Bruna and Kress, 2002; Wagner and Fortin, 2005), they should be evaluated for any given species in the multiple habitats or forest types in which it occurs.

Carapa guianensis (Meliaceae) is valued for both the high quality oil extracted from its seeds (Shanley and Medina, 2005) and as a timber resource (Dayanandan et al., 1999). Pure *C. guianensis* seed oil is used for medicinal purposes (Rodrigues, 1989), and in products such as soaps, shampoos, candles and insect-repellent torches (Boufleuer, 2001; Shanley and Medina, 2005). Nonetheless, *C. guianensis's* major economic use today is as insect-resistant timber often used in place of its heavily exploited relative, *Swietenia macrophylla* King, commonly known as mahogany. Very little, however, is known about *C. guianensis* population structure, and whether structure changes across forest types.

Measuring population structure in different habitats is a first step towards assessing sustainability of harvesting in different habitat types (Peters, 1996). Population structure in most forestry and ecological studies has been defined in terms of the size-class or diameter distribution of individuals, with frequency histograms showing the number or percentage of individuals in each size class (Knight, 1975; Peters, 1996). Quantifying species demographic structure provides data for ecological models assessing long-term population viability (Alvarez-Buylla et al., 1996). Since vital demographic rates are normally stage-dependent (Harper, 1977), determining the structure of a population is a first step that, when combined with demographic data, such as size-specific growth rate (Condit et al., 1998) can be the basis for management decisions (Bruna and Kress, 2002).

We compared the demographic structure and seedling recruitment of *C. guianensis* in occasionally inundated and *terra firme*, or upland, forests. The main study objectives were: (a) to assess the density, spatial distribution, and size class structure of *C. guianensis* in occasionally inundated and *terra firme* forests and (b) to use patterns of abundance, distribution and demographic structure to help infer key demographic stages or ecological variables that merit special focus for management of this economically important species.

2. Species description

At maturity, *C. guianensis* is a medium to large hardwood tree that can attain 2 m in diameter and 50 m in height (Pennington, 1981; McHargue and Hartshorn, 1983). Most authors agree that *C. guianensis* is predominantly a species of wet areas, although it is also found on a variety of drier sites (Pennington, 1981; McHargue and Hartshorn, 1983; Fournier, 2003). Its range includes the West Indies, Antilles, Central America south of Honduras, many parts of the Amazon region, and tropical Africa (Smith, 1965; Pennington, 1981; McHargue and Hartshorn, 1983). In Brazil, it is more commonly referred to as "andiroba", and Pennington (1981) provides a reference to other common names for this species.

The fruit is a spherical or subspherical capsule of dry dehiscent fiber with four valves (quadrants), each containing one to four seeds (Smith, 1965; McHargue and Hartshorn, 1983; Sampaio, 2000). These valves separate, open and free the seeds upon falling to the ground. *C. guianensis* has two predominant methods of secondary seed dispersal: water and frugivores, including scatter hoarding rodents (McHargue and Hartshorn, 1983; Plowden, 2004). Based on a 5-year Costa Rican study, McHargue and Hartshorn (1983) reported that *C. guianensis* produces good seed crops almost every other year. In our Brazilian study area, forest residents and technicians report a 2–3-year masting cycle (Klimas, personal communication). A large seed sustains successful *C. guianensis* germinants in shade, and seedlings are able to establish and grow under a closed canopy (Clark and Clark, 1985).

3. Study site

Field surveys were carried out within the 1200 ha experimental forest of the Brazilian Agricultural Research Corporation (Embrapa) in the southwestern portion of the state of Acre, Brazil. The study region has lightly undulating topography, with dominant vegetation classified as humid, moist tropical forest (Holdridge, 1978). The region has a pronounced 3-month dry season from June to August, and mean annual temperature is 24.5 °C. Brief intrusions of cold air from the South occasionally drop temperatures to 10 °C during the dry season (ZEE, 2000). According to weather data collected 25 km from the study site, maximum and minimum temperatures during the 2004–2005 study period, respectively, were 35 and 16 °C; relative humidity ranged from 71 to 91% with an average of 86%; and total rainfall was 2089 mm in 2004 and 1743 mm in 2005 (UFAC, 2005).

4. ==Methods==

4.1. Plot installation

We established four 400 m × 400 m (16-ha) plots, from June through July 2004 to determine distribution and density patterns of *C. guianensis* at the landscape level. These four plots were randomly selected within two distinct forest types, with adjacent plot corners at least 500 m apart. Two plots were established where the majority of the environment was classified as *terra firme* forest and two in occasionally inundated forest. We installed internal transects every 50 m to create eight 400 m × 50 m rectangles and used a central transect to bisect these rectangles. These internal

divisions created a grid system used to map *C. guianensis* individuals.

Occasionally inundated and *terra firme* forest were distinguished by flooding regimes. The occasionally inundated forests were potentially flooded yearly, during the peak of the rainy season (November through February). Fluctuations in yearly rainfall can produce years when not all occasionally inundated forests were flooded or flooded for varying periods (a few days to a month). These forests were not considered floodplain forests and did not have consistent yearly flooding. Soils in the occasionally inundated and *terra firme* forest were reported to be red and yellow ultisols and plintosols, respectively (Rodrigues et al., 2001).

4.2. Mapping adult individuals

C. guianensis trees ≥10 cm diameter at breast height (dbh) were inventoried in all four plots. A minimum of two researchers located trees by systematically walking parallel to the transect lines. After locating a tree, we recorded the y-coordinate based on a tape-measured distance. We visually estimated the x-coordinate based on distance to the proximate transect. We initially tested the accuracy of the x-coordinate by measuring the distance with a meter tape until an error of ±5 m was attained, subsequently using the estimated x-coordinate in place of a meter-tape measurement. In addition to the coordinates, we recorded plot number, canopy position [(dominant, co-dominant, intermediate or suppressed) from Smith et al. (1997)], dbh, microenvironment and reproductive status. Reproductive status was positive if seeds or associated dehiscent capsules were located either on the tree, on the ground underneath the tree, or if a seedling bank from a former year could only be clearly attributed to that tree. While at the landscape scale each of the four plots was assigned to one of two forest types (*terra firme* or occasionally inundated forest), each individual was also assigned to a "microenvironment", either upland (never flooded) or lowland (possibly flooded), based on a 1–2 m radius surrounding each tree.

4.3. Estimating regeneration

We randomly nested 32 10 m × 10 m subplots within each of the larger 400 m × 400 m plots, measuring individuals <10 cm dbh between August and October 2004. We only selected subplots for study if the entire 100 m² area was characterized by the same microenvironment as the larger, designated forest type. For example, if a selected subplot of *terra firme* fell in a lowland or transition zone, it was removed from the sample and another subplot was randomly selected for consideration. We also discarded selected subplots with trails or rivers within their boundaries.

Within each subplot, we tagged all seedlings (individuals < 1.5 m tall) and saplings (individuals ≥1.5 m tall and <10 cm dbh) and noted x,y coordinates. For seedlings, we measured basal diameter (at the level of the soil) and height. For saplings, we measured dbh and estimated height. While the seedling classification may have captured small saplings and could have been further divided, our goal was not to differentiate between those individuals still using seed reserves for growth and those relying on environmental resources, but to look at general classes of recruitment. We remeasured all tagged seedlings and saplings in 2005 to determine 10-month mortality, and diameter (basal or dbh) and height growth.

4.4. Data analysis

We used analysis of variance (Anova) to test for differences in adult, sapling and seedling densities and adult diameter distribution. For adult density comparisons, each forest type had two replicates (the 16-ha plots) and we calculated Anova estimates using average density values per forest type. We calculated Anova estimates for seedling and sapling densities partitioning the overall error into two parts: experimental error and sampling error, to account for replication in the 32 nested subplots. We treated forest type as a fixed effect. Since forest type and microenvironment were correlated, after initially testing to make sure that our results were consistent between these two designations, only forest type was used for all further Anovas. Tukey's HSD was used for all applicable multiple comparisons. We used a two-sample test of proportions to compare percentage values for tree reproduction of the various dbh classes and to calculate the ratio of non-reproductive (seedlings, saplings and individuals <20 cm dbh) to potentially reproductive individuals (dbh ≥ 20 cm) in the population. These subdivisions were used since results showed that the majority of individuals ≥20 cm dbh had evidence of reproduction, while this was not the case for individuals <20 cm dbh. For tree reproduction comparisons, we applied a Bonferroni correction on the alpha level. Since there were 21 comparisons between the seven diameter classes, we divided our *p*-value of 0.05 by 21. Therefore, *p*-values ≥0.0024 were considered statistically significant. We used a general linear model to compare the number of trees with evidence of seed production between the two forest types. We used a logit model, in R described as binomial proportion comparisons, to test for differences in the binary production values and differences between size classes in the different forest types. Indeed, R programming language was used for all analyses (R Development Core Team, 2006) and *p*-values ≤0.05 were considered statistically significant in all cases where we did not use a Bonferroni correction.

We characterized the spatial distribution of *C. guianensis* using the aggregation index *R* (Clark and Evans, 1954), corrected for edge effects (Donnelly, 1978). The aggregation index is based on measurement of nearest neighbor distances for each individual and provides an indication of whether a population has a clumped, random or uniform distribution. We used spatstat, an R package for spatial point pattern analysis (Baddeley and Turner, 2005) to calculate nearest neighbor distances based on the x,y coordinate reference system. We used the calculated z-value and associated p-value to determine whether the observed distribution was significantly different than the expected random pattern. This analysis was completed for sub-adults (defined as 10 cm ≤ dbh < 20 cm) and potentially reproductive adults (defined as dbh ≥ 20 cm) in each

experimental plot for the purpose of exploring whether sub-adults have a different spatial distribution than reproducing adults. Anova was used to test for significant differences in nearest neighbor distances between forest types.

The use of first nearest neighbors, however, does not differentiate an aggregated distribution from an even distribution of regularly sized clumps, and information is lost (Cressie, 1993; Dale, 1999). Therefore, Ripley's $K(r)$ function (Ripley, 1977 from Goreaud et al., 1999) and the edge-correction factor proposed by Ripley were also applied to the data. Ripley's $K(r)$ function determines the expected number of neighbors in a circle of radius d_s centered on an arbitrary tree in the point pattern. This circle begins at a specified radius and is increased until it encompasses the entire study region. The expected number of neighbors in the circle is defined as

$$\lambda \times K(r).$$

The intensity, λ, is the expected number of points per unit area

$$\lambda = \frac{N}{S};$$

where N is the number of points in the pattern and S is the study region area.

$$K(r) = \frac{1}{\lambda} \times \frac{1}{N} \times \sum \sum k_{ij};$$

where $k_{ij} = 1$ if the distance between i and j is less than r, and 0 otherwise. Since the number of trees should increase with an increasing circle radius, the linearized function $L(r)$ proposed by Besag (1977) was used to simplify pattern interpretation

such that:

$$L(r) = \sqrt{\left(\frac{K(r)}{(1-r)} \right)}.$$

For a Poisson pattern, $L(r) = 0$ at every distance r; for clustered patterns at distance r, $L(r) > 0$; and in the case of regularity at distance r, $L(r) < 0$ (Goreaud et al., 1999). This test was completed for sub-adults (defined as $10 \text{ cm} \leq \text{dbh} < 20 \text{ cm}$) and potentially reproductive adults (defined as $\text{dbh} \geq 20 \text{ cm}$).

We estimated confidence intervals using the Monte Carlo method. One thousand Poisson patterns were simulated and the confidence interval was defined for each r so that only the highest 5% and the lowest 5% of $L(r)$ values were outside the interval (Goreaud et al., 1999). We graphed results for $L(r)$ with their corresponding confidence intervals for all plots. If the graphed $L(r)$ functions for field data remained within the confidence intervals, it demonstrated a random distribution of individuals. Spatstat was also employed for all calculations of Ripley's $K(r)$ with the "iso" edge-correction factor used for the adjustment of edge effects (Baddeley and Turner, 2005).

5. Results

5.1. Adult structure

Almost twice as many *C. guianensis* trees ≥ 10 cm dbh were encountered in occasionally inundated versus *terra firme* forests (822 and 466, respectively). Thus, tree densities were higher in the former than the latter (25.7 ± 0.4 and 14.6 ± 3.9 trees ha^{-1}, respectively) ($\bar{x} \pm$ S.D.) (d.f. = 1, $F = 16.23$, $p = 0.056$), although the p-value only borders on

Table 1

Descriptive results comparing *Carapa guianensis* populations in occasionally inundated and *terra firme* forests

Forest type	Diameter class	Percent of individuals (%)	Crown class (percentage in each diameter class)				Reprod. indiv. (%)
			D	CD	I	S	
Occasionally inundated	$10 \leq \text{dbh} < 20$	40.0[***]	1	12	45	42	11
	$20 \leq \text{dbh} < 30$	30.3	4	49[***]	39	8	74
	$30 \leq \text{dbh} < 40$	18.7	14	73	11	2	98
	$40 \leq \text{dbh} < 50$	7.8	28	69	2	2	98
	$50 \leq \text{dbh} < 60$	2.7	55	45	0	0	95
	$60 \leq \text{dbh} < 70$	0.4	67	33	0	0	100
	$\text{dbh} \geq 70$	0.1	100	0	0	0	100
Percentage of all individuals ≥ 10 cm dbh			20	32	8	40	56
Terra firme	$10 \leq \text{dbh} < 20$	50.2	1	8	46	45	7
	$20 \leq \text{dbh} < 30$	24.7	1	26	56	17	74
	$30 \leq \text{dbh} < 40$	16.5	10	64	21	5	97
	$40 \leq \text{dbh} < 50$	5.2	33	46	21	0	100
	$50 \leq \text{dbh} < 60$	2.4	82	18	0	0	100
	$60 \leq \text{dbh} < 70$	0.9	75	25	0	0	100
	$\text{dbh} \geq 70$	0.2	100	0	0	0	100
Percentage of all individuals ≥ 10 cm dbh			28	41	7	24	53

Overall, statistical comparisons between these two forest types were not different except for the percentage of individuals in one dbh class and the percentage of individuals in one crown class within a given dbh class. For crown class, D, CD, I and S represent individuals in dominant, co-dominant, intermediate and suppressed crown classes, respectively. The last column indicates the percentage of total individuals within each diameter class that had signs of reproduction (seeds or a seedling bank).

[***] $p \leq 0.0005$.

statistical significance. For both forest types, the distribution of adults in dbh classes revealed a classic reverse-J distribution with a higher number of sub-adults (10 cm ≤ dbh < 20 cm) and smaller diameter trees and a decrease in the number of individuals in the larger diameter classes (Table 1). Further binomial proportion comparisons indicated that the percentage of individuals in each dbh class only differed with respect to forest type in the 10–20 cm dbh class (d.f. = 1, $p < 0.001$) (Table 1). Anova tests revealed that average dbh was significantly larger in the occasionally inundated versus *terra firme* forest (d.f. = 1, $F = 4.69$, $p = 0.031$).

In the occasionally inundated and *terra firme* forest plots, respectively, 52 and 69% of all adult trees ≥10 cm dbh were in the dominant or co-dominant categories, and it was almost entirely these trees that were reproductive. The number of reproductive trees (those with evidence of prior or current seed production) was significantly higher in occasionally inundated forest than in the *terra firme* forest ($p = 0.003$), based on a general linear model. There was, however, no significant difference in the percentage of reproducing individuals of *C. guianensis* in each dbh class between forest types, and the majority of trees <20 cm in both forest types showed no evidence of reproduction (Table 1).

Finally, assuming reproduction at dbh ≥20 cm, the sub-adult (10 ≤ dbh < 20 cm) to adult (dbh ≥ 20 cm) ratio in the occasionally inundated forest was significantly higher than in the *terra firme* forest (8.44 and 5.79, respectively) (d.f. = 1, $p = 0.025$). Thus, compared with the occasionally inundated forests, for every potentially reproductive adult in *terra firme* forest, there were fewer corresponding sub-adults.

5.2. Seedling and sapling structure

C. guianensis seedling densities (individuals < 1.5 cm tall) were almost three times higher in occasionally inundated plots than in *terra firme* plots (366 ± 511 and 104 ± 236 individuals ha^{-1}, respectively) ($\bar{x} \pm$ S.D.) (d.f. = 1, $F = 8.13$, $p = 0.005$) (Fig. 1a). Seedling densities in the 10–20 cm height class were statistically greater (d.f. = 1, $p < 0.0001$) in occasionally inundated forests, while in the tallest height classes (40–50 cm and 50–150 cm), they were significantly higher in *terra firme* forests (d.f. = 1, $p < 0.0001$ for both comparisons) (Fig. 1a). Number of seedling recruits (d.f. = 1, $F = 11.93$, $p = 0.001$) and mortality (d.f. = 1, $F = 5.84$,
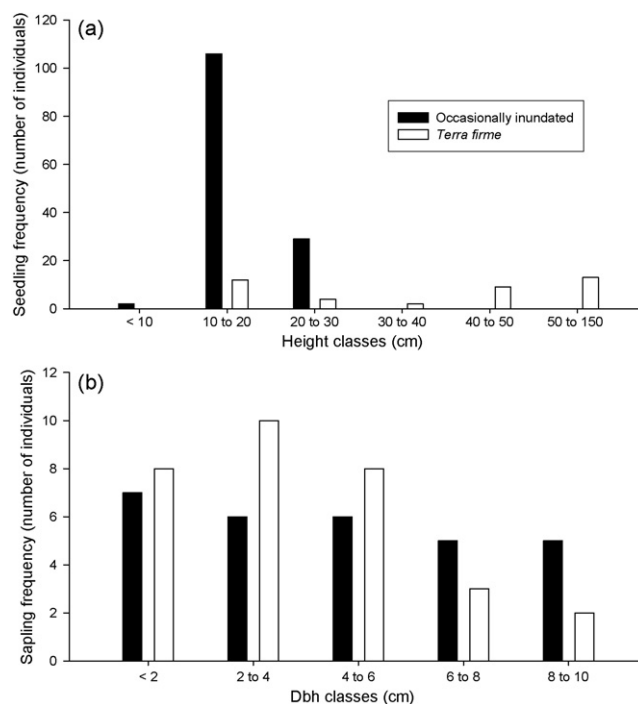

Fig. 1. The height-class distribution of 2004 *C. guianensis* seedlings (a) (height < 1.5 m) and the size-class distribution of 2004 *C. guianensis* saplings (b) (individuals ≥ 1.5 m tall and <10 cm dbh) in two contrasting forest types.

$p = 0.017$) were greater in occasionally inundated forest after a 10-month period, but percent recruitment and percent mortality were not different between forest types (Table 2).

There were no statistical differences in sapling densities between forest types when considering all saplings (individuals ≥ 1.5 cm tall and <10 cm dbh). Frequencies between forest types were also no different when dividing them into smaller dbh classes (Fig. 1b).

5.3. Spatial distribution

Spatial distribution of reproductive adults (dbh ≥ 20 cm) was aggregated in all forest plots (Fig. 2) (Table 3). The index of aggregation (R) for reproductive adults in occasionally inundated forests was statistically the same as that for the *terra firme* forests (0.9056 and 0.8258, respectively). Based on these values, we reject the null hypothesis of a strictly random pattern of distribution in all the plots.

Table 2
Total number (N) of seedlings (individuals <1.5 m tall) and saplings (individuals ≥1.5 m tall and <10 cm dbh) of *Carapa guianensis* observed in 2004 and 2005

	Seedlings		Saplings	
	Occasionally inundated forest	*Terra firme* forest	Occasionally inundated forest	*Terra firme* forest
Total *N* (2004)	231[**]	66	30	32
Total *N* (2005)	248	73	28	31
Mortality: *N* (%)	77[*] (33.3)	19 (28.8)	3 (10.0)	1 (3.1)
New recruits: *N* (%)	94[**] (40.7)	26 (39.4)	1 (3.3)	0

Number and percent of seedling and sapling mortality and new recruits between these two periods (10 months) is also shown. Statistical comparisons are between forest types.
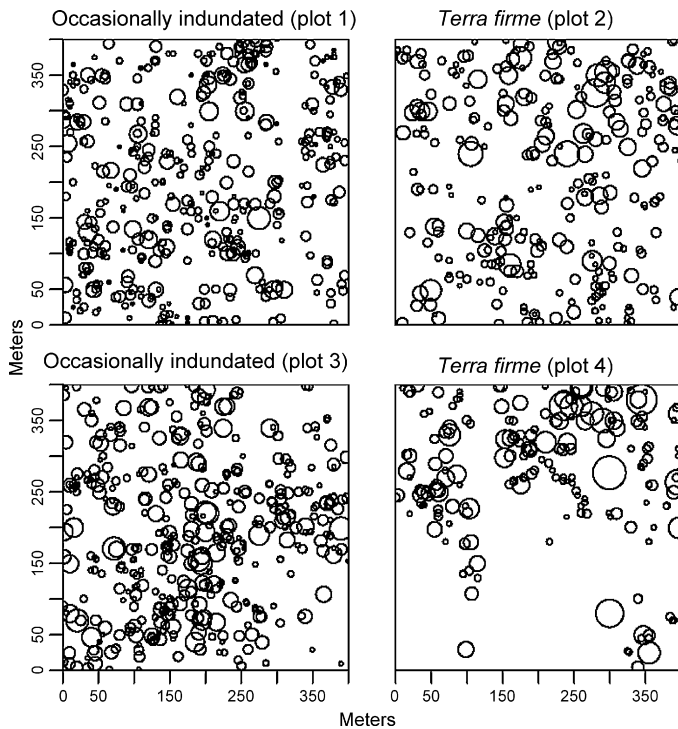[*] $p < 0.05$.
[**] $p < 0.01$.

Fig. 2. Spatial distribution of individuals ≥10 cm dbh in each of the four study plots. The size of the circle is directly correlated to the measured diameter of the individual it is representing.

When analyzed separately, sub-adults (10 cm ≤ dbh < 20 cm) exhibited a greater level of aggregation than reproductive adults (Table 3). Indeed, sub-adults in all plots, irrespective of forest type, were significantly different from a random distribution. Plot 4, representative of a *terra firme* forest (see Section 6), and which was dominated by a bamboo forest in approximately one third of the plot, had the highest level of aggregation.

Results from Ripley's $K(r)$ confirm a clumped distribution in all four plots for all trees ≥10 cm dbh (Fig. 3). Sub-adults again showed a greater degree of clumping than adults (results not shown). When $L(r)$ is outside the confidence interval, it is possible to reject the complete spatial randomness hypothesis

(with a risk of $\alpha = 10\%$) in favor of regularity or clustering at distance r (Goreaud et al., 1999). In the *terra firme* forest, plot 2 indicates middle range (30 m) and long-range (60 m) aggregation (Fig. 3). Very few individuals of *C. guianensis* were found in plot 4 in comparison with the other plots (Fig. 2), but individuals that did occur were aggregated.

Forest type was a significant predictor of nearest neighbor distances ($p = 9.1 \times 10^{-6}$), with those trees in *terra firme* being more distant from one another (15.3 ± 1.1 m) than those in the occasionally inundated forests (11.5 ± 0.4 m). Canopy class, reproductive status and all possible interaction terms were not significant for nearest neighbor comparisons.

6. Discussion

6.1. Adult density and distribution

We found that the density of one of the Amazon's most important timber trees far exceeds that of most other species. *C. guianensis* had 25.5 and 14.5 trees ≥10 cm dbh ha^{-1} in occasionally inundated and *terra firme* forest study areas, respectively. Other authors have found high densities of *Carapa* spp. in these two forest types: 5.6 trees ha^{-1} in eastern Amazonian *terra firme* forests and 6.7 trees ha^{-1} in occasionally inundated forests (Plowden, 2004), and 62 trees ha^{-1} on "swamp slopes" in Costa Rica (McHargue and Hartshorn, 1983). In contrast, Gullison et al. (1996) reported densities ranging from 0.31 to 1.6 trees ha^{-1} for *S. macrophylla* (dbh ≥ 2.5 cm). In southwestern Amazon, Wadt et al. (2005) reported densities of only 1.35 trees ≥10 cm dbh ha^{-1} for Brazil nut (*Bertholletia excelsa*).

6.1.1. Forest type influences

We found almost twice as many individuals ≥10 cm dbh in occasionally inundated versus *terra firme* forests ($p = 0.056$). Although these densities were not statistically significant at $\alpha = 0.05$, we considered this detected difference to be biologically significant, particularly for a study with only two replicates. McHargue and Hartshorn (1983) also found that *C. guianensis* was predominantly a species of swampy or

Table 3
Spatial distribution values for reproductive adults (dbh ≥ 20 cm) and non-reproductive sub-adults (10 cm ≤ dbh < 20 cm) in occasionally inundated and *terra firme* forests based on the application of Donnelly's (1978) nearest neighbor method

Forest type	Plot	N	R	p-Value	Average distance between trees (m) ($\bar{x} \pm$ S.E.)
Occasionally inundated					
Adults	1	264	0.9010	<0.0002	11.1 ± 0.4
Adults	3	229	0.9006	<0.0003	11.9 ± 0.5
Sub-adults	1	151	0.7586	<0.0001	12.4 ± 0.8
Sub-adults	3	178	0.9116	<0.0020	13.7 ± 0.6
Terra firme					
Adults	2	139	0.9152	<0.0060	15.5 ± 0.8
Adults	4	93	0.7256	<0.0001	15.1 ± 1.3
Sub-adults	2	138	0.8891	<0.0013	15.1 ± 0.8
Sub-adults	4	96	0.5942	<0.0001	12.1 ± 1.2

N is the number of individuals in a given plot and R is the index of aggregation. $R = 1$ if the spatial pattern is random, $R = 0$ when clumping occurs, and $R > 2.15$ when a uniform distribution pattern exists (Krebs, 1999).
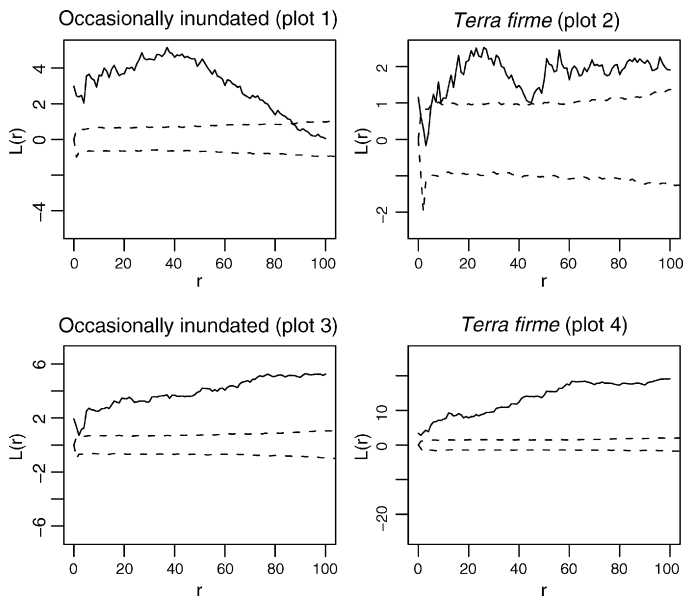
Fig. 3. Ripley's $K(r)$ analyses confirm a clumped adult distribution in all four plots. When $L(r)$ (continuous line) is outside the confidence interval (dotted lines), it is possible to reject the complete spatial randomness hypothesis (with a risk of $\alpha = 10\%$) in favor of regularity or clustering at distance r. Plot 2 displays middle-range (30 m) and long-range aggregation (60 m).

periodically inundated land, reporting lower densities on higher and better drained slopes and ridges in Costa Rica's La Selva forest.

Environmental factors at various scales affect species density and distributions (Clark and Clark, 2000), Valencia et al. (2004) found that soil type affected abundance differences for a variety of tropical trees in the Ecuadorian Amazon while Boll et al. (2005) found that soil moisture was the most important environmental predictor of occurrence for the tropical palm *Aphandra natalia*. The comparatively lower density of *C. guianensis* in the *terra firme* versus the occasionally inundated forests studied may be partially attributed to bamboo competition in one of our *terra firme* plots (Fig. 2, plot 4). Griscom and Ashton (2006) have observed that bamboo forests of southwestern Amazonia are frequently more widespread on *terra firme* than in floodplains, despite similar levels of disturbance on both forest types. Furthermore, Silveira (2001) reported that bamboo forests are common in more than half of the Brazilian state of Acre, suggesting that our plots with high density of bamboo may be ''representative'' of *terra firme* forests in our study area. Notwithstanding, the ability of *C. guianensis* to tolerate flooding, conferring a competitive advantage over other less flood tolerant species, may be the most likely explanation of adult density differences encountered. *Carapa* spp. can delay germination during water dispersal or germinate while floating (Scarano et al., 2003) and their large seeds have been hypothesized to provide the energy reserves necessary to produce a tall shoot to raise leaves above flood waters (McHargue and Hartshorn, 1983).

The influence of forest type can also change over time. While not evident in this data set, intense fires during the 2005 dry season increased mortality in one of the *terra firme* forest

plots (Klimas, personal observation). Tropical forests are becoming more susceptible to fire (Nepstad et al., 1999), and logging can exacerbate this phenomenon by opening up gaps, and creating standing fuel (Fearnside, 2005). If logging of *C. guianensis* increased, occasionally inundated forests with higher year-round moisture content may be more fire resistant and perhaps better suited for timber management.

6.1.2. Aggregated distributions

Both spatial analyses demonstrated aggregation of individuals for both forest types. Similar to Henriques and Sousa's 1989 finding in patches of disturbed tropical moist forest, we found smaller size classes to be more clumped than larger ones. Clumped distributions of trees are typical in both tropical dry (Hubbell, 1979) and humid forests (Clark and Clark, 1984; Boll et al., 2005). Aggregation seems to be highly linked with seed dissemination processes (Condit et al., 2000; Svenning, 2001; Svenning and Skov, 2005). Dispersal via scatter hoarding rodents transports nuts away from source plants, creating a more uniform distribution of fruits (Vander Wall, 2001). The large seeds of *C. guianensis* may confer a competitive dispersal advantage; heavier seeds of *Carapa procera* had a higher probability of being removed more than 30 m from the parent tree than lighter seeds of the same species (Jansen and Forget, 2001). These seeds may also be more likely to survive due to their larger seed reserves. Even with these establishment advantages, *C. guianensis* seeds still do not overcome the large-scale dispersal limitation that can result in aggregation, such that on a landscape level, spatial analyses reveal clumped distributions. Some differences in levels of aggregation were detected. Plot 4 (Fig. 2), of *terra firme* forest was partially dominated by a bamboo and associated with lower *C. guianensis* densities and higher levels of aggregation.

6.2. Size-class structure

When summarizing adult and seedling/sapling data sets, population densities in both forest types showed a reverse-J distribution, displaying a greater number of smaller size-class trees than larger size-class trees (Table 1). This type of structure is characteristic of shade-tolerant canopy trees that maintain a more or less constant rate of recruitment (Peters, 1996; Gibson, 2002). In *C. guianensis*, this structure may be attributed to the long-lived nature of the species and because mast intervals of 2–3 years are sufficient to maintain adequate recruitment levels. Slow rates of diameter growth in the smallest size classes (Condit et al., 1998) may also explain this population structure.

6.2.1. Seedling to sapling transitions

While overall population structure seems to indicate sufficient recruitment, we observed a gap in the transition from seedlings to saplings in the occasionally inundated forest, particularly in the 30–150 cm height range (Fig. 1a). Although there were fewer seedlings in the *terra firme* forest irrespective of size-class, they appeared more stable than in the occasionally inundated forest areas sampled.

Since this 1-year study is just a snapshot of historical events that shaped our study population structure, the cause and duration of this gap are not known, but could be attributed to an inundation that affected new and established seedlings, or an accumulation of small changes over time such as multiple years with low seed production or high predation, related to scatterhoarders, and/or insect infestation (Vander Wall, 2001). Higher seed densities in occasionally inundated forests (where we found significantly greater reproductive adult densities) may have attracted insects and led to greater seed loss through insect infestation (Vander Wall, 2001). Henriques and Sousa (1989) attributed recruitment mortality of *C. guianensis* in wet sites to damping-off (*Pythium* sp.) while stemborer (*Hypsiphyla* sp.) attacks were observed in larger juveniles and sub-adults (approximately equivalent to our own sapling size classes), presumably throughout their study area.

While models have shown that the population and growth rates are mostly controlled by mortality of reproductive adults (Caswell, 2001), a holistic long-term management plan should consider maintaining a constant base of recruits for this species. For long-lived tree species, it will take a long time before changes to the population structure due to decreased reproduction can be detected, but recovery from lack of recruitment may also be a lengthy process.

6.2.2. Adult seed production

The percentage of reproducing individuals in any given dbh class was not significantly different between occasionally inundated and *terra firme* forest. This suggests that regardless of forest type, individuals in a given diameter class have approximately the same probability of producing seeds. Further research is necessary to determine whether the quantity and quality of seeds produced differs between forest types. We did observe in our study, however, that a significantly greater percentage of individuals ≥ 10 cm dbh were in the dominant or co-dominant canopy positions in the *terra firme* when contrasted with the occasionally inundated forest plots (69% versus 52%).

Further research would also illuminate time needed to reach reproductive maturity between forest types. We found that seed production was initiated in most trees >20 cm dbh in all plots, yet do not know how long it took for them to attain this diameter. Vieira et al. (2005) documented highly variable diameter growth rates of *C. guianensis* trees growing in open forest with bamboo and dense *terra firme* forest.

6.3. Management implications

As a multiple-use species, *C. guianensis* plays both a timber and non-timber role in the diverse matrix of resources that encourage Amazonian forest conservation through sustainable use. Our research highlights several demographic variables that indicate *C. guianensis* management potential. Low densities of economically important tree species in many tropical forests are a major constraint to sustainable resource exploitation and a chronic management problem (Peters, 1996). Our study and others (McHargue and Hartshorn, 1983; Plowden, 2004;

Henriques and Sousa, 1989), however, suggest that in a variety of environments, *C. guianensis* is found at relatively high densities, favoring management and potentially suggesting comparatively higher yields (seed or timber) per hectare than other species. Furthermore, the higher densities in the occasionally inundated forest suggest that this forest type in particular may merit special attention for future management. Still, we found a higher percentage of adults in *terra firme* forests that hold dominant and co-dominant positions in the canopy—canopy positions that are almost a prerequisite for reproductive maturity based on our data. Whether these *terra firme* adults reach reproductive maturity more quickly than those in occasionally inundated forests merits further consideration when managing for *C. guianensis* seed production. The fact that both seedling mortality and recruitment are similar in the two forest types suggests that seeds and seedlings do well in both habitats, at least over the study interval.

In addition to the high densities, aggregation of *C. guianensis* individuals may facilitate resource accessibility. *C. guianensis* in both forest types presented a clumped distribution, which could facilitate a concentration of management activities such as trail construction, silvicultural treatments, and seed collection.

Bamboo dominance in one study plot may be indicative of future management challenges. Bamboo can rapidly colonize areas after disturbances such as logging or fire and is considered invasive by some (Okutomi et al., 1996; Blundell et al., 2003). Timber harvests in bamboo-rich sites, such as our plot 4 (Fig. 2), characterized by low adult densities, should only proceed with caution given the likelihood that disturbance would facilitate bamboo expansion.

This is the first study to explicitly compare *C. guianensis* population structure in *terra firme* and occasionally inundated forest; almost all research has focused on populations in wet sites. We found spatially similar aggregated distributions and size-class structures in both *terra firme* and occasionally inundated forests, suggesting that both forest types are suitable for *C. guianensis*. This new finding illustrates the potential for *C. guianensis* management in *terra firme* forests. Due to their borderline significant differences in tree densities and potential differences in reproductive potential, however, we recommend stratification by forest type when conducting further studies on key ecological/management variables of *C. guianensis*.

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