ECOLOGICAL REVIEW AND DEMOGRAPHIC STUDY OF *Carapa guianensis*

By

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This document is dedicated to my husband, my parents and my grandfather Frank Klimas. Thank you for everything.
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Both NTFPs and logging play important economic roles in Amazonian development, though not without environmental costs. Effective forest management, however, can mitigate some of these associated costs, particularly when based on an understanding of the ecological parameters under which sustainable harvest can exist.

*Carapa guianensis* Aublet. is a tropical tree with strong multiple-use characteristics, valued for both the high quality oil extracted from its seeds and as a timber resource. This thesis first provides a synthetic review of the most relevant ecological and management literature of *Carapa guianensis*. Then, I compare population structure of this economically important rainforest tree in two contrasting forest types. Main study objectives were (a) to assess the density, distribution, and size class structure of *C. guianensis* in occasionally inundated and *terra firme* forests; (b) to compare spatial distribution between the two forest types, using two different methodologies; and (c) to use patterns of abundance, distribution and demographic structure to help infer key demographic stages or ecological variables that merit special focus when implementing a
management scheme. Four 400 x 400 m plots, two in each forest type, were established to
determine distribution and density patterns of C. guianensis ≥ 10 cm at the landscape
level, and 32 10 x 10 m subplots were randomly nested within each of the larger plots to
measure individuals < 10 cm dbh. Carapa guianensis was 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 413 trees ha⁻¹
in occasionally inundated forests and 154 trees ha⁻¹ in terra firme forests, but interplot
variation of regeneration density was high. Annual recruitment was 94 seedlings (41%)
in occasionally inundated forest and 26 seedlings (39%) in terra firme. Both spatial
distribution methods revealed a tendency toward clumping in both forest types. High
densities and clumped distributions in both forest types are indices favorable for
sustainable species management, though reported growth rates for this species merit
further attention. Finally, several ecological variables were sufficiently different between
terra firme and occasionally inundated forests to recommend stratification by forest type
for further studies on growth and yield.
CHAPTER 1
INTRODUCTION

*Carapa guianensis* Aublet. (Meliaceae) is a key Amazonian species with both current and future economic potential. As with other species in the Meliaceae (*Swietenia macrophylla* and *Cedrela odorata*), *C. guianensis* is an important timber tree in the Neotropics (McHargue & Hartshorn 1983, Mabberley 1987, Dayanandan *et al.* 1999). It is also valued for the high quality oil extracted from its seeds (Shanley 2005). Pure *Carapa* seed oil is used for medicinal applications (Rodrigues 1989), with value-added products including soaps, shampoos, candles and repellent torches (Shanley 2005). This species is considered to have such great economic potential that the Amazonian State of Acre in Brazil has identified it as one of six priority species for extraction research (Acre 2000). The oil has an international demand. Between 1974 and 1985, Brazil exported between 200 – 300 tons of oil annually (Clay *et al.* 2000). In a market in Belém, the oil sells for R$15 per liter (approximately US $7). As a valuable timber and non-timber forest product (NTFP), resource exploitation is already occurring and promises to expand as demand for seed oil and timber advance into the interior of the Amazon via federally-funded highway development projects (Fearnside 2005).

Despite its economic importance, however, there is limited information about *C. guianensis* in the peer-reviewed literature. While there are research gaps in the study of every species, there is a paucity of basic ecological information available for this species and information on management is concentrated in theses and technical reports. In addition, very little is known about *C. guianensis* population structure, and whether
structure changes across forest types. In this thesis, I first provide a synthetic review of the most relevant ecological and management literature of *Carapa guianensis* and comment on possible avenues for future research. In the subsequent chapter, I compare the demographic structure and seedling recruitment of *C. guianensis* in occasionally inundated and *terra firme*, or upland, forests. Main study objectives were: (a) to assess the density, distribution, and size class structure of *C. guianensis* in occasionally inundated and *terra firme* forests; (b) to compare spatial distribution analyses using two different methodologies; and (c) to see whether measured 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.

Measuring population structure in different habitats can be a first step towards assessing sustainability of harvesting in different habitat types (Peters 1996). Quantifying species demographic structure provides the underlying data for use in ecological models for assessing long-term population viability (Alvarez-Buylla *et al.* 1996). Since vital demographic rates are normally stage-dependent (Harper 1977), the structure of a population can be indicative of its demographic future and can be the basis for immediate management decisions when long-term demographic monitoring is not feasible (Bruna & Kress 2002).

This thesis is structured so that the second and third chapters are independent articles ready for submission to peer-reviewed journals. As such, relevant conclusions are found at the end of these two chapters and I articulate overall conclusions in the final chapter (Chapter 4).
CHAPTER 2
ECOLOGY AND MANAGEMENT OF Carapa guianensis AUBLET

Abstract

Carapa guianensis Aublet. (Meliaceae) is a key Amazonian species with both current and future economic potential. As with other species in the Meliaceae (Swietenia macrophylla and Cedrela odorata), C. guianensis is an important timber tree in the Neotropics. It is also valued for the high quality oil extracted from its seeds. Despite its economic importance, however, there is limited information about C. guianensis in the peer-reviewed literature. The objective of this paper is to provide a synthetic review of the most relevant ecological and management literature of Carapa guianensis and comment on possible avenues for future research.

Introduction

Carapa guianensis Aublet. (Meliaceae) is a key Amazonian species with both current and future economic potential. As with other species in the Meliaceae (Swietenia macrophylla and Cedrela odorata), Carapa guianensis is an important timber tree in the Neotropics (McHargue & Hartshorn 1983, Mabberley 1987, Dayanandan et al. 1999). It is also valued for the high quality oil extracted from its seeds (Shanley 2005), and in a local market in Belém, Brazil, sells for R$15 per liter (approximately US $7). The oil also has international demand; Brazil exported between 200 – 300 tons of oil annually between 1974 and 1985 (Clay et al. 2000). Pure Carapa seed oil is used for medicinal applications (Rodrigues 1989), with value-added products including soaps, shampoos, candles and repellent torches (Shanley 2005). This species is considered to have such
great economic potential that the Amazonian State of Acre in Brazil has identified it as one of six priority species for extraction research (Acre 2000). As a valuable timber and non-timber forest product (NTFP), resource exploitation is already occurring and promises to expand as demand for seed oil and timber advance into the interior of the Amazon via federally-funded highway development projects (Fearnside 2005).

Despite its economic importance, however, there is limited information about *C. guianensis* in the peer-reviewed literature. There are crucial gaps in the basic ecological information available for this species, and information on management is concentrated in theses and technical reports. This paucity of published ecological data on tropical species, even economically important ones, is not uncommon (Wilson 1988). For example, *Swietenia macrophylla* King, or mahogany, is one of the best known tropical trees, yet little is known about the ecology of Amazonian populations. Even basic inventories are lacking for mahogany over most of its range (Gullison *et al.* 1996). A search of Web of Science’s Science Citations Index found only 128 results for *Swietenia macrophylla*, and an even smaller number of 47 citations for *C. guianensis*. In contrast, a search for loblolly pine (*Pinus taeda*), an important temperate timber tree, produced 1,568 results. While this search was likely limited to recent literature with an English-language bias, it still demonstrates that research on *C. guianensis* is lacking.

The objective of this paper is to provide a synthetic review of the most relevant ecological and management literature of *Carapa guianensis*. I provide a brief description of the species drawn mostly from the work of Terence D. Pennington, a taxonomic authority for *C. guianensis*. I then review data from peer-reviewed publications, the relatively rich “gray” literature (Canhos *et al.* 1996, Lancanilao 1997), and unpublished
reports and data to synthesize information on the ecology, uses and management of the species. I conclude with potential avenues for future research.

Ecology

Taxonomy and Species Description

The first botanical description of *C. guianensis* was from a specimen collected in Guiana by Aublet (Aublet 1775). *C. guianensis* belongs to the Meliaceae family, and is a large evergreen tree. Buttresses can be absent or as high as 1 to 2.5 m (Fournier 2003). The bark has characteristically wide fissures with horizontal splits, and on peeling reveals a pink-red underbark (Jankowsky 1990). In old-growth forests at La Selva, Costa Rica, *C. guianensis* can attain 2 m in diameter and 45 m in height (McHargue & Hartshorn 1983). Fournier (2003) reported that *C. guianensis* may reach a maximum height of 60 m, though he did not cite details of this observation. More typically, however, *C. guianensis* reaches heights of 25-30 m (Pennington 1981).

Leaf morphology of *C. guianensis* is well described by Pennington (1981). Leaves are paripinnate, without stipules and clustered at the end of branchlets. They usually have an apical dormant or glandular leaflet, which sometimes results in an odd pinnate leaf. Leaflets are opposite (Pennington 1981, Ferraz 2003, Fournier 2003). Its large leaves have a distinctive texture: coriaceous with a dull smooth surface and slightly intricately impressed fine venation below (Pennington 1981, Gentry 1993). Some sesquiterpenes (Andrade *et al.* 2001) and other compounds (Shu-Hua 2003) have been isolated from *C. guianensis* leaves and flowers, suggesting some protection against herbivory (Trapp & Croteau 2001, Shu-Hua 2003).

Though *C. guianensis* has been cited as *Carapa macrocarpa* (Ducke 1922) and *Carapa nicaraguensis*, Pennington (1981) and Holridge & Poveda (1975) note that
neither is taxonomically distinct from *C. guianensis*. *C. guianensis* is morphologically similar to the taxonomically distinct *C. procera*, and the two can be confused as seedlings and adults. In both species, seedling germination is hypogeal and cryptocotylar, and fused cotyledons and unfused petioles are present (Fisch *et al.* 1996). Though both have compound leaves when adult, *C. procera* puts out an average of six simple leaves at germination, while leaves of *C. guianensis* are compound at all stages, thus providing the best distinguishing characteristic for seedlings (Fisch *et al.* 1996). Adult plants are botanically distinguishable by inflorescence and leaflet morphology, and Pennington (1981) outlines these differences:

1. *C. guianensis* has sessile, subsessile flowers or very rarely short stout pedicellate flowers, predominantly 4-merous with 8 anthers, a 4-locular ovary, and (2-)3-4(-6) ovules per loculus; leaflets ± elliptic, with an acute or acuminate apex.
2. *C. procera* has flowers that are always slender pedicellate, predominantly 5-merous with 10 anthers (rarely with 6 petals and 12 anthers), a 5(-6)-locular ovary, and (2-)3-6(-8) ovules per loculus: leaflets generally oblong with a rounded or apiculate apex.

Pennington (1981) listed local names for *C. guianensis*, mentioning that there is not always a clear distinction between tree and timber (Table 2-1).

<table>
<thead>
<tr>
<th>Country</th>
<th>Names</th>
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<tbody>
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<td>England, US</td>
<td>Carapa, Crabwood</td>
</tr>
<tr>
<td>Belize</td>
<td>Bastard mahogany, Warawere</td>
</tr>
<tr>
<td>Brazil</td>
<td>Andiroba</td>
</tr>
<tr>
<td>Colombia</td>
<td>Masábolo, Tangarillo, Tangaré</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>Cedro bateo, cedro macho</td>
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<tr>
<td>Cuba</td>
<td>Najesí</td>
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<tr>
<td>Dominica</td>
<td>Acajou</td>
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<td>Dominican Republic</td>
<td>Cabirma de Guinea</td>
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<tr>
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<td>Surinam</td>
<td>Krappa, Krappaboom</td>
</tr>
<tr>
<td>Venezuela</td>
<td>Carapa</td>
</tr>
</tbody>
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Carruyo (1972), Prance & Silva (1975) and Fournier (2003) provide more variations and additional names for these and other countries.

**Geographic Distribution**

*Carapa guianensis* is widely distributed from Belize along the Atlantic coast of Central America (also on the Pacific slope of Costa Rica) to South America throughout the Amazon Basin (Carruyo 1972, Pennington 1981, McHargue & Hartshorn 1983). The species is also found in eastern Cuba, the Dominican Republic, the Windward Islands and Trinidad and Tobago (Figure 2-1) (Pennington 1981, Standley & Steyermark 1946, Mhecha *et al.* 1984)

![Figure 2-1: The geographic distribution of *Carapa guianensis*.](image)

*C. guianensis* occupies a wide range of niches within this geographic distribution. While most individuals are restricted to altitudes between 0 and 350 m (Carruyo 1972, Pennington 1981), Pennington (1981) stated that in Ecuador and Venezuela, especially in
the state of Yaracuy, *C. guianensis* also occurs on mountain slopes at elevations up to 1400 m. Fournier (2003) added that *C. guianensis* is found above 1000 m on Guadaloupe Island. Rainfall requirements also vary widely as *C. guianensis* has been reported on sites receiving 1,743 mm yr\(^{-1}\) (UFAC 2005) and above 3000 mm yr\(^{-1}\), with a temperature range of 20 to 35 °C (Fournier 2003).

Most authors agree that *C. guianensis* is predominantly a species of swampy or periodically inundated land, preferring marsh edges, swamp forests, alluvial riverbanks and periodically flooded plains, occasionally forming nearly pure stands under these conditions (Rizzini 1972, Pennigton 1981, McHargue & Hartshorn 1983, Fournier 2003). Gerry and Kryn (in Carruyo 1972) state that *C. guianensis* can grow in a range of sites with different soils, as long as the site is not too dry. Magalhães et al. (1986/1987), examining factors associated with species development in experimental plots, however, recorded greater *C. guianensis* heights in areas with more argisols.

In adult *C. guianensis* trees, extremely wet and extremely dry periods can induce a cambial dormancy and the formation of terminal parenchyma bands; this indicates that wet sites without inundation and without extremely dry periods may offer the best growth conditions for this species (Dünisch et al. 2002b).

**Genetics**

The genetic diversity of *C. guianensis* as measured by percent polymorphism (35%) or heterozygosity (0.12) is low in comparison with tropical tree species (Hall et al. 1994). Even taking into account the limitations of their study (small number of loci, exclusion of complex loci and use of the most parsimonious approach in considering the number of total loci), Hall et al. (1994) considered the genetic variability of *Carapa guianensis* low for a highly outcrossed, long-lived tree with wide seed dispersal (Hall et
Dayanandan et al. (1999) found no inbreeding in either saplings or adults of *C. guainensis*, but they did see a trend toward decreased allelic richness in the sapling cohort of an isolated fragment population. As *Carapa guianensis* grows predominantly in periodically inundated tropical lowland swamps interconnected by watercourses, the movement and change of river courses over time would aid in the migration of floating seeds to distant populations (Rädänen et al. 1992).

Dayanandan et al. (1999) developed and characterized three polymorphic microsatellite markers for *C. guianensis*. Vinson et al. (2005) developed five additional microsatellite markers to use in investigation of mating system, gene flow and paternity in *C. guianensis* in Pará, Brazil. There are limited genetic studies of *C. guianensis* and a more thorough study of paternity, mating patterns and gene flow is recommended for a better understanding of management needs. The continuation of work by Vinson et al. (2005) should provide an important first step in addressing this understanding.

**Population Dynamics**

Densities of *C. guianensis* can vary widely between and within regions. In Northeastern Brazil, adult densities (dbh > 15.9 cm) were estimated at 137 individuals ha^{-1} (Sousa 1997). The median adult diameter was 34.8 cm and 31% of the adults exceeded 44.9 cm (Sousa 1997). Plowden (2004) found maximum densities of 16 trees ha^{-1} (dbh ≥ 10 cm), with densities ranging from 0 to 20 trees ha^{-1} depending on the habitat type. A population of *C. guianensis* in Acre, Brazil showed an overall density of 20.1 trees (dbh ≥ 10 cm) ha^{-1} with a higher density (25.7 trees ha^{-1}) in occasionally inundated forest and a lower density (14.6 trees ha^{-1}) in *terra firme* forest (Klimas, unpublished data 2004). Figure 2-2 shows the distribution of trees in the four plots from this study. In an unlogged population of trees ≥ 10 cm diameter at breast height (dbh) in Acre, Brazil, mean, median
and mode dbh were 25.6 cm, 22.2 cm and 11.1 cm, respectively, and no trees were found with a dbh above 80 cm (Klimas unpublished data from the Western Amazon). The

![Figure 2-2: Spatial distribution of individuals ≥ 10 cm dbh in four study plots in the Northwestern Amazon (Acre, Brazil). The size of the circle is directly correlated to the measured diameter of the individual it is representing. Panels A and C represent occasionally inundated forest and B and D represent terra firme forest.](image)

frequency distribution of this same population in the Western Amazon is characterized by a type-I size class distribution, one that displays a greater number of small trees than
large trees, and an almost constant proportional reduction from one size to the next (Klimas unpublished data from the Western Amazon). Research in Northwestern Brazil found a clumped dispersion pattern for *C. guianensis* (Henriques & Sousa 1989) and similar research in Acre, Brazil revealed a tendency toward clumping that was more aggregated for juveniles (10 cm ≤ dbh ≤ 20 cm) (Klimas, unpublished data, 2004).

A rigorous study by Vieira *et al.* (2005) found that *C. guianensis* is older and grows more slowly than previous research had suggested. Authors found that *C. guianensis* was among the oldest and slowest-growing of the approximately 50 species measured. One individual of *C. guianensis* with a dbh of 17 cm was carbon-dated at 785 years old. Individuals that measured 37.5, 55.0, 56.0 and 84 cm were found to be 172, 180 ± 120, 187 ± 145 and 277 ± 75 years old based on radiocarbon measurements (Vieira *et al.* 2005). Ages without error bars were determined by extrapolating growth rates determined by multiple radiocarbon measurements (Vieira *et al.* 2005).

**Reproductive Ecology**

**Flowering and fruiting**

*C. guianensis* inflorescences are large, 20 - 80 cm long, branched, and axillary or subterminal. Flowers have a delicate musky fragrance (Pennington 1981). Petals are white or creamy with a light pink color externally (Fournier 2003). No observational research on pollinators was uncovered.

In plantings at an experimental station, fruit production began at 10 years. In Surinam *C. guianensis* trees generally begin to flower when they are 6-8 years old and begin fruiting when 10-12 years old (Willemstein 1975 from Plowden 2004). The months of flowering and fruitfall vary greatly by latitude/longitude and even within the same region (Rizzini 1971, Pennington 1981, McHargue & Hartshorn 1983, Viana & Silveira...
Fournier (2003) reports that fruits mature in eight months, although no experimental or observational data was cited to back up this statement. No research on environmental cues that trigger pollination or fruitfall were observed, although Pennington (1981) stated that in areas where fruitfall coincides with the rainy season, water becomes an important dispersal agent.

The fruit is a large globulose to slightly 4-angled dehiscent capsule with 4 valves (quadrants) that separates when the fruit falls to the ground, freeing the seeds (Gentry 1993). Each valve is woody or subwoody 5 - 12 cm long and 6 - 10 cm in diameter. There are 1-2 seeds per valve, which are angular due to mutual compression (Pennington 1981). Impressions on the valve wall indicate the number of seeds contained in the segment (McHargue & Hartshorn 1983). In Brazil, Plowden (2004) found that whole fruits contained an average of 8.7 \( \pm \) 0.5 seeds, while at La Selva, Costa Rica, McHargue and Hartshorn (1983) report 6-7 seeds per fruit.

**Seeds.** Individual fresh seeds usually weigh between 25-35 grams, but seeds weighing over 100 grams have also been recorded (Hall et al. 1994). McHargue & Hartshorn (1983) reported an average dry seed weight of 15.6 grams. Despite their weight, seeds are very buoyant. Seeds loose their viability rapidly (McHargue & Hartshorn 1983, Connor et al. 1998, Ferraz 2003). Sampaio (1999) recommends storing seeds in plastic bags in a temperature-controlled area (14°C and 80% RH; or 12°C and 30% RH) where viability can be maintained for up to seven months. For information on seed composition, see Loureiro et al. (1979), Sampaio (1999), Revilla (2000) and Andrade et al. (2001).
Production. An adequate estimate of the (potential) productivity of *C. guianensis* in a certain forest area requires information on the seed production per tree. As *C. guianensis* is a masting species and variability of seed production between trees in high (Plowden 2004) (Table 2-2). McHargue and Hartshorn (1983b) reported that the *C. guianensis* population at La Selva produces good seed crops about every other year; in 1971, 1974, and 1976 almost all trees produced abundant seeds, but in 1973 and 1975 very few trees fruited. Realistic production estimates must include a wide cross-section of trees measured over a number of consecutive years. Even these data should be replicated across regions before scaling up (or using local results that may not be relevant in distant regions).

Table 2-2: While there is little information on seed production per tree, reported values vary wildly. Below is a compilation of research on seed production.

<table>
<thead>
<tr>
<th>Seed production</th>
<th>Total Seed weight (kg)</th>
<th>Authors</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>754 – 3,944</td>
<td>11.8 – 61.5 (dry)</td>
<td>McHargue &amp; Hartshorn 1983</td>
<td>A few trees dominated total seed production</td>
</tr>
<tr>
<td>74</td>
<td>1.2</td>
<td>Plowden 2004</td>
<td>No studies cited to obtain this estimate</td>
</tr>
<tr>
<td>Not reported</td>
<td>50 - 200</td>
<td>Shanley &amp; Medina 2005</td>
<td></td>
</tr>
</tbody>
</table>

Dispersal. *Carapa guianensis* has two predominant methods of secondary seed dispersion: water dispersal and frugivores (McHargue & Hartshorn 1983b, Plowden 2004). When fruitfall occurs during the rainy season, this allows for seed dispersal via water. *C. guianensis* is preferentially found in areas that are subject to flooding, but variability in the timing of fruitfall does not allow for quantification of the overall importance of water as a dispersal agent.

After fruitfall, McHargue and Hartshorn (1983b) report that 80 to 90% of the seeds are removed or eaten. The major vertebrate predators of *Carapa* are collared peccaries
(Tayassu tajacu), white-lipped peccaries (Tayassu pecari), and large rodents such as agoutis (Dasyprocta punctata) and pacas (Agouti paca) (McHargue and Hartshorn, 1983). Based on a study by Guariguata et al. (2002), seed removal rates were uniformly high irrespective of forest site. Small exclusion cages were successful in reducing seed predation, suggesting that larger animals were probably responsible for removing Carapa seeds.

**Germination**

Scarano et al. (2003) report physiological variation regarding dormancy in response to seed flotation. Results showed that seed responses to floating were two-fold: they either germinated while floating, growing both shoots and roots, or germination was inhibited. As the length of floating increased, maintenance of seed viability diminished, and after 2-2.5 months, most seeds were no longer viable (Scarano et al. 2003).

The germination capacity of *C. guianensis* seedlings is high. Published values range from 41 to 94% germination after varying time periods (Sampaio 1999, Connor et al. 1998, Guariguata et al. 2002). Germination begins 6 to 10 days from when the seeds fall from the tree, and seeds remain viable for 2 to 3 months (Sampaio 1999). It has been hypothesized that the species’ large seeds provide the energy reserves necessary to produce a tall shoot to raise the leaves above the normal seasonal or annual flood waters (McHargue & Hartshorn 1983b). *Carapa* seeds are capable of germinating in the shade, and seedlings are able to establish and grow under a closed canopy (Clark and Clark 1985).

Seed germination studies have not clearly determined the most favorable environment for germination. McHargue and Hartshorn (1983) found that in well-drained soils, half-embedded and completely buried seeds had higher rates of germination. In
poorly-drained swamp soils, seeds on the surface or half-embedded had 90% germination. Neither buried seeds in the swamp soils nor surface-sowed seeds in the well-drained soils germinated. Results from Guariguata et al. (2002) also showed a significant treatment effect on the number of Carapa seedlings that established (41% from buried and 59% from surface sown seeds). The benefits of burial by terrestrial mammals may be important for reducing density-dependent mortality by moving seeds away from maternal fruiting trees where seed and seedling density is high (Guariguata et al. 2002), but whether it plays a significant role in increasing germination is still unclear.

**Uses**

*C. guianensis* seed oil is widely used in folk medicine in Brazil and other countries in the Amazon basin (Rodrigues 1989, Penido et al. 2005), with value-added products including soaps, shampoos, candles and as a repellent (Shanley 2005). The oil is also used to prepare cosmetics and as fuel for lanterns in rubber tapping communities (Boufleuer et al. 2005). Even with its value as a NTFP, Plowden (2004) asserts that *Carapa*’s major economic use today is its insect-resistant reddish timber often used in place of its heavily exploited relative, mahogany (*Swietenia macrophylla*).

**Seed oil**

Ethnographic questionnaires applied to nonindigenous Brazilian forest communities indicated that *C. guianensis* seed oil was used to treat arthritis; throat inflammations; to prevent insect bites; to heal insect bites, cuts, sores and bruises; diarrhea; diabetes; ear infection; as a digestive stimulant and to treat cervical cancer (treat pain in the vaginal region) (listed in order of frequency encountered) (Hammer & Johns 1993). Ferraz (2003) also reports that some indigenous groups use the bitter yellow oil from *C. guianensis* seeds as an insect repellent, especially against mosquitoes carrying
dengue and malaria. A method of obtaining a lipid extract from *C. guianensis* for cosmetic treatment of cellulite has even been patented (Rouillard et al. 1999), although no published research verifies its veracity.

Hammer and Johns (1993) found significant general bioactivity in the seed of *C. guianensis*. The presence of active principles such as alkaloids, triterpenoids, cardiac glycosides, carbohydrates and tannins support the notion that *C. guianensis* is an important source of pharmacologically active compounds and merits further study (Hammer & Johns 1993).

Mendonça et al. (2005) showed that crude oil preparations from *C. guianensis* had high insecticidal activity with LC$_{50}$ values of 57 μg/l against *Aedes aegypti*, although identification of the components present in the active samples that might be responsible for the larvicidal activity against *A. aegypti* is still needed. Miot et al. (2004) found that *C. guianensis* oil (100%) showed a superior profile of repellence compared to product absence, but its repellent effect was significantly inferior to DEET. These results, however, are based on only 4 subjects and open the doors for more expansive and rigorous testing of the oil’s effectiveness as an insect repellent. Miot et al. (2004) cited research from Gilbert et al. (1999) indicating that repellent candles made from *C. guianensis* oil burned for 48 hours protected 100% against bites of *Aedes aegypti* in a closed environment of up to 27 ± 10 m$^2$. The citation from Gilbert et al. (1999), however, only stated that toxicology measurements of *C. guianensis* candles have been made at Alfenas University, Minas Gerais, Brazil. More rigorous studies are still necessary to confirm results from these studies and better analyze the effectiveness of the oil’s repellent strength.
To obtain the oil, seeds are boiled in a large pot of water and left for 8 to 15 days to induce fermentation. Seeds are then shelled, and the pulp (seed endosperm) is mashed and kneaded by hand. The seed mass is then set out on a sloping sheet. Over the course of a week, the oil drips down a cloth wick into a collecting jar (Plowden 2004, Boufleuer et al. 2005). In addition to this method, extraction of oil can be done using small presses and filters more commonly used to extract oil from Brazil nuts or can be done on an industrial scale. Plowden (2004) found that it would take 14.43 kg of seeds to produce one liter of oil.

**Timber**

While the oil market is well-developed, *C. guianensis*’s major economic use today is its timber (Plowden 2004). The wood of *Carapa* is moderately heavy (0.70 to 0.75 g/cm³) with bright reddish-brown coloring. It is similar in many respects to that of true mahogany, but it is harder and heavier and lacks the lustre and color of mahogany (Pennington 1981). According to Pennington (1981), two types of *C. guianensis* timber are recognized by foresters: red and white. Red or Hill “crabwood” is said to be superior to white and is obtained from trees growing on higher land. White “crabwood” is derived from those growing on swampy flat ground. Carruyo (1972) and Jankowsky (1990) provide a more complete list of the physical properties of the wood. Timber from *C. guianensis* is considered variable; laboratory tests report both high and low resistance to brown and white rot fungi. This variability may stem from the two different timber types. The wood is easy to work and allows for a good finish. It is much sought after for construction of furniture, detailed boxes for jewelry, construction, window frames and doors, dividing walls, shutters, doorframes, molding, thin wood leaf, chipboard, and the final woodwork for boats and ships (SUDAM, 1979 from Sampaio 1999; Souza, 1997).
The Swedish Forest Products Research Laboratory has conducted a wide array of studies on the wood of *C. guianensis* and other species and is a valuable starting point for research on the wood properties of *C. guianensis* (Boutelje 1980). Finally, the wood is an excellent fuel source due to a high ignition temperature and therefore slow combustion (SUDAM, 1979 from Sampaio 1999; Sousa, 1997).

**Management Considerations**

As with most tropical species, knowledge about the site demands and the appropriate management of timber plantations is still limited (Dünisch et al. 2002b), and this is also true for management of *C. guianensis* in natural forest. Studies in plantations and natural forest have begun to identify factors that may affect future management of *C. guianensis*.

**Wood quality**

The low variability in wood density, flavonoid content that gives rise to *C. guianensis*’s decorative color, and a high fibre content all contribute to *C. guianensis*’s wood quality. Bauch & Dünisch (2000) found that these characteristics are maintained in plantation grown trees. *C. guianensis* produces mature wood (heartwood) at a very early age (four years in plantations), compared with development of adult wood in other tropical hardwoods (Bauch & Dünisch 2000). As heartwood is very important for furniture and veneer wood, this finding is promising for high-quality timber production under suitable plantation conditions (Bauch and Dünisch 2000), though seeds and seedlings are susceptible to attack by parasites and these attacks are more prevalent when grown under plantation conditions (see below).
Drought tolerance

*C. guianensis*, a pioneer species, exhibited different functional gas exchange and hydraulic traits than later successional lowland rainforest species in French Guiana (Huc *et al.* 1994). The authors believe that these results may reflect a competitive ability for water and nutrient uptake in the absence of soil drought. Maximum water uptake in *C. guianensis* was found in soils with a soil water potential of –25 to –28 kPa (Dünisch *et al.* 2002c). *C. guianensis* utilizes a strategy that increases its net assimilation rate under drought conditions compared to *Swietenia macrophylla* and *Cedrela odorata*. Trees use stored xylem water for transpiration during drier periods. While the absolute amount of stored xylem water is sufficient to compensate only short-term daily water deficits, good conditions for refilling xylem water at night often exist in tropical forests. Xylem water storage thus positively influences photosynthesis during drier periods (Dünisch & Morais 2002). Dünisch and Puls (2003) found that *C. guianensis* favors the compensation of unfavorable hydrological conditions to maintain growth during the entire year while related species (*Swietenia* and *Cedrela*) depend on a high water supply of the soil.

Morphological and anatomical studies on the structure of the roots and leaves also showed a better capacity for the regulation of water and nutrient uptake of *C. guianensis* compared to *Swietenia* and *Cedrela* (Dünisch *et al.* 1999). Noldt *et al.* (2001) were able to demonstrate special strategies to resist drought in by analyzing the anatomical structure and chemical characteristics of the fine roots of *C. guianensis*. They found that *C. guianensis* exodermis develops cells especially well adapted to drought. These adaptations to drought are very important for long-term survival of *C. guianensis* and with increasing evidence of current and future droughts in the Amazon (Nepstad 1999), these adaptations may select for survival of this species under changing climate
conditions. They may also facilitate management under a variety of conditions and facilitate management in areas where water limitation is a factor.

**Effects of parasites**

*C. guianensis* seeds and seedlings are susceptible to attack by the parasite (*Hypsipyla* sp.) (Pennington 1981). Becker (1973) records larvae of *H. grandella* Zell. from the shoots and those of *H. ferrealis* (Hamp.) from the seeds of *C. guianensis*. Plowden (2004) also mentions that seeds are susceptible to attack by fly maggots. Attack by *H. ferrealis* causes forking in seedlings - a problem for timber production, especially since this parasite is more prevalent when trees are planted in full sunlight (Carruyo, 1972). While full sunlight has been stated as the cause for attack, no experiments have been conducted to determine percent attack with different light availabilities. Other confounding variables such as soil moisture or planted seedling density may have more of an effect on seed and seedling susceptibility to attack.

Infested seeds are recognized by the sawdustlike substance coming out of 1-3 mm diameter holes in the seed coat through which larvae emerge. Seeds can sustain some seed damage by moths and still germinate (McHargue & Hartshorn 1983). Although I am not aware of any literature that speaks to the effect of seed infestation on oil quality, depending on how long the larvae had been feeding on the seed, larval infestation could reduce the quantity of seeds available for oil production. Soaking seeds in water for 14 days (changing the water daily), then germinating them in sealed clear plastic bags drowns *Hypsipyla* sp. and allows the seeds to become turgid (Fisch *et al.* 1996, Ferraz 2003).
**Growth and maturation**

Due to formation of vessel bands in the juvenile wood (false rings), *C. guianensis* is not suited to dendroecological studies (Dünisch *et al.* 2002b, Dünisch *et al.* 2002a). This makes determining tree age difficult, particularly since growth rates are variable between regions and forest habitats. A group of planted trees at La Selva, Costa Rica measured 10-15 cm in diameter, about 7-10 m tall after 6 years of growth, the same age as a group of shaded seedlings in a nearby swamp, most of which are below 1 m in height (McHargue & Hartshorn 1983b). In plantings done at the Experimental Station of Curuá-Una/PA, in full sunlight, with 2.5 x 2.5 m spacing and 80% survival, trees averaged a 1.8 m yr\(^{-1}\) height increase and a 1.10 cm annual dbh increase (Willemstein 1975 from Plowden 2004).

Growth rates also differ between forest and plantations. At about four years of age, growth rates of *C. guianensis* in primary forest was only approximately half that of trees from unfertilized plantations. Plantation grown *C. guianensis* exhibited rapid growth throughout the year with annual growth of about 1.14 cm. The intra-annual pattern of *C. guianensis* in the primary forest differed with an annual diameter growth of only 0.246 cm (Bauch and Dünisch 2000). The high variability of individual growth rates makes it difficult to use published growth rates from one region in another region, or even a neighboring site. This difficulty is enhanced if there are large differences between the sites (i.e. plantation vs. natural forest).

Measurements of the soil water supply in primary forest indicate that high soil water content can lead to growth depression or even short dormancy periods (Dünisch *et al.* 1999), although no dormancy was observed during the dry season (Bauch and
Dünisch 2000). Positioning plantations in areas that are not subject to periodic inundation may result in increased annual growth.

Variation in diameter and height increment due to light environment and other microenvironmental conditions is problematic for estimating timber yield and age to first reproduction in natural forest. As determined in Vieira et al. (2005), small diameter trees can survive in the understory for hundreds of years, making it difficult to estimate cutting cycles and timber yield. This environmental variation also makes it difficult to predict when trees will reach a size that supports seed production. More research is necessary to better determine average growth rates under a forest canopy and limiting microenvironmental factors that may limit growth.

**Reforestation**

*Carapa guianensis* was suggested as a species that holds promise for reforesting secondary forests (Sampaio 1999). Dünisch et al. (2002c) recommend it for the restoration of degraded areas. The physiological adaptations to drought mentioned above (Huc et al. 1994, Dünisch et al. 1999, Dünisch & Morais 2002, Dünisch & Puls 2003), the high germination rates (Connor et al. 1998, Sampaio 1999, Guariguata et al. 2002) and its high survival in plantations (Willemstein 1975 from Plowden 2004) are suggest its potential for establishment and survival. It also showed promise for reforestation in pasture and grasslands. *Carapa guianensis* had fast germination, high survival and relatively high performance when planted with the exotic grass *Saccharum spontaneum*. It also had the ability to resprout after fire (Hooper et al. 2002). While the authors did not mention attack by *H. ferrealis*, it is possible that they were concerned more with rapid establishment and growth than with adult tree form.
Dünisch et al. (2003) do not recommend monocultures of plants with low transpiration rates, such as *C. guianensis*, in the Central Amazon due to high water loss from interception and water runthrough in young monoculture stands. Authors instead recommend enrichment plantations where the positive effect of secondary vegetation stabilizes water fluxes.

**Avenues for Future Research**

While authors have touted the economic potential of *C. guianensis* in the literature, very little research has been done to quantify this potential or to look at sustainable harvest limits/challenges. This section outlines data still lacking to make informed decisions about sustainable management of this species as both a timber and non-timber resource. According to Hall and Bawa (1993), knowledge of the natural distribution, abundance, population structure and dynamics, and variation of these factors across a landscape is required in order to assess the sustainability of resource harvesting. Permanent plot networks in tropical forests may provide some information on these variables for *C. guianensis* (Losos & Leigh Jr. 2004, Viera et al. 2005), but in these cases, *C. guianensis* may form only a small percentage of the inventoried trees. A recent article examines the population structure and spatial structure of this species in two forest types in Acre, Brazil (Klimas, in preparation). This study, however, fails to provide information on the size-specific growth rate, fecundity and mortality of this species or other information on species dynamics, information that is essential for simple demographic models (Leftkovitch 1965).

Using genetic and evolutionary models in combination with demographic models may provide a more realistic projection of the efforts necessary for species management. These models incorporate loss of genetic variability for adaptive evolution, random
fixation of deleterious mutations or alleles by genetic drift and inbreeding depression (Hedrich & Miller 1992, Ellstand & Elam 1993). Only preliminary genetic studies exist for *C. guianensis*. The continuing work of Vinson *et al.* (2005) will allow a better understanding of management needs, and recent genetic surveys of *C. guianensis* in Acre, Brazil (Raposo) will provide valuable information on paternity and mating patterns. To truly capture the risks of management, however, estimates of effective population size, inbreeding coefficients and the genetic variation are important (Alvarez-Buylla *et al.* 1996).

Basic ecological information on this species is still unavailable. Research on pollinators, a key management variable is lacking. Silvicultural experiments to ascertain methods for improving growth rates, tree form and increasing seed production per tree would also provide valuable management data for both plantation and forest-grown *Carapa guianensis*. Methods of controlling *H. ferrealis* and *H. grandella* infestations in seedlings and saplings, respectively, and ways to promote/improve survival and growth of young *C. guianensis* individuals may also bear investigation. Experiments that explore underlying causes for seedling susceptibility to parasite attack would permit better management of early plantations.

Seed collection will likely affect seed predators. More research determining the broader ecosystem impacts of seed and timber collection may be beneficial. Similarly, broader faunal resources such as game meat are critically important for human inhabitants (Hill *et al.* 2003). The linkages between seed populations and seed predators is important to quantify (Forget 1996), both for ecologists and forest residents who rely on these animals for sustenance.
Economic and social analyses of commercialization barriers for small scale landowners is a key step toward utilization and management of this resource. Even with preliminary information on the market value of seed oil in different areas of the Brazilian Amazon (Shanley 2005), the costs of transportation to the nearest market, labor, investment in equipment and the trade-offs with current economic activities have not been fully analyzed, though see Plowden (2004) for preliminary labor estimates. From the forest to the final product, there is still a wealth of information yet to be discovered to better advise ecosystem managers and commercial producers of this species.
CHAPTER 3
POPULATION STRUCTURE OF *Carapa guianensis* IN TWO FOREST TYPES IN THE WESTERN BRAZILIAN AMAZON

**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 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 & Perez 2001). Logging and non-timber forest product (NTFP) extraction, however, incurs associated environmental costs (Peters 1996, Nepstad 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 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
To sustain, or even increase the abundance of an extracted product, detailed knowledge of species life history and demographic behavior is essential (Sunderland and Dransfield 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 & Ribeiro 2005). Since these variables can differ by habitat type (Bruna & Kress 2002, Wagner & Fortin 2005), they should be evaluated for any given species in the multiple habitats or forest types in which they occur.

*Carapa guianensis* is valued for both the high quality oil extracted from its seeds (Shanley 2005) and as a timber resource (Dayanandan *et al.* 1999). Pure *C. guianensis* seed oil is used for medicinal purposes (Rodrigues 1989), as well as in products such as soaps, shampoos, candles and insect-repellent torches (Boufleuer 2001, Shanley 2005). *C. guianensis*’s major economic use today, however, is as insect-resistant timber often used in place of its heavily exploited relative, *Swietenia macrophylla* King, commonly known as mahogany (Plowden 2004). 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), the structure of a population can be indicative of its demographic future and can be the basis for immediate management decisions when long-term demographic monitoring is not feasible (Bruna & Kress 2002).

We compared the demographic structure and seedling recruitment of *C. guianensis* in occasionally inundated and *terra firme*, or upland, forests. Main study objectives were: (a) to assess the density, distribution, and size class structure of *C. guianensis* in occasionally inundated and *terra firme* forests; (b) to compare spatial distribution between the two forest types, using two different methodologies; and (c) to use patterns of abundance, distribution and demographic structure to help infer key demographic stages or ecological variables that merit special focus when implementing a management scheme.

**Species Description**

*C. guianensis* is a medium to large hardwood tree that can attain 2 m in diameter and 50 m in height (Pennington 1981, McHargue & Hartshorn 1983). Most authors agree that *C. guianensis* is a predominantly pioneer species of wet areas, although it is also found on a variety of drier sites (Pennigton 1981, McHargue & Hartshorn 1983, Fournier 2003). It is found in the West Indies, Antilles, Central America south of Honduras, many parts of the Amazon region, and tropical Africa (Smith 1965, Pennington 1981, McHargue & 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 4 valves (quadrants).
that separate and open upon falling to the ground, freeing the seeds. It has two predominant methods of secondary seed dispersal: water and frugivores (McHargue & Hartshorn 1983b, Plowden 2004). Each valve contains between 1 and 4 seeds (Smith 1965, McHargue & Hartshorn 1983, Sampaio 2000). Annual seed production in this species is variable. Based on a 5-year study, McHargue and Hartshorn (1983) reported that *C. guianensis* produces good seed crops almost every other year. In Acre, forest residents and technicians report a 2-3 year masting cycle (personal communication).

**Study Site**

Field surveys were carried out within the 1,200 hectare experimental forest of the Brazilian Agricultural Research Corporation (Embrapa) in the northeastern portion of the state of Acre, Brazil (Figure 3-1). 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. The mean annual temperature is 24.5°. Brief intrusions of cold air from the South occasionally drop

![Figure 3-1: Location of the study plots at the Brazilian Agricultural Research Corporation’s experimental forest in Acre, Brazil (Figure adapted from Gomes 2001, with permission).](image)
temperatures to 10°C during the dry season (ZEE 2000). During the 2004-2005 study period, the maximum and minimum temperatures, respectively, were 35°C and 16°C; relative humidity ranged from 71 to 91% with an average of 86%; and total rainfall was 2,089 mm in 2004 and 1,743 mm in 2005 (UFAC 2005). Weather data were collected 25 km from the study site. Soils in the occasionally inundated forest were red and yellow ultisols; soils in the terra firme forest were plintosoils (Rodrigues et al. 2001).

Methods

Plot Installation

Four 400 x 400 m (16-ha) plots were established from June through July 2004 to determine distribution and density patterns of C. guianensis at the landscape level. Two plots were installed in areas where the majority of the environment was classified as “terra firme”, or upland forest and two in occasionally inundated forest, defined as level or concave areas on poorly drained ground or areas subject to periodic flooding. Terra firme was considered to be convex or level ground in well-drained areas (Azevedo 2005).

Internal transects were installed every 50 m to create eight 400 x 50 m rectangles. A central transect was used to bisect these rectangles. These internal divisions created a grid system used to map C. guianensis individuals. Appendix A contains additional information on the sampling design.

Mapping Adult Individuals

C. guianensis trees ≥ 10 cm diameter at breast height (dbh) were inventoried in all 4 plots. A minimum of two researchers located trees by systematically walking parallel to the transect lines. After locating a tree, the exact y-coordinate was recorded based on a tape-measured distance. The x-coordinate was visually estimated based on distance to the proximate transect. This accuracy of the x-coordinate was tested by measuring the
distance with a meter tape and an error of $\pm 5$ m was attained before continuing. In addition to the coordinates, plot number, canopy position (dominant, co-dominant, intermediate or suppressed) from Smith et al. (1997), dbh, microenvironment (terra firme or occasionally inundated) and reproductive status were recorded. Reproductive status was positive if there were seeds or associated dehiscent capsules located either on the tree or on the ground underneath the tree or if there was a seedling bank from a former year that could only be clearly attributed to that tree. While at the landscape scale, each of the 4 plots was assigned to one of two forest types (terra firme or occasionally inundated forest), we also assessed the “microenvironment” immediately surrounding each tree (approximately a 1-2 m diameter), assigning each individual to a microenvironment (again, either terra firme or occasionally inundated).

**Estimating Regeneration**

Thirty-two 10 x 10 m subplots were randomly nested within each of the larger plots to measure individuals < 10 cm dbh in August and October, 2004 (Appendix B). Subplots were only selected for study if the entire 100 m$^2$ area belonged to the same microenvironment as the larger, designated forest type. For example, only subplots that were clearly and totally defined as terra firme were accepted for study as a terra firme regeneration subplot. If a selected subplot fell in a lowlying area or transition zone, it was removed from the sample and another subplot was randomly selected for consideration. Selected subplots with trails or rivers within their boundaries were also discarded.

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

**Data Analysis**

Since analysis of variance (Anova) cannot be used if autocorrelations are present, we used correlograms from the ‘spatial’ package in R to test for spatial autocorrelation of tree diameter as a function of distance (Venables & Ripley 2002). Correlograms divide a range of data into bins and computes the average squared differences for pairs with separation in each bin. Results are returned only for those bins with 6 or more pairs; 50 bins were selected per plot. A logit model, in R described as binomial proportion comparisons, was used to test for differences in the binary production values and differences between size classes in the different forest types.

Following this test, Anova was used to test for differences in adult, sapling and seedling densities and adult diameter distribution. Forest type and microenvironment were treated as fixed effects. Nesting was used for the seedling and sapling anovas. Tukey’s HSD was used for all applicable multiple comparisons. A two-sample test of proportions was used to compare percentage values for tree reproduction of the various dbh classes. In this case, a bonferroni correction was used on the alpha level. R programming language was used for all analyses and a p-value of 0.05 was considered statistically significant.

I characterized the spatial distribution of *C. guianensis* using the aggregation index R (Clark & 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. Spatstat, an R package for spatial point pattern analysis (Baddeley & Turner 2005) was used to calculate nearest neighbor distances based on the x,y coordinate reference system. I 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 individuals (10 cm ≤ dbh < 20 cm), hereafter termed sub-adults, and reproductive adults (dbh ≥ 20 cm) in each experimental plot for the purpose of exploring whether sub-adults have a different spatial distribution than reproducing adults. These subdivisions were used since results showed that the majority of individuals dbh ≥ 20 cm had evidence of reproduction, while this was not the case for individuals < 20 cm dbh. Plowden (2004) found similar size-based production estimates. Anovas tested 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 $\lambda \cdot K(r)$. The intensity, $\lambda$, 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.
\[ K(r) = \frac{1}{\lambda} \times \frac{1}{N} \times \sum \sum \kappa_{ij}; \]

where \(\kappa_{ij}=1\) 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:

\[ L(r) = \sqrt{\frac{K(r)}{1-r}}. \]

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 analysis included all trees \(\geq 10\) cm dbh.

Confidence intervals were estimated 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). Results for \(L(r)\) were graphed with their corresponding confidence interval 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 & Turner 2005).

**Results**

**Adult Structure**

Almost twice as many *C. guianensis* trees \(\geq 10\) 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 (25.5 ± 0.2 and 14.5 ± 2.7 trees ha\(^{-1}\), respectively) \((p = 0.056)\) (Figure 3-2). For both forest types the distribution of
Figure 3-2: Density of *C. guianensis* individuals (dbh ≥ 10 cm) in four 16-ha study plots in two contrasting forest types.

Individuals in dbh classes revealed a classic j-distribution with a higher number of subadults (10 cm ≤ dbh < 20 cm) and smaller diameter trees and a decrease in the number of individuals in the larger diameter classes (Figure 3-3). Further binomial proportion

Figure 3-3: Size-class distribution of *C. guianensis* trees ≥ 10 cm dbh in two contrasting forest types.
comparisons indicated that the percentage of individuals per forest type only differed with respect to forest type in the 10 to 20 cm dbh class (p < 0.001) (Table 3-1). Correlograms showed no correlation between tree diameter and nearest neighbor distance (Figure 3-4). Anova tests were thus appropriate for data analysis, and revealed that average dbh was significantly higher in the occasionally inundated versus terra firme forest (p = 0.031).

The number of reproductive trees was significantly higher in occasionally inundated forest than in the terra firme forest (p = 0.003). 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 did not show evidence of reproduction (Table 3-1). 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.

Finally, assuming reproduction at dbh ≥ 20 cm, the non-reproductive to potentially-reproductive ratio in the occasionally inundated forest was significantly different than in the terra firme forest (8.44 and 5.79, respectively) (p = 0.025). Thus, compared with the occasionally-inundated forests, for every reproductive adult in terra firme forest, there are fewer corresponding non-reproductive sub-adults.

**Seedling and Sapling Structure**

As with individuals ≥ 10 cm dbh, C. guianensis seedling densities were significantly higher (almost triple) in occasionally inundated plots than in terra firme plots (p = 0.006), while sapling densities did not differ by forest type (Figure 3-5).
Table 3-1: Descriptive results comparing *Carapa guianensis* populations in occasionally inundated and *terra firme* forests. Overall, 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.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Diameter class</th>
<th>Percent of individuals (%)</th>
<th>Crown class&lt;sup&gt;a&lt;/sup&gt; (Percentage in each diameter class)</th>
<th>Reprod. indiv.&lt;sup&gt;b&lt;/sup&gt; (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>D</td>
<td>CD</td>
</tr>
<tr>
<td>Occasionally inundated</td>
<td>10 ≤ dbh &lt; 20</td>
<td>40.0***</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>20 ≤ dbh &lt; 30</td>
<td>30.3</td>
<td>4</td>
<td>49***</td>
</tr>
<tr>
<td></td>
<td>30 ≤ dbh &lt; 40</td>
<td>18.7</td>
<td>14</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>40 ≤ dbh &lt; 50</td>
<td>7.8</td>
<td>28</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>50 ≤ dbh &lt; 60</td>
<td>2.7</td>
<td>55</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>60 ≤ dbh &lt; 70</td>
<td>0.4</td>
<td>67</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>dbh ≥ 70</td>
<td>0.1</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Percentage of all individuals ≥ 10 cm dbh</td>
<td></td>
<td>20</td>
<td>32</td>
<td>8</td>
</tr>
<tr>
<td><em>Terra firme</em></td>
<td>10 ≤ dbh &lt; 20</td>
<td>50.2</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>20 ≤ dbh &lt; 30</td>
<td>24.7</td>
<td>1</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>30 ≤ dbh &lt; 40</td>
<td>16.5</td>
<td>10</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>40 ≤ dbh &lt; 50</td>
<td>5.2</td>
<td>33</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>50 ≤ dbh &lt; 60</td>
<td>2.4</td>
<td>82</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>60 ≤ dbh &lt; 70</td>
<td>0.9</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>dbh ≥ 70</td>
<td>0.2</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Percentage of all individuals ≥ 10 cm dbh</td>
<td></td>
<td>28</td>
<td>41</td>
<td>7</td>
</tr>
</tbody>
</table>

<sup>a</sup>Crown position: D=Dominant; CD=Co-dominant; I=Intermediate; S=Suppressed

<sup>b</sup>Reproductive individuals

*** p = 0.0005
Figure 3-4: Correlograms show no correlation between tree diameter and nearest neighbor distance, allowing use of anova for testing statistical differences. Panels A and C represent occasionally inundated forest and B and D represent *terra firme* forest.
Figure 3-5: Density of *C. guianensis* seedlings and saplings in two contrasting forest types.

Seedlings or saplings were found in 81% of the occasionally inundated subplots, but only 51% of the *terra firme* subplots. Occasionally inundated forest also had greater rates of seedling recruitment (*p = 0.001*) and mortality (*p = 0.017*) after a 10-month period, but percent recruitment and mortality were not different between forest types (Table 3-2).

These same sapling parameters did not differ with respect to forest type (Table 3-2).

Table 3-2: 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. Number and percent of seedling and sapling mortality and new recruits between these two periods (10 months) is also shown.

<table>
<thead>
<tr>
<th></th>
<th>Seedlings</th>
<th>Saplings</th>
<th>Occasionally Inundated Forest</th>
<th>Terra Firme Forest</th>
<th>Occasionally Inundated Forest</th>
<th>Terra Firme Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N (2004)</td>
<td>231**</td>
<td>66</td>
<td>30</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total N (2005)</td>
<td>248</td>
<td>73</td>
<td>28</td>
<td>31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mortality: N (%)</td>
<td>77* (33.3)</td>
<td>19 (28.8)</td>
<td>3 (10.0)</td>
<td>1 (3.1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>New Recruits: N (%)</td>
<td>94** (40.7)</td>
<td>26 (39.4)</td>
<td>1 (3.3)</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* * p < 0.05
** * p < 0.01
**Spatial Distribution**

Spatial distribution of reproductive adults (dbh ≥ 20 cm) was aggregated in all forest plots (Figure 3-6) (Table 3-3). Based on application of Donnelly’s (1978) nearest neighbor method, 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 0.5015).

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Figure 3-6: 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. Panels A and C represent occasionally inundated forest and B and D represent *terra firme* forest.
0.8258, respectively). These values indicate a rejection of the null hypothesis of a strictly random pattern of distribution in all the plots.

Table 3-3: 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.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Plot</th>
<th>N^a</th>
<th>R^b</th>
<th>p-value</th>
<th>Average distance between trees (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(x ± SE)</td>
</tr>
<tr>
<td>Occasionally</td>
<td>Adults</td>
<td>1</td>
<td>264</td>
<td>0.9010</td>
<td>&lt;0.0002</td>
</tr>
<tr>
<td>inundated</td>
<td>Adults</td>
<td>3</td>
<td>229</td>
<td>0.9006</td>
<td>&lt;0.0003</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>1</td>
<td>151</td>
<td>0.7586</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>3</td>
<td>178</td>
<td>0.9116</td>
<td>&lt;0.0020</td>
</tr>
<tr>
<td>Terra firme</td>
<td>Adults</td>
<td>2</td>
<td>139</td>
<td>0.9152</td>
<td>&lt;0.0060</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>4</td>
<td>93</td>
<td>0.7256</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>2</td>
<td>138</td>
<td>0.8891</td>
<td>&lt;0.0013</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>4</td>
<td>96</td>
<td>0.5942</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

^a Number of individuals.

^b 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).

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

Results from Ripley’s K(r) confirm a clumped distribution in all four plots (Figure 3-7). For this analysis, sub-adults and reproductive adults were analyzed as a unit. When L(r) is outside the confidence interval, it is possible to reject the complete spatial randomness hypothesis (with a risk of α=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 longer range aggregation (60 m) (Figure 3-7).

Figure 3-7: 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 (B) displays middle-range (30 m) and long-range aggregation (60 m). Panels A and C represent occasionally inundated forest and B and D represent *terra firme* forest.
Both forest type and microenvironment were significant predictors of nearest neighbor distances ($p = 9.1 \times 10^{-6}$ and $p = 0.0001$, respectively), with those trees in terra firme being more distant from one another ($15.3 \pm 1.1$ m) than those in the seasonally inundated forests ($11.5 \pm 0.4$ m). Canopy class, production and all possible interaction terms were not significant for nearest neighbor comparisons.

**Discussion**

**Density and Distribution**

I found that the density of one of the Amazon’s most important timber trees far exceeds that of most other species. *Carapa guianensis* had densities of 25.5 and 14.5 trees $\text{ha}^{-1}$ in occasionally inundated and terra firme forests, respectively. In contrast, Gullison *et al.* (1996) report densities ranging from 0.31 to 1.6 trees $\text{ha}^{-1}$ for *Swietenia macrophylla* ($\text{dbh} \geq 2.5$ cm). In the Western Amazon, Wadt *et al.* (2005) found densities of only 1.35 trees $\geq 10$ cm $\text{dbh} \text{ ha}^{-1}$ for Brazil nut (*Bertholletia excelsa*), another economically important tropical tree. Furthermore, I found extremely high densities in the occasionally inundated forest compared to the terra firme forest. McHargue and Hartshorn (1983) also reported that *C. guianensis* was predominantly a species of swampy or periodically inundated land, but is also found in lower densities on higher and better-drained slopes and ridges. The natural distribution and abundance of a species is partly a function of the spatial variability in available habitats and the species capacity to colonize these habitats (Hall & Bawa 1993).

**Size-class Structure**

The frequency distribution (Figure 3-3) shows that populations in both forest types show similar diameter distribution patterns. Peters (1996) describes this j-distribution as a “type-I size class distribution”, one that displays a greater number of smaller size-class
trees than larger size-class trees, and an almost constant proportional reduction from one size class to the next. This type of structure is characteristic of shade-tolerant canopy trees that maintain a more or less constant rate of recruitment (Peters 1996). While *C. guianensis* is a well characterized shade tolerant (Clark & Clark 1985), it is a masting species, and its ability to maintain constant recruitment over time in this population may speak to the ecological importance of this seed production strategy. The distribution suggests a demographically healthy population; many authors consider a type I structure the ideal of a stable, self-maintaining plant population (Meyer 1952, Leak 1965).

Not only were diameter distributions similar across forest types, but the percentage of reproducing individuals in any given dbh class was also 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 still necessary to determine whether the quantity of seeds produced differs between forest types. Similarly, further research may indicate a difference in the time it takes to reach a certain dbh between forest types. I found that seed production was initiated in the majority of trees > 20 cm dbh in all plots, yet do not know how long it took for them to attain this diameter. Viera *et al.* (2005) documented growth rates of five *C. guianensis* trees growing in open forest with bamboo and dense *terra firme* forest. They found that individuals of *C. guianensis* with dbh measurements of 17.0, 37.5, 55.0, 56.0 and 84.0 cm, had ages of 785, 172, 180 ± 120, 187 ± 145 and 277 ± 75, respectively. These data do not include individuals in occasionally inundated forests, but they clearly demonstrate high variability in growth rates. This variability in growth rates may prove problematic for sustainable harvest projections of *C. guianensis*
and other long-lived, slow-growing species. Since vital demographic rates are normally stage-dependent (Harper 1977), matrix models that explicitly consider the size (Leftkovitch 1965), dependent fecundity, growth and survival rates of individuals have been used to explore the effect of different harvesting regimes on the growth rate and structure of populations (Pinard 1993, Olmsted & Alvarez Buylla 1996, Zuidema & Boot 2002). High variability in growth rates confound projection matrices.

Forest type may influence time to seed production, but other variables may outweigh forest type effects. For example, light, which has been well correlated with relative height and spatial distribution (Nigh & Love 2004), has been shown to play an important role in stimulating seed production (Greene et al. 2002). In my study, the occasionally inundated plots consistently had higher numbers and densities across almost all size classes, suggesting a more robust population. In terra firme plots, however, a greater percentage of adults ≥ 10 cm dbh were in the dominant or co-dominant canopy positions, and it was in the terra firme plots where the proportion of reproductive to non-reproductive adults was greater. Perhaps in the terra firme, a greater proportion of adults reach the upper canopy where they have greater access to light, creating conditions in which a greater proportion of these adults produce fruits.

Forest type may have other effects due to microclimate variation between the higher terra firme forests and the more swampy occasionally inundated forest (Svenning 1999). Boll et al. (2005) found that soil moisture was the most important environmental predictor of occurrence for the tropical palm Aphandra. Valencia et al. (2004) also found that soil affected abundance differences for a variety of tropical trees. John and Sukumar (2004) found that species richness was weakly influenced by topography. While not
evident in this data set, intense fires, during the 2005 dry season, increased mortality in one of the *terra firme* forest plots (Wadt, personal communication). Recent research has indicated that tropical forests are becoming more susceptible to fire (Nepstad 1999). The effect of forest type may become important in conjunction with these environmental changes.

**Spatial Distribution**

While adult and seedlings densities differed between forest types, both spatial analyses demonstrated aggregation of individuals. Clumped distributions of trees are typical in both tropical dry (Hubbell 1979) and humid forests (Clark and Clark 1984). Aggregation seems to be highly linked with seed dissemination processes (Goreaud *et al.* 1999) and aggregation is ecologically beneficial; aggregation of conspecifics should increase pollination efficiency, outcrossing success, and species abundance (Hubbell 1979).

Adults occur in relatively large neighborhoods, probably due to competitive exclusion as the plants get larger with age. Seedlings, saplings and smaller diameter individuals occur in tighter clusters, since they are recruited by mature plants (Gibson 2002). Some differences in levels of aggregation were detected. Plot 4 (Figure 3-6), representative of a *terra firme* forest, was partially dominated by a bamboo. Very few individuals of *C. guianensis* were found in this area, which led to lower densities and higher levels of aggregation for trees in this plot.

Another *terra firme* forest plot (plot 2) showed both middle range and long range aggregation (Figure 3-7). The middle range aggregation may be due to seed dispersal close the parent tree and the long-range dispersal could be due to water or animal transport of seeds. Water is a crucial transport agent for *C. guianensis* as seeds fall during
the rainy season in some areas (Pennington 1981, Raposo 2002). Agoutis (Dasyprocta leporina) and collared peccaries (Tayassu tajacu) also disperse seeds while foraging (McHargue & Hartshorn 1983).

Both Clark & Evans and Ripley’s K(r) demonstrated aggregation of individuals. As expected, Ripley’s K(r) was more appropriate for showing whether aggregation occurred at different distances. Both methods, however, indicated that the local population of C. guianensis was aggregated irrespective of forest type. Aggregation is common in a variety of other tree species (Boll et al. 2005, Svenning & Skov 2005) and has been most often related to dispersal limitation (Condit et al. 2000, Svenning 2001, Svenning & Skov 2005).

Management Implications

These results highlight several demographic variables that merit special focus for species management. First and foremost, C. guianensis densities are extremely high compared to almost any tropical species. Low densities of economically important conspecific adult trees in many tropical forests are a major constraint to sustainable resource exploitation and a chronic management problem (Peters 1996). My study and others (McHargue & Hartshorn 1983, Plowden 2004), 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 extremely high densities in the occasionally inundated forest suggest that this forest type in particular may merit special attention for future management; there were simply more trees present.

These high densities which favor management, however, may be counterbalanced with excessively low growth rates. Growth differences between forest types might be the
most important demographic variable for determining timber harvest cycles. The extremely slow *C. guianensis* growth rates reported by Viera et al. (2005) from *terra firme* forests serve as cautionary signals if hoping to manage for sustainable timber production.

For non-timber resources, differences in key demographic variables, such as age to first reproduction, could play a major role in resource management. My study results do not provide direct data on age to first reproduction, but I did find that proportionally more adults in terra firme forests are reproductively mature, perhaps tied to light access. While it is unclear whether these terra firme adults reach reproductive maturity more quickly than those in occasionally inundated forests, this merits further study for management purposes.

Highly dispersed timber and non-timber resources present a major challenge to managing tropical forests because it is not economically feasible to access these disparate resources. I found that *C. guianensis* in both forest types presented a clumped distribution, which could facilitate a concentration of management activities such as trail construction and seed collection.

In conclusion, this study found spatially similar distributions of *Carapa guianensis* in both terra firme and occasionally inundated forests studied. Tree densities and reproductive potential, however, were sufficiently different to recommend stratification by forest type for further studies on growth and yield.
CHAPTER 4
CONCLUSION

While there is still considerable scientific debate over whether and how natural resource extraction can be sustained over the long term from tropical tree populations (Nepstad 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), as well as the paucity of published ecological data on tropical species.

The objective of this thesis was to provide a synthetic review of the most relevant ecological and management literature of *Carapa guianensis* to identify gaps in current research and recommend avenues for further study. In the second chapter, I compared the demographic structure and seedling recruitment of *C. guianensis* in two forest types, occasionally inundated and *terra firme*, or upland forests. Main study objectives were: (a) to assess the density, distribution, and size class structure of *C. guianensis* in occasionally inundated and *terra firme* forests; (b) to compare spatial distribution analyses using two different methodologies; and (c) to use patterns of abundance, distribution and demographic structure to help infer key demographic stages or ecological variables that should be the subject of special focus when implementing a management scheme.

The synthetic review revealed that although authors have touted the economic potential of *C. guianensis* in the literature, very little research has been done to quantify this potential or to look at sustainable harvest limits/challenges. Gaps in information on *C. guianensis* pollinators and species genetics were identified. There is still a need for
silvicultural experiments to ascertain methods for improving growth rates, tree form and increasing seed production per tree. Methods of controlling *H. ferrealis* and *H. grandella* infestations in seedlings and saplings, respectively, and ways to promote/improve survival and growth of young *C. guianensis* individuals may also bear investigation.

Seed collection will likely affect seed predators. More research determining the broader ecosystem impacts of seed and timber collection may be beneficial. Similarly, broader faunal resources such as game meat are critically important for human inhabitants (Hill *et al.* 2003). The linkages between seed populations and seed predators is important to quantify, both for ecologists and forest residents who rely on these animals for sustenance.

Economic and social analyses of commercialization barriers for small scale landowners is a key step toward utilization and management of this resource. From the forest to the final product, there is still a wealth of information yet to be discovered to better advise ecosystem managers and commercial producers of this species.

Research on the population structure provided encouraging results for a species with such great economic potential. In contrast with many tropical tree species, the local population of *C. guianensis* at the Embrapa forest has a high density of trees per hectare: 20.1. The population survey also confirmed the importance of microhabitat, with seasonally inundated plots having a ~55% higher density than upland forest plots (25.7 versus 14.6 trees hectare⁻¹). Seedling recruitment in the study plots slightly exceeded mortality in both habitats, which indicates a currently healthy population. Based on application of Donnelly’s (1978) nearest neighbor method, the index of aggregation (R) for all individuals was 0.9056 in the seasonally inundated plots and 0.8258 for the upland
dry forest plots, significantly different than a random distribution. All individuals showed a significant tendency toward clumping and this was even more pronounced for non-reproductive juveniles. Low density of conspecific adult trees is a major constraint to sustainable resource exploitation, but this study and others (McHargue & Hartshorn 1983, Plowden 2004) reveal a high density and clumped distribution, two factors that favor management and encourage further research.

Measuring population structure in different habitats can be a first step towards assessing sustainability of harvesting in different habitat types (Peters 1996). Quantifying species demographic structure provides the underlying data for use in ecological models for assessing long-term population viability (Alvarez-Buylla et al. 1996). Since vital demographic rates are normally stage-dependent (Harper 1977), the structure of a population can be indicative of its demographic future and can be the basis for immediate management decisions when long-term demographic monitoring is not feasible (Bruna & Kress 2002). This demographic data coupled with tree growth rates, survival and seed production data could form the basis of an ecological model to measure sustainable harvest rates of both the timber and non-timber resources that *C. guianensis* yields. Unless information on harvest limits and suggested management techniques is available for *C. guianensis*, resource extraction will likely be based on maximizing short-term economic revenue and not on managing a stable or increasing resource base.
APPENDIX A
PLOT INSTALLATION

To open the 400 m transects that defined the plot boundaries, we determined the initial compass direction (normally 90 or 0 degrees). A support for the level (a branch) was cut and the compass was placed on the support. Two branches/poles where placed in the line of sight of the compass to begin a straight line. Field technicians and ‘mateiros’ then used the branches as a reference to cut a straight line through the forest following the determined compass direction. Reference branches were placed no more than every 10 m apart (more frequently in hilly terrain) so that the compass direction was apparent. A compass was used to check the placement of the reference branches throughout. A metric tape was used to measure the distance cleared until 400 m was reached. After clearing each transect, the metric tape was used to go back and re-measure each transect. This method was used for all transects bordering the plot as well as the internal transects cleared to facilitate tree identification and location.
APPENDIX B
RANDOM SELECTION OF REGENERATION SUBPLOTS

These subplots were selected by dividing each plot into 16 quadrats with one-hundred 10 x 10 m subplots. Excel’s random number generator was used to select random numbers from 1 to 16 and then again to select random numbers from 1 to 100. These random numbers were paired to select the 32 subplots. The selected sub-plots were mapped on graph paper and located in the field.
LIST OF REFERENCES


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BIOGRAPHICAL SKETCH

Christie Ann Klimas was born on July 23, 1978, in Cleveland, Ohio. She received a B.S. in environmental science with a biology concentration at Southampton College, Long Island University. During nine months of her undergraduate studies, she worked as an intern for Brookhaven National Lab at their Free-Air Carbon Dioxide Exchange (FACE) site in North Carolina. The FACE system facilitates CO₂ enhancement of entire forest stands. Following graduation, she spent 1.5 years as a research specialist at Columbia University’s Biosphere 2 Center in Arizona where she again studied plant carbon uptake under CO₂ enhancement. In 2001, she was awarded a Rotary Ambassadorial Fellowship to conduct research in Acre, Brazil. This preliminary research prepared her for master’s level study at the University of Florida in 2003. This thesis was supported by a Tropical Conservation and Development Assistantship and an Environmental Protection Agency STAR (Science to Achieve Results) Fellowship. In 2006, she was awarded a National Science Foundation IGERT (Integrative Graduate Education and Research Traineeship) fellowship to continue doctoral studies at the University of Florida.