

MODELING COMPATIBILITY OF TIMBER AND NON-TIMBER HARVESTS OF A  
MULTIPURPOSE AMAZONIAN SPECIES: ASSESSING SUSTAINABILITY THROUGH  
ECOLOGICAL AND ECONOMIC ANALYSES

By

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To Mark, Elizabeth and my parents: Thank you for your constant support and understanding

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## LIST OF ABBREVIATIONS

AIMEX	Association of Timber Industry Exporters in the State of Pará
CV	Coefficient of Variation
CV <sub>p</sub>	Coefficient of Variation (population level)
DBH	Diameter at Breast Height
EMBRAPA	The Brazilian Agricultural Research Corporation
INMET	Brazilian National Institute of Meteorology
IPGRI	International Plant Genetic Research Institute
$\lambda$	Population Growth Rate
$\lambda_s$	Stochastic Population Growth Rate
$\lambda_T$	Population Growth Rate calculated by Tuljapurkar's Approximation
MTF	Multiple-use Forest Management
NPV	Net Present Value
NTFPs	Non-timber Forest Products
PCCs	Pearson Correlation Coefficients
P <sub>i</sub>	Probability of Survival
PV	Present Value
RIL	Reduced Impact Logging
SE	Standard Error
UFAC	Federal University of Acre
xCV <sub>i</sub>	Coefficient of Variation (between individuals)

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MODELING COMPATIBILITY OF TIMBER AND NON-TIMBER HARVESTS OF A  
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This dissertation examines the relative compatibility of timber vs. non-timber forest product (NTFP) harvest of *Carapa guianensis* for population persistence and income generation in two forest types in the Brazilian Amazon. *C. guianensis* is a multi-use tropical tree valued for its seed oil and its high-quality timber. This dissertation focused on variable components of sustainable harvest, including quantifying patterns of natural seed production, modeling sustainable seed and timber harvests based on underlying demographic data collection, and simulating economic returns from seed and timber harvests by calculating the equal annual equivalent (EAE) of revenues associated with modeled simulations of seed and timber harvests. Our study demonstrated that multiple variables interact at different scales to influence seed production. Climatic cues were central to setting overall patterns in phenophases and seemed to best explain why high seed production years were consistent across both forest types examined. Individual tree attributes contributed to seed production heterogeneity within habitats; dbh, and cross-sectional canopy area showed positive, quadratic relationships with seed production, while vine load negatively affected seed production, irrespective of forest

type. In our upland forest sites, demographic parameters suggested that no tested levels of seed and timber extraction were sustainable; quasi-extinction simulations indicated population decline regardless of harvest levels. Removing 10% of the total seed production proved feasible and consistent with a stable or increasing population in occasionally inundated forests, though the quasi-extinction threshold of less than 3 individuals dbh  $\geq$  10 cm per hectare was reached within the 500-year time interval. We also found the potential for compatibility between seed and timber harvest in occasionally inundated forests. Our results suggested that 10% annual seed harvests were compatible with 100% timber harvests (of trees  $\geq$  50 cm) twice a century, the equivalent of approximately two trees per hectare. Revenue from 100% timber harvests (of individuals  $\geq$  50 cm every 25-years) exceeded that of 10% seed harvests when evaluated separately and applying labor costs of R\$23 per kilogram of oil (US\$12.88). When we dropped those labor costs to R\$12 (US\$6.72), however, seed harvest EAE surpassed that of timber harvest. In practice, however, benefits could accrue from both annual seed harvest revenues and periodic logging of *C. guianensis* individuals. Findings add to the ecological understanding of the mechanisms contributing to variable yearly seed production and represent an important first step in providing information geared toward encouraging ecological best management practices while maintaining profitable harvest scenarios.

## CHAPTER 1 INTRODUCTION

This dissertation examines the relative compatibility of timber vs. non-timber forest product (NTFP) harvest of *Carapa guianensis* for population persistence and income generation in two forest types in the Brazilian Amazon. The central dependent variables in this study are seed oil, timber production and price/cost variables. As such, each chapter of my dissertation addresses one of these variables. This dissertation is structured so that the second, third and fourth chapters are independent articles ready for submission to peer-reviewed journals. Relevant conclusions are found at the end of these three chapters and I articulate overall conclusions in the final chapter (Chapter 5).

*Carapa guianensis* Aublet. (Meliaceae), common name “andiroba”, is a multiple-use species. As with other species in the Meliaceae family (*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). The oil also enjoys international demand: between 1974 and 1985, Brazil exported between 200 – 300 tons of oil annually (Clay *et al.* 2000). 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), exploitation of *C. guianensis* promises to expand as market demand for seed oil and timber advances concomitantly into the interior of the Amazon with federally funded highway development projects (Fearnside 2005).

## Modeling Variability in Seed Production

*C. guianensis* management must take into account species value and productivity as both a timber and non-timber resource. Chapter 2, therefore, specifically addresses the NTFP resources and seeks to illuminate natural patterns of *C. guianensis* seed production and variability and how these patterns are related to underlying habitat heterogeneity, tree attributes and climatic cues. Unsustainable resource extraction can stem from a lack of understanding of species biology (Peters 1996). This is further complicated in cases where the resource of interest is tree fruits or seeds: most polycarpic woody plants exhibit variable years of high and low seed production at the population-level (Herrera *et al.* 1998). In chapter 2, we tested the hypothesis that seed production is influenced by multiple interacting factors across scales (climatic cues, habitat heterogeneity, and tree attributes). To do this, we recorded reproductive phenophases of *C. guianensis* and quantified *C. guianensis* seed production over 5 years, using a Poisson regression to see how seed production was related to predictor variables at each scale. We predicted that: 1) Climatic cues, like rainfall, would be most important in determining population-level seed production due to potential for large-scale resource limitation; 2) Seed production would be significantly higher in occasionally inundated forests based on observations by forest residents and previous research that documented higher *C. guianensis* densities in swamp forests; and 3) Tree attributes such as dbh and vine load would be strongly implicated in determining seed production potential. Findings from this study add to the ecological understanding of the mechanisms driving variable yearly seed production, particularly in tropical trees, while also contributing species-specific information for *C. guianensis* management.

## Ecological Viability of Combined Timber and Non-Timber Harvests

Determining ecologically sustainable harvest limits is necessary for developing appropriate forest management strategies, though effective simulation modeling of tropical forests managed for NTFP and timber is a significant challenge (Ribeiro do Valle *et al.* 2007). We used information on variable seed production along with other demographic data to parameterize a matrix model developed to examine sustainable harvests levels of both timber and seeds for this species (chapter 3). We question whether management of *Carapa guianensis*, a tree species valued for both its high quality timber and its seed oil, can be managed sustainably for both seed and timber harvests. Matrix models are powerful tools for identifying population trends and responses to management regimes (Leftkovitch 1967, Crowder *et. al.* 1994, Olmsted & Alvarez Buylla 1995), setting harvest limits from a population that are compatible with its continued existence (Nantel *et al.* 1996, Ratsirarson *et al.* 1996) and identifying key life stages as management targets (Crouse *et al.* 1987). In addition, matrix models can be used to simulate sustainable harvest levels for timber, NTFPs, or a combination of management strategies for single species, an important factor given that one third to almost half of timber species also have NTFP value (Martini *et al.* 1994, Ndoye & Tieguhong 2004, Herrero-Jáuregui *et al.* 2009). Our objectives were: 1) to quantitatively assess the impact of seed and timber harvesting on *C. guianensis* in stochastically varying environments, 2) to determine whether the impact of harvest varied between occasionally inundated and upland (*terra firme*) forests, and 3) to simulate potential ecologically viable harvest scenarios of *C. guianensis* seeds, timber, or seeds and timber. We hypothesized that intensive seed collection would still result in sufficient seedling recruitment to ensure continued species persistence, and that *terra firme*

forests would allow even more intensive seed harvests as seeds in this environment may be “safe-site” limited. Therefore, collection of seeds that would otherwise perish would allow for increased seed harvest levels without impacting future population viability.

### **Economic Revenue from Sustainable Harvest**

Quantifying revenue from harvest is particularly important in cases where an individual species provides multiple economic benefits, generating a potential conflict of interest in deciding whether to prioritize one use over another. Such “conflict of interest” is common in the Amazon. Herrero-Jáuregui *et al.* (2009) found that 46% of the 200 timber species in the state of Pará, Brazil also provided non-timber forest products. Multiple-use species should be managed to maximize their economic or social value under constraints of ecological sustainability. The determination of how to do this is often left to the forest resident or manager, using imperfect and general information on the benefits of different forest management strategies (Macpherson 2007). Availing quality information to managers should improve both ecological and economic decision-making, though detailed knowledge of sustainability does not always translate into sustainable management practices (Gaoue & Ticktin 2009), and expected economic gains are not always realized (Putz *et al.* 2000). Therefore, this research (chapter 4) was conducted, partly, to enhance the economic information available to the forest manager, in particular the potential revenue associated with different harvesting strategies of *Carapa guianensis*. We modeled the equal annual equivalent (EAE), a function of net present value (NPV), of revenues associated with modeled simulations of sustainable seed and timber harvests. Our specific objectives were 1) to simulate and compare the revenue from ecologically viable seed and timber harvests of *C.*

*guyanensis* in stochastically varying environments; and 2) to simulate the EAE of revenues from seed and timber harvest under different market prices for both seed oil and timber. Sustainable harvest simulations are based on a stochastic ecological matrix model parameterized with data from a demographic study in the southwestern Amazonian state of Acre, Brazil (See Chapter 3).

CHAPTER 2  
MODELING VARIABILITY IN SEED PRODUCTION: A 5-YEAR STUDY TO EXPLORE  
THE INFLUENCES OF TREE ATTRIBUTES, HABITAT HETEROGENEITY, AND  
CLIMATE CUES

**Introduction**

Seasonal patterns in tropical plant phenology are assumed to represent adaptive responses to proximate cues (De Steven *et al.* 1987), though these cues are still unknown for the majority of tropical plants (Stevenson *et al.* 2008) and can vary significantly by species (Rivera *et al.* 2002, Diaz & Granadillo 2005, Sing & Kushawaha 2006). Understanding the mechanisms that underlie the seasonal phenology of individual tropical species and communities is increasingly important in efforts to understand the potential impacts of climate change on tropical plants (Cleland *et al.* 2007, Stevenson *et al.* 2008), how plant populations may be affected by more frequent weather abnormalities like droughts (IPCC 2007, Cox *et al.* 2008), and even phenology's adaptive evolution (Elzinga *et al.* 2007). Quantifying the relevant cues underlying plant phenology of species may indicate those species most vulnerable to expected abiotic changes. For species that are important sources of marketable resources, ecological vulnerability may translate into an economic and social vulnerability for persons depending on resource revenue, an already vulnerable community (Rodrigues *et al.* 2009). A better understanding of the underlying mechanisms of reproductive phenology can improve species management options, especially for species whose seeds are a marketable resource.

Temperature and photoperiod are likely the best studied climatic cues influencing tropical phenology (Elzinga *et al.* 2007, Stevenson *et al.* 2008) and have also been hypothesized to affect subsequent seed output (Kelly and Sork 2002). Climatic variables

are clear cues for some species (Kelly *et al.* 2000, Schaumber *et al.* 2002, Monks & Kelly 2006), but remain inconsistent for others (Sork & Bramble 1993, Piovesan & Adams 2001). While much research on climatic cues that influence variable seed production has focused on temperate tree species, there is evidence that temperature and rainfall also influence flowering of tropical plants (Bernier 1988, Díaz & Granadillo 2005). Low minimum temperatures signal bud development in peninsular Malaysia and Sarawak (Ashton *et al.* 1988). Several studies have shown that rainfall patterns are responsible for seasonal cycles of growth, and flowering of some species in tropical environments (Borchert *et al.* 2004, McLaren & McDonald 2005, Brearly *et al.* 2007). Dry season severity is another factor, as many tropical forest plants require a threshold level of drought before successful flowering (Alvim 1960; reviewed by Kozlowski & Pallardy 2002). Climatic variation is often captured by year-to-year quantification of the number of individuals flowering and subsequent seed production; most polycarpic woody plants exhibit variable years of high and low seed production at the population-level (Herrera *et al.* 1998).

Distributions and abundances of many species are influenced by local heterogeneity in physical habitat variables (Webb & Peart 2000, Svenning *et al.* 2006), including soil nutrients (Gartlan *et al.* 1986, Baillie *et al.* 1987), drainage (Newbery *et al.* 1986, Hubbell & Foster 1986), soil texture (Davies *et al.* 1998) light availability (Lieberman *et al.* 1995) and topography (Poore 1968, Ashton 1976, reviewed in Whitmore 1984). The importance of habitat heterogeneity in representing resource availability for plant growth, maintenance and reproduction is reflected in the

predominance of classifications such as “forest type” – a term we use to distinguish localized heterogeneity in our study site.

While the interaction between habitat and climatic factors may influence phenology and seed production at the population-level, individual characteristics are also important in determining the flowering and subsequent seed production of specific trees. Since plants accumulate resources over time, size, as expressed by tree diameter, is positively correlated with seed production (Ares & Brauer 2004, Snook *et al.* 2005, Kainer *et al.* 2007). Other associated factors, such as liana loads in crowns, have been found to reduce fruit production (Stevens 1987, Kainer *et al.* 2006) and suppress tree growth (Clark & Clark 1990, Grauel & Putz 2004). There is also evidence that some trees are consistently high producers (Snook *et al.* 2005), perhaps due to correlations with larger crown size (Kainer *et al.* 2007) or the underlying genotypic characteristics of individuals (Vander Wall 2001).

This study tests the hypothesis that seed production is influenced by multiple interacting factors across scales (climatic cues, habitat heterogeneity, and tree attributes). To do this, we first recorded reproductive phenophases of *C. guianensis* and quantified *C. guianensis* seed production over 5 years, using a Poisson regression to see how seed production was related to predictor variables at each scale. We chose *C. guianensis* as a model species because it is an economically important tropical tree that demonstrates pronounced temporal variability in seed production. We predicted that: 1) Climatic cues, like rainfall, would be most important in determining population-level seed production due to potential for large-scale resource limitation; 2) Seed production would be significantly higher in occasionally inundated forests based on

observations by forest residents and previous research indicating that the species is found in higher densities in swamp forests (McHargue & Hartshorn 1983); 3) Tree attributes such as dbh and vine load would be strongly implicated in determining seed production potential. In addition to adding to the ecological understanding of the mechanisms contributing to variable yearly seed production, findings from this study also contribute to species management: *C. guianensis* is a tropical tree valued for its high quality timber and seed oil (Shanley & Medina 2005).

## ***Methods***

### **Study Species**

*C. guianensis* is a shade-tolerant tree found in both canopy and sub-canopy levels in a variety of tropical forest types. Mature *C. guianensis* trees can reach heights of 30 meters (Ferraz *et al.* 2002) and diameters of 2 meters (Fournier 2003). Tree size may not reliably predict age; carbon-dating of two individuals in a nearby forest in the southwestern Amazon estimated the age of a 37.5 dbh individual at 172 years while a 17 cm dbh individual was aged at 785 years (Vieira *et al.* 2005).

This species exhibits prolonged synchronous flowering (Hall *et al.* 1994), although the timing and length of this phenophase varies by region (Leite 1997). Pollinators include stingless bees (Apidae) and butterflies (Riodinidae and Lycaenidae) (Maués 2006). Seeds are enclosed in a dehiscent capsule that normally breaks open upon impact with the ground, freeing seeds for germination or dispersal via water or frugivores (McHargue & Hartshorn 1983a, Plowden 2004). Seeds are subject to attack by *Hypsipyla ferrealis* moth larvae. *H. ferrealis* larvae eat the endosperm, but in some cases don't consume enough to prevent seed germination or cause seedling mortality.

Partial endosperm consumption can result in smaller seedlings due to diminished seed reserves (McHargue & Hartshorn 1983b).

Some authors have published rough estimates of seed production ranging from 50 to 200 Kg of seeds per tree (Shanley *et al.* 1998, Shanley 2005). Other published seed production estimates are based on samples of fewer than 10 trees (Ranklin 1978, McHargue & Hartshorn 1983a, Plowden 2004, Guedes *et al.* 2008), though more comprehensive surveys of production were recently conducted in Amazonian floodplain forests (Londres 2009) and in the northwestern Brazilian state of Roraima (Tonini *et al.* 2008). Annual variability in seed production of this species, however, is still poorly understood, including the proportion of trees that suspend production over multiple years, an important factor in calculating overall yield and potential revenue. There may also be local variation in seed production due to differences in forest types: *C. guianensis* is preferentially a species of periodically inundated swamp forests (McHargue & Hartshorn 1983), though more recent research has shown high densities in a variety of environments, including *terra firme* and occasionally inundated forest (Klimas *et al.* 2007, Londres 2009).

*C. guianensis* seeds reportedly provide food for many species of peccaries, rats and large rodents (McHargue & Hartshorn 1983b, Fournier 2003). Both field observations and conversations with local hunters, however, indicate that *C. guianensis* seeds are not a favorite food for game animals near our study site. Using motion-activated cameras in highly altered forests, Silva (2009) found that rats (*Proechimys* spp.) and acouchis (*Myoprocta pratti*) were the most common visitors to sites with *C. guianensis* seeds. These animals made only rare visits during the dry season, when

other food is scarce (Silva, 2009). On the other hand, faunal interest in seeds may be somewhat higher in less disturbed forests.

### **Study Site and Forest Types**

The study was carried out in the 1200 ha forest reserve of the Brazilian Agricultural Research Corporation (EMBRAPA) (latitude 10° 01' 28" S and longitude 67° 42' 19" W), in the southwestern portion of the State of Acre, Brazil. Average annual temperature is 24.5°C with a dry season from June to August (INMET 2009). The region has slightly hilly topography including upland habitat (*terra firme*) and occasionally inundated areas. This region is close to the southwestern limit of the species' range and these forests differ from the floodplain forests where most *C. guianensis* research has been conducted (Guariguata *et al.* 2002, Plowden 2004, Londres 2009). We established four 400 x 400 m (16-ha) plots within the reserve: two in areas of predominantly *terra firme* forest, and two in occasionally inundated forest.

### **Tree Attributes and Climatic Variables**

For each *C. guianensis*  $\geq 10$  cm dbh in the four plots, we recorded spatial coordinates, canopy position [(dominant, co-dominant, intermediate or suppressed) from Smith *et al.* (1997)], diameter at breast height (dbh), tree height, crown cross-sectional area, vine-loading, tree abnormalities, and reproductive status. The latter three variables were assigned binary values. Trees with  $\geq 75\%$  of their crowns loaded with vines were given a value of 1, whereas trees with  $<75\%$  were assigned a value of 0. Tree abnormalities were defined as any characteristic that differed from most trees and could negatively affect tree function, such as evidence of a previous burn, forked trunks (a potential indication of prior insect attack), and damaged or absent crowns. Reproductive status was determined based on evidence of seed production either on or

below the tree. Crown cross-sectional area was measured along two axes: maximum crown diameter and a second diameter at a right angle to maximum diameter. An ellipsoid formula was used to convert axis diameters to crown area (Kainer *et al.* 2007). Total tree height was measured with a SUUNTO optical height meter PM-5/1520 (clinometer), using a surveyor's tape to determine distance from clinometer to tree.

Rainfall and temperature data were collected daily at noon at the Federal University of Acre (UFAC) approximately 8 km from our study site. Monthly mean temperature was averaged from the daily compensated mean temperatures for a given month and maximum and minimum temperatures also represented monthly averages of these daily values (INMET 2009).

### **Phenology**

We monitored the phenophases of *C. guianensis* from September 2005 to June 2009 for a random sample of trees in each of the two forest types, stratified by diameter class. We selected this sample from the larger sample of all inventoried individuals in three of the plots via random sampling; one plot was excluded due to time constraints involved with weekly seed collection. Trees with crowns overlapping with other conspecifics and those whose seeds fell into adjacent rivers were excluded from the phenology sample and replaced by another randomly selected individual that met the criteria. Initially, we observed 53 trees located in occasionally inundated forest and 23 in *terra firme*. After the first year, we added 28 additional randomly selected trees in *terra firme* forest, for a total of 51 trees. Diameter classes were  $15 \text{ cm} \leq \text{dbh} \leq 20 \text{ cm}$ ;  $20 \text{ cm} < \text{dbh} \leq 30 \text{ cm}$ ;  $30 \text{ cm} < \text{dbh} \leq 40 \text{ cm}$ ; and  $40 \text{ cm} > \text{dbh}$ . Sample sizes per class ranged from 7 to 18 trees depending on natural density and probability of reproduction (Klimas *et al.* 2007).

We used binoculars to conduct crown observations (O'Brien *et al.* 2008) twice a month, beginning in September 2005. We recorded presence/absence of new leaves, flowers and falling fruits. We also checked the ground below canopies, looking for additional evidence of phenophases, such as the presence of fallen flowers. If we observed flowers either on the ground below the canopy or in the canopy, the individual was classified as “flowering.” *C. guianensis* flowers are small and ground observations served both to validate binocular observations and identify flowering trees where flowering was limited and canopy flowers were hidden from view. Once three or more individuals from the entire sample population initiated flowering, we intensified monitoring from twice a month to weekly, which continued until the end of fruitfall. Based on observations of flowering and fruitfall outside of peak periods and rapid progression through phenophases, we monitored phenology weekly from September 2007 until June 2009 (Table 2-1).

Table 2-1 The number of *Carapa guianensis* trees monitored for estimates of seed production each year and the time period in which production was quantified.

Quantification period	Measurement period (weeks)	Number of trees	
		Occasionally inundated	<i>Terra firme</i>
Nov/2004 – Mar/2005	17	19	20
Jan/2005 – Feb/2006	5	30	24
Jan/2006 – Feb/2007	5	29	23
2007-2008	Continuous	53	51
2008-2009	Continuous	53	50

### **Below-Tree Seed Counts**

We quantified weekly seed production by collecting fallen seeds under a random subset of trees selected from the phenology study population. The measurement period

and number of sample trees in each environment varied annually. For our study “annual seed production” refers to the ecological seed production period for this species which can extend from November of one year to June of the following year in this region. In 2004-2005, we collected seed production weekly throughout a 17-week “peak” seedfall period. In 2005-2006 and 2006-2007, we collected weekly seed production during 5-week “peak” seedfall periods (Table 2-1). From September 2007 to July 2009, we collected seeds at weekly intervals throughout the year to account for seed production outside of peak periods, and measured production for each of the 104 trees in the phenology dataset (Table 2-1). Sampled trees were visited weekly on the same day or within a two-day period if rain or inclement weather delayed seed collection. Within 24 hours of collection, seeds were taken to an onsite laboratory, where we counted and recorded total fresh weight of each tree’s production. Seeds were subsequently dried at 105°C, and after 24 hours, seed dry weight was recorded, and water content of seeds as a percent of fresh weight calculated.

Measured seed production for the first three years likely underestimated total annual seed production due to non-continuous sampling. To allow for graphical presentation of average seed production per tree, we calculated the percentage of each year’s seed production that occurred outside observed 5- and 17-week “peaks” during 2007-08 and 2008-09, respectively. We then added the average off-peak seed production (converted to seed number and weight) to estimate total annual seed production measured for 2004-2007. These calculations assume that we captured the true peak of seedfall, which is corroborated by our year-round phenological observations. An average of 1% and 18% of total seedfall in 2007-09 occurred outside

of the 17-week peak period in occasionally inundated and *terra firme* forest, respectively. An average of 24% and 40% of total seedfall in 2007-09 fell outside of the 5-week peak period in occasionally inundated and *terra firme* forest, respectively. We converted measured individual seed production to per hectare estimates by multiplying the average seed production per tree by the average number of trees with dbh  $\geq$  15 cm per hectare for each forest type, the size when we found trees were likely reproductive (Klimas *et al.* 2007).

### **Seed Removal and Infestation**

Seed counts below trees did not include seeds that had been removed during the week-long interval between collection visits. Seed removal before visits indicates a potential revenue loss, though not necessarily an ecological loss; removed seeds include eaten (predation) and dispersed seeds (VanderWall *et al.* 2005). Determining seed fate was outside the scope of this study, but it is ecologically relevant for species maintenance. We were interested in estimating the extent of seed loss during the course of a week, to determine whether more frequent seed collection trips were warranted. In addition to our weekly quantification of seed production, in 2007-2009 we used a second method to estimate seed production by collecting and counting all fruit husks below parent trees. Fruit husk counts have the potential to better represent actual seedfall in species with high seed removal: the fibrous capsules decompose slowly, and each mature seed leaves a clear mark within the husk (Forget 1996). We counted the total number of fruit husks (including those for intact fruits) and divided by 4, the mean number of husks per fruit, to estimate fruit numbers. To estimate the number of seeds per fruit, we counted the number of seeds for all intact fruits or imprints for those that could be mounted in the lab. We obtained 315 such “intact fruits” in 2007-08 and

341 in 2008-09. The mean number of seeds per fruit was multiplied by the husk-based estimate of fruit number to estimate seed production prior to removal; this comparison was done for overall annual production without separation by forest type. This number was compared with measured seed production to estimate the extent of weekly seed removal.

*Hypsipyla ferrealis* Hampson (Pyralidae) moth larvae commonly attack *C. guianensis* seeds. Infested seeds can be recognized by 1-3 mm diameter holes created when larvae enter and exit the seeds (McHargue & Hartshorn 1983b). In some cases, larvae were found in relatively intact seeds, and in other cases, complete consumption of the endosperm was observed. Collected seeds were carefully examined for evidence of *Hypsipyla ferrealis*. Seeds with entrance holes were classified as infested, irrespective of hole size or stage of infestation.

## **Data Analysis**

### **Modeling variation in fruit production**

We modeled fruit production using a Poisson regression as a function of multiple predictor variables using the SAS procedure PROC GLIMMIX (version 9.2). Quantitative tree variables tested included dbh, tree height and crown cross-sectional area.  $\text{Dbh}^2$  was also included based on research that found a quadratic relationship between dbh and fruit production for *Bertholletia excelsa* (Wadt *et al.* 2005). Class variables included (1) forest type, (2) vine cover and (3) abnormalities. Quantitative climate predictor variables also were tested, including total annual rainfall (from the year that flowering and fruit development occurred), rainfall during the annual 3-month dry season from June to August prior to flowering, rainfall during the five-month wet season from January to May that preceded flowering, and the annual mean maximum temperature, mean

minimum temperature and average temperature. Since seed production in each tree was measured weekly, a repeated measures structure was utilized, with the variance-covariance matrix structure specifically accounting for within-tree correlation of observations. Pearson-adjusted residuals were plotted to verify that the assumptions of Poisson regression were met. In all cases, homoscedasticity and normality of the residuals were verified. Non-significant variables were dropped sequentially (based on p-values), using a backward stepwise model selection procedure to determine our final model. We also ran the model using 5-week peak seedfall periods each year to confirm that sampling methods (different temporal measurement periods between years) did not affect the model results. If results were significant in both models (all data and 5-week peak seedfall model) and the direction of the effect was the same, we assumed that significance of results was not an artifact of sampling methodology. If this was not the case, or results were only marginally significant, we verified the direction and magnitude of interactions by looking at plots of LSM and performing multiple comparison tests using Scheffe's method. We used the SAS procedure PROC CORR to identify and potentially eliminate model variables that were correlated. Tree height was correlated with dbh (pearson correlation coefficient (PCC) = 0.64),  $\text{dbh}^2$  (PCC = 0.60) and crown cross-sectional area (PCC = 0.59), and was thus eliminated from the model because these multiple correlations could potentially lead to multicollinearity problems. Moreover, dbh is an easily- and commonly-measured variable whereas height measurement is often problematic in dense tropical forest. Total yearly rainfall also was dropped from the model. It was correlated with both dry season rainfall (PCC = 0.66) and rainfall during the 5-month rainy season (PCC = 0.63), the latter two being more

biologically relevant drivers in determining flowering and fruiting than the more general yearly mean. Finally, we dropped mean temperature which was correlated with maximum (PCC = 0.86) and minimum temperatures (PCC = 0.76).

### **Synchronicity in fruiting**

We used Kelly and Sork's (2005) methodology to calculate three measures of seed production variability. First, to estimate variability in individual tree seed production ( $xCV_i$ ), we calculated the coefficient of variation (CV) of seeds tree<sup>-1</sup> for each tree over the 5-year study period. We then took the mean of these individual tree CVs and calculated variability in seed production at the population level (CV<sub>p</sub>) by taking the mean number of seeds tree<sup>-1</sup> for all sample trees over the 5-year period. Finally, we calculated synchronicity by calculating the Pearson correlation coefficients for all possible pairs of trees in the sample and calculating the mean of these CVs ( $xPCC$ ) (Snook *et al.* 2005). The entire sample population from both forest types was used to calculate synchrony.

## **Results**

### **Phenology**

*C. guianensis* individuals displayed two flowering peaks over a 12-month period in 2007-2009. One peak initiated during the height of the dry season and concluded at the start of the rainy season, followed by a second smaller peak during the rainy season (Figure 2-1).

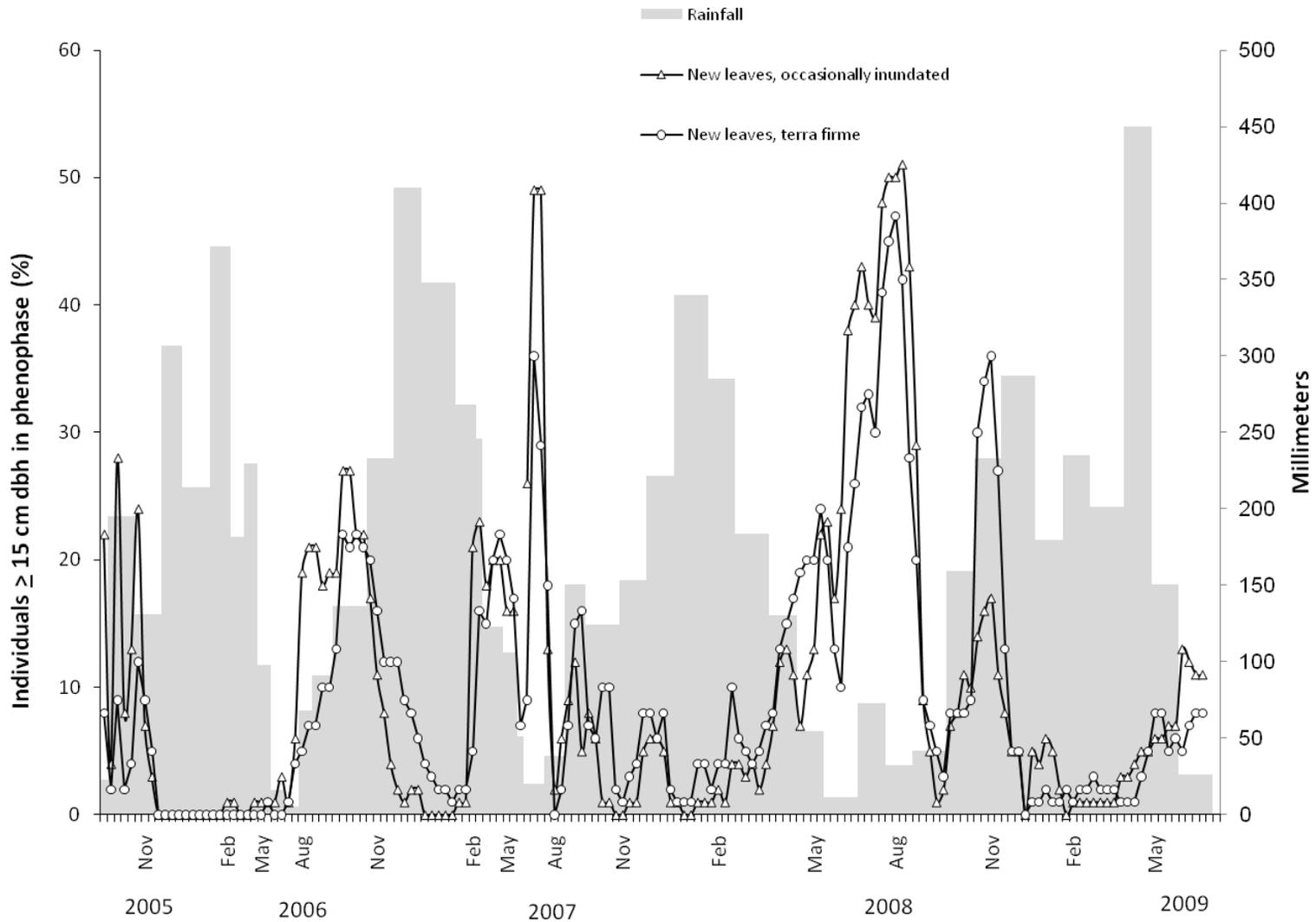


Figure 2-1 Percentage of individuals with new leaves (top panel) flowering (middle panel) and with observed fruitfall (bottom panel) in *terra firme* and occasionally inundated forests superimposed on monthly precipitation values (mm).

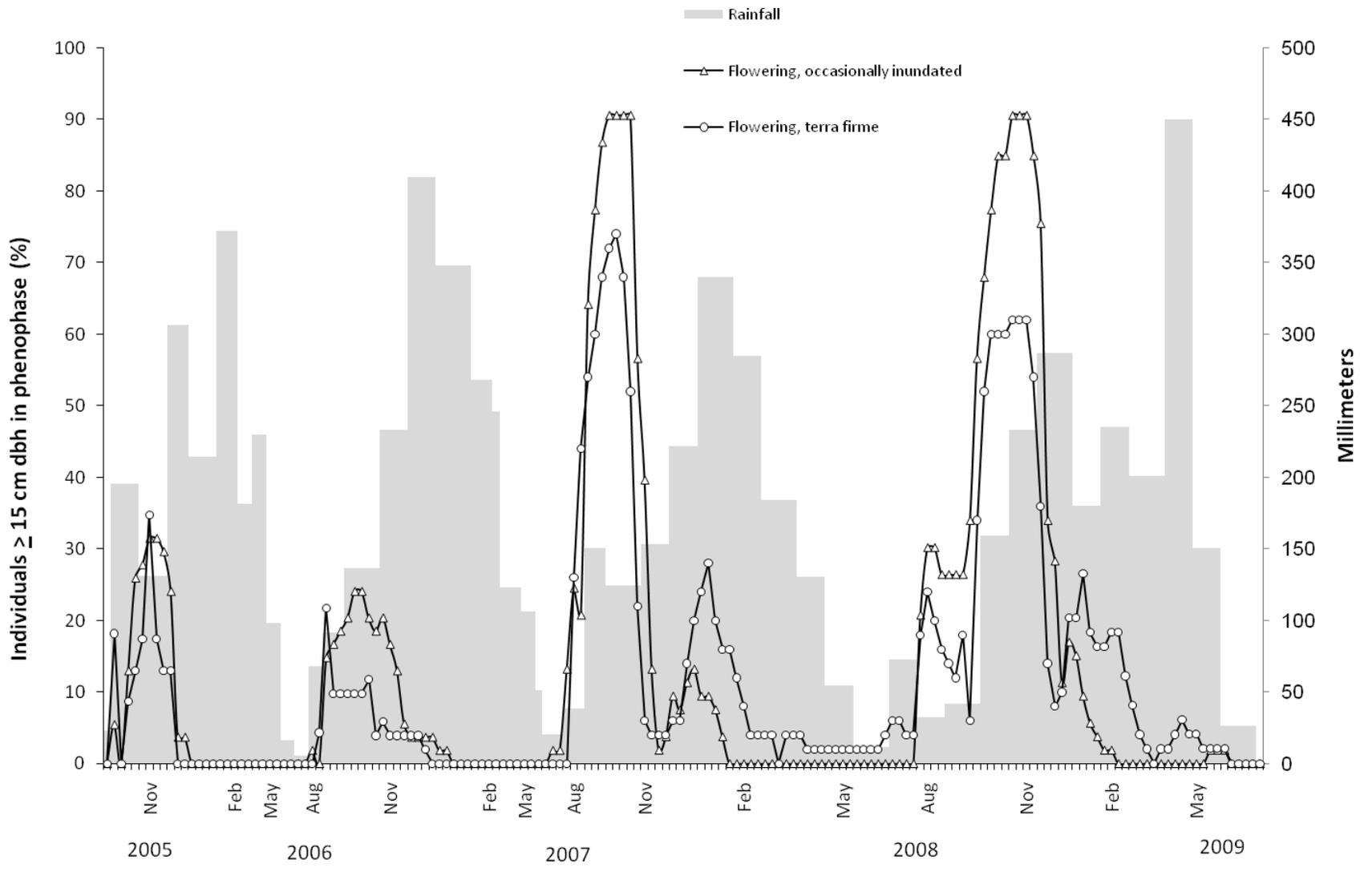
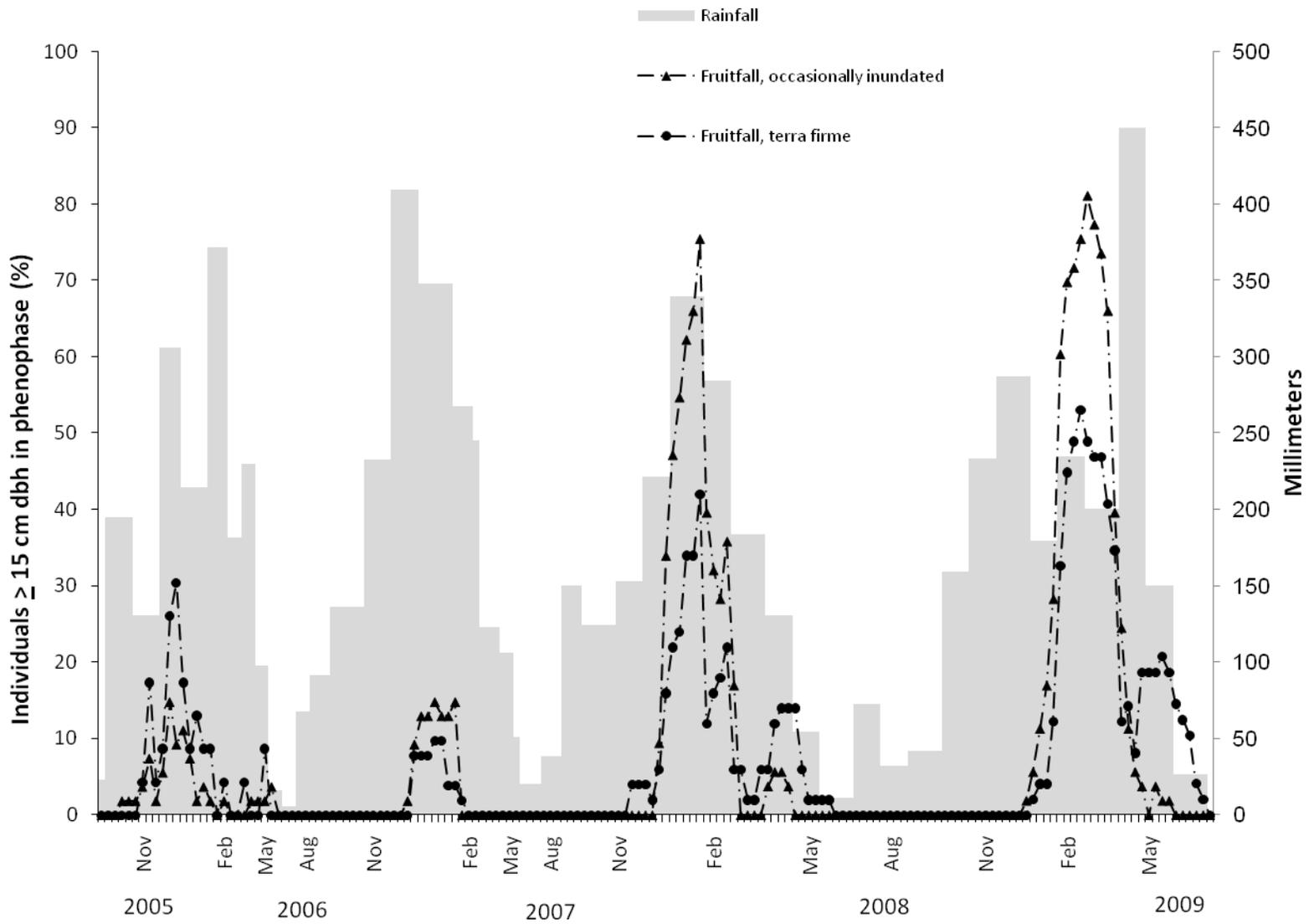


Figure 2-1. Continued



As the first set of flowers matured into fruits over 4 months, some trees flowered again joined by trees that had not yet flowered that year; a lower percentage of trees flowered during the second peak (Figure 2-1). Trees in *terra firme* forest comprised the majority of individuals flowering and fruiting during this second peak, whereas very few trees in the occasionally inundated forest flowered during this later peak (Figure 2-1).

The percentage of flowering individuals increased in concert with increase in precipitation that marked the beginning of the rainy season in all years (Figure 2-1). In 2006, the greatest percentage of flowering individuals in occasionally inundated forest occurred 1-month after the peak in *terra firme* forest. Otherwise, we observed the greatest number of individuals with flowers in both forest types concurrently for all other years, though this period lasted longer in occasionally inundated forest than in *terra firme* forest in 2007 (Figure 2-1).

Fruitfall commenced 4 months after the onset of flowering, near the end of the rainy season, and mirrored the dual peaks seen in the flowering phenophase (Figure 2-1). Peak percentage of individuals with falling fruit was consistently timed close to the time of the annual peak in rainfall. An anomalous high rainfall period at the end of the first fruitfall peak, however, was observed in 2009 (Figure 2-1). We observed no difference in fruiting peaks between forest types.

### **Seed Production**

Seed production, or the average number of seeds produced per tree, varied greatly by year with the highest years producing over 9 times more than the lowest years (Figures 2-1 & 2-2). While seeds were collected over more months in 2007-2008 and 2008-2009, even when off-peak seed production estimates were added to the measured seed production for the first three years, the average number of seeds

produced per tree was much greater in 2007-08 and 2008-09 (Figure 2-2). This was true in both occasionally inundated and *terra firme* forests.

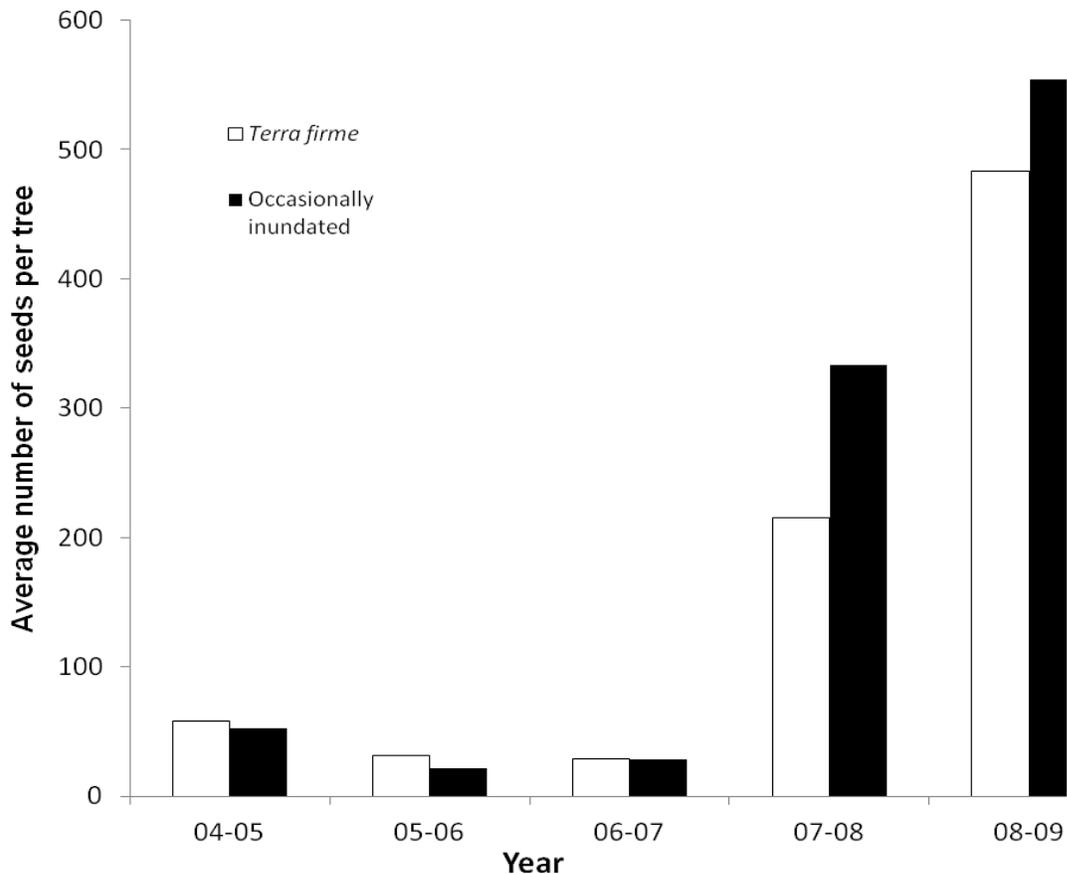


Figure 2-2 Average number of *Carapa guianensis* seeds per tree. Estimates include measured seed production data plus an estimate of non-measured seed production for the first three study years, when seed production was quantified only during a 5 to 17-week peak period.

Forest type, various tree attributes, and several climatic cues explained seed production variation for our 5-year study (Table 2-2). Seed production was significantly different between forest types ( $p < 0.0001$ ) (Table 2-2) with higher seed production in occasionally inundated forest. Results differed based on the 5-week peak seedfall model, indicating that forest type was not a significant predictor of seed production ( $p <$

0.0967). When we further explored forest type effect in the 5-week model, however we found significantly higher seedfall in occasionally inundated forests (Table 2-3), but only in years 2007-08 and 2008-09. Seed production in 2008-2009 in both forest types was higher than seed production in other years (either forest type). Seed production in occasionally inundated forest in 2007-2008 was also higher than seed production in the three prior years (both forest types) as well as same-year *terra firme* seed production (Figure 2-3). Trends indicated that trees in occasionally inundated forest produced more seeds per tree than those in *terra firme* forest (Figure 2-2). The proportion of trees with seeds was also higher in occasionally inundated forest in 2007-2008 and 2008-2009 with over 80% of selected trees producing seeds. The percentage of trees producing in *terra firme* forests was approximately 50% in 2007-2008, equal to the 2004-2005 percentages, although mean seed production per tree in 2004-2005 was lower.

Table 2-2 Results explaining variation in seed production, calculated using PROC GLIMMIX to perform a Poisson regression

Variable	Denominator DF	Estimated parameters	F-value	Pr > F
Intercept	103	-58.5281	22.48	0.0001
Forest type (OI)	103	0.4502	22.60	<0.0001
Dbh	103	0.3394	136.59	< 0.0001
Dbh <sup>2</sup>	103	-0.0041	110.35	< 0.0001
Crown cross-sectional area	103	0.0040	6.91	0.0099
Vine load (0)	103	0.6584	27.78	< 0.0001
Dry season rainfall (3 months)	4	0.03178	48.88	0.0022
Wet season rainfall (5 months)	4	-0.0209	92.67	0.0038
Mean maximum temperature	4	0.5932	36.36	0.0007

Table 2-3 Results of the model explaining variation in seed production when only 5-week peak seedfall periods were used for all years. (For brevity, estimated parameters for year and year x forest type interactions are not shown)

Variable	Denominator DF	Estimated parameters	F-value	Pr > F
Intercept	104	-9.2197	-10.56	< 0.0001
Forest type (OI)	104	1.4163	2.81	<0.0967
Dbh	104	0.5330	121.16	< 0.0001
Dbh <sup>2</sup>	104	-0.00641	95.25	< 0.0001
Vine load (0)	104	0.9647	23.96	< 0.0001
Year	4		107.75	< 0.0003
Year*Forest type	4		11.79	< 0.0176

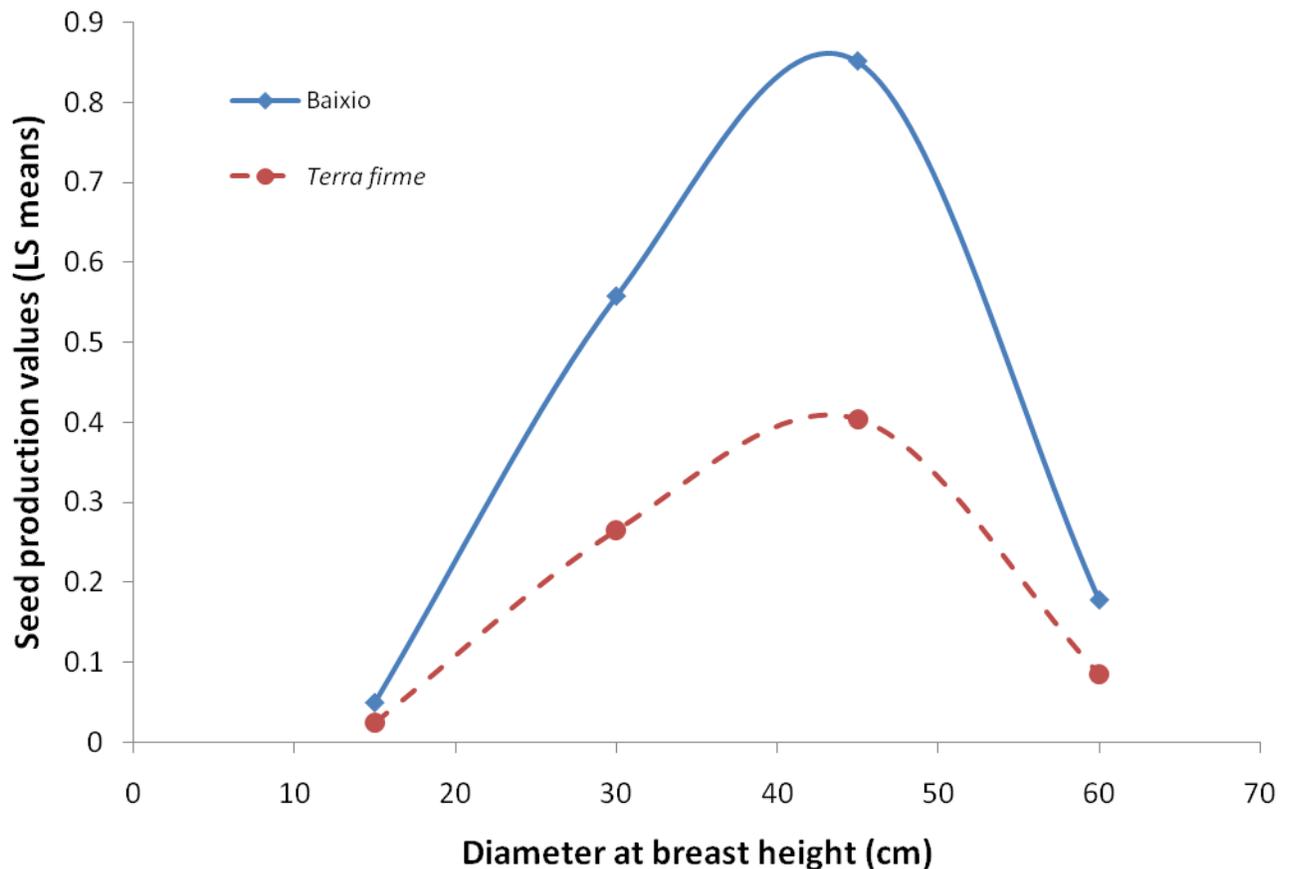


Figure 2-3 Relationship between d.b.h. and seed production using least squared mean values.

Table 2-4 The average number of seeds per hectare ( $\bar{x}$ ) and standard error (SE) for *Carapa guianensis* in kilograms.

Year	<i>Terra firme</i>		Occasionally inundated	
	Seeds per hectare ( $\bar{x} \pm \text{SE}$ )	Seed weight per hectare (kg) ( $\bar{x} \pm \text{SE}$ )	Seeds per hectare ( $\bar{x} \pm \text{SE}$ )	Seed weight per hectare (kg) ( $\bar{x} \pm \text{SE}$ )
2004-2005	445 ± 180	1.11 ± 1.485	919 ± 343	8.24 ± 3.25
2005-2006	176 ± 98	0.93 ± 3.90	287 ± 174	3.45 ± 0.96
2006-2007	157 ± 98	0.18 ± 1.30	383 ± 201	3.06 ± 2.49
2007-2008	1995 ± 727	24.04 ± 7.98	6264 ± 1044	80.26 ± 10.73
2008-2009	4575 ± 935	55.96 ± 0.09	10421 ± 1776	121.83 ± 0.19

Estimates of seed production per hectare varied broadly from hundreds to thousands of seeds, depending on the year (Table 2-4). We did not add off-peak seed production to these numbers; our seed production per hectare underestimated seed production in the first three years. Seed production per hectare (whether measured by seed number or weight) was higher in occasionally inundated forest than in *terra firme* forest due to greater seed production per tree, and a higher density of trees per hectare. Still, variability was high in both forest types. Multiple other measured variables also explained *C. guianensis* seed production, including dbh, dbh<sup>2</sup>, crown cross-sectional area, vine load, dry season rainfall, wet season rainfall and mean maximum temperature (Table 2-2). Overall, tree crown cross-sectional area had a slightly positive impact on seed production ( $p = 0.0099$ ). Although we assumed that this relationship would have been stronger without the confounding effect of non-producing trees, this was not the case; removing non-productive trees resulted in a weaker relationship. Crown cross-sectional area, however, was not significant in the model that used only 5-week peak seedfall (Table 2-3). The relationship between dbh and seed production was also significant and slightly positive ( $p < 0.0001$ ). There was a quadratic relationship between dbh and seed production: seed production increased with dbh until 40-50 cm,

then decreased (Figure 2-3). Vine load was negatively correlated with seed production, such that those trees with  $\geq 75\%$  crown vine load had significantly less seed production ( $p < 0.0001$ ). None of the interaction terms were significant in explaining seed production variation and were not included in the final model.

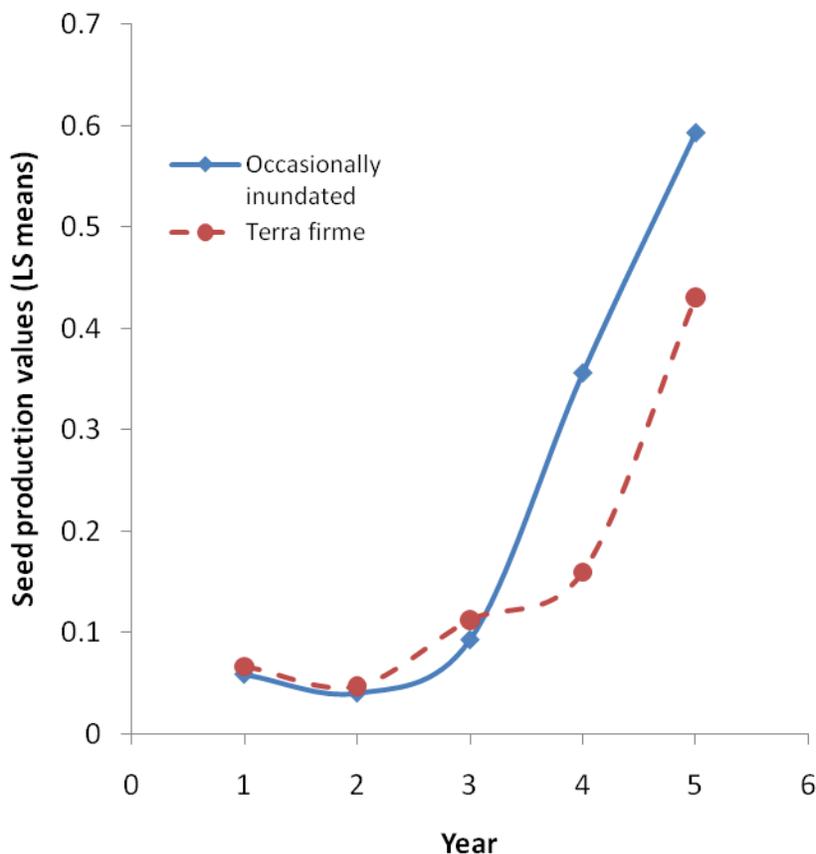


Figure 2-4 Relationship between year and seed production using least squared mean values.

Rainfall during the 5-month “wet period” from January to May was negatively correlated with seed production. This was also true for mean maximum temperature. Conversely, rain measured during the region’s 3-month dry season was positively correlated with seed production.

## Seed Removal and Infestation

Based on the number of fruit husks and an average seed number per fruit of  $8.9 \pm 3.7$  (SD), we estimated a 2007-2008 pre-removal seedfall of  $26,010 \pm 10,754$  seeds. The actual number of seeds collected and weighed that year was 28,373. In 2008-2009, the average seed number per fruit was  $8.8 \pm 3.2$ . Thus, we estimated pre-removal seedfall at  $51,541 \pm 18,742$  seeds. The actual number of seeds collected in 2008-2009 was 53,557, within the range of variation of our husk-based estimates of seedfall.

Seed infestation by *H. ferrealis* in 2007-2008, was: 14.6% and 15.5% for occasionally inundated forest and *terra firme*, respectively. In 2008-2009, infestation was 12.0% and 11.6% for occasionally inundated forest and *terra firme*, respectively.

## Synchronicity in Fruiting

Variability in seed production at the population level was moderate ( $CV_p = 1.25$ ). Individual variation was also moderate ( $xCV_i = 1.24$ ). The mean pairwise Pearson correlation coefficient, however, indicated low seed production synchrony in this population of *C. guianensis* ( $xPCC = 0.276$ ).

## Discussion

Using the tropical tree *Carapa guianensis* as a model species, this study demonstrates that multiple variables interact at different scales to influence seed production. At the largest scale, climatic cues (rainfall and temperature parameters) were central to setting overall patterns in phenophases and seemed to best explain why high seed production years were consistent across both forest types (or habitats) examined. Habitat heterogeneity, including species abundance, spacing between individuals (Klimas *et al.* 2007) and underlying abiotic factors may be the primary reason for significantly higher seed production in occasionally inundated forest ( $F =$

22.60, Table 2-2), though climatic variables had a much stronger predictor effect (Table 2-2). At the smallest scale, individual tree attributes contributed to seed production heterogeneity within habitats; dbh, and cross-sectional canopy area showed positive, quadratic relationships with seed production while vine load negatively affected seed production irrespective of forest type. These central ecological findings can also help inform management of this economically important multiuse species.

### **Annual Patterns in Flowering and Fruitfall**

We observed two periods of flowering and seed production during a 12-month cycle in both forest types in 2007-2009. Initiation of flowering was closely tied to the climatic rainfall variable. Flowering occurred at the beginning of the rainy season during the first two years and peaked immediately prior to the initiation of the rainy season in the last two years of the study (Figure 2-1). Our findings are consistent with other research that indicates that flowering peaks in seasonally dry forests tend to come at the end of the dry or start of the rainy season (Van Schaik *et al.* 1993); reproductive events generally occur during the period of low photosynthetic activity or after high rates of reserve accumulation (Fenner 1998). Indeed, Van Schaik *et al.* (1993) found that 67% of flowering peaks fell within one-month of the onset of the rainiest period for 53 tropical forest sites. This timing, prior to the onset of some of the season's heaviest rains, may be conducive to pollination. Flowering near the onset of the rains is also strategic for reproductive success. Only 4 months separated the first evidence of flowers from the initiation of fruitfall (though see Fournier 2003); germinating seeds were thus well-positioned for water dispersal and seedlings unlikely to be limited by available soil moisture during germination, though excessive rains can increase seedling death due to fungal rot (Rigamonte-Azevedo personal communication).

While there is evidence for flowering induction with a reduction in photoperiod that coincides with the rainy season (Rivera & Borchert 2001), we did not test this hypothesis: our dataset shows annual consistency in flowering times, the relative lack of synchrony indicates control of phenology by site-dependent temporal variation in water status as opposed to photoperiodic control (Borchert 1994). Episodic rains prior to the onset of heavier rains may have been the actual impetus for flowering; several species in Venezuela responded to episodic rains with increasing water potentials, flowering and new leaf production (Díaz & Granadillo 2005). Individual trees, however, differed in flower initiation: some trees concurrently had buds, flowers, developing fruits and fruitfall. This variation may promote genetic recombination if spatial non-aggregation of flowering trees forces longer-distance pollen dispersal. The timing of flowering, however, is likely also related to the timing of vegetative phenology of this species: initiation of flowering coincided with the peak in the number of individuals with new leaves (Figure 2-1). Reproductive events require substantial carbon reserves and the increased photosynthetic capacity of plants after leaf flush may help provide the necessary reserves for this large-seeded species.

### **Seed Production Variation by Forest Type**

We found significantly higher seed production per tree in occasionally inundated forest which was further increased by higher densities in this forest type, though this effect was not one of the strongest effects ( $F=22.6$ , Table 2-2). *C. guianensis* has long been considered predominantly a species of flooded forests (Pennington 1981, McHargue & Hartshorn 1983a, Fournier 2003), though previous research found high densities of individuals in *terra firme* forest (Klimas *et al.* 2007). Unmeasured micro-environmental characteristics, such as soil moisture or nutrient availability, may favor

survival and growth of this species in inundated environments and also explain some of the differences in seed production between these forest types. Density differences, however, might be the underlying cause of seed production differences: increased spacing among trees in *terra firme* forest may lower pollination visitation, thus reducing seed set and subsequent seed production. While euglossine bees, an observed flower visitor of *C. guianensis* (Maués 2006) commonly visit plants sequentially over a wide geographic area (trapping) (Janzen 1971), some large euglossine bees show local site fidelity (Ackerman *et al.* 1982).

### **Influence of Forest Type Across Years**

*C. guianensis* seed production per tree varied greatly between years ( $xCV_i = 1.24$ ,  $F=107.75$ , Table 2-3). Average seed production per tree in 2007-2008 was more than four times higher than average seed production during any of the first three years of our study, and average production in 2008-2009 was more than nine times higher (Figure 2-2, Table 2-5). Large oscillations of seed output by individuals between high- and low-production years may be the rule among polycarpic plants (Herrera *et al.* 1998), though some studies have found that seed production on a population-level can remain relatively constant between years, even with high variation in individual production (Kainer *et al.* 2007).

Our study showed that *C. guianensis* had variable seed production between years ( $CV_p = 1.25$ ) and between individuals ( $xCV_i = 1.24$ ). Indeed, the  $CV_p$  for *C. guianensis* was higher than the median value of 1.10 for 108 tropical species (Wright *et al.* 2005), but below the  $CV_p$  of a strict masting species (i.e. 1.6) (Kelly 1994), which often suspend population-level seed production in some years. Still, calculations of CVs for

seed output are less reliable with less than 10 years of data (Kelly 1994) and these results could be improved with longer-term monitoring.

Table 2-5 Number of individuals sampled and average seed weight per tree ( $\bar{x}$ ) and standard error (SE) for *Carapa guianensis*. This table includes only measured seedfall; data shown do not include estimates of off-peak seed production not measured in the first 3 years of this study.

Production	<i>Terra firme</i>		Occasionally inundated		N	Total Seed wt tree <sup>-1</sup> (kg) ( $\bar{x} \pm SE$ )
	n	Seed wt tree <sup>-1</sup> (kg) ( $\bar{x} \pm SE$ )	n	Seed wt tree <sup>-1</sup> (kg) ( $\bar{x} \pm SE$ )		
2004-2005	20	0.12 ± 0.16	19	0.43 ± 0.17	39	0.27 ± 0.11
2005-2006	24	0.10 ± 0.42	30	0.18 ± 0.05	54	0.14 ± 0.19
2006-2007	23	0.02 ± 0.14	29	0.16 ± 0.13	52	0.10 ± 0.10
2007-2008	51	2.59 ± 0.86	53	4.19 ± 0.71	104	3.41 ± 0.56
2008-2009	50	6.03 ± 0.01	53	6.67 ± 0.02	103	6.36 ± 0.01

The interaction between forest type and year was also significant in our “peak” seedfall model (Table 2-3). In this model, year was used to represent climatic variation rather than season rainfall or temperature. The latter variable types were measured annually, and therefore had to be excluded from this analysis to avoid over-parameterization of the model and non-convergence. Perhaps part of this interaction and likely the observed lower seed production in *terra firme* forest, can be explained by a 2005 fire in one of our *terra firme* plots that stressed trees and reduced stored reserves available for reproduction. This fire, however, coincided with an especially severe Amazonian drought that would have affected both forest types. Indeed, percentage of individuals flowering and total seed production were low in both forest types in 2005 and the subsequent year. Phillips *et al.* (2009) found a highly significant decrease in biomass immediately after the 2005 drought in 55 plots distributed throughout the Amazon basin (as compared with the multi-decadal period immediately

prior); lower biomass production is linked to reduced reserves for reproduction and leaf flush (though see Huerte *et al.* 2006, Saleska *et al.* 2007). Samantha *et al.* (2010) found reductions in both PAR and surface shortwave radiation during the drought, further limiting species potential to rebuild stored reserves. Because we did not collect data prior to the drought, we are unable to determine whether our results represent natural seasonal fluctuation in phenology and seed production or whether they are partially the response of trees to severe drought stress.

### **Variation by Tree Attributes**

Individual tree attributes, particularly size, were also important in explaining seed production variation, an expected relationship since vital demographic rates are normally stage- or size-dependent (Harper 1977). Indeed, the strength of the impact of dbh on seed production was higher than any of the other predictor variables ( $F=136.59$ ). We found a quadratic relationship between seed production and dbh; trees in the middle diameter classes ( $30 < \text{dbh} < 50$ ) were better producers than both smaller and larger trees (Figure 2-4), a relationship also evident for *Bertholletia excelsa* (Kainer *et al.* 2007). This contrasted with results for the related *Swietenia macrophylla* and two other tropical trees, which showed a more linear increase in seed production with increasing diameter (Snook *et al.* 2005, Nabe-Nielsen *et al.* 2009), though larger individuals had been eliminated from the study populations through logging, effectively eliminating the ability to detect production patterns of larger-diameter trees.

Our data revealed an expected, though relatively weak, negative association between vine load and seed production ( $F=27.78$ , Table 2-2) (Stevens 1987), a finding consistent for other tropical species (Nabe-Nielsen *et al.* 2009, Wright *et al.* 2005, Kainer *et al.* 2006). Nonetheless, Londres (2009) found no significant effect of lianas on

seed production for *C. guianensis* in a flooded forest near the mouth of the Amazon. Their sample, however, included very few trees with lianas and these were weighted heavily toward larger, better producing individuals.

### **Influence of Climate Cues**

Mean annual maximum temperature was negatively correlated with *C. guianensis* seed production. Temperature may not have independently affected seed production in our study; the three years with the highest annual mean maximum temperature also had the least dry season rainfall (PCC = -0.43). Indeed, very few cases have demonstrated that phenological patterns are triggered by temperature and not by covariates, such as cloud cover, day length and solar elevation (Stevenson *et al.* 2008). Combined, these generate substantial seasonal variation in tropical irradiance (Van Schaik *et al.* 1993), often associated with temperature changes, which may affect tropical phenological patterns (Wright *et al.* 1999, Stevenson 2004, Zimmerman *et al.* 2007). Indeed, 2005 was characterized by lower available sunlight due, in part to significant aerosol loads in the atmosphere from biomass burning (Bevan *et al.* 2007, Koren *et al.* 2007). The negative association between temperature and seed production, however, may have been due to plant drought stress: higher temperatures in 2005 coincided with the severe drought. Recent research has shown an interaction between temperature and drought stress on plants (Adams *et al.* 2009, Allen *et al.* 2010) due, in part to increasing respiration rates with temperature (Hartley *et al.* 2006), but our study did not collect data to test this hypothesis.

Three-month dry season rainfall was positively correlated with seed production. Conversely, five-month wet season rainfall was negatively correlated with seed production. Slightly higher than normal dry season rains may allow trees access to a

seasonally scarce resource, increasing stored reserves available for flowering and fruiting. Too much rain during the dry season, however, is likely detrimental. Threshold levels of drought synchronize flowering and enhance seed set in some tropical forest plants (Alvim 1960). Since a minimum flower abundance may be necessary to attract pollinators (Van Schaik *et al.* 1993), this drought-influenced synchrony may facilitate pollinator activity. Our results correlating dry-season rainfall with seed production are not unique in the region; Kainer *et al.* (2007) found a highly significant, though weak, positive correlation between number of fruits of *Bertholletia excelsa* and 5-month dry season rainfall.

Rainfall data is also influenced by the occurrence of the El Niño southern oscillation. Wright *et al.* (1999) found that a 2-year cycle of high, then low community-level fruit production was observed twice for Barro Colorado Island, Panama, when a mild dry season followed an El Niño event. Zuidema & Boot (2002) found a significant drop in fruit production coinciding with low rainfall in an El Niño year. There may be a pattern with data from our study; the El Niño years 2004-2005 and 2006-2007 were associated with low fruitfall while the La Niña year of 2007-2008 was associated with high levels of seed production. *Bertholletia excelsa* trees in the region also had high levels of seed production in 2008 and 2009; and relatively low seed production in 2006 and 2007 (Wadt & Kainer, unpublished data), similar to the trends observed for *C. guianensis*, though *B. excelsa* takes 14 months to mature from flower to fruit. The El Niño year in 2005 coincided with the severe drought caused by anomalous North Atlantic warming (Marengo *et al.* 2008). If results from these species are an indication of

basin-wide trends, El Niño years or drought years may be associated with decreased seed production for tropical species.

### **Management Considerations**

While we observed high interannual variation in seed production, seed production on a population-level occurred in all years, a positive implication for seed extraction and management. We found consistency in seed production in both forest types; high seed production in occasionally inundated forest coincided with high seed production in *terra firme* forest. In some years, harvest may not be viable in either forest type; years where expected harvests generate two to twelve kilograms of seeds per hectare (Table 2-4) may not generate sufficient revenue to justify time invested in seed collection. One way to reduce harvest costs is to focus on trees that show evidence of being top-producers (Kainer *et al.* 2007, Snook *et al.* 2005); a subset of monitored *C. guianensis* trees in this study showed evidence of consistently superior seed production.

The percentage of plants flowering was a good indicator of future fruit abundance for *C. guianensis*, a finding described in similar studies (Foster 1982, Heideman 1989). Anticipating years with high seed production prior to the onset of flowering, however, may be difficult. This study does not have the temporal length necessary to predict patterns in seed production variability between years. Indeed, difficult-to-predict, variable cycles may be the norm for this species. Further monitoring, however, may indicate a maximum number of high production years before the plant must rebuild resources.

The two production peaks per annum observed in our study may facilitate management. Leaving seeds from the second smaller production peak in the forest may be sufficient to maintain species recruitment, though this second peak was not

forthcoming in low production years. Results from population models often suggest that very low seedling establishment: rates, as low as 1-3% for an Amazonian herb (Bruna 2003), are sufficient for positive population growth rates . Londres (2004) found that seed production of *C. guianensis* far exceeds harvest levels for a community in the eastern portion of the Brazilian Amazon basin; the community harvested only 0.1% of the total estimated annual seed production in the area (Londres 2009). Excessive extraction in our study area is not likely in the short-term. Current local market prices of R\$14-15 for a 60 kilogram mesh bean-sack of *C. guianensis* seeds and limited demand in the state of Acre effectively limit interest in large-scale collection.

Though there was little evidence of seed predation by vertebrates in the study region, seed infestation by *H. ferrealis* larvae affected 11.6 to 15.5% of viable seeds. Leaving fallen seeds in the forest facilitates the rapid spread of larvae to non-infested seeds. Larval damage can be minimized by frequent seed harvest coupled with rapid storage and/or oil processing. Seeds can be stored prior to oil extraction, but the larvae must be killed either by drying seeds at high temperatures or submerging seeds in water for 24 hours (Ferraz 2003); solar drying spreads *H. ferrealis* infestation (RECA, personal communication). Still, infested seeds can be used for oil extraction. When we experimentally extracted seed oil via a small press, we included seeds with evidence of *H. ferrealis* entry with non-infested seeds. The quantity of oil extracted was dependent almost completely on the weight of the seed sample ( $r^2=0.98$ ) (Klimas, unpublished data), but seed quality was not tested.

This study is an important first step in management of a species with variable inter-annual fruiting, and can help predict years with high fruit production crucial for

economic revenue. We recommend further study of temporal seed production trends and variability as our study represents only a snapshot in the life of this long-lived species.

CHAPTER 3  
VIABILITY OF COMBINED TIMBER AND NON-TIMBER HARVESTS FOR ONE  
SPECIES: AN EXAMPLE USING *CARAPA GUIANENSIS*

**Introduction**

There is growing consensus that sustainable use has a significant role to play in nature conservation globally (Brechin *et al.* 2002, Heywood & Iriondo 2003, Nepstad *et al.* 2009). While preservation via protected areas is a cornerstone of conservation (Brooks *et al.* 2009) and an essential part of any strategy to conserve tropical forest diversity, protected areas inevitably include an incomplete set of the regional biota and are often embedded in a modified and fragmented landscape. Even if protected areas are locally effective, they encompass only 9.8% of tropical forests and 11.1% of Amazonia (Schmitt *et al.* 2008), often too small to be comprehensively effective (Janzen 1986). Luckily, managed and secondary forests can also provide important conservation benefits, including provision of ecosystem services (Daily 1997, Bhagwat *et al.* 2008, Gardner *et al.* 2009) and species habitat for biodiversity conservation (Lamb *et al.* 2005, Scales & Marsden 2008). Maintenance of these forested areas adjacent to or nearby protected areas could complement protected areas by creating a forested mosaic at the landscape-level.

Recognizing and increasing the conservation value of lands outside protected areas is a necessary component of any long-lasting conservation effort (Harvey *et al.* 2008, Ros-Tonen *et al.* 2008). In the Brazilian Amazon, existing legislation has the potential to promote forest cover on private land: Brazilian law currently requires maintaining 80% of a private landholding in the Amazon as forest reserve (Medida Provisória 2001). Enforcement is often lax, however, suggesting that this legislation is not likely to maintain forest cover on privately-owned lands while deforestation for

conversion to other land uses remains a competing and economically attractive alternative. Managing forests for services and products that yield economic benefits is another way to enhance the value of standing forests while providing benefits to the landowner, thus encouraging forest persistence. This option has the benefit that economic incentives for management are applicable to diverse groups, including private landowners, forest residents, indigenous groups and smallholders charged with management of conservation units. Smallholders alone control over 16% of the Amazon (Barreto *et al.* 2005, Lima *et al.* 2006), more than the area currently under legal protection. Social and economic benefits derived from standing forests must be competitive with benefits derived from forest conversion to other land uses, however, since private owners are not expected to manage primarily in the public interest (Zarin *et al.* 2007).

While market valuation of some benefits, like ecosystem services and carbon storage is still developing (Engel *et al.* 2008, Stickler *et al.* 2009), multiple forest resources already provide concrete economic benefits, including timber and non-timber forest products (NTFPs). Logging provides clear economic benefits (Veríssimo *et al.* 1992, Lentini *et al.* 2003, AIMEX 2005), although it does not provide a continuous flow of benefits unless it is specifically managed to do so (Oliveira *et al.* 1998, Oliveira 2000), which is rarely the case: indiscriminant one-entry logging remains the predominant form of timber extraction (Putz *et al.* 2000). Timber extraction can also provide conservation benefits: half of Borneo's remaining forests (approximately 200,000 km<sup>2</sup>) that have active forestry concessions maintain significant wildlife conservation value (Meijaard *et al.* 2005) and biodiversity (Whitmore & Sayer 1992), making them a viable component

of multi-functional conservation landscapes (Meijaard *et al.* 2005). Logging, however is an intensive and extensive land use that has significant drawbacks: removing the stem causes significant forest disturbance (Verissimo *et al.* 1992), increases forest susceptibility to fire (Laurance *et al.* 1998, Cochrane *et al.* 1999, Alencar *et al.* 2004), and typically permits new forest access and conversion (Walker 2003, Fearnside 2005). In contrast, NTFP harvest can provide a more consistent (Pearce *et al.* 2003) cash flow from harvesting a diversity of species over the course of a year, and may or may not provide similar revenue levels as logging, but likely over longer time frames (i.e., decades). NTFP harvests are generally less destructive than logging, though harvest of stems, bark and apical meristems imply harvest of whole trees (Ticktin 2004). Harvests are typically easier to sustain over years or decades and add to the perceived value of the forest (Chopra 1993, Gunatilake *et al.* 1993, Marshall *et al.* 2003), but alone, may not provide enough revenue to promote forest maintenance. NTFP harvest can also affect persistence of populations (Peres *et al.* 2003, Peters 1996), alter forest structure (Belcher & Schreckenberg 2007) and ecosystem processes at many levels (Ticktin 2004) and may be insufficient to lift communities out of poverty (Morsello 2006).

Another option, combining these two types of forest products through multiple-use forest management (MFM) is increasingly envisioned as a preferable alternative to timber-dominant management models (García-Fernández *et al.* 2008). Limited research, however, has focused on the relative compatibility of coupling timber and NTFP harvests (though see Snook 2000, Guariguata *et al.* 2008, Menton *et al.* 2009, Guariguata *et al.* 2010). Still, thoughtful harvest of multiple forest products seems

increasingly necessary to compete with relatively lucrative activities, like conventional logging and cattle ranching (Pearce 1996, Pearce *et al.* 2003).

Determining ecologically sustainable harvest limits is necessary for developing appropriate forest management strategies, despite the significant challenge to produce effective simulations of tropical forests managed for both NTFPs and timber (Ribeiro do Valle *et al.* 2007). Matrix models are powerful tools useful for identifying population trends and responses to management regimes (Leftkovitch 1967, Crowder *et al.* 1994, Olmsted & Alvarez Buylla 1995), setting harvest limits from a population that are compatible with its continued existence (Nantel *et al.* 1996, Ratsirarson *et al.* 1996) and identifying key life stages as management targets (Crouse *et al.* 1987). In addition, matrix models can be used to simulate sustainable harvest levels for timber, NTFPs or a combination of management strategies for single species, an important factor in determining appropriate management strategies for the third to almost half of timber species that also have value for their NTFPs (Martini *et al.* 1994, Herrero-Jáuregui *et al.* 2009).

We employ matrix models to examine sustainable use of *Carapa guianensis*, one such multiple-use species. We question whether management of *C. guianensis*, a tree species valued for both its high quality timber and its seed oil, can be managed sustainably for both seed and timber harvests. Our objectives were: (1) to quantitatively assess the impact of seed and timber harvesting on *C. guianensis* in stochastically varying environments, (2) to determine whether the impact of harvest varied between occasionally inundated and *terra firme* forests, and (3) to simulate potential ecologically viable harvest scenarios of *C. guianensis* seeds, timber, or seeds and timber. We

hypothesized that intensive seed collection would still result in sufficient seedling recruitment to ensure continued species persistence. Wadt *et al.* (2007) found that high levels of seed harvest (up to 71%) were compatible with population persistence and simulation models indicate that extreme reductions in recruitment are necessary for population declines (Bruna 2003). We also hypothesized that *terra firme* forests would allow even more intensive seed harvests as seeds in this environment may be “safe-site” limited. Klimas *et al.* (2007) found that *C. guianensis* seedling densities were almost three times higher in occasionally inundated forests than in *terra firme* forests, perhaps due to the limited availability of suitable germination sites. Therefore, collection of seeds that would otherwise perish would allow for increased seed harvest levels without impacting future population viability. We examined sustainable harvests of *C. guianensis* in two of the forest types in which it occurs naturally, and at different densities and abundances (Klimas *et al.* 2007). Vital rates, key demographic variables that form the basis for matrix models, depend on individual size (Harper 1977), species distributions and abundances between habitats (Bruna & Kress 2002, Wagner & Fortin 2005), and habitat heterogeneity (Webb & Peart 2000, Svenning *et al.* 2006) due to variation in physical variables (Gartlan *et al.* 1986, Hubbell & Foster 1986, Davies *et al.* 1988, Lieberman *et al.* 1995, Whitmore 1984).

## **Methods**

### **Study Species**

Mature *C. guianensis* trees can reach heights of 30 meters (Ferraz *et al.* 2002) though neither tree height nor dbh reliably predicts age. Carbon-dating of two individuals in our study region estimated the age of a 37.5 dbh individual at 172 years while a 17 cm dbh individual was aged at 785 years (both of these ages are based on

extrapolating growth rates determined by multiple radiocarbon measurements) (Vieira *et al.* 2005). Fruitfall coincides with the rainy season, with an onset around December and cessation by early June in our study region (See Chapter 1). *C. guianensis* has no seed bank and germination occurs rapidly, often within two-weeks of seedfall (Klimas, personal observation). Seeds are enclosed in a dehiscent capsule that normally breaks open with ground impact, freeing seeds for germination or dispersal via water or frugivores (McHargue & Hartshorn 1983, Plowden 2004).

*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 & Medina 2005) which sells both locally and in international markets; Brazil exported between 200-300 tons of oil annually between 1974 and 1985 (Clay *et al.* 2000). Pure *C. guianensis* 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, Brazil identified it as one of six priority species for extraction research (Acre 2000).

### **Study Site**

We carried out field measurements within four 400 m x 400 m (16-ha) plots established within the 1200 ha experimental forest of the Brazilian Agricultural Research Corporation (Embrapa) in the eastern portion of the state of Acre (latitude 10° 01' 28" S and longitude 67° 42' 19" W). Average annual temperature is 24.5°C with a dry season from June to August (INMET 2009). The region has rolling topography including upland habitat (*terra firme*) and occasionally inundated areas. Two plots were established where the majority of the environment was classified as *terra firme* forest and two in

occasionally inundated forest (Klimas *et al.* 2007). All individuals  $\geq 10$  cm dbh were inventoried in these plots and tree canopy position (dominant, co-dominant, intermediate or suppressed), spatial coordinates, and diameter at breast height (dbh) were measured.

### Individual Survival Rates and Diameter Growth

Growth rates used in the demographic model were based on the average growth rate of individuals in a given size class. We installed dendrometer bands on a stratified random sample of over 500 trees in 2003, controlling for location (forest type) and diameter at breast height (dbh) categories (Table 3-1). Following a 9-month period of band adjustment, annual circumference growth was monitored between May and June of 2004 through 2009, recording measurements during the dry season to reduce variance (Sheil 1995, 1997 but see Baker *et al.* 2003). Annual circumference increment was divided by pi to convert to annual diameter increment. Tree mortality of all marked individuals was recorded annually during growth measurements.

Table 3-1 Number of trees with dendrometer bands installed in 2003 and measured in 2004. N reflects original tree numbers sampled in 2004 prior to subsequent tree mortality.

<i>Forest type</i>	<i>Diameter class (cm)</i>	<i>N</i>
Occasionally inundated	10 to 20	104
	20 to 30	70
	30 to 40	39
	40 to 50	20
	50 +	15
	Total	248
<i>Terra firme</i>	10 to 20	100
	20 to 30	71
	30 to 40	40
	40 to 50	22
	50 +	9
	Total	242

We monitored seedling and sapling survival and growth in 32 10 m x 10 m subplots within each of the larger 400 m x 400 m plots (Klimas *et al.* 2007). We noted  $x$ ,  $y$  coordinates and annually monitored all seedlings (individuals < 1.5 m tall) and saplings (individuals  $\geq$  1.5 m tall and < 10 cm dbh) in each subplot from 2005 to 2009, between May and July. For seedlings, we annually measured basal diameter (soil level) and stem height; for saplings we measured dbh (Klimas *et al.* 2007), calculating annual growth increments by increases in seedling height and sapling dbh, respectively. We measured smaller saplings using digital calipers, marking the measurement location with a permanent marker to ensure year-to-year consistency. For larger saplings, we sprayed paint around a circular piece of metal the same size as the diameter tape, taking annual measurements by placing the diameter tape within the non-painted area.

For seedlings and saplings, we calculated survival based on observed mortality each year in each forest type. For seedling growth, we pooled individuals from both forest types to calculate annual growth, because high mortality substantially decreased the approximately 900 seedlings tagged over the 5-year study. Likewise, survival of only 76 saplings did not leave representative sample sizes for calculating growth by year and forest type, and thus sapling measurements were also pooled across forest types.

### **Parameter Estimation for Transition Matrices**

The population was classified into eight size classes considered biologically relevant: seedlings (individuals < 1.5 m tall); seedlings that regressed in growth but survived (also <1.5 m tall); saplings (individuals  $\geq$  1.5 m tall and < 10 cm dbh); 10 cm  $\leq$  dbh < 20 cm; 20 cm  $\leq$  dbh < 30 cm; 30 cm  $\leq$  dbh < 40cm; 40 cm  $\leq$  dbh < 50 cm; and dbh  $\geq$  50 cm. Our justification for the given size classes was based on differences in size-specific mortality and fertility. Mortality rates were very high for all newly

germinated seedlings, with survival increasing substantially when seedlings reached a height of approximately 1.5 m. Individuals in the 10-20 cm dbh class had a low probability of producing seeds (Klimas *et al.* 2007); dbh was then quadratically related to seed production (Chapter 2).

Every year, we observed a significant fraction of seedlings that regressed. In most cases, these seedlings were dead the following year, but some survived. Since seedling cannot regress back into the seed stage (Figure 3-1), we divided our fertility entries of average size-specific seedling production into the first and second rows of the matrix based on the proportion of seedlings that grew or regressed, respectively (Figure 3-2).

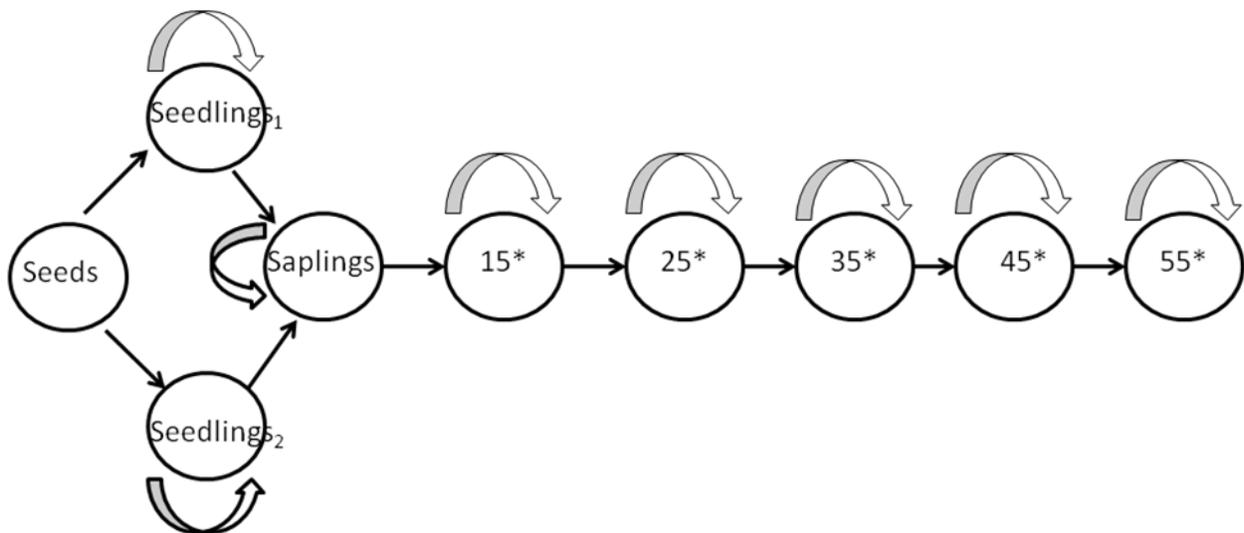


Figure 3-1 The life cycle of *C. guianensis* with straight arrows indicating the probability that an individual will grow ( $G_i$ ) from one stage to the next during time interval  $t$ . Curved arrows indicate the probability that an individual will survive and remain in a given size class ( $P_i$ ) during time interval  $t$ . Starred stages can produce seeds, though not all individuals or stages produce seeds in any given year. Numbers represent the midpoint of dbh size classes. Seeds are not included in the matrix as they germinate rapidly and become either seedlings that experience positive growth (Seedlings<sub>1</sub>) or seedlings that experience negative growth (Seedlings<sub>2</sub>) during the one-year time interval  $t$

	Seedling <sub>1</sub>	Seedling <sub>2</sub>	Sapling <sub>3</sub>	15 <sub>4</sub>	25 <sub>5</sub>	35 <sub>6</sub>	45 <sub>7</sub>	55 <sub>8</sub>
Seedling <sub>1</sub>	$P_1 = \sigma_1 - G_1$	0	0	$F_4 * P_{\text{pos}}$	$F_5 * P_{\text{pos}}$	$F_6 * P_{\text{pos}}$	$F_7 * P_{\text{pos}}$	$F_8 * P_{\text{pos}}$
Seedling <sub>2</sub>	0	$P_2 = \sigma_2 - G_2$	0	$F_4 * P_{\text{neg}}$	$F_5 * P_{\text{neg}}$	$F_6 * P_{\text{neg}}$	$F_7 * P_{\text{neg}}$	$F_8 * P_{\text{neg}}$
Sapling <sub>3</sub>	$G_1 = \sigma_1 * (g_1/c_1)$	$G_2 = \sigma_2 * (g_2/c_2)$	$P_3 = \sigma_3 - G_3$	0	0	0	0	0
15 <sub>4</sub>	0	0	$G_3 = \sigma_3 * (g_3/c_3)$	$P_4 = \sigma_4 - G_4$	0	0	0	0
25 <sub>5</sub>	0	0	0	$G_4 = \sigma_4 * (g_4/c_4)$	$P_5 = \sigma_5 - G_5$	0	0	0
35 <sub>6</sub>	0	0	0	0	$G_5 = \sigma_5 * (g_5/c_5)$	$P_6 = \sigma_6 - G_6$	0	0
45 <sub>7</sub>	0	0	0	0	0	$G_6 = \sigma_6 * (g_6/c_6)$	$P_7 = \sigma_7 - G_7$	0
55 <sub>8</sub>	0	0	0	0	0	0	$G_7 = \sigma_7 * (g_7/c_7)$	$P_8 = \sigma_8 - G_8$

Figure 3-2 Matrix entry calculations, where:  $F_i$  = average size-class specific fertility;  $\sigma_i$  = size-class specific survival probability;  $g_i$  = size-class specific growth rate (mm/year);  $c_i$  = category width (100mm for most size classes, excluding seedlings and saplings which differed in their category width limits);  $P_{\text{neg}}$  = probability that a seedling will experience negative growth its first year;  $P_{\text{pos}}$  = probability that a seedling will experience positive growth its first year; Seedling<sub>1</sub> = seedlings that experience positive growth during their first year after germination; Seedling<sub>2</sub> = seedlings that experience negative growth during their first year after germination

We used the SAS procedure PROC LOGISTIC (version 9.2) to calculate logistic regressions of survival and growth against size for individuals  $\geq 10$  cm dbh; we calculated survival and growth values taken from these fitted regressions at the midpoint of each size class, using logistic regression implemented in the R programming language (R Development Core Team 2006) to calculate the probability of growing from stage  $i$  to stage  $i+1$  in the transition matrix. Combining the data from all size classes to estimate logistic regressions of survival and growth minimizes errors from small sample size in larger size classes; estimates of survival and growth for classes with few marked individuals are susceptible to chance variation around the true value (Caswell 2001, Morris & Doak 2002). Growth and survival curves were calculated: 1) for the entire dataset combining data from all years and both forest types, 2) per year using pooled matrices of individuals from both forest types and 3) annually for each forest type.

We calculated transition probabilities by multiplying the probability of survival ( $P_i$ ) by the probability of growth ( $G_i$ ) from  $i$  to  $i+1$  (Figure 3-2). We calculated the probability that a given individual would transition from stage  $i$  to  $i+1$  as the inverse of the average duration in a given stage (Caswell 2001), based on average size-specific growth from dendrometer band measurements. Seedling and sapling transitions were the inverse of the average duration in a given stage based on height growth and diameter growth, respectively (Figure 3-2).

Fertility values were based on the average seed production of an individual in a given size class converted to observed seedling frequencies. We quantified weekly size-class specific seed production by collecting fallen seeds under a random subset of

trees in both forest types. We used a combination of measured annual seed production from 07-08 and 08-09 and estimated seed production (for methodological details, see Chapter 1).

### **Matrix Modeling**

We compared transition matrices between years and forest types, using population growth rate and bootstrapped estimates of variability to determine whether matrices were the same (indicating that we should pool all matrices before running matrix projections) or whether differences between matrices, either between years or forest types, warranted using separate annual transition matrices for each forest type. Confidence intervals for each estimate of  $\lambda$  were calculated using bootstrapping: we recalculated average growth in each size class each year based on a random reselection of individual growth rates. The upper and lower 95% confidence intervals of 2000 bootstrap runs were estimated using bootstrap percentile intervals (Caswell 2001) (Table 3-3). We used MATLAB (2002) for all analyses unless otherwise stated.

Population matrix models use the equation  $n(t+1) = An(t)$ , where  $n(t)$  and  $n(t+1)$  are column vectors that contain the population structure at time  $t$  and  $t+1$ , and  $A$  is a square  $m \times m$  matrix containing the transition probabilities among categories during one year (Caswell 2001). In our case,  $m = 8$  for all matrices in both forest types, where  $m$  is the number of size classes. In this equation, the population structure at time  $t+1$  is obtained by multiplying the structure at time  $t$  with the transition matrix that contains information on the dynamics of the population. When repeating this process many times, the population structure (relative to the initial population structure) and population growth rate become stable. In this situation, the rate at which the population grows (the asymptotic population growth rate) is equal to the dominant eigenvalue ( $\lambda$ ) of matrix  $A$ ,

an inherent characteristic of the transition matrix. The stable population structure is equal to the right eigenvector of the matrix  $A$  (Caswell 2001). The long-term behavior of the population is determined by  $\lambda$ . If  $\lambda \geq 1$ , the population is viable and is stable or increases; if  $\lambda < 1$ , the population is not viable and declines.

### **Elasticity Calculations and Ranking**

We also calculated elasticity values for the vital rates underlying each 8 x 8 transition matrix. Elasticity analysis is often used to demonstrate the sensitivity of population growth rate to variations in vital rates (survival, growth and reproduction), allowing for analysis of effectiveness of management interventions at changing population growth (Rogers-Bennett & Leaf 2006, Carslake *et al.* 2009). While most studies have calculated deterministic sensitivities (Horvitz & Schemske 1995, Pascarella & Horvitz 1998, Meekins & McCarthy 2002), we calculated vital rate sensitivities since each matrix element is composed of underlying vital rates, each of which may contribute to multiple matrix elements (Franco & Silvertown 2004, Morris & Doak 2005). Elasticities predict the relative change in population growth rate ( $\lambda$ ) given a proportional, infinitesimal change in a vital rate, holding all other elements constant; elasticity ( $e_{ij}$ ) is the slope of  $\log \lambda$  plotted against  $\log a_{ij}$  (Caswell 2001). The elasticities of  $\lambda$  with respect to a vital rate are often interpreted as the “contributions” of each of the vital rates to  $\lambda$  since the elasticities of  $\lambda$  with respect to the vital rate always sum to one (De Kroon *et al.* 1986). We used vital rate means and a matrix definition to calculate deterministic elasticities of  $\lambda$  to vital rates, using symbolic functions to take derivatives (based on a modification of code by Morris & Doak 2002). We also ranked elasticities for each year’s model in each forest type.

## Modeling Environmental Stochasticity

We incorporated environmental stochasticity into simulated population projections using independent and identically distributed (iid) environmental states using MATLAB code based on Morris & Doak (2002). We assumed that the 5 years of our study (4 transition matrices) represented the range of typical conditions, each of which was equally likely to occur in the future; for each year 1 of the 4 matrices was chosen at random for each forest type and used to simulate population growth. To calculate the mean stochastic population growth rate ( $\lambda_s$ ) and associated 95% confidence intervals, we simulated population growth over 50,000 years. We used Tuljapurkar's approximation (Tuljapurkar 1982, 1990) as a second method for estimating  $\lambda_s$  of *C. guianensis* based on the assumption that the variation among the annual matrices was not large.

## Sustainable Harvest Simulations

We used computer simulations to explore possible sustainable harvesting regimes by varying the percentage of seeds collected annually and the number of *C. guianensis* individuals harvested for timber. We simulated seed harvest by modifying the transition matrix such that between time  $t$  and time  $t + 1$  fecundity values were proportionally reduced, with harvest levels varying from 50% to 95% (i.e. the fraction of seeds remaining after the simulated harvest varied from 50% to 5%).

For timber, we harvested only individuals  $\text{dbh} \geq 50$  cm, the legal minimum diameter limit for *C. guianensis* in the Brazilian Amazon (Resolução N. 406) and our largest size class, using a 25-year harvest cycle. Although this cutting cycle is likely unsustainable (Gardingen *et al.* 2006), particularly given that *C. guianensis* is a slow growing species (Vieira *et al.* 2005), we used the 25-year cutting cycle to reflect on-the-

ground harvest realities. Since timber is normally logged during the dry season from June to August (INMET 2009), we simulated post-reproductive timber harvests (after all seeds had fallen, and a percentage were harvested) (See Chapter 1). We also ran simulations with annual seed harvests combined with 25-year timber harvests. All simulations were run under the stochastic environmental conditions simulated using independent and identically distributed (iid) environmental states.

### **Quasi-Extinction Threshold Calculations**

We also determined the extinction time cumulative distribution function (CDF), the single most informative metric of a population's viability (Morris & Doak 2002). Since  $\lambda_s$  is a long-term metric of population growth or decline under stochastically changing environmental conditions, the CDF provides us with an estimate of the probability that a population will fall below a certain number of individuals in the short-term. For our simulations, we used a time-horizon of 500 years and a quasi-extinction threshold of 100 individuals, equivalent to approximately three individuals dbh  $\geq$  10 cm per hectare. These simulated densities would be a drastic reduction from our original densities of 25.7 and 14.6 individuals dbh  $\geq$  10 cm per hectare in occasionally inundated and *terra firme* forests, respectively (Klimas *et al.* 2007). The CDF was calculated based on 20 runs with 5,000 separate realizations of population growth (Morris & Doak 2002).

## **Results**

### **Vital Rates and Parameter Estimation**

Pooled average diameter growth was 2.89 mm ( $\pm$  2.76 mm SD) per year, suggesting that an individual would take an average of 35 years to grow to the next size class. Class transition periods varied broadly from 17 to 769 years, the range limits for individuals at the highest and lowest growth extremes, respectively. Size-class

dependent growth followed similar patterns; annual diameter increment was low with high variability (Figure 3-3). There was also variation in growth between years with a comparatively higher average growth in the first transition years (05-06), which was consistent throughout all dbh classes and in both forest types. Growth trends were not significant, however, due to high variability. The sample size used to calculate annual growth increment decreased slightly over the study period due to tree mortality and dendrometer band damage.

Matrix entries indicating stasis (survival and maintenance in the same size class) were consistently high (greater than 90%) for individuals  $\text{dbh} \geq 10$  cm, in both forest types. Overall seedling survival was consistently higher across all years in *terra firme* forest, while sapling survival was lower across all years (Table 3-2). Higher fecundity values in 07-08 and 08-09 were due to the variable annual seed production of *C. guianensis*; fecundity values were also significantly higher in occasionally inundated than in *terra firme* forest (See Chapter 1). Average fecundity per size class was highly variable between years. This was, in part, due to temporally variable seed production, but individuals suspending seed production also dropped the contribution of certain size classes in some years. This was most obvious in the largest size class; individuals in this size class ( $\text{dbh} \geq 50$  cm) tended to produce seeds in only two of the four measured years (08–09).

### **Matrix Modeling**

We constructed population projection matrices for each forest type in 05-06, 06-07, 07-08 and 08-09. Upper and lower confidence intervals (CIs) represent bootstrapped estimates of variability from random selection of individual growth rates. We found differences between transition matrices between years and forest types.

Population growth rate ( $\lambda$ ) was  $> 1$  in occasionally inundated forest for all four annual matrices; in *terra firme* forest,  $\lambda$  was  $> 1$  in only one of the four (Table 3-3). Confidence intervals around  $\lambda$  were tight (Table 3-3), therefore we used four separate annual transition matrices for each respective forest type in all our simulation models. The differences between the forest types were great enough and the uncertainty around the estimates small enough to warrant different transition matrices (Table 3-2).

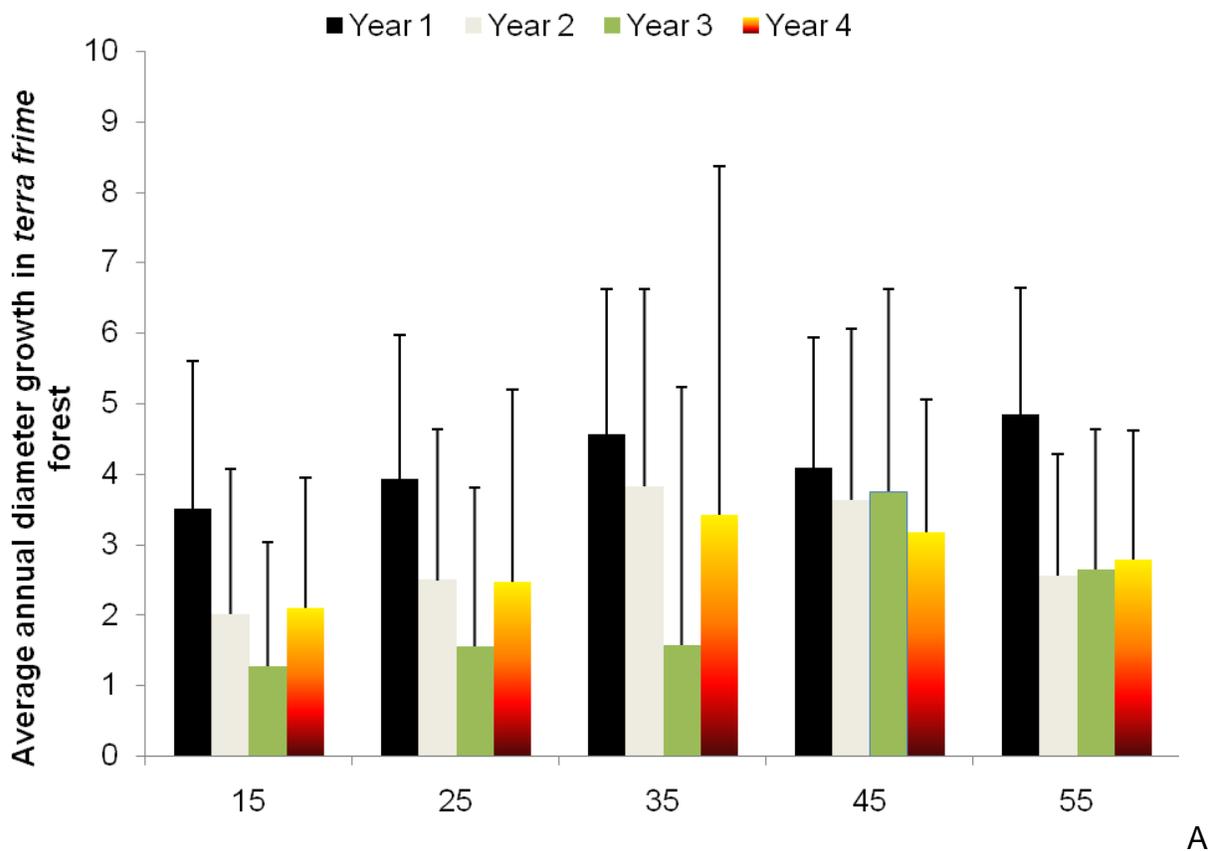


Figure 3-3 Annual size-class dependent diameter growth (mean + SD) of *C. guianensis* in *terra firme* forest (a) and occasionally inundated forest (b). Years included are 2005-2006, 2006-2007, 2007-2008 and 2008-2009.

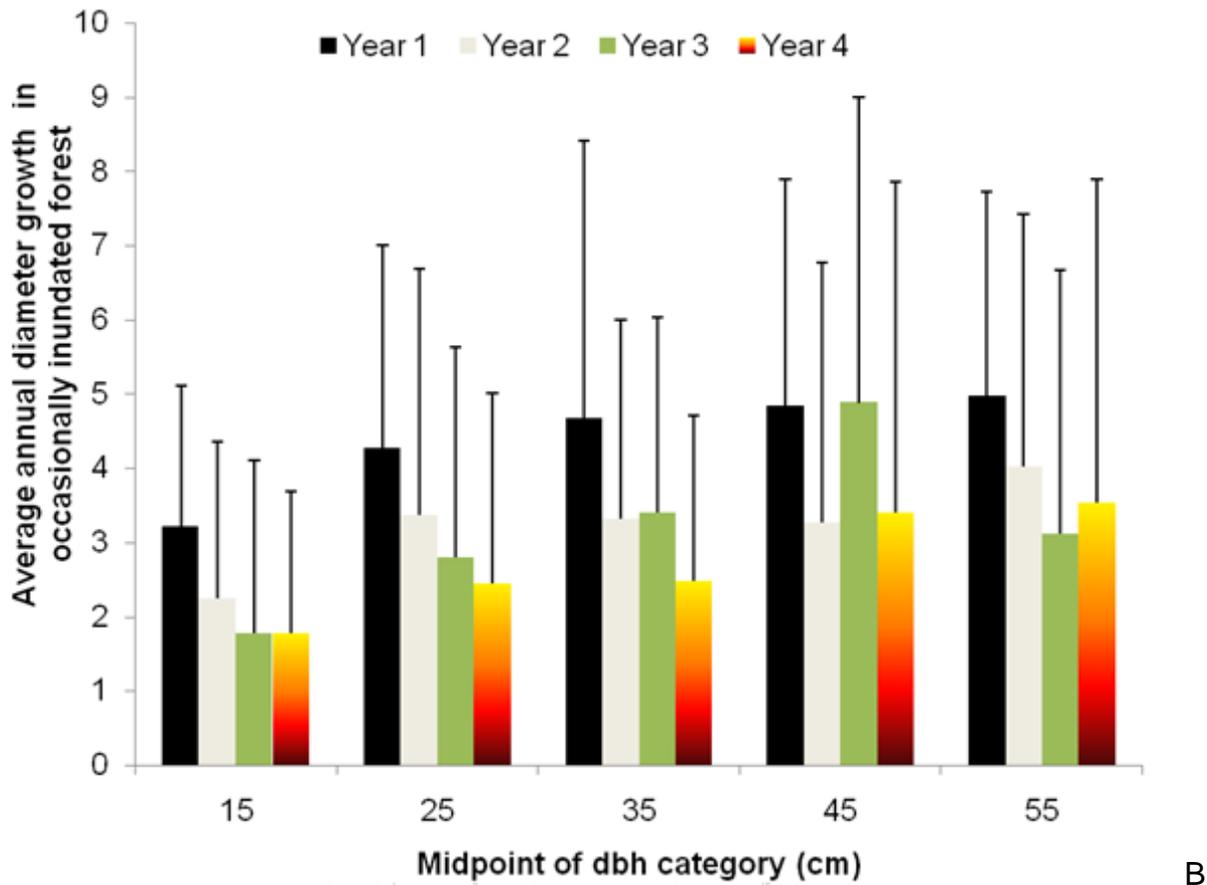


Figure 3-3. Continued

### Elasticity Calculations and Ranking

The overall importance of types of vital rates was fairly consistent in both forest types (Figure 3-4). Stasis, the relative probability of surviving but remaining in the same size class, had the highest proportional contribution to population growth rate. Fecundity values had some of the lowest proportional contributions to  $\lambda$ , though growth transitions were also low. Results from the pooled matrices in each forest type show general elasticity trends. Stasis had the greatest effect on population growth rate and stasis of different size classes consistently dominated the top four elasticity ranks, though the relative ranks of stasis of different size classes varied between years and forest types (Table 3-4). Stasis not only dominated elasticity rankings, but also stasis of the four top-

Table 3-2 Leftkovitch, or size-dependent, demographic matrices for *Carapa guianensis* in two forest types: occasionally inundated and *terra firme*. For each forest type, there are four annual transition matrices. Matrix entries are: seedlings, saplings, 10 cm ≤ dbh < 20 cm, 20 cm ≤ dbh < 30 cm, 30 cm ≤ dbh < 40cm, 40 cm ≤ dbh < 50 cm, dbh ≥ 50 cm.

Size class	Year 1: Occasionally inundated forest								
Seedling <sub>1</sub>	0.2166	0	0	0	0	49.6665	83.0504	0	
Seedling <sub>2</sub>	0	0	0	0	0	43.5165	72.7664	0	
Sapling	0.0113	0	0.9638	0	0	0	0	0	
10-20cm	0	0	0.0027	0.9643	0	0	0	0	
20-30cm	0	0	0	0.0326	0.9515	0	0	0	
30-40cm	0	0	0	0	0.0421	0.9404	0	0	
40-50cm	0	0	0	0	0	0.0464	0.9253	0	
> 50cm	0	0	0	0	0	0	0.0475	0.9438	
	Year 2: Occasionally inundated forest								
Seedling <sub>1</sub>	0.2359	0	0	0	1.5885	8.5099	158.2206	0	
Seedling <sub>2</sub>	0	0.1581	0	0	1.1767	6.3036	117.2005	0	
Sapling	0.0126	0.0085	0.9052	0	0	0	0	0	
10-20cm	0	0	0.001	0.965	0	0	0	0	
20-30cm	0	0	0	0.0229	0.9588	0	0	0	
30-40cm	0	0	0	0	0.0318	0.9588	0	0	
40-50cm	0	0	0	0	0	0.0318	0.9588	0	
> 50cm	0	0	0	0	0	0	0.0355	0.9956	
	Year 3: Occasionally inundated forest								
Seedling <sub>1</sub>	0.2843	0	0	1.4786	17.3035	12.5663	14.9277	4.8205	
Seedling <sub>2</sub>	0	0.0457	0	4.2509	49.7475	36.1281	42.9173	13.859	
Sapling	0.0116	0.0018	0.9633	0	0	0	0	0	
10-20cm	0	0	0.0021	0.9711	0	0	0	0	
20-30cm	0	0	0	0.018	0.9597	0	0	0	
30-40cm	0	0	0	0	0.0271	0.9495	0	0	
40-50cm	0	0	0	0	0	0.0344	0.9416	0	
> 50cm	0	0	0	0	0	0	0.0387	0.9761	

Table 3-2. Continued

	Year 4: Occasionally inundated forest							
Seedling <sub>1</sub>	0.1845	0	0	19.0448	55.2516	76.3062	100.9983	45.8275
Seedling <sub>2</sub>	0	0.2204	0	3.1441	9.2085	12.7176	16.833	7.6379
Sapling	0.0163	0.0195	0.962	0	0	0	0	0
10-20cm	0	0	0.0022	0.9672	0	0	0	0
20-30cm	0	0	0	0.018	0.9617	0	0	0
30-40cm	0	0	0	0	0.0218	0.9552	0	0
40-50cm	0	0	0	0	0	0.0263	0.9476	0
> 50cm	0	0	0	0	0	0	0.0317	0.9769
Size class	Year 1: Terra firme forest							
Seedling <sub>1</sub>	0.2444	0	0	0	4.7672	4.8234	40.682	0
Seedling <sub>2</sub>	0	0	0	0	2.7241	2.7562	23.2468	0
Sapling	0.0155	0	0.8072	0	0	0	0	0
10-20cm	0	0	0.0052	0.9216	0	0	0	0
20-30cm	0	0	0	0.0334	0.9083	0	0	0
30-40cm	0	0	0	0	0.0396	0.8989	0	0
40-50cm	0	0	0	0	0	0.0407	0.8893	0
> 50cm	0	0	0	0	0	0	0.0405	0.9186
	Year 2: Terra firme forest							
Seedling <sub>1</sub>	0.4848	0	0	0	4.8259	2.7075	18.7164	0
Seedling <sub>2</sub>	0	0.1535	0	0	0.6894	0.3867	2.6737	0
Sapling	0.0414	0.0131	0.8404	0	0	0	0	0
10-20cm	0	0	0.0033	0.9289	0	0	0	0
20-30cm	0	0	0	0.0185	0.9223	0	0	0
30-40cm	0	0	0	0	0.0261	0.9185	0	0
40-50cm	0	0	0	0	0	0.0309	0.9171	0
> 50cm	0	0	0	0	0	0	0.0332	0.9513
	Year 3: Terra firme forest							
Seedling <sub>1</sub>	0.4878	0	0	0	0.7326	2.4643	4.348	1.9549
Seedling <sub>2</sub>	0	0.0464	0	0	0.7326	2.4643	4.348	1.9545
Sapling	0.0121	0.0012	0.96	0	0	0	0	0
10-20cm	0	0	0.0029	0.9568	0	0	0	0
20-30cm	0	0	0	0	0.0158	0.9782	0	0
30-40cm	0	0	0	0.0115	0.9773	0	0	0
40-50cm	0	0	0	0	0	0.0203	0.9749	0
> 50cm	0	0	0	0	0	0	0.0247	0.9999

Table 3-2. Continued

	Year 4: <i>Terra firme</i> forest							
Seedling <sub>1</sub>	0.5312	0	0	0	6.477	9.4558	22.6187	24.9721
Seedling <sub>2</sub>	0	0.2295	0	0	0.7623	1.1128	2.662	2.939
Sapling	0.0242	0.0105	0.9234	0	0	0	0	0
10-20cm	0	0	0.0051	0.9337	0	0	0	0
20-30cm	0	0	0	0.0205	0.9326	0	0	0
30-40cm	0	0	0	0	0.0247	0.9325	0	0
40-50cm	0	0	0	0	0	0.0277	0.9333	0
> 50cm	0	0	0	0	0	0	0.0297	0.9656

Table 3-3 Population asymptotic growth rates ( $\lambda$ ) calculated from the Leftkovitch model for populations of *Carapa guianensis* in Acre, Brazil.

Forest type	Year	$\lambda$	Lower CI	Upper CI
Occasionally inundated	Pooled	1.0029		
	1	1.0038	1.0037	1.0157
	2	0.9956	0.9956	1.0070
	3	0.9961	0.9912	1.0029
	4	1.0167	1.0082	1.0399
<i>Terra firme</i>	Pooled	0.9706		
	1	0.9460	0.9380	0.9465
	2	0.9550	0.9546	0.9595
	3	1.0006	1.0005	1.0020
	4	0.9841	0.9750	0.9850

ranked size classes summed to proportional contributions of 0.8433-0.9222 and 0.7205-0.9692 in occasionally inundated and *terra firme* forests, respectively.

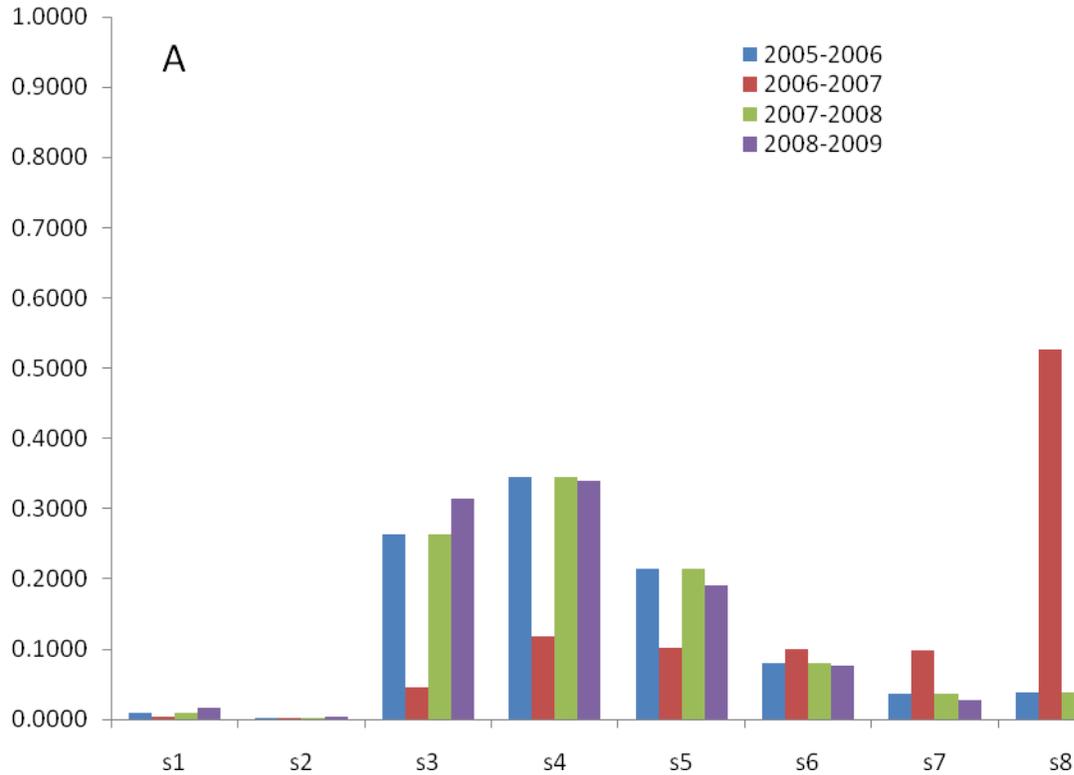


Figure 3-4 Elasticity values for *Carapa guianensis* vital rates in two forest types: occasionally inundated (A, C, E) and *terra firme* (B, D, F). For each forest type and vital rate, y-axis values vary and there are four elasticity bars, one for each transition matrix. The first two panels (A, B) display the elasticity of  $\lambda$  to changes in the vital rate survival (s1-s8). The second two panels (C, D) display the elasticity of  $\lambda$  to changes in the vital rate growth (g1-g7). The last two panels (E, F) display the elasticity of  $\lambda$  to changes in fertility, or the number of average seedlings produced by an individual in a given size class. The first five fertilities (f4-f8) represent seedlings that grow the first year; the second five fertilities (2f4-2f8) represent seedlings that shrink or experience negative growth the first year.

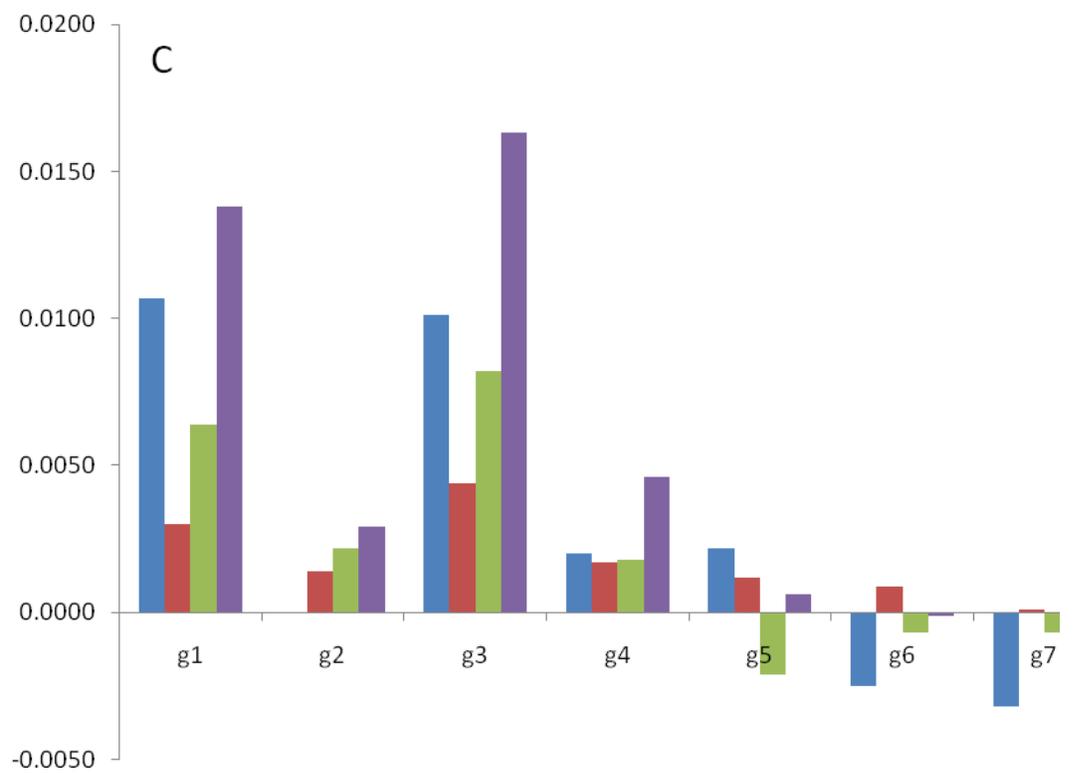
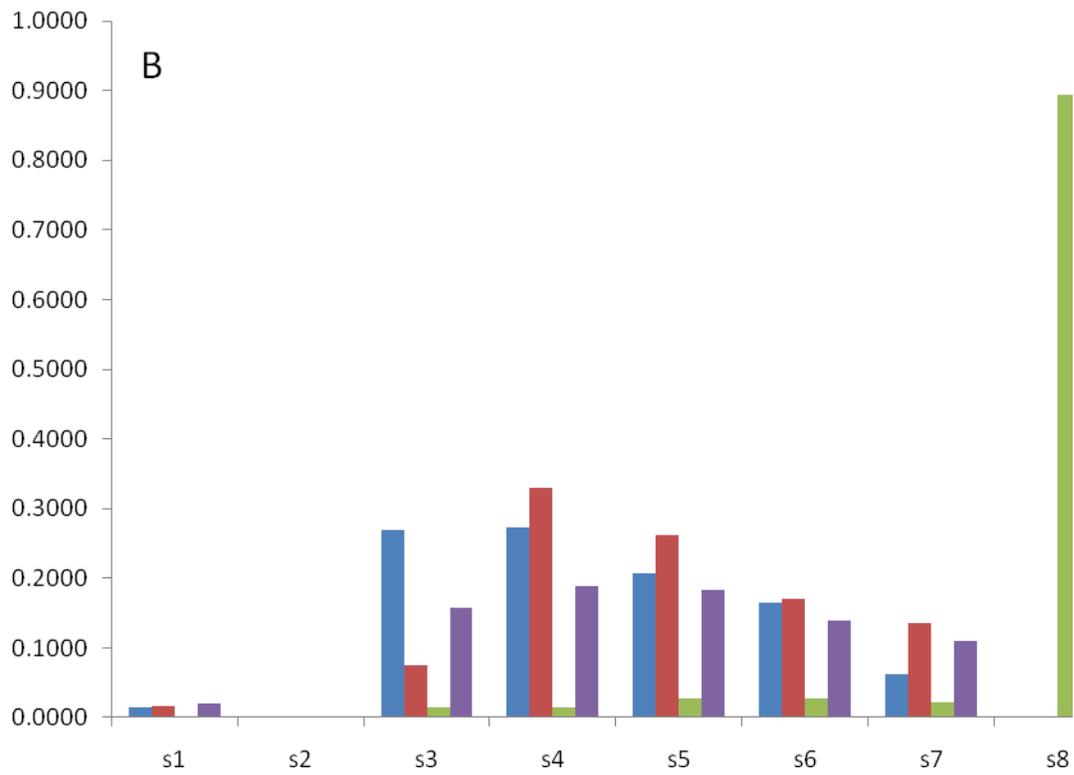


Figure 3-4. Continued

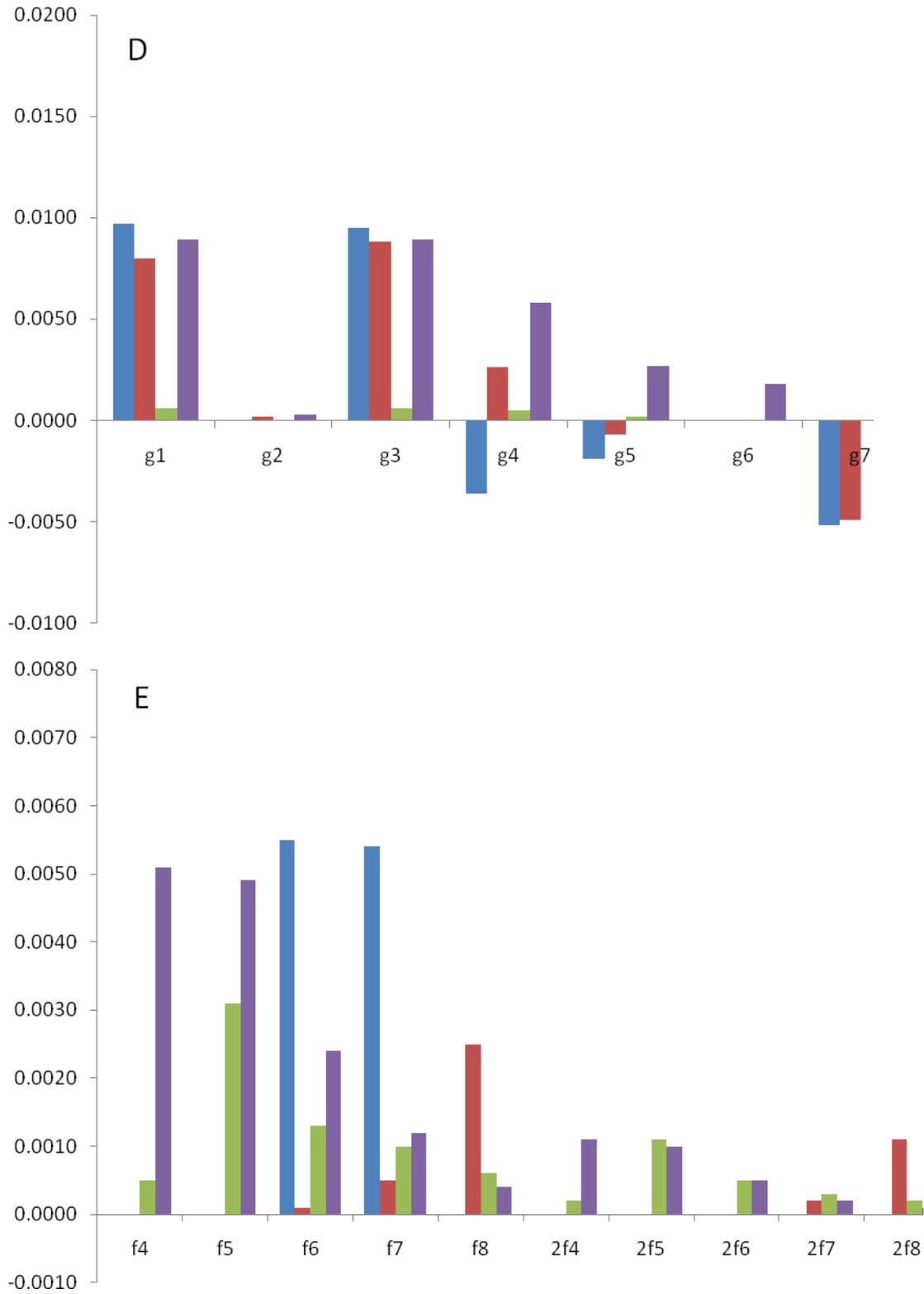


Figure 3-4. Continued

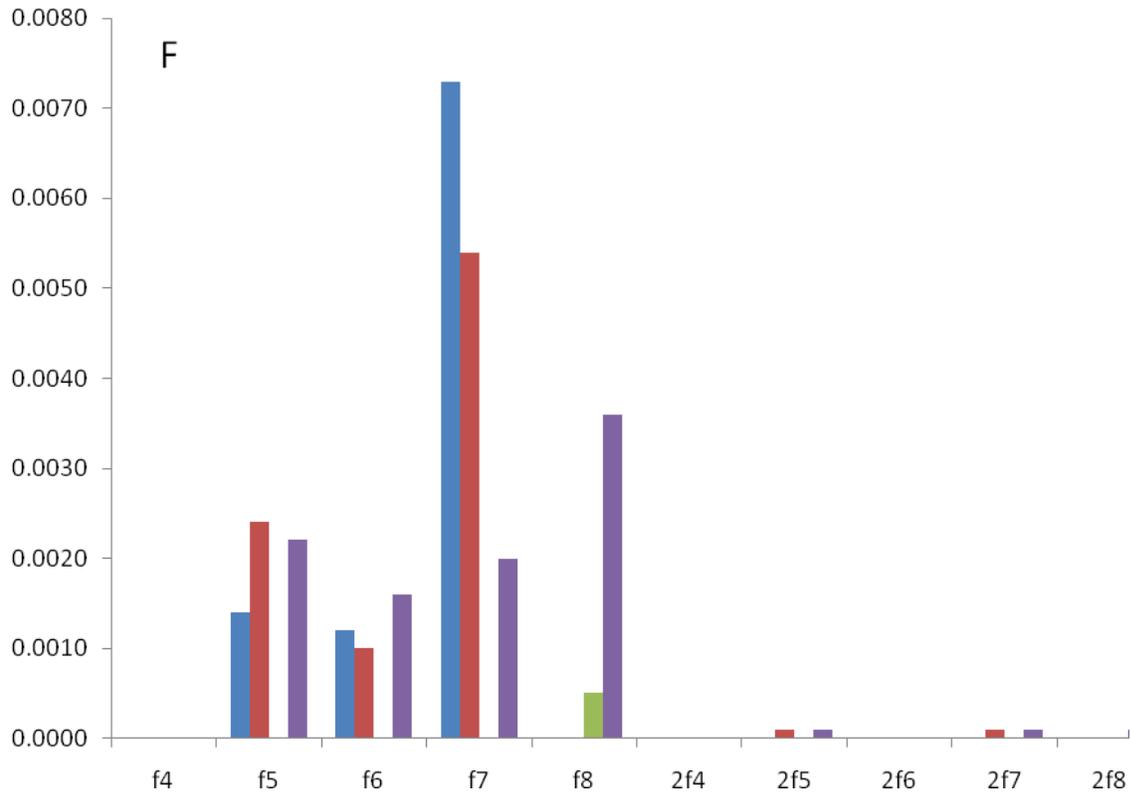


Figure 3-4. Continued

Table 3-4 Ranking of top four vital rate elasticity values in order of importance and their contribution to population growth rate ( $\lambda$ ). Midpoints of dbh categories are noted in parentheses.

	Occasionally inundated		<i>Terra firme</i>	
	Elasticity ranks	Elasticity values	Elasticity ranks	Elasticity values
Year 1	(15)	0.2721	(15)	0.3816
	(saplings)	0.2693	(25)	0.2459
	(25)	0.2063	(35)	0.1683
	(35)	0.1648	(45)	0.1137
Year 2	(55)	0.5261	(15)	0.3303
	(15)	0.1187	(25)	0.2611
	(25)	0.1018	(35)	0.1710
	(35)	0.0993	(45)	0.1351
Year 3	(15)	0.3443	(55)	0.8931
	(saplings)	0.2643	(35)	0.0269
	(25)	0.2139	(25)	0.0265
Year 4	(35)	0.0807	(45)	0.0227
	(15)	0.3401	(55)	0.1917
	(saplings)	0.3137	(15)	0.1888
	(25)	0.1917	(25)	0.1829
	(35)	0.0767	(saplings)	0.1571

Table 3-5 Simulated stochastic population growth rate ( $\lambda_s$ ) with simulated 95% confidence intervals and stochastic growth as calculated by Tuljapurkar's approximation ( $\lambda_T$ ) for populations of *Carapa guianensis* in Acre, Brazil. Simulations were conducted with no harvesting, varying levels of seed harvest, timber harvest, and combined seed and timber harvests. All transition matrices had an equal probability of selection.

Forest type	Harvest	$\lambda_s$	95% Conf. Int.		$\lambda_T$
<b>Occasionally inundated</b>	No harvest	1.0028	1.0004	1.0053	1.0028
	10% seeds	1.0017	0.9993	1.0040	1.0017
	20% seeds	1.0005	0.9982	1.0028	1.0004
	30% seeds	0.9991	0.9969	1.0014	0.9991
	50% timber 25-yr cutting cycle	1.0026	1.0003	1.0048	
	100% timber 25-yr cutting cycle	1.0022	1.0001	1.0044	
	10% seeds & 50% timber	1.0014	0.9992	1.0036	
	10% seeds and 100% timber	1.0012	0.9991	1.0033	
<b>Terra firme</b>	No harvest	0.9704	0.9678	0.9731	0.9704
	10% seeds	0.9697	0.9670	0.9724	0.9696
	20% seeds	0.9688	0.9661	0.9716	0.9687
	30% seeds	0.9679	0.9651	0.9707	0.9678
	50% timber 25-yr cutting cycle	0.9681	0.9659	0.9702	
	100% timber 25-yr cutting cycle	0.9672	0.9651	0.9693	
	10% seeds & 50% timber	0.9671	0.9650	0.9693	
	10% seeds and 100% timber	0.9663	0.9642	0.9684	

### Modeling Environmental Stochasticity

The simulated stochastic population growth rate ( $\lambda_s$ ) in occasionally inundated forest indicated an increasing population ( $\lambda_s = 1.0028$ ), and a declining population in *terra firme* forest ( $\lambda_s = 0.9704$ ) (Table 3-5). The 95% confidence intervals for stochastic population growth indicated an increasing population in occasionally inundated forest in the absence of harvest, but when even low levels of seed harvest (10%) were simulated, the lower CI dropped below one. In *terra firme* forest, in contrast, both  $\lambda_s$  and

the upper bound of the simulated confidence interval remained below one even in simulations without harvest (Table 3-5). Tuljapurkar's approximations corroborated simulated stochastic population growth rates (Table 3-5).

### **Sustainable Harvest Simulations**

No levels of timber or seed harvest were considered viable in *terra firme* forest with a  $\lambda_s < 1$ , though a major caveat of our study is that we have only 4 transition matrices for a species that can live hundreds of years (Vieira *et al.* 2005). If the observed environmental conditions were characteristic of expected future conditions, we would expect a decline in the *terra firme* population. Indeed quasi-extinction simulations indicated that there was a 100% probability that the population would have less than 3 individuals dbh  $\geq 10$  cm per hectare after 93 years in the absence of either seed or timber harvest. Multiple harvesting options, however, were available to sustainably manage *C. guianensis* in occasionally inundated forest.

Simulations predicted population growth in occasionally inundated forest with harvest regimes of 10% and 20% of total seed production, but the lower 95% CI was below one for both of these harvest scenarios (Table 3-5). Timber harvests of both 50% and 100% of individuals with dbh  $\geq 50$  cm were also sustainable, and the probability that the population would have fewer than 3 individuals dbh  $\geq 10$  cm remained zero for the 500 years modeled. While we found this surprising since stasis had some of the highest elasticity values; however, modeled harvest levels were extremely low, involving fewer than 2 trees per hectare every 25-years in occasionally inundated forests. Since smaller individuals (< 50 cm dbh) comprised a larger part of the per-hectare densities, simulations did not reduce the population to fewer than 3 individuals dbh  $\geq 10$  cm per hectare until almost 1000 years in the future. Simulations that limited recruitment, while

simultaneously harvesting larger individuals, affected both recruitment of individuals into the smaller dbh classes and seed production in the larger dbh classes, leading to cumulative distribution functions (CDFs) reaching 1.0 after 150 years.

Low seed harvest levels (10%) were also potentially compatible with both 50% and 100% harvest in the largest size class (dbh  $\geq$  50 cm) every 50 years, though the CDF indicated a 100% probability that these management scenarios would lead to fewer than 3 individuals dbh  $\geq$  10 cm per hectare during the 500 year time interval modeled. This model also does not include increased mortality accompanying harvest, and may overestimate the lower confidence bound (Table 3-5).

## **Discussion**

### **Sustainable Stochastic Harvest Estimates in Contrasting Forest Types**

Our results indicate that some populations of *C. guianensis* may be suitable for extraction of seeds, timber, or a combination of both. High simulated harvests were not sustainable across all habitats, however. In our *terra firme* sites, demographic parameters suggested that no tested levels of seed and timber extraction were sustainable; quasi-extinction simulations indicated population decline regardless of harvest levels. While we hypothesized that safe-site limitation would make seed harvests more viable in this forest type, the low survival of individuals dbh  $\geq$  10 cm made both seed and timber harvests non viable. While *C. guianensis* does occur in *terra firme* forests, it is considered more competitive in forests with some flooding regime (Pennington 1981, McHargue & Hartshorn 1983a, Fournier 2003). Furthermore, our study region is close to the southwestern limit of the *C. guianensis* range, perhaps further compromising population resilience (Kawecki 2008).

In contrast, our modeling results revealed that a diversity of harvest regimes would be ecologically sustainable in occasionally inundated forests. In exploring sustainable seed harvests, removing 10% of the total seed production proved feasible and consistent with a stable or increasing population (Table 3-5), though the quasi-extinction threshold of less than 3 individuals dbh  $\geq$  10 cm per hectare was reached within the 500-year time interval. High levels of seed harvest normally do not prevent species persistence (Bruna 2003), which led us to hypothesize that even higher levels of harvest would be viable. Indeed, 10% of seed harvest is relatively low in comparison with studies reporting sustainable seed harvest levels in excess of 50% of population-level production for *Bertholletia excelsa* (Zuidema & Boot 2000) and *Sclerocarya birrea* (Emanuel *et al.* 2005). Nonetheless, current market demand for *C. guianensis* seed oil is minimal in our study region, and would not likely support higher ( $>$  10%) seed harvest levels. In the mouth of the Amazon basin, however, where *C. guianensis* is a major component of the dominant flooded forests and the seed oil market is more-developed, demand is indeed high and Londres (2009) reported that still local seed production far exceeded the estimated 0.1% harvest levels.

We also found the potential for compatibility between seed and timber harvest in occasionally inundated forests. Our results suggested that 10% annual seed harvests were compatible with 100% timber harvests (of trees  $\geq$  50 cm) twice a century, the equivalent of approximately two trees per hectare. Our simulations were based on growth data from best-fit logistic regressions, but we expect that incorporating growth variability into the model would decrease  $\lambda$  (Gaillard *et al.* 1998).

Matrix models with limited classes can inflate  $\lambda$  values if a small proportion of individuals pass rapidly through the life cycle and reach reproductive size at a very young age, which has led some authors to recommend integral projection models (IPMs) to correct these unrealistically fast transitions (Zuidema *et al.* 2010, though see Ramula & Lehtilä 2005). Nonetheless, we used regressions that related growth and size over the entire size range to calculate our average growth for each dbh class, a method that resembles the IPM approach (Zuidema *et al.* 2010). Finally, category width does not always inflate  $\lambda$ ; individuals that pass rapidly through the matrix but produce few recruits likely have less of an inflationary impact (Zuidema *et al.* 2010), though we are unsure if this is the case for *C. guianensis*.

### **Elasticity Calculations and Ranking**

Elasticity analyses indicate that stasis of varying size classes, measured by the vital rate survival, contributes the most to population growth rate. This is consistent with other demographic studies that found survivorship and growth contribute the most to  $\lambda$  (Pinerio *et al.* 1984, Horvitz & Schemske 1995, Olmsted & Alvarez-Buylla 1995, Morris & Doak 2005), and likely indicate that selection for high mean survival is higher than selection acting on any other vital rate (Morris & Doak 2005, Forbes *et al.* 2010). Even though  $\lambda$  was most sensitive to sapling and adult (individuals dbh  $\geq 10$  cm) survivorship, high observed survival (over 90%) for individuals dbh  $\geq 10$  cm (Table 3-2) could not be easily increased. Indeed, the lower stasis values measured for individuals in *terra firme* forests were partly responsible for the decreasing growth rate ( $\lambda < 1$ ) seen in the transition matrices for this forest type. Some of the increased mortality that led to reduced stasis values may have resulted from 2005 drought-related fire (Marengo *et al.* 2008) in one of the *terra firme* plots. Still, we also observed higher mortality of pole-

sized trees in *terra firme* areas unaffected by fire (unpublished data), perhaps due to drier soil conditions associated with forest type. To explore drought effects, we changed drought year frequency from the observed four to every 10 years, whereby  $\lambda_s$  increased to 0.9759 (CIs 0.9731, 0.9787). If the observed drought represents a rare “catastrophe” for this population, our iid model may severely underestimate  $\lambda_s$  due to over inclusion of deleterious population-level effects, especially for the drier *terra firme* forests.

Our ranking of elasticities indicated that the importance of survival (stasis) on  $\lambda_s$  was consistent in both forest types and throughout our 5-year study period (Figure 3-4). *C. guianensis* is a long-lived species (Vieira *et al.* 2005), however, and continued demographic monitoring may indicate higher importance of other vital rates during some years, though see (Forbes *et al.* 2010). Indeed, Doak *et al.* (2005) found that the mean standard error of model predictions declined with higher sampling intensity and more importantly, duration. The high elasticity of survival in the largest dbh class in some years (Figure 3-4) also serves as a cautionary note for timber harvest. While we observed long-term growth in the occasionally inundated forest ( $\lambda_s > 1$ ) even with low levels of timber extraction, the periodic high elasticity of this dbh class merits prudence.

Still, fecundity and growth should continue to be considered in *C. guianensis* management strategies. Pfister (1998) found that vital rates with low elasticities tend to have high variance. Gaillard *et al.* (1998) notes that vital rates with high variation can have larger effects on population growth rate than rates with high elasticity. Favorable environmental conditions, however, may enhance multiple vital rates (Morris & Doak 2002). Years of high fruit production coincided with years of high growth for the related *Swietenia macrophylla* (Snook *et al.* 2005), though other studies have indicated a trade-

off between seed production and growth in any given year for other species (Norton & Kelly 1988, Koenig & Knops 2000).

### **Limitations of the Harvesting Models**

While five years of survival, growth and reproductive measurements would be adequate for some species, this study only begins to delve into the variation in environmental conditions likely experienced over the lengthy lifetime of a *C. guianensis* individual. We also found high variation in some of the vital rates: both seed production and growth were characterized by high variability around mean values. Large sampling variability in the estimated transition rates increases the uncertainty in the estimated matrix and quantities derived from it, such as the population multiplication rate and sensitivities of matrix elements (Gross *et al.* 2006), though  $\lambda$  was relatively insensitive to variations in these vital rates, in comparison with variations in survival.

Our model did not include any spatial components, though previous research has shown aggregation of *C. guianensis*, especially juveniles (Klimas *et al.* 2007). We also attributed the mean growth within a dbh class to all individuals instead of modeling individual growth. There is some evidence that individual trees with a history of rapid growth contribute disproportionately to population growth (Zuidema *et al.* 2009), but this phenomenon does not easily translate to *C. guianensis* management guidelines.

### **Implications for Multi-Use Management**

Results from this study indicate harvests of timber and NTFPs may be complementary in some situations, even for the same species. Significant income pulses from periodic timber harvests of *C. guianensis* could complement a more steady revenue stream from annual seed harvests – all of which could be integrated with harvest of other timber and NTFPs. Increasing household forest-based revenues may

also increase the likelihood that forests will not be converted to other land uses (Barros 2002, Morton *et al.* 2006). Furthermore, multiple-use forest management can lead to increased employment opportunities and diversification of household incomes (Mollinedo 2000, Campos *et al.* 2001, Mollinedo *et al.* 2001) without thwarting the central food security role of NTFPs as key subsistence products and buffers in times of food shortages (Lipper 2000, Pattanayak and Sills 2001).

Management guidelines for integrating timber and NTFP harvests will necessarily be different, and perhaps more complex, than those for any one product type. Marking future crop trees prior to logging should integrate not only timber species, but also NTFPs (Rockwell *et al.* 2007; Guariguata *et al.* 2008). Minimizing residual damage may be facilitated in areas where communities or landowners have considerable knowledge of individual trees. If some larger dbh individuals of *C. guianensis* are found to contribute disproportionately to seed production, as is the case for some species (Snook *et al.* 2005, Kainer *et al.* 2007), they could remain unlogged until their seed production diminished beyond some theoretical threshold. Previous research indicated a quadratic relationship between seed production and diameter for *C. guianensis* in both forest types: smallest and largest size classes rarely contributed to seed production (See Chapter 1). This quadratic relationship has been documented for other species where logging had not previously occurred (Wadt *et al.* 2005, but see Snook *et al.* (2005) and Nabe-Nielsen *et al.* (2009) for logged examples. This suggests that temporal separation of seed and timber harvests merits consideration. If this quadratic pattern holds across other multi-use species (timber and fruits/seeds), harvest of the largest individuals may have a relatively small impact on future population dynamics,

though our elasticity results indicate the importance of maintaining high survival for non-logged individuals. However, because the largest and oldest individuals of a population tend to positively correlate with size and number of hollow stems (Lindenmayer *et al.* 1993, 2000, Fox *et al.* 2008), targeted logging of these top dbh individuals may not be economically viable, although incidence of heart rot varies by species (Fox *et al.* 2008).

In contrast to this temporal separation of timber-seed harvests, spatially setting aside areas with high densities of good seed producing trees would eliminate potential logging damage. In areas where desirable timber trees are mixed with good seed producers and delaying timber extraction is not economically viable, reduced-impact logging techniques such as vine-cutting and directional felling can be used to mitigate damage (Pinard *et al.* 1995, Dykstra & Heinrich 1996). Conversely, if careful analysis indicates that an individual is more valuable for timber than for its seed production, logging may be an appropriate decision.

Tropical forest conservation increasingly relies on multiple products and services valued in rapidly-changing markets and landscapes. *C. guianensis* is one potential species for such multi-use management. Our results indicate potential compatibility of timber and seed harvests in occasionally inundated forests of Acre, Brazil. Further research to determine whether these results hold for other economically important tropical species could increase the diversity of management options for Amazonia.

## CHAPTER 4 ECONOMIC REVENUE FROM SUSTAINABLE SEED AND TIMBER HARVESTS OF *CARAPA GUIANENSIS*

### **Introduction**

Integrating different revenue sources within management regimes may be the future of tropical forest management. While logging is currently one of the main forest uses in the Amazon due to its importance in the regional economy and the high present value associated with single-entry timber extraction (Verissimo *et al.* 1992, Lentini *et al.* 2003, AIMEX 2005), it is also one of the most intensive and extensive sources of forest management. While the principle of present value maximization is the driving force that determines land use in a market economy (Klemperer 1996), indicating that timber extraction will likely retain its importance in tropical forest management (Pearce *et al.* 2003), logging has significant drawbacks: it removes the entire individual, requiring decades for stem replacement given growth rates, incurs significant extraction costs (Holmes *et al.* 2002), can increase forest flammability (Nepstad *et al.* 1999), and encourages conversion of forest to other land use (Asner *et al.* 2005).

Management of non-timber forest products has also been touted as an economically-viable method of forest management. NTFP harvesting can contribute to the economic livelihoods and welfare of forest residents, can result in less ecological destruction than timber harvesting and other forest uses (Ticktin 2004), and may add to the perceived value of standing tropical forest (Chopra 1993, Gunatilake *et al.* 1993, Marshall *et al.* 2003). However, NTFP overharvesting does occur (Gaoue & Ticktin 2009), causing alteration or degradation to the resource and affecting species persistence (Peres *et al.* 2003, Ticktin 2004). NTFP harvests also may not be sufficient to lift communities out of poverty (Morsello 2006).

If linked, however, multiple-use forest management could provide the best of both worlds, pooling the income periodically available from timber harvest within a backdrop of steady income from NTFP harvest. Proponents of diversified forest management highlight the fact that integrating multiple forest values provides a social and financial edge in comparison with timber-dominant management models (Panayotou & Ashton 1993, Salick *et al.* 1995, Scherr *et al.* 2003). Indeed, multiple-use management of tropical forests (MTF) is not a new concept (Panayotou & Ashton 1992, Salick *et al.* 1995), but rather is the standard in most smallholder and community managed forests (Whitmore 1990). The combined extraction of xate (*Chamaedorea* spp.) and timber in community forests in Guatemala is one successful example of MTF (Guariguata *et al.* 2008); management for chicle, honey, game and timber in Mexico is another community-managed MTF regime acknowledged for its success (Snook 2000). There are, however, still multiple ecological, social, and economic barriers to widespread successful implementation of MTF (García-Fernández *et al.* 2008, Ros-Tonen *et al.* 2008).

While there is a growing body of literature on the economics of timber harvest (Boltz *et al.* 2001, Merry *et al.* 2009) as well as on economic returns from individual NTFPs (Varghese & Ticktin 2008, Avocèvou-Ayisso *et al.* 2009), there is still limited research on the compatibility of timber with non-timber forest management (though see Snook 2000, Guariguata *et al.* 2008, Menton *et al.* 2009, Guariguata *et al.* 2010). Most studies have highlighted the ecological benefits of not just focusing on timber without incorporating the economic opportunities and trade-offs associated with multiple use management (though see Boscolo & Vincent 2003, Menton *et al.* 2009). Quantifying

revenue from harvest is particularly important in cases where an individual species provides multiple economic benefits, generating a potential conflict of interest in deciding whether to prioritize one use over another. Such “conflict of interest” is common in the Amazon: Herrero-Jáuregui *et al.* (2009) found that 46% of the 200 timber species in the state of Pará, Brazil, also provided non-timber forest products, and reportedly at least one third of 305 Amazonian timber species also provide NTFPs (Martini *et al.* 1994).

Multiple-use species should be managed to maximize their economic or social value under constraints of ecological sustainability. The determination of how to do this is often left to the forest resident or manager who frequently uses imperfect and general information on the benefits of different forest management strategies to make a decision that meets particular objectives (Macpherson 2007). Even if detailed knowledge of sustainability does not always translate into sustainable management practices (Gaoue & Ticktin 2009) and expected economic gains are not always realized (Putz *et al.* 2000), improving the information available to managers should enhance both ecological and economic decision-making.

This study augments the economic information available to forest managers, in particular the potential revenue associated with different harvest strategies of the multipurpose tropical tree *Carapa guianensis*. *C. guianensis* is valued for both the high quality oil extracted from its seeds (Shanley & Medina 2005) and its mahogany-like timber (McHargue & Hartsorn 1983, Mabberley 1987). Pure *C. guianensis* seed oil is used for medicinal applications (Rodrigues 1989), with value-added products including soaps, shampoos, candles and repellent torches (Shanley & Medina 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).

*C. guianensis*, timber and seed harvests can be mutually compatible: a quadratic relationship between size and seed production found in previous research (See Chapter 2) coupled with relatively low numbers of individuals in the larger harvest classes indicated that in some cases, larger individuals could be harvested for timber in conjunction with low levels of seed harvest while maintaining positive population growth (See Chapter 3). Other species also demonstrate this quadratic relationship between size and seed production (Soehartono & Newton 2001, Kainer *et al.* 2007); in these cases, the largest individuals could potentially be harvested for timber, leaving mid-sized individuals for seed production. A continuum of options may be more appropriate, however, especially for communities that have knowledge of individual trees. For example, trees that have consistent low seed production or are past their reproductive “prime” may be suitable candidates for selective logging. Spatial segregation of timber and NTFP management units is another approach for concurrent timber and NTFP management (Guariguata *et al.* 2010).

A comparison of revenue generated by individual tree harvest and seed collection would allow forest managers to better choose a management strategy that meets their economic objectives. We provide one such comparison using *C. guianensis*, modeling the equal annual equivalent (EAE), a function of net present value (NPV), of revenues associated with modeled simulations of sustainable seed and timber harvests. Our specific objectives were 1) to simulate and compare the revenue from ecologically

viable seed and timber harvests of *C. guianensis* in stochastically varying environments; and 2) to simulate the EAE of revenues from seed and timber harvest under different market prices for both seed oil and timber. Sustainable harvest simulations are based on a stochastic ecological matrix model parameterized with data from a demographic study in the southwestern Amazonian state of Acre, Brazil (See Chapter 3). Here, we only provide a brief, summative explanation of this detailed ecological model necessary to understand the integration of ecological parameters within the context of our economics model.

## Methods

### Study Site and Field Measurements

We carried out field measurements within the 1200 ha experimental forest of the Brazilian Agricultural Research Corporation (Embrapa) in the eastern portion of the state of Acre (latitude 10° 01' 28" S and longitude 67° 42' 19" W). The region has rolling topography including occasionally inundated areas and upland habitat (*terra firme*). Two 400 m x 400 m (16-ha) plots were established where the majority of the environment was classified as *terra firme* forest and two in occasionally inundated forest (Klimas *et al.* 2007). We inventoried and monitored survival of all individuals  $\geq 10$  cm diameter at breast height (dbh) from 2004 to 2009. We also recorded canopy position (dominant, co-dominant, intermediate or suppressed), spatial coordinates, and initial diameter at breast height (dbh) for each tree (measured in 2004). We installed dendrometer bands on a random subset of over 500 trees stratified by dbh and forest type to measure annual growth. Using this subset, we also measured cross-sectional crown area, tree height, tree commercial height and tree form. We measured crown cross-sectional area along two axes: maximum crown diameter and a second diameter formed at a right

angle to the former, and subsequently applied an ellipsoid formula to convert axis diameters to crown area (Kainer *et al.* 2007). Tree heights were measured with a Suunto optical height meter PM-5/1520 (clinometer), using a surveyor's tape to determine distance from clinometer to tree. We recorded both total and commercial tree height; commercial height was measured to the highest defect-free point on the tree trunk and excluded if tree form invalidated commercial harvest. We made notations of any abnormalities that affected trunk form, such as evidence of a previous burn, forked trunks (a potential indication of prior insect attack), and damaged or absent crowns.

Rainfall and temperature data were collected daily at noon at the Federal University of Acre (UFAC), approximately 8 km from our study site. Average annual temperature was 24.5°C with a dry season from June to August. Monthly mean temperature was averaged from the daily compensated mean temperatures for a given month. Maximum and minimum temperatures also represented monthly averages of these daily temperature values (INMET 2009).

### **Seed Oil Extraction and Price Estimates**

We conducted interviews with key informants for market data on the price received for *C. guianensis* seed oil in 3 locations in the state of Acre from December to February of 2009. We utilized snowball sampling (Vogt 2005): initial interviews led to referrals that generated more interviews with individuals or companies engaged in either purchase of seed oil or in oil extraction.

We visited different areas throughout the state where individuals or co-operatives extracted seed oil to estimate yield in kilograms of seeds needed to make 1L of *C. guianensis* seed oil, the dominant marketable unit of oil. We also noted any procedural

differences in oil extraction between sites. We used a prior study to calculate labor costs associated with oil extraction (Londres 2004).

### **Timber Value**

We used two sets of allometric volume equations to determine stem volume of harvested *C. guianensis* individuals, which we then multiplied by price/m<sup>3</sup> and the number of trees available for harvest. The first equation of tree volume was developed by Segura & Kanninen (2005) based on measurements of 19 trees destructively sampled trees in Northern Costa Rica, including 3 *C. guianensis* individuals. Their best-fit model for stem volume was:

$$V_{\text{stem}} = \exp(c + a \ln \text{DBH})$$

where  $c = -8.70 \pm 1.77$  and  $a = 2.41 \pm 0.40$  (Segura & Kanninen 2005). These models, however, were constructed using individuals with diameters between 60 and 105 cm, and tended to overestimate tree biomass and volume outside the specified diameter range.

Thus, we also used a second set of volume equations specific to *C. guianensis* from an Amazonian data set of measured dbh and commercial tree heights from Pará, Brazil (Silva *et al.* 1984). Equations that include both commercial height and dbh are normally better at predicting the actual volume, though commercial tree height can be difficult to measure with accuracy (Segura & Kanninen 2005). Silva *et al.* (1984) used 183 *C. guianensis* sample trees to find constants most appropriate for volume equations, and parameterization did not include destructive harvests (Silva *et al.* 1984). The best-fit model for *Carapa* tree volume (without bark) was:

$$V = \exp(-9.20315 + 2.01914 \ln d + 0.76028 \ln h)$$

where  $V$  is the stem volume without bark,  $d$  is the dbh, and  $h$  is the commercial height excluding stump; these values did not include losses during log processing (Silva *et al.* 1984). We used a dbh of 50 cm ( $d$ ) and the average height of sampled individuals with dbh  $\geq$  50 cm ( $h$ ) to solve for timber harvest volume; a dbh of 40 cm was used to calculate illegal harvests of individuals ranging in diameter from 40 to 50 cm. While using this lower dbh limit may underestimate initial harvest of typically larger diameter trees, it should be more representative of future harvests. Slow growth rates mean that most individuals will be harvested soon after they reach harvestable diameter. Indeed, *C. guianensis* individuals spend an average of 20 years to grow from 40 to 50 cm dbh and from 50 to 60 cm, but the standard deviation of growth was high (55 years). We think that these slow growth rates, coupled with high variability, warrant conservative estimates of return from timber harvests. Finally, to determine the current timber market price, we interviewed researchers at Embrapa specializing in timber extraction.

### **Sustainable Harvest Simulations Under Simulated Environmental Stochasticity**

This study builds on a previously developed stochastic ecological simulation model developed in MATLAB (2002). We simulated stochastic environmental conditions using the independent and identically distributed environmental states represented by four transition matrices (See Chapter 3 for additional information on model construction). We assumed that the four years of our study represented the range of typical environmental conditions, each of which was equally likely to occur in the future. Each modeled year, 1 of 4 transition matrices was chosen at random and used to simulate population growth. To explore possible sustainable harvesting regimes in the simulation model, we reduced

average fecundity (to simulate seed harvest) and the number of individuals in the largest size classes (to simulate timber harvest) (See Chapter 3).

These stochastic simulation model results indicated compatibility of seed and timber harvests in occasionally inundated forest under certain harvest levels. Harvests of 10% of annual seed production combined with 100% timber harvests every 25 years maintained the simulated stochastic population growth rate above one ( $\lambda_s = 1.0012$ ) indicating an increasing population, though the lower 95% confidence interval of  $\lambda_s$  fell below one (0.9991, 1.0033). These same harvest levels simulated a decreasing population in *terra firme* forests ( $\lambda_s = 0.9663$ ), but since population dynamics are not normally considered in harvest decisions, we also calculated revenue from these harvest scenarios. Since the stochastic model used size-class specific estimates of seedling fecundity (average number of seedlings produced by an individual in a given dbh class), we associated the model with estimates of average seed production per individual in a given dbh class based on quantification of five years of seed production in the study area (See Chapter 2).

Timber harvest scenarios included both legal and illegal timber harvests. Only individuals  $\geq 50$  cm dbh are legally harvestable based on current Amazonian forest law (Resolução N. 406), and legal cutting cycles vary from 25- to 35-years in Amazonia (Instrução Normativa 05/2006, Resolução N. 406). Some authors state that this shorter cycle is likely not sustainable (Gardingen *et al.* 2006) and *C. guianensis* is a slow growing species (Vieira *et al.* 2005, Chapter 3). Indeed our model results indicated that timber harvests of the largest individuals ( $\geq 50$  cm dbh) were not sustainable in *terra firme* forests, though harvests were arguably sustainable in occasionally inundated

forest (but the lower 95% confidence interval indicated potential for non-sustainable harvest).

### **Net Present Value of Seed and Timber Harvests**

To calculate seed harvest revenues, the results indicating ecologically sustainable seed harvest levels from MATLAB matrix model results were converted to estimates of oil yield and multiplied by different observed market prices to generate estimates of expected revenue from yearly seed harvests. For timber harvests, the number of individuals harvested at 50-year intervals was multiplied by the volume estimates from the two allometric equations and then multiplied by the market price of a cubic meter of *C. guianensis* timber. The present value (PV) of all future harvests was calculated using the equation:

$$PV = V_h * e^{(-r*t)}$$

where  $V_h$  is the yearly harvest value,  $r$  is the discount rate and  $t$  is the year. Revenues from future seed harvests and logging entries were discounted at 4%, 8% and 20% to examine the impact of discounting on the profitability of long-term management.

We calculated the net present value of annual seed harvests and both 25 and 35-year timber harvests based on simulations; these NPVs were then converted to a per-hectare EAE (see below). The NPV of each year's seed harvest was stored as a vector and summed over the 51-71 years of the model (the temporal period was based on 3-timber cutting cycles) to determine the NPV of seed harvest over that same time period. We deducted labor costs per kilogram of seed oil processed based on an estimated daily wage of R\$23 (the minimum salary in Acre for agricultural workers, equal to US\$12.88 on 7/19/2010). Based on Londres (2004), two full days of labor yields two kilograms of oil (or 1 day per 1 kg). Londres' estimate included 4 hours for cooking

seeds, 4 hours for breaking them and removing the endosperm (30 days later), and 15 hours to prepare the seed pulp for oil extraction and mix for 15 minutes 3 times per day (for 15 days). Seed collection was combined with other activities (Londres 2004) and was not assigned a time cost. In addition to using a labor cost of R\$23 (US\$12.88), we also calculated revenue using a labor cost of R\$12 (US\$6.72 on 7/19/2010) per kilogram of oil to assess how sensitive revenue was to labor cost. We used a similar methodology to calculate the NPV of our 25- and 35-year timber harvests. We simulated and summed the NPV harvests 500 times to create a NPV distribution for both seed and timber harvests; these simulations represent how ecological variability may influence expected revenue.

We used these NPV sums to calculate the equal annual equivalent (EAE). The EAE allows comparison of land uses that have different investment time periods (annual vs. periodic harvests) by combining all costs and benefits into a single annual sum that is the equivalent to all cash flows during an analysis period spread uniformly over the period (Jacobson 1998).

$$\text{EAE} = \text{NPV} * \frac{i(1+i)^t}{(1+i)^t - 1}$$

where  $i$  is the discount rate, and  $t$  is the number of years. The EAE allowed for comparison of different cutting cycles (i.e. 35-year cutting cycles vs. 25-year cutting cycles). All EAE results are expressed on a revenue per hectare basis.

## Results

### Seed Oil Value

Prices for *C. guianensis* seed oil in 2009 varied throughout the state of Acre. A soap-making company, Tawaya, in the state's most western city of Cruzeiro do Sul paid

R\$15/kilogram (US\$8.40 on 7/19/2010) of seed oil. A community cooperative, RECA in the neighboring state of Rondônia, sells *C. guianensis* seed oil for R\$25/kilogram (US\$14 on 7/19/2010), and published values for the northern Amazon were R\$3 (US\$1.68 on 7/19/2010) in 1999 (Plowden 2004).

Oil extraction methods observed at both the community cooperative in Rondônia and in Cruzeiro do Sul used dried seeds and yielded comparable kilograms of oil. In Rondônia, one kilogram of seeds yielded 0.432 ( $\pm 0.036$  SD) kilograms of unfiltered oil, using a mechanical steel press after 30 minutes. Using agricultural equipment modified to break and press seeds and extract oil in Cruzeiro do Sul, one kg of seeds yielded 0.450 kg of oil after pressing for one hour and 40 minutes. Manual extraction results in comparable oil yields, but time for extraction is much greater than that using the modified agricultural equipment (RECA communication). We chose to use the estimate of oil yield from Rondônia (0.432 kilograms of oil per 1 kilogram seeds) in our seed harvest NPV calculations since it was comparable to manual extraction yield and provides a conservative estimate of oil yield. Because labor costs (time expended) were highly variable and poorly quantified in these sites, we instead adopted detailed estimates from Londres (2004) as outlined in our methods.

### **Timber Value**

The local stumpage price of a standing *C. guianensis* tree was R\$40 to R50/m<sup>3</sup> (US\$22.40 to US\$28 on 7/19/2010). Commercial heights of individuals ranged from 8.5 to 20 m, with a tendency toward lower heights, and average commercial height of all individuals  $\geq 50$  cm dbh (12.6 meters) was used to calculate timber volume. Prices for extracted *C. guianensis* stems were R\$150/m<sup>3</sup> on a log deck (US\$83.99 on 7/19/2010) and between R\$600 –R\$ 900/m<sup>3</sup> (US\$335.95-\$503.92 on 7/19/2010) when processed

at sawmills in the capital city of Acre, Rio Branco (with a 3:1 yield ratio) (Figueiredo, personal communication). Since most communities in Acre do not have the training or equipment necessary to extract timber, or process at on-site sawmills, we used stumpage price to calculate timber revenues.

### **Net Present Value of Seed and Timber Harvests**

We found that revenue from 100% timber harvests (of individuals  $\geq 50$  cm every 25-years) exceeded that of 10% seed harvests when evaluated separately and applying labor costs of R\$23 per kilogram of oil (US\$12.88 on 7/19/2010). When we dropped those labor costs to R\$12 (US\$6.72 on 7/19/2010), however, expected seed harvest revenue jumped by a factor of 6 or more, surpassing the EAE of timber harvest (Table 4-1). These trends also were consistent for 35-year cutting cycles (results not shown), though EAE of both seed and timber harvests for this longer cutting cycle were less than in simulated 25-year cycles. Revenue patterns were consistent in both occasionally inundated and *terra firme* forests, though expected revenue from both seed and timber harvests was consistently higher in occasionally inundated forests (Table 4-1; Table 4-2). The obvious caveat here is that timber extraction only included *C. guianensis*. Most selective logging is not exclusive to one species, but rather includes a mix of valuable timber species.

Table 4-1 Expected revenue per hectare of *C. guianensis* seed and timber harvest in an occasionally inundated forest (A) and *terra firme* forest (B) in Acre, Brazil. All revenues indicate the total revenue over 51-years or 3 timber cutting cycles (mean, minimum and maximum values are from 500 simulations). The seed price is based on the market value of 1 kg of processed seed oil; timber price is based on the value of a m<sup>3</sup> of timber. Prices and revenues are expressed in the Brazilian *real* (plural: *reais*) currency (1 real = US\$0.56 7/19/2010). For timber, the first revenue listed is calculated using multi-species allometric equations derived from Costa Rican sites (Segura & Kanninen 2005). The second timber revenues in parentheses are based on allometric equations of *C. guianensis* (Silva *et al.* 1984). Revenues for a 20% discount rate were approximately zero and are not shown.

<b>A: Occasionally inundated forest</b>		<b>Seeds</b>					<b>Timber</b>			
<b>Discount rate</b>	<b>Harvest</b>	<b>Labor (R\$)</b>	<b>Price (R\$)</b>	<b>Simulated EAE Range (R\$)</b>			<b>Price (R\$)</b>	<b>Simulated EAE Range (R\$)</b>		
				<b>Mean</b>	<b>Min</b>	<b>Max</b>		<b>Mean</b>	<b>Min</b>	<b>Max</b>
4%	10% seeds and 100% timber	23	25	0.29	0.13	0.46	40	0.79 (0.83)	0.73 (0.76)	0.83 (0.89)
	100% illegal timber harvest	23	25				40	1.99 (2.11)	1.89 (2.02)	2.07 (2.22)
	10% seeds & 100% timber	12	25	1.90	1.07	2.92				
8%	100% illegal timber harvest	12	25							
	10% seeds & 100% timber	23	25	0.03	0.01	0.06	40	0.10	0.10	0.10
	100% illegal timber harvest	23	25	0.22	0.09	0.34		0.30	0.29	0.31
	100% illegal timber harvest	12	25							



Table 4-2 Expected revenue per hectare of *C. guianensis* seed and timber harvest in an occasionally inundated and *terra firme* forest in Acre, Brazil. All revenues indicate the total revenue over 51-years or 3 timber cutting cycles (mean, minimum and maximum values are from 500 simulations). The seed price is based on the market value of 1 kilo of processed seed oil using R\$25 (US\$14 on 7/19/2010) market price and a labor cost of R\$23 (US\$12.88) or R\$12 (US\$6.72); timber price is based on a stumpage value of R\$40 (US\$22.40) per m<sup>3</sup> of timber. Prices and revenues are expressed in the Brazilian real (plural: reais) currency (1 real = US\$0.56 7/19/2010). Timber revenue estimates were calculated using Segura and Kanninen's (2005) multi-species allometric equations from Costa Rican sites. Revenues for a 20% discount rate were approximately zero and are not shown.

Discount rate	Harvest	Labor (R\$)	Occasionally inundated forest			Terra firme forest		
			Simulated EAE Range (R\$)			Simulated EAE Range (R\$)		
			Mean	Min	Max	Mean	Min	Max
4%	10% seeds and	23	1.07	0.95	1.19	0.40	0.33	0.47
	100% timber	12	2.68	1.90	3.66	0.84	0.54	1.20
	100% illegal timber harvest		1.99	1.89	2.07	0.73	0.67	0.79
8%	10% seeds &	23	0.13	0.11	0.15	0.06	0.05	0.07
	100% timber	12	0.32	0.20	0.43	0.11	0.07	0.17
	100% illegal timber harvest		0.30	0.29	0.31	0.12	0.11	0.12

Timber and seed extraction, however were not mutually exclusive at some levels modeled (10% seeds and 100% timber). These combined harvest levels had a  $\lambda_s$  greater than one for occasionally inundated forests (See Chapter 3), indicating ecologically viable harvests, and positive revenue in each forest type (Table 4-2).

Annual oil harvests varied considerably between years and between forest types due to annual variability in seed production (Figure 4-1). In contrast, timber harvests showed relatively little variation due to tree slow annual growth increment. The number of individuals that grew to harvestable size within the 25-year cutting cycles was low, reflecting, harvest intensities of less than three individuals per hectare, even with harvests of all individuals dbh  $\geq$  40 cm (Table 4-3). Based on distributions of NPVs for

10% seed harvest predicted from 500 simulations (Figure 4-2), we observed an expected decrease in NPV with increasing discount rate. We also observed ecological variability as seen in the variation around mean NPV; as discount rate increased this ecological variability had less impact on expected revenue.

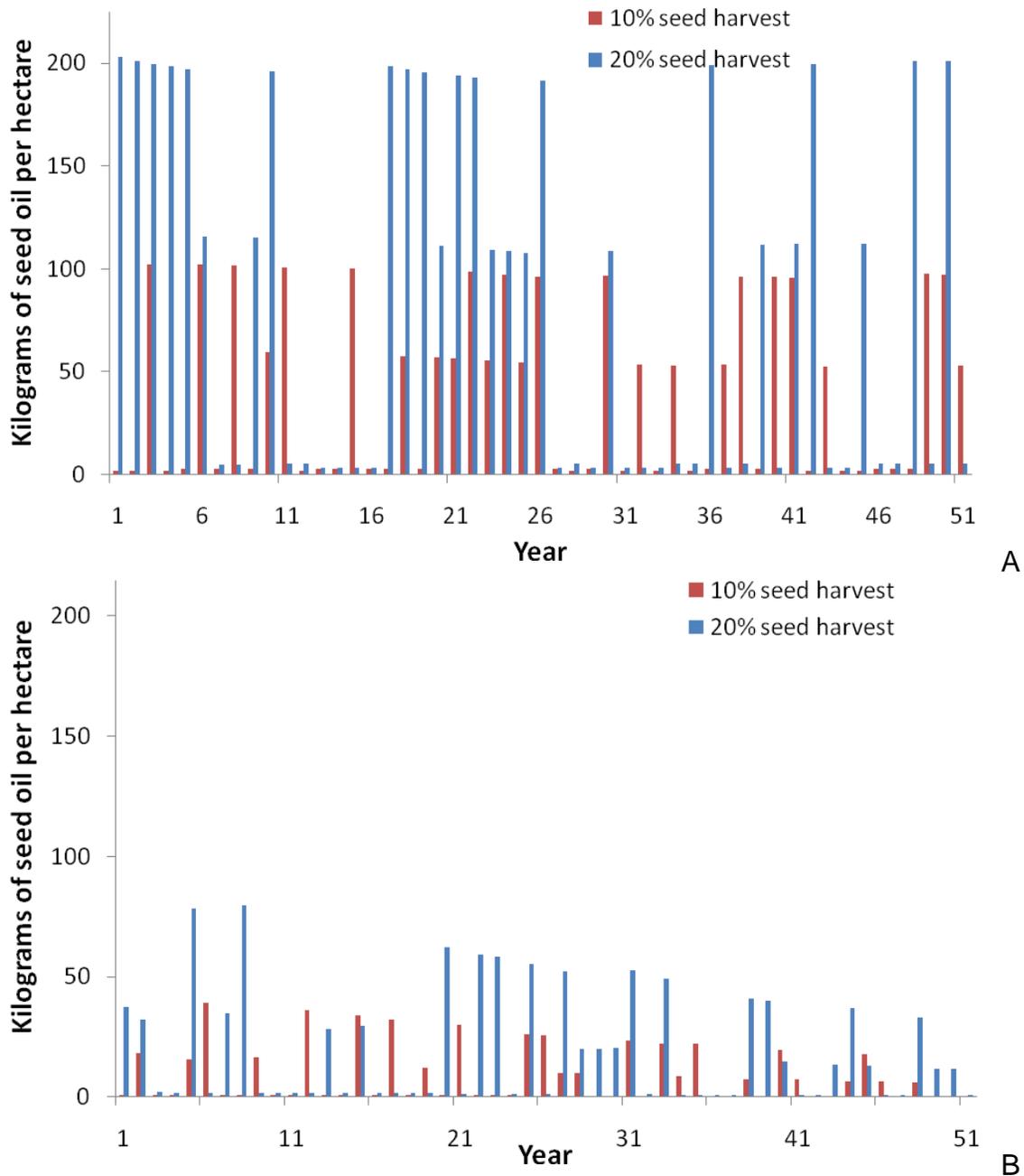


Figure 4-1 Potential annual seed oil production per hectare with harvests of 10% and 20% of the seed crop in occasionally inundated (A) and *terra firme* forest (B). Variability is due to modeled variability in seed production between years.

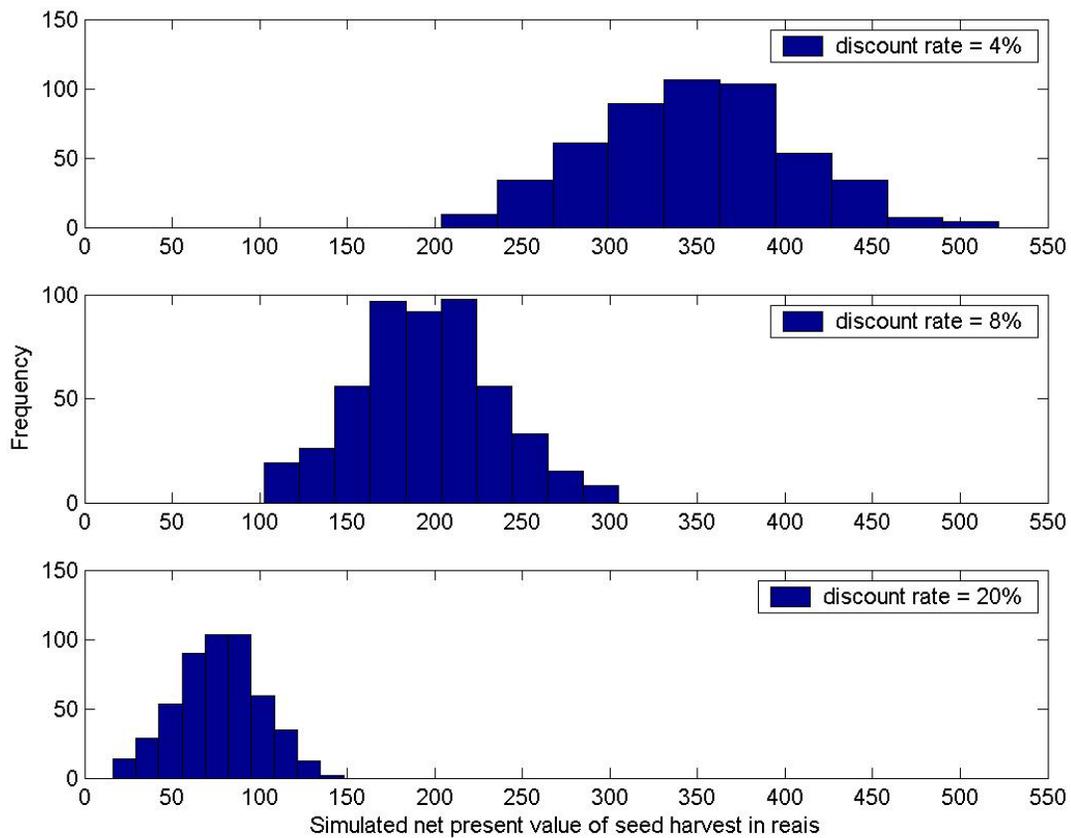


Figure 4-2 Histograms of the distributions of NPVs for 10% seed harvest predicted from 500 simulations using a market price of R\$25 and a labor cost of R\$12; variability is due to differences in expected seed production based on modeled ecological stochasticity.

Table 4-3 Average number of individuals harvested per hectare for timber based on a 25-year cutting cycle.

Harvest Number of individuals per hectare	Year	Occasionally inundated forest		<i>Terra firme</i> forest	
		dbh $\geq$ 50 cm	dbh $\geq$ 40 cm	dbh $\geq$ 50 cm	dbh $\geq$ 40 cm
	1	0.87	2.97	0.53	1.27
	26	1.76	2.99	0.41	1.10
	51	1.62	2.61	0.26	0.45

## Discussion

When identifying potential management regimes for tropical forests, civil society prefers activities that are biologically feasible, ecologically sustainable, economically efficient, socially acceptable and operationally feasible. While very few alternatives pass all these tests (Alavalapati & Zarin 2004), our study found that both 10% seed harvests and 100% timber harvests of *C. guianensis* (individuals dbh  $\geq$  50 cm) were both profitable and arguably ecologically sustainable, though in occasionally inundated forests only. Timber harvest of *C. guianensis* was economically superior to income from seed harvest when the full cost of seed oil extraction was included, but when labor costs were halved, revenues from seed harvests were competitive or superior to timber harvests (Table 4-1). Reducing labor costs was based on the assumption that individuals involved in the seed processing were not always earning the equivalent of a daily minimum wage, therefore we may have overestimated the true opportunity cost of their labor. In practice, however, benefits could accrue from both annual seed harvest revenues and those from periodic logging revenues of *C. guianensis* individuals.

### Shadow Prices

Labor costs differed between the two *C. guianensis* products. For modeling, we assumed no labor costs for timber extraction because timber prices modeled were based on stumpage values (standing trees harvested by loggers). Our modeled labor costs for seed collection and oil extraction (R\$23 per kilo of oil extracted) may have overestimated the true cost of labor due to shadow prices. A shadow price differs from a financial price in that it reflects the true opportunity cost of the resource in question. While oil extraction takes 2-5 months without the use of mechanized equipment (Londres 2004, Plowden 2004), the associated work is not continuous because of

significant time lapses as oil drains during different processing stages. Thus, parts of the oil extraction process can be combined with other household activities. If, however, communities plan on increasing seed harvests to above 20% of total seed production simulated here, seed collection and processing would require substantially greater amounts of time. The costs of extensive seed collection are not included in this study due to the expectation that market demand is not sufficient to warrant this scenario.

Transport costs and potential capital investment also differed between *C. guianensis* timber and seeds. For timber, transport costs to market and capital expenditures are included in our estimates of stumpage prices. We also assumed no transport costs for marketing seed oil since this was the case for individuals involved in small-scale oil extraction in Acre at the time of our study (personal observation). Community members travelled to urban centers on a relatively frequent basis to visit relatives and conduct other transactions. When marketing of seed oil was combined with these pre-planned trips, the opportunity cost was effectively zero. Because *C. guianensis* oil can be stored after processing (RECA, personal communication), often in repurposed containers such as 1 L soda bottles, we did not subtract any oil transport costs from our expected net present value of seed harvest. If, however, communities were to invest in larger-scale extraction operations, a more thorough analysis of initial capital investment costs would be necessary (including receptacles for oil storage and transport).

### **Model Assumptions**

This model only incorporates logging of one species at very low densities. This scenario is limited in scope; most logging currently includes other valuable timber species identified in pre-harvest inventories. Additionally, we may have overestimated

the expected revenue from timber harvest since we did not include mortality from tree felling in our model. Holmes *et al.* (2002), however, only estimated additional mortality at 2.6% when multiple timber species are harvested using logging practices designed to reduce negative environmental impacts on a given stand. Our simulated harvest intensities were low, including the equivalent of 1-3 individuals per hectare at each 25-year interval (Table 4-3). Still, additional mortality could affect stasis (survival) of this species, one of the most important demographic factors in predicting *C. guianensis* population growth rates (See Chapter 3). This omission, however, is perhaps compensated for by the fact that we do not assume higher growth (due to increases in light) immediately after timber harvests as is common in some logging models (Boltz *et al.* 2001, Valle *et al.* 2007). As our logging intensities are low, increased growth would affect only a few individuals. Increased growth is also reportedly short-lived, both in the Brazilian Amazon (Silva *et al.* 1995) and Surinam (De Graaf *et al.* 1999, Dekker & De Graaf 2003).

### **Limitations of Model Results**

Population stability is a precondition to sustainable revenues over time. As evidenced by our timber simulations in *terra firme*, timber extraction decreased over the interval of just 3-cutting cycles (Table 4-3). Simulating increased timber harvests cannot be justified, since *C. guianensis* growth rates were some of the slowest in the Amazon (Vieira *et al.* 2005). Revenues from timber harvests could potentially be higher with increased processing, however. Prices of *C. guianensis* timber jumps R\$100 just by removing it from the forest to a log deck; this, however, requires labor, training, and an associated time cost.

In terms of *C. guianensis* seeds, harvests may be higher in other Amazonian regions where higher average seed production has been reported (Tonini *et al.* 2008, Guedes *et al.* 2008, Londres 2009), although their production estimates were based on fewer years of observations and *C. guianensis* shows pronounced variation in seed production between years (See Chapter 2). The market for *C. guianensis* seed oil is also more-developed in the Northeastern Brazilian Amazon; these markets might be able to absorb higher oil production than smaller markets in the state of Acre. It is important, however, to exercise caution when hypothesizing about prospective gains from increased product extraction. Local and regional markets cannot always absorb the volume of products that could result from highly intensified extraction (Padoch 1988, Padoch & Pinedo-Vasquez 1996, Shanley *et al.* 2002).

### **Best Management Practices for Multiple-Use *C. guianensis* Management**

Maximizing stumpage value while achieving a minimum level of nontimber benefits likely requires harvesting rules that are more complex than the simple diameter-limit system implemented in most parts of the Amazon and used in this study (Boscolo & Buongiorno 1997, Buongiorno *et al.* 1995). Designing these systems requires a great deal of silvicultural expertise as well as the capacity to monitor logging operations. Monitoring may be easier to implement in communities that have a good knowledge of diverse tree species (and perhaps individual trees) and a low opportunity cost of labor (Boscolo & Vincent 2003). Spatial separation of management units, or specialized management, where some stands are managed more intensely for timber and other stands more intensely for NTFPs, is one management option (Binkley 1997, da Silva Dias *et al.* 2002, Zhang 2005, Guariguata *et al.* 2010). Boscolo & Vincent (2003) found that specialized management might be superior for combined biodiversity conservation

and production of timber at low discount rates. Specialized management units might be useful for *C. guianensis* timber and NTFP combined management as well. Communities could identify those trees that should remain unlogged for their value as seed-producers, either because they are not fit for timber or are consistently high seed producers. Research on *Bertholletia excelsa* (Kainer *et al.* 2007) and *Swietenia macrophylla* (Snook *et al.* 2005) have documented the latter, while also noting individuals that produce few to no seeds which could be targeted for logging. Field observations of *C. guianensis* in our study site also indicated a subset of trees with consistently lower seed production. Planning timber management to target these marked low seed producers is one way to minimize impact of timber harvest on the seed resource. This requires informed planning and organization, which are not consistently found in Amazonian communities (Shanley *et al.* 2002), though this may be changing. Initiatives are underway in Brazil to train tropical foresters in bridging the gap between timber and NTFP use, ecology and management (Pinto *et al.* 2008, Shanley & Medina 2005).

Managing timber resources for continued extraction (as opposed to depletion harvesting) has a short history in the Amazon basin; there is no experience beyond the first harvest (Zarin *et al.* 2007). In selective logging, first harvests yield high timber volumes because they take place in forests that have not been anthropogenically disturbed for hundreds of years. Second cuts are not nearly as profitable (Keller *et al.* 2007, Macpherson 2007), and concerns about viability and returns associated with future timber harvests can lead to land use conversion for cattle ranching and slash-and-burn agriculture (Veríssimo *et al.* 1992, Nepstad *et al.* 2001) in the absence of other

economic incentives from forest management between cutting cycles. Our combined returns for seed and timber harvest of *C. guianensis* indicate a potentially viable economic opportunity that is sustainable in certain forest types. Combining extraction of NTFPs with timber may provide the needed incentive for maintaining forest cover until regrowth is sufficient for the next timber harvest. This is even more important if the current timber cutting cycles are unsustainable (Gardingen *et al.* 2006) and therefore adjusted upwards, further reducing the expected value from future harvests of timber only. This study found significant estimated revenue from both timber and seed harvest of *C. guianensis*, though this revenue is not likely sufficient to move communities out of poverty. Combining this income with harvest of other resources in the context of multiuse management may be an economically viable management strategy in Amazonia, preferable to some current single-resource extraction management systems.

## CHAPTER 5 CONCLUSION

Taken together, the three papers in this dissertation allow for a better understanding of the ecological and environmental mechanisms that influence *C. guianensis* natural seed production and variability, how the ecology of the species constrains both seed and timber harvests in two different forest types, and the potential economic revenue from simulated ecologically sustainable harvests. The first paper demonstrated variable seed production between years and between individuals. Multiple variables interacted at different scales to influence seed production. At the largest scale, climatic cues (rainfall and temperature parameters) were central to setting overall patterns in phenophases and seemed to best explain why high seed production years were consistent across both forest types (or habitats) examined. Habitat heterogeneity, including species abundance, spacing between individuals (Klimas *et al.* 2007) and underlying abiotic factors, may be the primary reason for significantly higher seed production in occasionally inundated forest ( $F = 22.60$ , Table 2-2), though climatic variables had a much stronger predictor effect (Table 2-2). At the smallest scale, individual tree attributes contributed to seed production heterogeneity within habitats; dbh, and cross-sectional canopy area showed positive, quadratic relationships with seed production, while vine load negatively affected seed production, irrespective of forest type.

Mean annual maximum temperature was negatively correlated with *C. guianensis* seed production, perhaps due to its often strong correlation with irradiance (Van Schaik *et al.* 1993, Stevenson *et al.* 2008). Three-month dry season rainfall was positively correlated with seed production, while five-month wet season rainfall was negatively

correlated. Higher than normal dry season rains may allow for increased available reserves for fruiting and flowering. Too much rain, however, may inhibit synchronization of flowering (Alvim 1960) and reduce pollinator visits (Van Schaik *et al.* 1993). *C. guianensis* had significantly higher seed production in occasionally inundated forest, with higher densities in this forest type further amplifying production. The interaction between forest type and year was also significant in our “peak” seedfall model (Table 2-3). Perhaps part of this interaction, and likely the observed lower seed production in *terra firme* forest, can be explained by a 2005 fire in one of our *terra firme* plots, which stressed trees and reduced stored reserves available for reproduction. This fire, however, coincided with an especially severe Amazonian drought that would have affected both forest types. Indeed, percentage of individuals flowering and total seed production were low in both forest types in 2005 and the subsequent year. Still, our study cannot confirm this fire hypothesis since we do not have data prior to the drought.

The second paper focused on sustainable harvest scenarios for *C. guianensis*. Results indicated that some populations of *C. guianensis* may be suitable for extraction of seeds, timber, or a combination of both. No levels of timber or seed harvest were considered viable in *terra firme* forest with a  $\lambda_s < 1$ , though a major caveat of our study is that we measured only 4 transition matrices for a species that can live hundreds of years (Vieira *et al.* 2005). If the observed environmental conditions were characteristic of expected future conditions, we would expect a decline in the *terra firme* population. Indeed quasi-extinction simulations indicated that there was a 100% probability that the population would have less than 3 individuals dbh  $\geq 10$  cm per hectare after 93 years,

even in the absence of seed or timber harvests. Multiple harvesting options, however, were available to sustainably manage *C. guianensis* in occasionally inundated forest.

Simulations predicted population growth in occasionally inundated forest with harvest regimes of 10% and 20% of total seed production, but the lower 95% CI was below one for both of these harvest scenarios (Table 3-5). Timber harvests of both 50% and 100% of individuals with dbh  $\geq$  50 cm were also sustainable, and the probability that the population would have fewer than 3 individuals dbh  $\geq$  10 cm remained zero for the 500 years modeled. We found this surprising since stasis had some of the highest elasticity values; however, modeled harvest levels were extremely low, involving fewer than 2 trees per hectare every 25-years in occasionally inundated forests. Since smaller individuals (< 50 cm dbh) comprised a larger part of the per-hectare densities, simulations did not reduce the population to fewer than 3 individuals dbh  $\geq$  10 cm per hectare until almost 1000 years in the future. Simulations that limited recruitment, while simultaneously harvesting larger individuals, affected both recruitment of individuals into the smaller dbh classes and seed production in the larger dbh classes, leading to cumulative distribution functions (CDFs) reaching 1.0 after 150 years.

We also found the potential for compatibility between seed and timber harvest in occasionally inundated forests. Our results suggested that 10% annual seed harvests were compatible with 100% timber harvests (of trees  $\geq$  50 cm) twice a century, the equivalent of approximately two trees per hectare. The longevity of *C. guianensis*, seen in its high stasis rates, compensated for slow annual growth. Indeed, the importance of survival (stasis) on population growth rate (based on elasticity calculations) was consistent in both forest types and throughout the 5-year study.

The third paper focused on comparing the economic revenue associated with the simulated ecologically sustainable seed and timber harvests from the previous paper. Quantifying revenue from harvest is particularly important in cases where an individual species provides multiple economic benefits, generating a potential conflict of interest in deciding whether to prioritize one use over another, as is the case for *C. guianensis*. When we modeled the EAE of expected economic revenue from both seed and timber harvest over a 51-year period, we found that revenue from 100% timber harvests (of individuals  $\geq 50$  cm every 25-years) exceeded that of 10% seed harvests when evaluated separately and applying labor costs of R\$23 per kilogram of oil (US\$12.88 on 7/19/2010). When we dropped those labor costs to R\$12 (US\$6.72 on 7/19/2010), however, expected seed harvest revenue jumped by a factor of 6 or more, surpassing the EAE of timber harvest (Table 4-1). Reducing labor costs was based on the assumption that individuals involved in the seed processing were not always earning the equivalent of a daily minimum wage; therefore, we may have overestimated the true opportunity cost of their labor. In practice, however, benefits could accrue from both annual seed harvest revenues and those from periodic logging revenues of *C. guianensis* individuals. A major caveat of this study is that we simulated timber extraction of *C. guianensis* solely. Most selective logging includes a mix of valuable timber species.

### **Research Significance**

Few studies have attempted to place an economic value on the flow of goods and services from logging compared with multi-use forest management (MTF). This dissertation does not offer a comprehensive comparison of these two strategies when managing an entire forest, which remains a challenge (Valle *et al.* 2007). It does,

however, delve into this issue for one species. This represents an important first step in providing information geared toward encouraging ecologically-sound best management practices, while maintaining a profitable harvest scenario. The goal of sustainable forest management is not to perpetuate poverty in forest-based communities, and as such, combining NTFP harvests with other management strategies may be necessary to truly improve livelihoods for forest residents. NTFP harvest alone is currently insufficient (Morsello 2006). Therefore, there is growing interest in incorporating economic analysis with the more common delineation of ecological sustainability of resource harvests to determine whether sustainable harvest levels are expected to be economically viable.

Similarly, there is a growing trend toward analysis of MTF. This includes valuation of diverse forest “goods,” for example managing for carbon storage in logged stands (Boscolo & Buongiorno 1997, Boscolo & Vincent 2003). Both logging and NTFP harvest can be legitimate components of good forest management (García-Fernández *et al.* 2008, Guariguata *et al.* 2008, Guariguata *et al.* 2010). In addition, one third to one half of timber species are multi-use, indicating that they also have value for their NTFPs (Martini *et al.* 1994, Herrero-Jáuregui *et al.* 2009). For MTF to progress, we must combine ecological and economic research to rationally determine the best forest management approaches at the local, regional or national level, including the best management approaches for individual species valued for multiple products. Perhaps incorporating economics with ecological studies can better clarify best management practices under MTF.

### **Evolution of Research and Collaboration Interests**

The initial idea for this research, and my interest in forest management, was formed during a one-year Rotary Ambassadorial Fellowship in Acre, Brazil from 2001-

2002. During this time, I worked as part of a project funded by the International Plant Genetic Research Institute (IPGRI) titled “Conservation-through-use of forest genetic resources in Latin America.” The Acre-based field team worked with four species, one of which was *C. guianensis*. My contribution was predominantly resource mapping of two of these species. Interested in continuing my contribution to research on the viability of forest management as an alternative to forest conversion, I began graduate studies at UF. My graduate project was developed in partnership with Dr. Lúcia Wadt, a researcher I had met during my Ambassadorial Fellowship. The project initially drew heavily on addressing the question of variable returns from *C. guianensis* seed harvest due to natural variability in seed production, but grew to include population modeling and economic viability.

This research would not have been possible without my collaboration with Dr. Wadt, Embrapa, and the research team we assembled. While I made frequent trips to Brazil, data collection for phenology and seed production was weekly. A team of students and field technicians at Embrapa made this long-term data intensive project possible. In turn, I began mentoring/advising two M.S. students at the Federal University of Acre, focusing on statistical assistance in data analysis and helping these students publish in international journals. My partnership with Dr. Wadt also enabled me to join a multi-site project in Brazil that addressed management of NTFPs in Amazon on a more regional scale. Through continued collaboration with this team, I seek to conduct joint research, plan new projects, and assist in building the capacity of upcoming scientists both in the U.S. and abroad with the general goal of educating

concerned global citizens capable of addressing the major societal and environmental challenges, such as improved forest management in the Amazon.

### **Future Research**

The long-term dataset from this dissertation will continue to generate answers to interesting ecological and applied questions. We intend to compare results from this model with results generated via integral projection models, a more sophisticated and arguably more effective modeling technique for modeling the dynamics of long-lived plant species (Zuiedema *et al.* 2010). We also plan to explore in more depth the sources of differences in the long-term growth rate between these two forest types under stochastic environmental conditions using recently developed stochastic life table response experiments (Caswell 2010, Davison *et al.* 2010). Lastly, another hope is procure funding for more applied questions such as the best oil extraction methods and oil filtration techniques most appropriate for small communities. The dual economic potential of this species may also lead to increased market research.

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## BIOGRAPHICAL SKETCH

During and after completion of her undergraduate degree, Christie Klimas' research focused on the role of forests in global climate change and the carbon cycle. In North Carolina, she worked for Brookhaven National Lab at the Free-Air Carbon dioxide Exchange (FACE) site. The FACE system allows for CO<sub>2</sub> enhancement of entire forest stands. Klimas examined the effects of rising atmospheric carbon dioxide levels coupled with seasonal temperature increase on plant photosynthetic carbon uptake. This work led her to the Biosphere 2 in Arizona where she studied plant carbon uptake in a more controlled environment. She learned a key component of climate change research: forests play a crucial role in the carbon cycle, and it is hoped that they will help mitigate the effects of increasing atmospheric CO<sub>2</sub>. However, the benefits that forests provide are being compromised by rapid and unprecedented changes in forest use and abuse.

To learn more about the human dimensions of environmental change, Klimas spent eleven months in Acre, Brazil as a Rotary Ambassadorial Scholar. She collaborated with rubber tapping communities to inventory reproducing adults of two species of rainforest trees *Carapa guianensis* (andiroba) and *Euterpe precatoria* (açai), which have broad potential markets in various industries from food to medical. This investigation was part of a larger research initiative, which focuses on economic incentives that may encourage communities to seek sustainable use of the forest. Klimas had the privilege of joining other researchers, university faculty, government officials and motivated individuals in the pursuit of solutions to local problems that collectively compose some of the greatest existing scientific challenges. Concurrently frustrating, euphoric, rewarding and challenging, it was her first experience with applied science. As with all of her research endeavors, the more she learned, the more she

realized she still needed to learn. It was the desire to improve her research efforts that led her to the interdisciplinary master's program at the University of Florida (UF).

Her experience with the master's program at UF has strengthened her desire to continue collaborative research on using the earth's resources in a way that balances ecological concerns with a respect and improved quality of life for resource users. Klimas hopes to remain in academia as a professor using science, interdisciplinary knowledge and her collaborative skills to mentor others. Research is an exciting, challenging and constantly changing field and she plans to use the skills and knowledge acquired through community-based work in Brazil, research experience and Florida's interdisciplinary program to apply rigorous science to help solve/clarify some of the most intractable problems faced in tropical regions. Through dissemination of my results, she hopes to contribute to economically sound, socially equitable development in the Amazon and throughout the globe. Klimas received her PhD from the University of Florida in 2010. She is currently teaching at DePaul University in Chicago, Illinois and resides with her husband and daughter.