The Ecology and Harvest of Andiroba Seeds for Oil Production in the Brazilian Amazon

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*Andiroba (*Carapa guianensis *Aubl.: Meliaceae) is a canopy tree found in moist tropical forests in Amazon, Central America and Africa. Manual and mechanical methods have been used to extract oil from its seeds for use in insect repellent and traditional medicine, and as an ingredient in mosquito repellent candles and medicinal soap. Forest communities need a better understanding of the ecological and economic aspects of andiroba seed and oil production to decide if and how collecting more of these seeds can be done sustainably and profitably. I worked with Tembé Indians in the eastern Brazilian Amazon in 1998–99 to investigate the ecology and economics of andiroba seed production. We found that andiroba tree (≥10 cm DBH) density in mostly intact forest near Tekohaw village averaged 6.5 trees ha^{-1}. While some trees started reproducing in the 10–20 cm DBH class, 46–63 per cent of trees ≥30 cm DBH had flowers or fruits in the two seasons observed. Trees reached peak flowering in the mid-rainy season in March, and most fruit fell in the early dry season in June and July. In 1999 a group of forty-six reproducing trees yielded an average of 0.8 kg of seeds tree^{-1}. Up to 29 per cent of these seeds had been infested by moth and fly larvae, partially consumed by mammals or germinated. Each tree produced an estimated average of 1.2 kg seeds with 33 per cent being removed by mammals. This production is much less than the 50–300 kg seeds per tree averages cited in other accounts. The study's one measurement of seed transformation to oil (14.4 kg seed to a litre oil yield)*

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was less efficient than the 3.4–9 kg seed to oil (litre) ratio reported in other accounts. Given the extensive time needed to collect and process seeds, this enterprise would provide minimal financial reward with the typical selling price of $3 per litre. It may be worthwhile for some communities to collect seeds from the most productive trees for sale to dealers or buy a seed press to increase processing efficiency. Andiroba density could be readily planted in forest gaps and secondary forests to increase seed supply for human harvesters and wildlife.

INTRODUCTION

FOREST PEOPLES THROUGHOUT the tropics use a wide variety of fruits for food, oil, dyes and other purposes. While the ethnobotany of these products is often well known, the ecological and economic aspects of harvesting and processing fruits from wild populations of rainforest trees has received much less attention. Such information is needed for specific products to evaluate the sustainability of harvest and commercial viability of selling the processed product under a range of ecological and market conditions. An examination of the harvest of the seeds of *Carapa guianensis* Aublet (Meliaceae) provides a good opportunity to explore these questions for one of the most commonly used non-timber forest products (NTFP) in the neotropics. In Brazil, the species is best known as andiroba (Sampaio 2000).

In spite of the market interest, there is little information about the ecological and economic aspects of harvesting and processing andiroba seeds for oil production. These questions include the amount of seed production per tree and area of forest, the efficiency of seed collection and processing, and impacts of insect and mammals predation on seeds. Insect larvae can infest andiroba seeds when the fruits are first forming in the canopy and after the seeds fall to the ground (Becker 1973). If infestation progresses too far, these seeds lose their usefulness for oil extraction. Mammals can impact human seed harvest by immediately consuming seeds that fall to the ground and, in the case of agoutis, removing and burying seeds where they presumably become more difficult for people to find. Forest-based communities need this type of information to decide if and how they can conduct this enterprise sustainably and profitably.

In 1998 and 1999 we investigated a variety of variables related to the ecology and production of oil from the seeds of andiroba in the Alto Rio Guamá Indigenous Reserve in eastern Pará state, Brazil. While a few families in this area occasionally collected andiroba seeds to make oil for personal use, no one in this or neighbouring villages had intensively harvested these seeds for commercial purposes.

The main objectives of the study were to: (*a*) assess the density of the andiroba resource near Tekohaw; (*b*) investigate the flowering and fruiting phenology of the species; (*c*) estimate the quantity and quality of seed production in relation to seed predation; (*d*) estimate the seed-to-oil conversion ratio; (*e*) quantify the time involved in harvesting and processing andiroba seeds; and (*f*) estimate the net financial return for village collectors under a range of ecological and marketing conditions.

Natural History and Use of Andiroba

Andiroba is a medium-sized canopy tree found in the West Indies, Central America south of Honduras, many parts of the northern Amazon region and tropical Africa (Pennington 1981; Record and Hess 1943). Its fruit is a four-valved woody capsule that generally splits open when it matures, falls and hits the ground (Pennington 1981). Depending on the region, the capsule typically contains four to sixteen oil-rich seeds that can germinate well in different habitats (Hall et al. 1994; McHargue and Hartshorn 1983a). The buoyancy of these seeds helps andiroba become widely established in moist forests (Scarano et al. 2003) such as riparian swamps and creek banks; it is sometimes found in nearly pure stands in flood-plain forests (McHargue and Hartshorn 1983a). The adaptable species is also found in more upland (terra firme) forests of the Amazon (Le Cointe 1947; Record and Hess 1943) where its nutrient-rich seeds are often dispersed by agoutis (*Dasyprocta* sp.; Rankin 1978).

Amazon forest peoples have long extracted the yellow bitter oil from andiroba seeds to use externally as an insect repellent, and to relieve muscle aches and rheumatism; internally, it has been used in cough preparations (Duke and Vasquez 1994; Rodrigues 1989; Shanley et al. 1998; van den Berg 1982). The oil has also been used as raw material for making soap. This soap in-dustry was so important in the 1940s that the Brazilian government temporarily banned logging of the species to protect it (Record and Hess 1943).

Andiroba's major economic use today is its insect-resistant reddish timber often used in place of its heavily exploited relative, Honduras mahogany (*Swietenia macrophylla* King). As mosquito-borne diseases such as malaria and dengue continue to plague people in the region, there is new demand for andiroba oil to make medicinal soap and non-toxic insect repellent candles (MMA/SCA et al. 1998).

The processes used to extract oil from andiroba seeds have been described in several ethnobotanical accounts in the Amazon. The process usually begins by boiling and then setting the seeds aside to initiate fermentation and decomposition (Pinto 1956). This apparently begins the unbinding of fatty acids from the protein, carbohydrates, fibre and other materials in the seed endosperm. Mashing the kernels and setting them out in the sun further separates the oil and allows it to leach out. This process has been used by indigenous groups in the Guianas and Brazil (Plotkin et al. 1991; Shanley et al. 1998; van Andel 2000). More oil is sometimes obtained by squeezing the mashed seeds in a *tipiti* (Pinto 1956; Shanley et al. 1998), a cylindrical woven tube, typically used to squeeze water out of mashed manioc (*Manihot esculenta* Crantz). Industrial processing of the seeds involves breaking them into small pieces and then pressing the oil out with hydraulic presses (Pinto 1956). In both the traditional and mechanical processes there are variations that use more or less heat in the final stage. Whether the seed mass is heated in the sun or an oven, the resulting oil ends up with a higher point of solidification (Pinto 1956; Shanley et al. 1998). This product is best suited for making soap. Processing that involves cooler temperatures produces oil that better retains its liquid form, more desirable for use as a medicine or insect repellent.

RESEARCH METHODOLOGY

Habitat Preferences and Density of the Resource

This study was primarily conducted with Tembé Indians living in the village of Tekohaw on the Gurupi river as part of a larger study to explore the ecological and economic potential of a variety of NTFP in the reserve. To assess the density of andiroba and five other marketable NTFPs near Tekohaw, we conducted an inventory in January 1998 in two 100 ha (1,000×1,000 m) blocks that included a cross-section of habitats within 2 km of the village. The density of andiroba trees ≥ 10 cm diameter at breast height (DBH; 1.5 m above ground) was quantified through inventories in a total of 12 ha in a series of belt transects. Each block had six 10×1,000 m transects (1 ha per transect) running north–south from an east–west midline. Transects were located through stratified random sampling (three transects in each half of the midline). Each transect was divided into forty 10×25 m sections that were classified according to habitat type. The two blocks together were composed of 58 per cent upland forest (terra firme), 13 per cent alluvial forest that was occasionally flooded (baixo), 12 per cent secondary forest (recovering from fire caused by agricultural activities or unintentional forest fire), 4 per cent grotas (small seasonal streams flowing through forest), 5 per cent varzea (seasonally flooded forest) and 9 per cent of several aquatic habitats (lakes or major streams).

Flower and Fruit Production

We sampled the population to estimate the proportion of trees, by diameter class, that were reproductively active. Sampling was conducted from the late rainy season through the early dry, which was the peak period of andiroba flowering and fruit formation as indicated by Tembé elders and our earlier observations. We also wished to estimate the time to pass from bud, to flower, to fruit, to fruit fall, and the proportion of flowering trees that yielded fruit, so that collectors could use their observations of flowering early in the season to gauge the potential quantity and timing of fruit production later in the year.

The first part of the study was conducted by using trees located in the initial inventory, and additional trees found in April and May 1998 by a survey team searching intact areas of alluvial and terra firme forest near the village. We recorded the DBH of 153 trees and noted the presence or absence of flowers or fruit in the canopy and fruit on the ground. In March 1999, a second survey team spent eight days revisiting previously marked trees and located additional andiroba trees in the vicinity of Tekohaw. Thus, in 1999, DBH and presence or absence of reproductive materials were noted for 203 trees that included most of the 153 trees first observed in 1998. These results were analysed to estimate the proportion of trees that were reproductively active in each diameter class.

We further investigated andiroba's reproductive pattern by monitoring forty-six trees from the second survey that had flowers or fruits visible in the canopy. None of these trees had been harvested in the recent past by anyone in the village. To ensure that fruit counts were derived from individual study trees, this group did not include trees where two neighbouring trees were both producing fruit in the same season. At the beginning of the observations, investigators cleared away underbrush, old andiroba fruits and seeds, from under the study tree canopies to assist finding all new fallen fruit. From early April through late July 1999 these trees were visited about five times per week. During each visit the investigator noted the presence of flowers and fruits in the canopy and on the ground, and removed whole fruits, separate capsule valves, and seeds found under or near the edge of the canopy of each tree. Daily flowering and fruiting observations were analysed by size class and month to evaluate the rate of progression from flowering to fruit production and fruit fall.

Seed Predation, Production and Harvest Efficiency

The percentage of seeds produced that can be found and used by people for oil production was assessed by counting the fruit materials collected under the forty-six study trees described in the previous section. Complete fruits, separate capsules and loose seeds were counted; seeds were weighed individually and categorised by their condition (good: whole, mature; bad: immature, chewed by mammals, infested with insect larvae or germinating) and position in the capsule valve (lone, inside, outside).

While agoutis and other mammals immediately consumed parts of some seeds and carried away others, they did not appear to remove inedible woody valves from below the tree. Since these valves contain a distinct impression of seeds in them, the total amount of fruit and seeds produced per tree was estimated by adding the number of whole fruits found to the number of seeds that would have been contained in the separate valves that were also found (for similar method, see Forget 1996; McHargue and Hartshorn 1983a). The average per cent seed removal by mammals per month from all study trees combined was estimated by subtracting the actual quantity (number and weight) of seeds found by investigators from the estimated total seed production. Similar estimates were made for the level of partial consumption by mammals and infestation by insects. Partial mammal consumption was indicated by teeth marks on seeds. Tembé hunters examined some of these seeds to make a qualitative evaluation of which animals were responsible for this type of consumption. Infected seeds were recognised from the outside by holes in the thin shell, brown frass and an orange jelly-like exudation. Seeds in the early stages of infection had multiple small larvae that had eaten small tunnels in the white endosperm. Kernels in later stages of parasitism were devoid of healthy seed material. Seeds were collected on an almost daily basis while monitoring these study trees so insect attacks were all attributed to infection of fruits in the canopy.

Since human collectors may not always be able to pick up andiroba seeds on a daily basis, we conducted a separate small study to assess the impact of insect infestation and rate of germination of seeds left on the ground for several weeks. The second variable was investigated since germinating seeds would progressively use up the oil-rich endosperm. In this study four sets of sixteen andiroba seeds in good condition were placed in plastic mesh bags (35×45 cm) in late March 1999. These fine-mesh bags (2 mm mesh size) were placed on the forest floor in locations about 10–15 m apart near the area of the andiroba study trees. The seeds were examined almost daily for twenty-eight days. Observations noted the presence of insect entry holes, and the emergence and status (live or dead) of a root radicle. Results were analysed to track the rate of initial insect predation and germination.

Extracting Oil from Andiroba Seeds

Many forest dwellers collect andiroba seeds and extract oil from them through a manual process. Between April and June 1999 we interviewed one Tembé woman about the method for processing andiroba seeds. We collected quantitative data on the amount of time required for the seed cracking and mashing stages for five batches of fifty seeds and measured the ratio of seed weight to oil volume for one batch of seeds. Four other batches of seeds were processed to obtain a larger sample size for this ratio, but the family unfortunately consumed most of the oil before the final results could be measured.

We obtained information on the same topics by interviewing one man on Marajó Island (the delta island in the mouth of the Amazon river) who collected and manually processed seeds. One entrepreneur in Belém who bought large quantities of andiroba seeds from different forest communities in the eastern Amazon provided some general information about his mechanised process of making andiroba oil and the yield obtained.

RESULTS

Habitat Preferences and Density of the Resource

In the initial survey fifty-four andiroba trees were found in four habitat types among the 12 ha of various areas that were inventoried. The species was primarily found in intact terra firme (upland) and alluvial forests (Table 1). It was particularly common in grotas, narrow strips of extra moist land that adjoined occasional minor streams flowing through terra firme and alluvial forests. These areas typically had very high densities of açai palm trees (*Euterpe oleracea* Mart). One tree was found by a permanent stream, but this was too small a sample to generalise about andiroba's association with this type. The mean density of andiroba was 6.5 ± 1.4 (SE) trees per ha in Block 2, which contained mostly intact terra firme and alluvial forest; the density of andiroba trees was 2.5 ± 1.4 trees per ha in Block 1, which had a mixture of intact forest, secondary forest, seasonally flooded forest and aquatic habitats. In both blocks the maximum estimated density based on individual plots was sixteen trees per ha. The inventory revealed that andiroba was suited to intact terra firme and alluvial forest and wet areas integrated into these forest types (Table 1). No trees were found in secondary terra firme or alluvial forests that were in early stages (less than ten years) of regrowth from slash-and-burn farming activities, the forest adjoining the main river that is seasonally flooded, the grassy area that becomes a lake during the rainy season, and areas adjoining a major stream.

Table 1
Density of Andiroba Trees in Habitats Near Tekohaw

Habitat type	*Andiroba trees (%)*	*Area of survey (ha)*	*Andiroba density (trees ha^{-1})*
Terra firme (upland forest)	72.2	7.00	5.6
Baixo (occasionally flooded forest)	18.5	1.50	6.7
Grota (forest with ephemeral stream)	7.4	0.43	9.4
Secondary stream	1.9	0.05	20.0
Young secondary forest (terra firme or baixo forest)	0.0	1.45	0.0
Forest near seasonally flooded lake	0.0	0.55	0.0
Seasonally flooded lake	0.0	0.45	0.0
Major stream	0.0	0.58	0.0

Note: Fifty-four trees in initial inventory.

In late April and early May when two-to three-person teams searched almost exclusively for andiroba trees, it only took a team an average of 2.28 ± 0.21 minutes between the time it left one tree until it found another. It took only a minute or less in 50.6 per cent of these cases for 174 sets of consecutively located andiroba trees. These frequent encounters indicate that potential harvesters can easily locate hundreds of andiroba trees in their optimal forest types.

Flower and Fruit Production

In the 1998 survey 49.7 per cent of the 153 trees checked had either fruits in the canopy or fruit parts on the ground. It was not known, however, if fruit valves found on the ground were produced in the current or previous year since andiroba litter fall is particularly persistent (Smith et al. 1998). This survey showed that a small percentage of trees in the 10–20 cm DBH class were reproductively active (Table 2). More trees began producing fruits in the 20–30 cm DBH class; and 63.0 per cent of trees that were ≥30 cm DBH had produced fruits within the past year. The 1999 survey showed that 33 per cent of the 203 trees visited were either flowering or had already produced young fruits by the third week of March in that year. A comparison of tree size to reproductive activity again showed that trees < 30 cm DBH rarely produced flowers or fruits while 46.1 per cent of trees ≥30 cm DBH had either fruits or flowers in the first month of the survey (Table 2).

Table 2
Relationship of Reproductive Activity to Diameter in Andiroba Trees Near Tekohaw

	1998 Survey		*1999 Survey*	
*DBH size class (cm)**	*Trees in size class*	*Fruit parts on ground (%)*	*Trees in size class*	*Reproductive in March (%)*
5–10	4	0.0	6	0.0
10–20	30	6.7	9	0.0
20–30	45	44.4	60	13.3
30–40	32	62.5	73	45.2
40–50	19	63.2	43	44.2
≥50	3	66.7	12	58.3

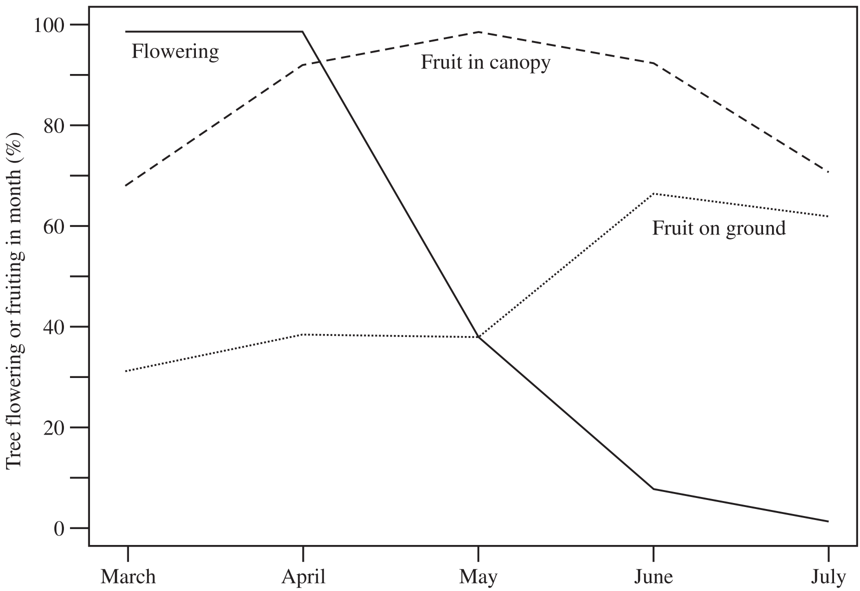
Note: * Size class upper limit is 0.1 cm less than maximum value listed in range.

The criteria for choosing the forty-six study trees for the production study was that they all flowered at some point during observations in March and April 1999. This proportion declined to 39 per cent in May and dropped to 2 per cent at the beginning of the dry season in July (Figure 1). The proportion of trees with fruit in the canopy during March was 70 per cent. This figure reached 100 per cent in May, and then declined to 72 per cent in July. In March, 33 per cent of the study trees dropped fruit on the ground during at least one day. This figure rose to a maximum of 66 per cent in June and July. The amount of fruit left in the canopy of study trees at the end of the observation period in July was very low so fruit fall likely ended for the season in the following month.

Seed Predation, Production and Harvest Efficiency

The average ±SE weight of 2,134 seeds collected during the monitoring period was 16.7 ± 0.1 g, but seeds that were whole and mature (good condition) weighed significantly more than those that had been damaged due to various factors (one-way ANOVA; $F = 151.36$, $df = 1$; $p \leq 0.001$; Table 3). This included seeds that had been subject to one or two of the following conditions: insect predation, mammal predation, immature seeds and germinating seeds. Immature seeds came from green fruits that had apparently aborted. Most of these fell in April. According to Tembé hunter examination of teeth marks on seeds partially eaten by mammals,

Figure 1
Fruiting Phenology of Andiroba Study Trees Near Tekohaw (March–July 1999)



the major consumer was the red-rumped agouti (*Dasyprocta leporina*) (Figure 2a). Other mammalian seed consumers apparently included pacas (*Agouti paca*) and brocket deer (*Mazama* spp.). Insect larvae were responsible for the largest cause of degradation of andiroba seeds. Most of these were microlepidopteran moth caterpillars (probably Pyralidae); fly maggots (probably Stratiomiyidae) also attacked some seeds (Figure 2b). Average seed weight was lowest for a small group of seeds that had germinated (Table 2). These seeds had apparently been produced from flowering that occurred well before the peak in March.

Table 3
Average Weight of Andiroba Seeds by Condition

	Number of seeds	*Weight (mean ± SE) (g)*
Good condition—whole mature	1,817	17.3 ± 0.1
Bad condition	317	13.3 ± 0.3
Insect predation	158	14.6 ± 0.4
Immature	25	14.1 ± 1.4
Mammal predation	81	13.5 ± 0.5
Insect predation and immature	23	11.1 ± 1.2
Mammal and insect predation	13	10.6 ± 1.0
Mammal predation and immature	6	4.7 ± 0.8
Germinating	11	3.4 ± 0.6
All seeds	2,134	16.7 ± 0.1

Figure 2
Andiroba Seed Predation

(a) Andiroba seeds chewed by *agouti*
(b) Insect larvae feeding in rotting andiroba seed

It was unusual to find whole fruits, but twenty-seven complete ones found during the monitoring revealed the mean number of valve capsules per fruit was 3.89 ± 0.06. While most fruits had four valves with seeds, a small percentage only had three capsule valves or had a small fourth valve with no associated seed. These whole fruits contained an average of 8.67 ± 0.48 seeds. Additional partial fruits were examined showing that one capsule valve contained up to four seeds with a mean value of 2.27 ± 0.07 seeds ($n = 240$ valves). The shape of a seed indicated whether it came from a capsule with one, two, three or more seeds. A seed's average weight varied both according to the number of seeds in the valve and its position within it. Not surprisingly, the highest average weight was that of seeds from valves with a lone seed. The next heaviest were seeds in a valve with two seeds, followed by outer seeds in valves with three or more seeds. Inner seeds from valves with three or four seeds were the smallest (Table 4). The dominance of seeds coming from valves with three or more seeds indicates that the average number of seeds per valve calculated from the smaller sample of valves collected may underestimate the true figure.

Table 4
Average Weight of Andiroba Seeds by Position in Valve

	Number of seeds	*Weight (mean ± SE) (g)*
Lone seed in valve	49	20.7 ± 1.0
Seed in valve with 2 seeds	117	17.8 ± 0.7
Outside seed in valve with ≥3 seeds	1,068	17.1 ± 0.2
Inside seed in valve with ≥3 seeds	456	15.5 ± 0.2

As indicated by the phenological observations, the quantity of fruits produced by the andiroba study trees was low from March through May, increased substantially in June, and peaked in July (Table 5). The proportion of seeds found in good condition ranged from 61 to 83 per cent in four of the five months of observation. The noticeable exception was in May when 78 per cent of the seeds found were in bad condition. The amount of available seeds was also lowest in this month. The total estimated seed production for the observation period was about seventy-four seeds (1.2 kg) per tree.

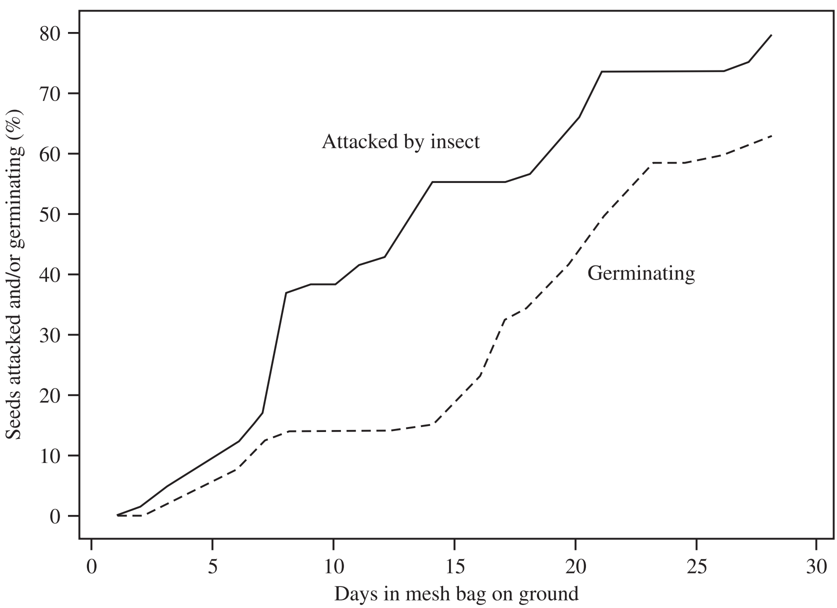
Table 5
Estimated Production and Harvest Efficiency of Seeds from Forty-six Andiroba Trees by Month at Tekohaw in 1999

	March	*April*	*May*	*June*	*July*	*Total*
Seeds found						
Number	131	225	106	710	1,107	2,279
Weight (g)	1,949	3,801	1,050	11,400	19,196	37,397
Average weight seed^{-1} by condition (g)						
Good	17.5	19.1	21.7	16.9	17.7	–
Bad	10.8	11.5	6.6	14.8	15.4	–
All	14.9	16.9	9.9	16.1	17.3	–
% In good condition	61.1	71.1	21.7	60.7	82.8	–
Estimated seed production						
Number	316	319	264	800	1,695	3,395
Weight (g)	4,701	5,397	2,619	12,839	29,395	55,702
Average weight tree^{-1} (g)	102	117	57	279	639	1,211
Harvesting efficiency						
Estimated % seeds found	41.5	70.4	40.1	88.8	65.3	–
Average seed weight found tree^{-1} (g)	42	83	23	248	417	813
Collecting days	16	15	20	18	17	86
Average seed weight found tree^{-1} day^{-1} (g)	3	6	1	14	25	–

The human harvesting efficiency as measured by the proportion of seeds found compared to the estimated total number of seeds produced averaged 67 per cent with the low point again occurring in May (Table 5). This means that wildlife carried away about 11–59 per cent of the seeds on the ground per month from March to July (average 33 per cent for this period) while people were also harvesting seeds once every one to three days. Mammals would presumably consume more seeds in the absence of human harvesting. The most sobering figure of this study was that these forty-six reproducing trees collectively yielded only 37.4 kg of seeds in eighty-six days of collecting. This yielded an average of 9 g of seeds collected per tree per day, and up to 29 per cent of these seeds were impaired or useless for oil extraction. Considering only fruit fall in the peak month of July, this average was 25 g of seeds per tree per day (Table 5). It is important to note that seed production was not evenly divided among these trees. The three most productive trees accounted for 33 per cent of the estimated total seed production by weight, and the ten most productive trees accounted for 66 per cent of the total.

The seed fate ground experiment showed that while andiroba seeds lying in a mesh bag were protected from mammal predation, they were subjected to increasing insect attacks the longer they lay there. By the end of the first week, an average of 17.2 per cent of the sixteen seeds in each of the four bags had been pierced by at least one insect entry hole (Figure 3). This figure jumped to 56.3 per cent by the end of the second week and reached 81.3 per cent by the end of the month. The rate of seed germination lagged somewhat behind these levels of insect attack. An average of 15.6 per cent of the seeds in each bag had sprouted by the end of the second week. By the end of the 28-day monitoring period, 64 per cent of the seeds had germinated, but the emergent radicle had already died on 93 per cent of these. This experiment demonstrated that even in the absence of mammal seed predation, human harvesters would have to gather fallen seeds once every few weeks in order to collect seeds in good enough condition to make oil.

Figure 3
Rate of Ground-level Insect Attack and Germination of Andiroba Seeds



Extracting Oil from Andiroba Seeds

According to one andiroba collector’s wife, transforming andiroba seeds to oil was a multi-stage process that began by boiling the seeds for at least half an hour (Figure 4a). She then set the seeds aside in a shady place for several weeks. When the seeds were dry, this woman, her husband and two to three children processed the seeds. A few people cracked open the seeds’ brown shell with a machete or wooden spoon. Other people scooped the soft seed endosperm out with metal spoons onto a metal sheet (Figure 4b). This process took an average of 0.98 ± 0.05 seeds (16.34 ± 0.80 g) per person per minute (n = 5 batches of 50 seeds). Next the seed meat was mashed and kneaded by hand into a large pasty lump (Figure 4c). This process was repeated several times over the next few days. Finally, the seed mass was set on the sloping metal sheet in direct sun. Over the course of a week, andiroba oil slowly dripped down a cloth wick into a collecting jar (Figure 4d). The mass is periodically re-mashed. The total time of oil preparation is four to five weeks.

Figure 4
Processing of Andiroba Seeds

(a) Boiling seeds
(b) Removing shells from dried seeds
(c) Mashing seed meat
(d) Leaching oil from seed meat

This same family transformed one batch of good quality andiroba seeds to oil between early April and May 1999. This batch that started with 149 seeds weighing 2568.5 g yielded 178 ml (163.8 g) of oil. This 6.4 per cent yield by weight indicates it would take 14.43 kg of seeds to produce 1 litre of oil. Five other measured batches of seeds weighing 5–10 kg each were processed between June and August 1999, but unfortunately the family consumed most of the oil before yield data were recorded.

DISCUSSION

Habitat Preferences and Density of the Resource

Andiroba trees at Tekohaw were found in both terra firme and alluvial forests with concentrations near small streams flowing through these areas. This is consistent with observations of this species in many other parts of its neotropical range (McHargue and Hartshorn 1983a; Pennington 1981; Sampaio 2000). In addition to andiroba's ability to respond well to changes in water conditions (Dünisch et al. 2002), its broad adaptability is also enhanced by its large seeds. If fruits drop in a flooded section of forest during a rainy season, the buoyant seeds can be dispersed by water and the sizeable endosperm can fuel rapid growth of a seedling to rise above the temporarily inundated forest (Scarano et al. 2003). When andiroba's fruits fall on land, some mammals readily disperse its large nutrient-rich seeds (McHargue and Hartshorn 1983a). Its fine roots are also well adapted to seasonal drought conditions (Noldt et al. 2001).

Densities of species found in other terra firme forest inventories have ranged from 0.3 to 9 trees per ha in surveys conducted in Brazil (Sampaio 2000), Costa Rica (McHargue and Hartshorn 1983a) and Surinam (Willemstein 1975). This range matches andiroba densities found in this study near Tekohaw. Higher densities have been recorded at a swamp forest in Costa Rica (62 trees per ha; trees ≥10 cm DBH [McHargue and Hartshorn 1983a]) and north-eastern Brazil (137 trees per ha; trees ≥15 cm DBH [Henriques and de Sousa 1989]).

Andiroba was noticeably absent from large areas of secondary forest in the vicinity of Tekohaw. These patches were created both by a large unintentional forest fire that burned irregularly through the area in the early 1980s and smaller areas that were recovering from slash-and-burn agriculture in the previous decade (Plowden 2001). The lack of andiroba in these areas may be due to its shade-tolerant nature and higher growth rate in natural forest gaps and enriched planting systems than in open fields or monoculture plantations (Dünisch et al. 2003; Huc et al. 1994). These traits are important to consider if communities wished to enhance andiroba density for oil or timber production.

The relatively high density of andiroba trees in both terra firme and alluvial forests near Tekohaw made it a relatively easy resource to locate. Small teams found hundreds of trees within several weeks. It took longer to locate one andiroba tree than the average 1.2 minutes it took a Tembé collector to find a host tree with harvestable titica (*Heteropsis flexuosa* [Kunth] Bunting) vine aerial roots, but it was much faster finding andiroba than copaíba (*Copaifera* spp.) trees sought for oleoresins. Five-person teams searching the same forest for *Copaifera* trees never found more than nine trees in one day (Plowden 2001). The efficiency of finding andiroba trees for seed collection, however, is reduced by the necessity of finding trees that are mature and actually producing seeds in that season. Once a group of trees that are reproducing are located, the number that can be potentially visited in one day increases as the collector establishes the most direct paths between these trees in the forest. It initially took two days for a researcher to visit all forty-six study trees. Within two weeks, it was possible to complete the rounds of these trees in just over half a day. While villagers would frequently hunt and collect a variety of NTFP during a single day for personal use, these relative harvesting efficiencies are important to compare for potentially marketable NTFP since the Tembé tend to focus on only one product per day when collecting it for commercial purposes.

Flowering and Fruit Production

Observations made during part of the reproductive cycle in andiroba at Tekohaw confirmed a pattern noted at other sites. Flowering may occur year round (Pennington 1981), but it is often concentrated in the rainy season and fruits generally mature and drop during the dry season (Sampaio 2000; Willemstein 1975). In the Amazon region, where the capsule fruits are typically 6–8 cm in diameter, fruit takes five to six months to mature (Le Cointe 1947; Pennington 1981; Willemstein 1975). This process of maturation takes up to eight months in north-eastern Brazil and Costa Rica where fruit capsules are larger (9–14 cm; Henriques and de Sousa 1989; McHargue and Hartshorn 1983a), and may even take up to a year (Pennington 1981; Record and Hess 1943).

As seen at Tekohaw and the rest of Pará, andiroba flowers in February and March. Further west in the state of Amazonas, this process begins in December (Sampaio 2000). Flowering can start as early as August in some parts of the Amazon, north-eastern Brazil, Costa Rica and Surinam (Henriques and de Sousa 1989; McHargue and Hartshorn 1983a; Shanley et al. 1998; Willemstein 1975). Trees are generally in flower for three to six weeks (Willemstein 1975). As found in this study, fruiting peaks have been observed elsewhere between March and July (Henriques and de Sousa 1989; McHargue and Hartshorn 1983a; Sampaio 2000; Willemstein 1975). Individual trees produced fruit in Surinam for about four weeks (Willemstein 1975). In Costa Rica, trees appear to have good fruit production about every other year (McHargue and Hartshorn 1983b).

The lesson from this study and its comparison to observations of flowering and fruiting patterns in other locations is that andiroba seed production may be concentrated in a few months or spread out over much of the year. In places where it is concentrated, harvesting will be more efficient for people. If this concentration occurs in the rainy season when many other fruits are available, human harvesting may have little conflict with other mammal consumers. If fruit fall peaks in the dry season (as observed in this study) when fewer fruit resources may be available, human collectors may compete more directly with wildlife for the andiroba seeds that make it to the ground.

In Surinam, andiroba trees generally begin to flower when they are 6–8 years old and begin fruiting when 10–12 years old (Willemstein 1975). Based on growth rates from plantations (Bauch and Dünisch 2000), this is consistent with Henriques and de Sousa's (1989) classification of adult *C. guianensis* trees as ones that are ≥16.0 cm DBH. Hall et al. (1994), however, consider reproductive trees of this species to be ones that are ≥35 cm DBH. At Tekohaw some trees that were <20 cm DBH did produce fruits, but they accounted for a very small proportion of individuals in this size class. It seems more reasonable to classify trees as adults at this site when they are >20 cm DBH since at least 44 per cent of the andiroba trees observed in this size class (20–30 cm DBH) or larger in 1998 had fruits on the ground (Table 2). More precise studies of andiroba growth rates and average size and age of maturity will allow harvesters to better assess the total potential harvest from a given population and evaluate how long it would take for measures such as enrichment planting to add to increase the andiroba resource base in an area.

Seed Production

The average size of whole fruits found in Tekohaw, and the Amazon region in general, seems to be smaller than in north-eastern Brazil and Costa Rica. The average range of seeds per fruit (8–16) is larger in South America than Central America (Henriques and de Sousa 1989; McHargue and Hartshorn 1983a; Pinto 1956; Record and Hess 1943). The average number of seeds per valve is predictably higher in Amazon sites (2.27 in this study) than places with fewer seeds per fruit, for example in Costa Rica, where McHargue and Hartshorn (1983a) found 1.67 seeds per valve. The average weight per seed is correspondingly higher in Costa Rica where the range was 25–35 g per seed with some large seeds weighing more than 100 g (Hall et al. 1994; McHargue and Hartshorn 1983a). Reported figures for andiroba seeds in Brazil range from the 16.7 g per seed found in this study, to 21 g per seed (Pinto 1956), and 20–30 g per seed (Fisch et al. 1995).

It is much harder to define the typical range for total annual production of seeds from this species because no comprehensive studies have been done. Estimates of andiroba seed production in Brazil have ranged from 50–200 kg $tree^{-1}$ $year^{-1}$ (Le Cointe 1947; Shanley et al. 1998). McHargue and Hartshorn (1983a) found an average of 2,500 seeds per tree (estimated weight 80.2 kg) from three trees at La Selva in Costa Rica. Rankin (1978) collected an average of 484 seeds per tree from ten trees in Trinidad in one season. Since many other seeds had been removed by mammals, she estimated total seed production at 1,826 seeds per tree (31–58 kg depending on average seed weight) based on McHargue and Hartshorn's (1983a) ratio of *C. guianensis* tree size to estimated seed production in Costa Rica. Tembé Indians in the Guamá river area of the same reserve as this study estimated that andiroba trees yielded about 10–30 kg of seeds per year.

These literature estimates of total andiroba seed production are clearly much higher than the average of 74 seeds (1.2 kg per tree) estimated from the forty-six trees in this study. This low average may have reflected an off year for the trees in the study, but it would have been even lower if the study had investigated a random sample of trees that included ones with no reproductive activity. The important lesson of comparing these widely divergent estimates is to recognise that realistic seed production estimates for a population need to be based on a wide cross-section of trees investigated for a number of consecutive years. Forget (1996) showed that seed production was steady for two years in andiroba's close relative *C. procera* DC and then dropped to 50 per cent of these levels in the third year. As found in this study, he also showed that a few trees dominated total seed production in a given year. Four of his twenty study trees produced 68 per cent of the total seed yield in one year.

Seed Predation and Harvest Efficiency

Other authors have routinely noted the infection of andiroba seeds by insect larvae. The best documented attackers are *Hypsipyla ferrealis* Hampson and its infamous shoot-borer relative *H. grandella* Zeller (Lepidoptera, Pyralidae). Both are small moths that plague various Meliaceae trees including andiroba and mahogany (Becker 1973; McHargue and Hartshorn 1983b; Record and Hess 1943). Two studies in Costa Rica estimated that *H. ferrealis* attacked an average of 36.3–50 per cent of *C. guianensis* seeds (Becker 1973; Santander and Albertin 1978). Rankin (1978) found that an average of 29 per cent of seeds from *C. guianensis* in Trinidad were infected by larvae or pupae of an unknown phycitinid moth (Pyralidae) in a different genus than *Hypsipyla*. The 10.6 per cent of seeds found infected by insect larvae in this study clearly underestimated the infection rate since seeds in bad condition were not collected for detailed examination during May and the first three weeks of June.

The degree to which larval infection would reduce the quantity of seeds available for human collection and oil production would depend both on how long the larvae had been feeding on the seed before it fell and how long the seed lay on the ground before the collector picked it up and processed it. Becker (1973) found *H. ferrealis*' developmental process from egg eclosion to adult emergence lasted an average of thirty-five days, therefore regular collection from trees would reduce loss to insects, since some infected seeds retained most of their endosperm at the time of collection, while others were already completely converted to larval biomass and waste. My finding that insects also steadily infect healthy seeds on the ground reinforces the need for timely collection of fallen seeds.

The role of mammals also needs to be considered to fully evaluate the intensity of predation on andiroba seeds. In addition to ones that Tembé hunters identified as andiroba seed consumers, peccaries (*Tayassu* spp.) have been prominently noted as *C. guianensis* seed eaters in Costa Rica (McHargue and Hartshorn 1983a). Using piles of seeds placed in various forest sites in Trinidad, Rankin (1978) observed that an average of 24 per cent of *C. guianensis* seeds were initially attacked by insect and mammal predators. Another 61 per cent were removed from the site without attack. Many of these were presumably scatter-hoarded and buried by agoutis. So while 85 per cent of these seeds were apparently destroyed on site or removed, only 59 per cent were actually lost because some of the seeds removed by agoutis were not subsequently consumed. Andiroba seeds that are buried do not germinate any better than seeds on top of the ground (Guariguata et al. 2002), but seeds dispersed by agoutis may have a better chance of surviving than ones left under the parent tree because they are less likely to be attacked by insect larvae that focus on these concentrations of seeds (Forget et al. 1999; Rankin 1978).

The average estimated amount of seed removal by mammals from the study trees at Tekohaw was 33 per cent (Table 5) although this intensity varied from 11 to 60 per cent in the five months of observation in 1999. The extent of agouti predation in general may be influenced by the density of its population, which may vary with the intensity of indigenous hunting. Informal observations of hunter catches at Tekohaw demonstrated that this animal was often killed. Agouti densities in moderately to heavily hunted areas throughout the Brazilian Amazon were 38 per cent of the levels found in areas with little or no hunting, although the differences were not statistically significant (Peres 2000). It is also possible that andiroba seed removal rates by agoutis in this study were lower than observed by Rankin (1978) because her seed piles were available for animals to eat for many days, while wildlife usually only had access to freshly fallen seeds for 24–48 hours between the times the researcher visited each study tree. The variability of agouti predation on *Carapa* seeds within a season is also likely determined by the abundance of other fruits. Rankin (ibid.) found that *C. guianensis* was a highly preferred seed food for agoutis because of its nutritive value and lack of noxious chemicals. The only species whose seeds were more preferred did not have a shell that required as much handling time. Forget (1996) noted that the percentage of seeds that were removed and cached steadily increased as the fruiting season of *C. procera* proceeded in French Guiana; this was accompanied by a decline in the proportion of seeds that were immediately consumed. This is consistent with Henry's (1999) finding that agoutis ate primarily fleshy fruits when these were abundant in the rainy season. As the year progressed they gathered more seeds for immediate consumption and cached them for food during the dry season when few fleshy fruits were available.

People wishing to collect andiroba seeds for oil production may view agouti consumption of these seeds in several ways. A tree with abundant fruits is likely to be a focal tree in the home range of an agouti as long as fruits are regularly falling (Silvius and Fragoso 2003). Since human collectors wish to use their time efficiently as well, they would probably concentrate their efforts on the most actively reproducing trees during their most productive times. This situation potentially makes agoutis and human collectors direct competitors for this resource. Daily human collection must cut considerably into the amount of seeds that agoutis can gather and vice-versa because agoutis will feed on seeds encountered on the ground for many days (Rankin 1978). To a certain extent, people can compensate for this loss to wildlife by collecting seeds from more trees. Rather than trying to devise schemes to completely shut off agouti seed predation, a longer-term but still self-serving view would indicate that allowing agoutis to take a healthy share of this resource helps enhance the regeneration of this important tree and maintains a healthy population of an important game animal. A challenging and so far unanswerable question is whether intensive human harvesting has a detrimental impact on agoutis by reducing the amount of food available to them when other potential resources are at a minimum. If this was found to be true, one strategy to balance the needs of both humans and agoutis would be to restrict harvesting from certain heavily producing trees each season. It is also necessary to assess if systematic seed removal by people could ultimately reduce the level of seedling establishment of andiroba.

Extracting Oil from Andiroba Seeds

So far only anecdotal information is available about the yield of andiroba oil from traditional methods of processing the seeds. Estimates vary from 3.4 kg of seeds to a litre of oil (Souza, personal communication) to 5.56 kg (Shanley et al. 1998), and even 9.1 kg of seeds to a litre of oil (van Andel 2000). Tembé in the Guamá area of the reserve stated they used about 9 kg of seeds to make a litre of oil. These are all better yields than the 14.4 kg seeds per litre of oil ratio found in this study.

Assuming that andiroba seeds in the same region contain roughly the same amount of oil, the components of processing that may account for these yield differences are the length of time the seeds are boiled, the amount of time they are left in the shade, the extent to which the softened seed mass is mashed, and the duration and temperature at which the seed mass is left in the sun for the oil to leach out. Pinto (1956) states that industrial processing has a 30–34 per cent seed-to-oil ratio by weight compared to traditional processing that has a maximum yield of 18 per cent by weight. Since this oil has an average density of 0.92 g per ml (ibid.), this is equivalent to needing 5.11 kg of seeds for a litre of oil. An industrial andiroba oil maker, however, stated he only achieves a 10 per cent yield of oil by weight (Morais, personal communication). Further field studies are clearly needed to better document the yield using traditional methods.

Conclusions

Compared to many other potentially commercial NTFP resources found in Tekohaw and other parts of the Brazilian Amazon, andiroba is a relatively abundant tree. Its seeds are easily collected, the traditional process for extracting is readily usable and sellable oil is well known in Tembé villages, and oil extraction requires little cost for materials. Initially, harvesting and processing andiroba seeds to produce a marketable oil seemed to offer an easy new economic option for people in this reserve. This study, however, provided some concrete evidence that other factors reduced the economic attractiveness of this product in this area. While andiroba density was relatively high compared to many other NTFP, trees generally had to be ≥30 cm DBH to produce a reasonable amount of fruit, and only a portion of trees in the population produced seeds in any given year. Even if a strategic collector visited only the most productive trees in their peak fruiting seasons, a significant amount of seeds would be lost to insect and wildlife predation. In contrast to their two main commercial NTFP that needed little or no processing to sell, Tembé people understood that making andiroba oil required regular attention over a period of several weeks. If the time devoted to collecting and processing seeds is combined, this venture would barely net a few dollars per day of labour because the oil sells for about $3 per litre. The returns would be more favourable during years when trees are particularly productive since this would reduce the amount of time needed to collect seeds. Since manual processing is time consuming, however, and has poorer yields than mechanical methods, it is not surprising that some forest dwellers only collect seeds and sell them to businesses that make oil in small urban-based factories (Morais, personal communication). For communities with access to abundant andiroba populations, though, purchasing a seed-oil press may be a sound long-term investment since seeds would yield more oil in less time.

The question of how systematic andiroba seed removal by people might affect other mammalian consumers and the regeneration potential of the trees remains open. If human harvesting seemed economically viable, one method of maintaining the resource for people and wildlife would be to consider enrichment planting of seeds in some forest gaps since they germinate easily (Fisch et al. 1995; Scarano et al. 2003) and thrive in these situations (Dünisch et al. 2003).

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