

Flowering phenology and pollination biology of *Ceiba pentandra* (Bombacaceae) in Central Amazonia

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ABSTRACT. The flowering and fruiting phenology, floral biology, pollination ecology, and breeding system of the emergent tree *Ceiba pentandra* were studied in the Brazilian Central Amazon. Of the 21 trees studied, 17 flowered once or twice during the 6-y study period. The mass flowering and relatively high production of nectar per flower (mean of 310 µl) resulted in a high nectar production (over 200 l per tree per season). Flowers were visited by a wide range of nocturnal (bats, marsupials, night monkeys, hawk moths) and diurnal (bees, wasps, hummingbirds) animals, but only phyllostomid bats, especially *Phyllostomus hastatus* and *Phyllostomus discolor*, played a relevant role promoting cross-pollination. Pollinations which occurred in the early morning by diurnal floral visitors were ineffective since pollen tubes did not traverse the style and reach the ovary before stylar abscission. Despite the apparently normal growth of the self-pollen tubes, controlled pollinations carried out in one tree revealed no fruit set by selfing and 16.8% fruit set by crossing. Progeny analysis from this 'self-incompatible' tree using isozyme markers showed that fruits resulting from mixed-pollination (i.e., 50% self- plus 50% cross-pollen on the stigma) set only 1.6% of selfed seeds. The percentage of outcrossed seeds in fruits resulting from open-pollination in two neighbouring planted trees, which flowered in isolation and concomitantly, was estimated at 91% and 71%. Two isolated trees did not set any fruits despite massive flowering, whereas two others set large quantities of seed, supporting data in the literature stating that variable degrees of self-fertility may occur in this species.

RESUMO. A fenologia de floração e de frutificação, a biologia floral, a ecologia de polinização e o sistema reprodutivo da árvore emergente *Ceiba pentandra* foram estudados na Amazônia Central Brasileira. Dezesete das 21 árvores estudadas (doze nativas e nove plantadas de sementes de procedência desconhecida) floriram uma ou duas vezes cada uma durante os seis anos do estudo. A maior parte das árvores nativas floriu massivamente somente em 1993 e 1996, enquanto que algumas das árvores plantadas floriram massivamente somente em 1992 e 1997.

A floração massiva e a relativamente alta produção de néctar por flor (média de 310 µl de néctar secretado por flor por noite) resultaram em uma alta produção de néctar por árvore (mais de 200 l de néctar por árvore por estação de floração). As flores de *C. pentandra* foram visitadas por uma grande variedade de animais noturnos (morcegos, marsupiais, macacos-da-noite, mariposas) e diurnos (abelhas, vespas, beija-flores), mas somente morcegos, especialmente *Phyllostomus hastatus* e *Phyllostomus discolor*, parecem exercer papel relevante promovendo a polinização cruzada. Não foram detectadas diferenças na capacidade dos tubos polínicos originados do auto-pólem e do pólem cruzado de se desenvolverem até o ovário e penetrarem nos óvulos. Polinizações que ocorreram no início da manhã foram inefetivas, uma vez que os tubos polínicos não tiveram suficiente tempo para atravessarem o estilete antes da sua abscisão. Apesar do aparente desenvolvimento normal dos tubos polínicos oriundos do auto-pólem, polinizações controladas executadas em uma árvore resultaram em nenhuma produção de frutos em flores auto-polinizadas e em 16,8% de produção de frutos nas flores que sofreram polinização cruzada. A produção natural de frutos (polinização aberta) na mesma árvore foi estimada em 0,7%. O uso de marcadores isoenzimáticos na análise genética da progênie dessa mesma árvore 'auto-incompatível' revelou que, em frutos resultantes de polinizações mistas (isto é; uma mistura contendo 50% auto-pólem e 50% pólem cruzado, depositada no estigma), apenas cerca de 1,6% das sementes foram originadas por eventos de auto-fecundação. A proporção de sementes originadas por fecundação cruzada em frutos formados naturalmente em duas árvores plantadas e vizinhas, que floriram isoladamente e concomitantemente em 1992, foi de 91% e 71%, respectivamente. Duas árvores isoladas não produziram frutos, apesar de intensa floração, enquanto que outras duas também isoladas frutificaram em abundância. Essas observações reforçam dados da literatura que indicam a ocorrência de níveis muito variáveis de auto-fertilidade entre as árvores dessa espécie.

KEY WORDS: Amazonia, bat-pollination, Bombacaceae, breeding system, *Ceiba*, mating system, *Phyllostomus*, pollination, reproductive biology, tropical trees

INTRODUCTION

Ceiba pentandra (L.) Gaertn. (Bombacaceae), the silk-cotton or kapok tree, is an emergent, fast growing tree species with a pan-tropical distribution. Native populations occur in tropical America and west Africa, while populations in south-east Asia were probably introduced by man (Baker 1965). Studies carried out in west Africa, south-east Asia and the Pacific Islands indicate that this species is visited and pollinated by pteropodid bats (Baker & Harris 1959, Cox 1983, Elmqvist *et al.* 1992, Harris & Baker 1959, Wodzicki & Felten 1975). Despite adaptations for bat-pollination, the palaeotropical trees of *C. pentandra* exhibit relatively high levels of self-fertility: Toxopeus (1948) stressed that *C. pentandra* is a highly self-pollinating species in south-east Asia, and later he reported that only 16% outcrossing occurred in Java plantations (Toxopeus 1950); Baker (1955, 1965) considered individuals of *C. pentandra* in Africa 'fully self-fertile' and that 'only a single viable seed . . . could be the founder of a new colony'; van der Pijl (1956) explained the fruiting of *C. pentandra* in the

Pacific Islands as the result of the introduction of self-fertile forms; and Elmquist *et al.* (1992) reported that 10% of geitonogamously pollinated flowers developed fruits in a tree in Samoa, but these flowers have not been bagged to avoid visits from bats.

In the neotropics, bats and other nocturnal and diurnal vertebrates have been observed as visitors and potential pollinators of the silk-cotton tree. Carvalho (1960) described bats with a large wingspan, which he supposed to be *Phyllostomus hastatus*, visiting *C. pentandra* flowers near Belém, eastern Amazonia. Villa (1966) noted the bats *Artibeus jamaicensis* and *Leptonycteris nivalis* visiting *C. pentandra* flowers in Mexico. Heithaus *et al.* (1975), working in a seasonal forest in Costa Rica, captured seven bat species with *C. pentandra* pollen on their fur. Toledo (1977) recorded that three non-flying mammals, various unidentified bats, seven species of hummingbirds and 26 other birds, as well as several insects, visited the flowers of *C. pentandra* in south-eastern Mexico, and this author considered the possibility of pollination by non-hovering birds. Effective pollination of *C. pentandra* by diurnal animals was also proposed by Janson *et al.* (1981) in south-eastern Peru, where these authors observed three monkey species (*Saimiri sciureus*, *Cebus apella*, and *Ateles paniscus*) visiting the flowers and suggested that these animals may have a significant role in the pollination of *C. pentandra*. The mating system of neotropical populations of *C. pentandra* has been studied only by Murawski & Hamrick (1992) on Barro Colorado Island, Panama. These authors, using isozyme markers, found a range from complete selfing to complete outcrossing among the 11 trees studied and considered that a combination of several ecological and genetic factors may be the cause of the wide range in the degree of self-fertility observed among trees of this species.

The main goal of this study is to provide data on the floral phenology, floral biology, pollination ecology, and breeding system of *C. pentandra* in Central Amazonia and to compare data from this area with studies in peripheral areas of the range of this species. Because of the problems of working with a canopy emergent tree, we have detailed observations for only a few individuals. We report observations on the floral biology and the behaviour of the flower visitors made from platforms placed in the canopies of *C. pentandra* trees in two different localities. We also provide a gross estimate of some reproductive parameters (total flower and fruit production, fruit set, nectar secretion and sugar concentration) which are still poorly quantified for this species, and report the results of hand self- and cross-pollination experiments, including the relative performance of the self- and cross-pollen tubes, carried out on one tree. More knowledge is necessary regarding the reproductive biology of this species in Central Amazonia since native populations of *C. pentandra*, at least in the Brazilian and Peruvian Amazon, have suffered a drastic reduction over the last two decades due to overexploitation by the plywood industry (Gentry & Vasquez 1988).

MATERIALS AND METHODS

The species

Neotropical populations of *C. pentandra* range from northern Central America and the Antilles to the southern boundary of the Amazon Basin in Brazil and Peru. In Central Amazonia, *C. pentandra* (locally called 'sumaúma') occurs in the lowland, seasonally flooded habitat ('várzea') along the sedimentary quaternary basin of the white-water rivers. It is a striking emergent tree, up to 60 m tall, with large plank buttresses. The trunk is covered with conical, sharply pointed spines. Sumaúma is a deciduous tree, shedding its digitate-compound leaves during the dry season, when mass flowering occurs.

The inflorescences are fascicles that are borne mainly at the ends of the branches, with buds initiated in the axils of leaves just before the latter are dropped. The flowers have nocturnal anthesis, with 1–20 flowers opening per inflorescence per night. The five petals, five staminal filaments and pistil are creamy white giving a mostly whitish colour to the flowers and inflorescence, spotted with the gold-yellow of the anthers. Most flowers are inclined or pendant, thus giving a globose appearance to the whole inflorescence.

The fruits are elliptic, pendant, brown capsules that dehisce by five valves. In each capsule there are 66–250 ovoid seeds, 4–6 mm in diameter, weighing 45–65 mg, surrounded by the pale yellow silk cotton, which develops from the endocarp. The seeds have a 'float structure' in their basal portion, indicating that in addition to wind dispersal, they can also be dispersed by water.

Flowering and fruiting phenology

Flowering and fruiting were monitored monthly, between 1992 and 1997, in eight young (20-y-old in 1992) planted trees on the campus of the Instituto Nacional de Pesquisas da Amazônia (INPA) in the Manaus urban area, Amazonas, Brazil (c. 03°08'S, 60°00'W), and in 10 wild trees located in or near Manaus, most of them on the Catalão Peninsula at the junction of the Negro and Solimões Rivers. The flowering and fruiting phenologies of two additional wild trees were followed in 1996 and 1997, and that of one planted tree at the INPA's Estação Experimental de Silvicultura Tropical, 60 km N of Manaus, between 1992–1995. All 12 wild *C. pentandra* were large, mature trees, 40–60 m tall, except for tree 12a, which was smaller and younger. Flowering was scored as 'massive' when all main and secondary branches of the tree set flower, or as 'partial' when only 1–2 main branches set flower. No intermediate situation was found. The same criterion was used for fruiting.

The total number of flowers and fruits set by trees 1 and 2 were estimated using four 1-m × 1-m quadrats set at random in the canopy shadow area beneath each tree. The pistils, immature fruits, and valves inside each quadrat were removed and counted weekly during the flowering and fruiting periods. A 10-m radius circle around the trunk base was considered as the pistil and valve shadow area for each tree.

Floral biology and pollination ecology

Some initial observations and captures of floral visitors were made in a 30-m tall tree located on the bank of the Uraricoera River, Maracá Biological Reserve (c. 03°20'N, 61°20'W), Roraima, Brazil, in March 1988. Floral events and behaviour of floral visitors were observed from a platform placed between two branches within the crown. Visitors were captured with a 4.0-m × 2.8-m nylon mist-net placed beside the platform.

Detailed observations on the floral biology and visitor behaviour were made from August to September 1993, a period during which trees 1 and 2 (located 15 m apart) flowered. Studies were made using a platform placed on top of a 20 m scaffold beside tree 1. On the INPA campus, the bats were captured with 12-m × 2.8-m mist-nets suspended from two branches and placed just below the canopy 20–22 m above ground. Bats foraging near the platform were also caught directly by hand as they alighted on the inflorescences.

The following sequence of floral parameters was noted: anthesis, odour release, nectar secretion, pollen liberation, and receptivity of stigmas. Nectar secretion was measured at 2-h intervals with a 15 µl capillary tube in 10 flowers of different inflorescences from tree 1. The sugar concentration of the nectar was estimated every 2 h for the same flowers using a pocket refractometer. Samples of pollen attached to the bats' fur were collected for further analysis using the technique described by Beattie (1971).

Hand pollinations

A series of hand self-, cross-, and mixed-pollinations were carried out using flowers of tree 1, accessible from the platform, and pollen from tree 2. Flowers from tree 2 were obtained with the aid of a ladder and a 16-m pruning hook. A mixture of self- and cross-pollen was used to carry out mixed-pollinations. The pollen load for the mixed-pollinations was obtained by loading the pollen of five flowers from tree 1 and five flowers from tree 2 in a Petri dish, thoroughly mixing the mass of pollen, and depositing the mixture on the stigma with a spatula. For these three pollination treatments, buds were opened, emasculated and enclosed with paper bags just before anthesis. Pollinations were carried out at 20h00–21h00, after which flowers were again covered until 10h00–11h00 the next morning. In the diurnal cross-pollination treatment, buds were emasculated before anthesis and rebagged and pollinated at 06h00–06h30 the following morning. To check for apomixis, flowers were emasculated and bagged without further treatment and unbagged at 10h00 the following morning. A series of untreated flowers were tagged the morning following anthesis to monitor natural fruit-set. Most hand self- or cross-pollinated flowers were left to census for fruit-set, but 32 pistils were fixed in FAA (formalin, acetic acid, 70% ethanol in proportions 5:5:90 v/v) at 12, 24, 48 and 72 h following pollination to allow further observation of pollen germination and pollen tube growth using fluorescence microscopy and aniline blue staining (Martin 1959). The proportion of penetrated ovules in self- and cross-pollinated pistils

was assessed by scraping out ovules and scoring for the presence of pollen tube 'tails' at the micropyle. Comparisons of the proportion of penetrated ovules in self- and cross-pollinated pistils were tested with a t-test of means. All proportions were arcsine-transformed prior to statistical analysis.

Determination of male parentage of the seedlings

To estimate the proportion of selfed and outcrossed seeds in fruits resulting from mixed- and open-pollinations, we used starch gel electrophoresis to characterize tree 1, tree 2 and their seedlings at the cytosolic phosphoglucose isomerase (PGI) locus. Seeds from fruits sired by mixed- and open-pollinations were germinated in a glass house and leaf samples of those seedlings, tree 1 and tree 2 were assayed for the PGI locus as described in Gribel & Abbott (1996). Trees 1 and 2 are neighbouring trees (15 m apart) which flowered in isolation and concomitantly in August 1992, when no other flowering trees were found in the study area, except tree 15 located 60 km away. Therefore, it was assumed that these two trees exchanged pollen only between themselves during the flowering period of 1992.

RESULTS

Flowering and fruiting phenology

Most wild trees flowered massively in 1993 and 1996, while some of the planted trees flowered massively only in 1992 and 1997 (Table 1). Four cultivated trees at INPA campus did not flower at all during the 6-y study period. Massive flowering was followed by 'massive' fruiting (i.e., at least one fruit formed per inflorescence) in all cases except for two spatially isolated trees: the wild tree 12 in 1993 and 1996, and the cultivated tree 15 in 1992. In contrast, tree 13, which flowered prematurely in July 1996, and tree 12b, which flowered in relative isolation in 1997, set fruits massively. No partial flowering episode resulted in fruits.

The number of flowers per m² of canopy shadow (i.e. number of valves/5 + number of pistils + immature fruits per square) was 2085 ± 444 for tree 1 and 845 ± 203 for tree 2 (mean ± SD). Therefore, total flower production per tree, within the 10-m radius, was estimated to be 655 000 and 265 000, respectively. The total fruit production for trees 1 and 2 (given the number of fruits per m² of canopy shadow = number of valves inside quadrat/5) was estimated to be 4930 and 5890 fruits, respectively. Fruit-set per tree (number of fruits/number of flowers per square × 100%) was estimated to be 0.75% for tree 1 and 2.22% for tree 2.

Floral biology

Anthesis started at dusk, usually between 18h15–18h30. By 18h45–19h15 the flowers were open and the anthers and stigmas were exposed. The stigma was wet and seemed to be receptive just following anthesis. Anther dehiscence

Table 1. Flowering and fruiting in 17 *C. pentandra* trees in the Manaus area between 1992 and 1997.

Tree number	Status ¹	Phenology ²	Intensity and month of activity in ³					
			1992	1993	1994	1995	1996	1997
1	P	Fl	M (Aug)	nf	nf	nf	nf	M (Aug)
		Fr	M (Oct)	nf	nf	nf	nf	M (Oct)
2	P	Fl	M (Aug)	P (Aug)	nf	nf	nf	M (Aug)
		Fr	M (Oct)	nf	nf	nf	nf	M (Oct)
3	P	Fl	nf	nf	nf	nf	nf	M (Aug)
		Fr	nf	nf	nf	nf	nf	M (Oct)
4	P	Fl	nf	nf	nf	nf	nf	M (Aug)
		Fr	nf	nf	nf	nf	nf	M (Oct)
7	W	Fl	nf	M (Aug)	nf	nf	nf	nf
		Fr	nf	M (Oct)	nf	nf	nf	nf
8	W	Fl	nf	M (Aug)	nf	nf	died	—
		Fr	nf	M (Oct)	nf	nf	died	—
9	W	Fl	nf	M (Aug)	nf	nf	nf	nf
		Fr	nf	M (Oct)	nf	nf	nf	nf
10	W	Fl	nf	M (Aug)	nf	nf	M (Aug)	nf
		Fr	nf	M (Oct)	nf	nf	M (Oct)	nf
10a	W	Fl	nf	M (Aug)	nf	nf	M (Aug)	nf
		Fr	nf	M (Oct)	nf	nf	M (Oct)	nf
11	W	Fl	nf	M (Aug)	P (Apr)	nf	M (Aug)	P (Aug)
		Fr	nf	M (Oct)	nf	nf	M (Oct)	nf
11a	W	Fl	nf	nf	nf	nf	nf	P (Aug)
		Fr	nf	nf	nf	nf	nf	nf
12	W	Fl	nf	M (Aug)	nf	nf	M (Aug)	P (Aug)
		Fr	nf	nf	nf	nf	P (Oct)	nf
12a	W	Fl	nf	nf	nf	nf	M (Aug)	nf
		Fr	nf	nf	nf	nf	M (Oct)	nf
12b	W	Fl	nf	nf	nf	nf	nf	M (Aug)
		Fr	nf	nf	nf	nf	nf	M (Oct)
13	W	Fl	?	?	?	?	M (Jul)	nf
		Fr	?	?	?	?	M (Set)	nf
14	W	Fl	?	?	?	?	M (Aug)	?
		Fr	?	?	?	?	M (Oct)	?
15	P	Fl	M (Aug)	nf	nf	nf	?	?
		Fr	nf	nf	nf	nf	?	?

1. P, planted; W, wild.

2. Fl, flowering; Fr, fruiting.

3. M, massive flowering or fruiting; P, partial flowering or fruiting; nf, no flowering or fruiting; ?, no data.

usually occurred as the stamens were exposed, but in the absence of wind or in conditions of high humidity, pollen release was sometimes postponed by up to 1 h. The flowers lasted just one night, and petals, stamens, and the style abscised during the following morning.

The flowers had $108 \pm 36 \mu\text{l}$ ($n = 10$) of nectar accumulated around the ovary just after the petals opened at 19h00. The secretion rate decreased from anthesis to 03h00, when it ceased. The total volume secreted by a flower per night was $310 \pm 75 \mu\text{l}$ ($n = 10$). The nectar contained 19.7% (range 18–21%) sugar (sucrose equivalents) at the beginning of the night, and became increasingly more dilute, reaching 11.5% (range 10–13%) by the end of the secretion period (Figure 1). Due to the pendant or tilted orientation of most flowers in the inflorescences, the nectar usually dripped from the flowers, causing a 'sweet rain' beneath the trees during the period of nectar secretion.

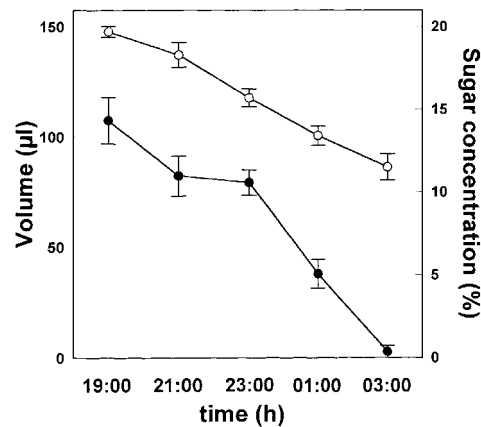


Figure 1. Cumulative nectar production (●) and sugar concentration (○) in nectar of *Ceiba pentandra* flowers (mean \pm SE, n = 10 flowers).

Controlled pollinations

The ovaries of all hand self-pollinated flowers were retained for 5–7 d, during which time they showed some enlargement, but after that they aborted at an abscission layer in the pedicel 25–30 mm below the receptacle. Most cross-pollinated flowers were also similarly aborted within 7 d. Diurnally cross-pollinated flowers were aborted 24–48 h following anthesis, as were the bagged unpollinated flowers (apomixis controls).

The pollination tests (Table 2) revealed that tree 1 was functionally self-incompatible since none of the 407 selfed flowers set fruit. No fruit was produced in the non-pollinated flowers (apomixis controls) nor in the diurnally cross-pollinated flowers. Fruit-set in naturally pollinated flowers was only 0.7%. Deposition of self-pollen mixed with cross-pollen negatively affected fruit-production ($\chi^2 = 6.49$, $df = 1$, $P = 0.011$) and number of seeds per fruit ($F = 4.21$, $df = 1$, $P = 0.044$) compared with cross-pollination.

Male parentage of the seedlings

Electrophoretic studies of PGI revealed that trees 1 and 2 differed in this dimeric enzyme, with tree 1 exhibiting a three-banded phenotype (i.e., the

Table 2. Pollination tests, fruit-set and number of seeds per fruit in a tree of *Ceiba pentandra* in the Manaus area.

Treatment	Pollen load	Pollination time	Number of flowers treated	Fruit-set (%)	Seeds/fruit (mean \pm SD)
Apomixis control	–	–	158	0.0	–
Self-pollination	100% self	20:00	407	0.0	–
Cross-pollination	100% cross	20:00	286	16.8	170.5 \pm 41.5 (n=46)
Mixed-pollination	50% self 50% cross	20:00	241	8.7	147.0 \pm 43.6 (n=19)
Diurnal cross-pollination	100% cross	06:00	47	0.0	–
Open-pollination	?	?	282	0.7	104.4 \pm 36.1 (n=20)

Table 3. Maternal and offspring genotypes at PGI-2 and estimate of percentage of outcrossed seeds in fruits of *Ceiba pentandra* resulting from mixed- and open-pollinations.

Maternal tree (genotype)	Offspring genotypes			total	Estimate of outcrossed seeds (%)
	<i>aa</i>	<i>ab</i>	<i>bb</i>		
Tree 1 (<i>ab</i>)					
Mixed-pollination	2	254	241	497	98.4
Open-pollination	5	103	114	222	91.0
Tree 2 (<i>bb</i>)					
Open-pollination	–	61	110	171	71.3

heterozygous genotype designated *ab*) and tree 2 having a single-banded phenotype for the PGI enzyme of lower electrophoretic mobility (i.e., the homozygous genotype *bb*). A quarter of the mixed-pollinated progeny resulting from selfing in tree 1 was expected to exhibit the homozygous *aa* genotype, whereas no seedling with this genotype could be found among the progeny resulting from crossing. In tree 2, any seedling resulting from selfing should exhibit the homozygous *bb* genotype, whereas the expected progeny genotypic ratio was 1 *ab*:1 *bb* among seedlings resulting from crossing. The use of electrophoresis to estimate the ratio of outcrossed seedlings (Table 3) suggested that tree 1 was predominantly outcrossed (91 and 98% of outcrossed seeds in fruits sired by open- and mixed-pollinations, respectively), whereas tree 2 seemed to be somewhat more self-fertile (71% of outcrossed seeds in fruits resulting from open-pollination).

Pollen tube performance

Fluorescence microscopy showed that both self- and cross-pollen grains germinated on the stigma and produced tubes growing toward the ovary, where, at 24 h post-pollination, some 25–30% of the ovules were penetrated. The proportion of penetrated ovules increased slightly between 24–48 h and 48–72 h, reaching a maximum of 42–45% for both treatments (Figure 2). The proportion

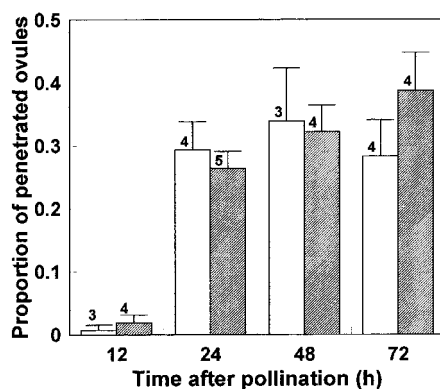


Figure 2. Proportion of ovules penetrated by pollen tubes in self- and cross-pollinated pistils (white and striped bars respectively) of *Ceiba pentandra* 12, 24, 48 and 72 h following pollination. Column heights indicate a mean of 3–5 pistils and error bars represent the upper half of 95% confidence intervals. The numbers above the bars represent the number of pistils assessed.

of ovules penetrated by self- and cross-pollen tubes were not significantly different within each time period (t-test of means, $P > 0.05$). The absolute percentage of penetrated ovules should be interpreted with caution because an unknown proportion of them could have been penetrated despite the lack of a visible 'pollen tail'. The data, however, can be used as an estimate of the minimum proportion of penetrated ovules and to compare the relative performance of self- and cross-pollen tubes, since any bias probably affected both treatments equally. The 10 diurnal cross-pollinated pistils examined under fluorescence microscopy had no trace of the presence of pollen tubes in the placental region and no ovules with pollen tube penetrations 24 h after pollination.

Flower visitors

Eight mammalian species visited the flowers of *C. pentandra* on the INPA campus: five phyllostomid bat species (*Phyllostomus discolor* (Wagner), *Phyllostomus hastatus* (Pallas), *Artibeus jamaicensis* Leach, *Artibeus concolor* Peters, and an unidentified glossophagine bat), two species of marsupials (*Caluromys philander* L. and *Didelphis marsupialis* L.) and a species of night monkey (*Aotus* sp., from a group formed by individuals released on the INPA campus 14 y ago). *Phyllostomus hastatus* and *P. discolor* were the only nocturnal visitors to *C. pentandra* flowers at the Maracá site.

Thirty-two bats were captured in mist-nets placed near the crown of flowering trees on the INPA campus: 24 *P. discolor*, four *P. hastatus*, three *A. concolor* and one *A. jamaicensis*. Additionally, six *A. concolor* were captured directly by hand at inflorescences near the platform. At the Maracá site, four *P. discolor* and four *P. hastatus* were captured. All captured bats in the two study areas had pollen on their fur and microscopic analyses of their pollen loads revealed only *C. pentandra* pollen.

Phyllostomus hastatus (head/body length 110–130 mm, weight 80–115 g) and *P. discolor* (head/body length 70–80 mm, weight 35–45 g) were the most frequent flower visitors in the two areas. Flock sizes for these two bat species were visually estimated at 30–50 individuals for *P. hastatus* and more than 100 individuals for *P. discolor* during the flowering peak on the INPA campus. At the Maracá site, more than 100 individuals of each *Phyllostomus* species visited the flowers of the study tree at the beginning of the night. Flocks of these bats arrived at the trees at both sites at dusk, around 18h35–18h45. Both species flew around the crowns several times before initiating flower visits. *Phyllostomus hastatus* activity was much more intense during the first hour after flower opening, whereas *P. discolor* had a more or less constant activity until midnight. During their visits, which lasted 1–5 s, individuals of these two bat species landed on the inflorescence with their wings extended backwards (Figure 3) or 'embraced' the cluster of flowers, introduced their head into the flowers, and lapped the nectar. Visits by these phyllostomid bats knocked considerable numbers of pistils/young fruits off the tree, but these probably were unpollinated or rejected selfed and crossed pistils for which an abscission layer had already



Figure 3. *Phyllostomus discolor* visiting an inflorescence of *Ceiba pentandra*. Note the flower's mainly downward inclination.

formed in the pedicel. Captured individuals of *P. discolor* and *P. hastatus* carried dense pollen loads on their heads and ventral body and wing surfaces.

Artibeus concolor (head/body length 55–60 mm, weight 18–22 g) was more commonly observed and photographed at the end of the flowering season, and these bats repeatedly visited the same pair of inflorescences in a restricted part of the crown. These small bats landed and walked on the inflorescence, keeping their wings closed during visits. They, too, carried heavy pollen loads on their heads and ventral body surfaces. During the most intensive period of *P. hastatus* activity, when these bats vocalize intensely, individuals of *A. concolor* were not observed at the tree. No observations were made on the visiting behaviour of *A. jamaicensis*, but this species could be confused with the other more frequent bat visitors because of its intermediate size between the two *Phyllostomus* species. The single captured individual of *A. jamaicensis* had a very sparse dust of pollen on its fur. Glossophagine bats were not captured in either area, but a few instances of their typical hovering visits were observed at the Manaus trees during the final week of the flowering period.

Unidentified nectar-seeking hawk moths were occasionally observed visiting flowers of tree 1 at the end of the flowering season and then only late at night, after the more intensive period of bat activity. *Caluromys philander* and *Didelphis marsupialis* walked along branches searching for inflorescences. Both species spent up to 30 s lapping the nectar in each inflorescence and apparently did not damage the flowers although some young fruits were dislodged during their visits. *Caluromys philander* was observed foraging alone or in pairs, and *D. marsupialis* was always observed alone. Both species visited trees 1 and 2 only during the two weeks of most intensive flowering. The night monkey *Aotus* sp. moved more quickly than the marsupial species and frequently jumped between

branches to reach the inflorescences. Night monkeys were always observed foraging in groups of five individuals in both monitored trees on INPA's campus. Their activities in the inflorescence apparently did not damage the opened flowers but caused young fruits to drop. Diverse bee species (*Centris*, *Xylocopa*, *Bombus*, *Trigona* and *Apis* spp.), wasps (*Polybia*), and an unidentified hummingbird visited the flowers to collect residual nectar or pollen during the early daylight hours.

DISCUSSION

Flowering phenology, floral biology and pollinators

The 6 y of observations on the flowering of *C. pentandra* in this study were not enough to show a clear picture of the frequency of reproductive events in this species, but they do confirm previous observations that neotropical populations flower in non-annual periods (Baker 1965, Frankie *et al.* 1974, Murawski & Hamrick 1992). The trees in the Maracá and Manaus areas (located 370 km N and 312 km S of the equator, respectively) appear to have adjusted their phenology to flower during the local dry seasons, i.e., November–March in Maracá (Thompson *et al.* 1992) and August–October in Manaus (Ribeiro 1976).

Ceiba pentandra is a massively flowering tree that attracts assemblages of nocturnal and diurnal animals to flowers. Sugar concentration and volume of nectar secreted by each flower are within the range cited for most chiropterophilous species (Baum 1995, Eguiarte *et al.* 1987, Faegri & van der Pijl 1979, Gribel & Hay 1993, Gould 1978, Heithaus *et al.* 1974, Helversen & Reyer 1984, Hopkins 1984, Lack 1978, Lemke 1985, Kress & Stone 1993, Ramirez *et al.* 1984, Voss *et al.* 1980). However, the total amount of nectar offered by each tree individually is, to our knowledge, higher than that of any other studied species. The estimate of *c.* 650 000 flowers set by tree 1 (a relatively young and small tree that flowered for the first time during the study period) means that *c.* 200 l of nectar (and *c.* 30 kg of sugars) were available to floral visitors during the 5 wk flowering period. During the flowering peak, a tree such as this can probably secrete >10 l of nectar (with >1.5 kg of dissolved sugar) per night. Older and bigger trees, usually with 30–35 m of crown diameter, certainly produce still more impressive amounts of floral reward.

The combination of floral features (shape, colour, odour, time of anthesis, and period of nectar production) in *C. pentandra* indicates a pronounced adaptation for pollination by nocturnal animals, especially bats. An ecologically remarkable floral event, previously cited by Toxopeus (1950), Baker (1983) and Murawski & Hamrick (1992), is the abscission of the style, together with the petals and anthers, during the morning following anthesis. Ovaries from diurnal hand pollinations (effected at 06h00) presented no penetrated ovules, indicating that the pollen tubes had not traversed the style into the ovary before stylar abscission. Thus, diurnal pollinations have no importance in *C.*

pentandra reproduction. This strict adaptation for nocturnal pollination differentiates *C. pentandra* from other bat-pollinated Bombacaceae such as *Ceiba acuminata* (Baker *et al.* 1971) and *Pseudobombax ellipticum* (Eguiarte *et al.* 1987), where diurnal floral visitors may have some role in fruit- and seed-set. Failure to observe this essential aspect of *Ceiba pentandra* floral biology has led some authors to suggest possible effective diurnal pollinations by monkeys (Janson *et al.* 1981), birds (Toledo 1977), or insects (Toxopeus 1950).

Glossophagine bats were not a common visitor of *C. pentandra* flowers in either of our study areas, although they are frequent visitors to other chiropterophilous plants such as *Couepia longipendula* Pilger, *Caryocar villosum* (Aubl.) Pers. and *Bauhinia longicuspis* Spruce ex Benth. in the Manaus area (Rogério Gribel, unpubl. data). At first sight this seems surprising, since *C. pentandra* floral morphology allows glossophagine bats to take nectar during their hovering flight visits. This contrasts with other non-glossophagine bat-pollinated or non-flying mammal-pollinated Bombacaceae, such as *Pseudobombax tomentosum* (Mart. et Zucc.) A. Robyns and *Ochroma pyramidale* (Lam.) Urban, which have large, erect, funnel-shaped flowers which make difficult or preclude typical glossophagine hovering visits (Gribel 1988, Gribel *et al.* 1990). The rarity of glossophagines at *C. pentandra* flowers may be a predator-avoidance response due to the intense activity of *P. hastatus* in these areas. *Phyllostomus hastatus* is an omnivorous bat that can prey on small vertebrates (Gardner 1977), including glossophagine bats, at least in captivity (Dunn 1933).

Although the three nocturnal non-flying mammals observed in this study made legitimate visits (i.e., non-destructive visits, touching the anthers and stigmas) it is likely that they have a negligible role in *C. pentandra* cross-pollination when compared with bats, because of the scarcity of their visits and their relatively limited ability to move between scattered emergent *C. pentandra* trees. The foraging behaviour of the small phyllostomid bat *Artibeus concolor*, repeatedly visiting few inflorescences in a restricted area of the canopy, probably promotes high levels of geitonogamous pollination and can be important for the fruit-set of self-compatible trees. However, *Phyllostomus hastatus* and *P. discolor* are clearly the main pollinators of *C. pentandra* in both study areas. The following behavioural features of both *Phyllostomus* species contribute to their effectiveness as pollinators of *C. pentandra*: (1) high frequency of their visits, (2) foraging in large groups that presumably move between trees, (3) potential to cover large distances, (4) non-destructive visits on the inflorescences, and (5) foraging activity during the first half of the night, which permits the pollen tubes to traverse the style before its abscission in the morning.

Probably only a small fraction of the nectar produced is available to be consumed by floral visitors since the tilted or pendant orientation of most flowers allows drainage of the nectar droplets, and this waste of nectar is intensified during the bat's visits when the branches are shaken. Perhaps this floral orientation has an adaptive value: the fast decline in nectar availability during

visitations would force the bat flocks to move to other trees, promoting cross-pollination. Abundant resources concentrated in small, irregularly distributed patches during ephemeral and unpredictable periods favour group foraging by phyllostomid bats (Ayensu 1974, Baker 1973, Fleming 1982, Howell 1979, Lemke 1984, 1985). Group foraging has been observed for *P. discolor* in several studies (Gribel & Hay 1993, Heithaus *et al.* 1974, 1975; Kress & Stone 1993, Sazima & Sazima 1977). Foraging in large groups, *P. hastatus* and *P. discolor* share the resources available in a given tree and may be forced to move to another tree to satisfy their energetic demands, promoting cross-pollination. *Phyllostomus hastatus* and *P. discolor* have a high potential as long-distance cross-pollinating vectors. The foraging territory of *P. hastatus* may extend up to 20 km around the roosting site (Williams & Williams 1970; but see McCracken & Bradbury 1981 for a smaller estimate of the *P. hastatus* foraging area). *Phyllostomus discolor* was found carrying pollen of *Ceiba aesculifolia* for distances greater than 1 km overnight in Costa Rica (Heithaus *et al.* 1975).

The data from this study, carried out in areas separated by 700 km in a north/south direction, together with observations by Carvalho (1960) in Belém (located 1300 km east of Manaus), indicate that the *C. pentandra*-*Phyllostomus* pollination system may be regionally widespread. Body size and visiting behaviour of *P. hastatus* and *P. discolor* resemble those of some medium-sized Pteropodidae bat species, such as *Epomophorus gambianus*, which pollinates *C. pentandra* in Ghana (Baker & Harris 1959, Harris & Baker 1959; compare the photographs of bats on *C. pentandra* flowers in Harris & Baker (1959) with Figure 3). The similarity in selective pressures exerted by the main pollinators in both neotropical and palaeotropical regions may have contributed to the success of *C. pentandra* in colonizing extensive tropical areas and diverse habitats while keeping the same basic floral structure and function despite geographically (and genetically) widely disjunct populations.

Breeding system

Ceiba pentandra seems to be somewhat variable in its breeding and mating system throughout its distribution range (Baker 1955, 1965; Elmquist *et al.* 1992, Murawski & Hamrick 1992; Toxopeus 1948, 1950). The results reported in this paper provide experimental (tree 1) and circumstantial (tree 12 in 1993 and tree 15 in 1992) evidence that cross-pollination may be essential for fruit and seed production in some trees and that successful geitonogamy is probably not widespread in Central Amazonia.

A possible explanation for the self-fertility exhibited by *C. pentandra* in the palaeotropical region may be the putative recent bottleneck in population size during the colonization period in Africa and Asia, when selection favoured selfing individuals and probably purged deleterious mutations from the population (Baker 1955, Barrett & Shore 1989, Leberg 1992). In contrast, in the historically large populations in the core neotropical area of distribution, such as those in Central Amazonia and Central America, higher levels of outcrossing

and an accumulation of recessive deleterious mutations could be expected (Lande & Schemske 1985). In other bombacaceous taxa, such as *Eriotheca gracilipes* (Oliveira *et al.* 1992), *Chorisia speciosa* and *C. chodatii* (Gibbs & Bianchi 1993) self-pollen tubes are also as successful at penetrating ovules as crossed ones. In these species, which set no fruit by self-pollination, self-pollen tubes that penetrate ovules effect fertilization, and a resting zygote with initial endosperm nuclei divisions is present at the time selfed flowers abscise.

Finally, our results have implications for the conservation biology of *C. pentandra* in the Amazon region. It seems possible that, despite a mixed mating system, many *C. pentandra* trees in Central Amazonia require cross-pollination to set fruits and seeds. The native populations of *C. pentandra* have suffered intensive exploitation by the plywood industry throughout the Brazilian, as well as the Peruvian, Amazon (Gentry & Vasquez 1988). The density of *C. pentandra* trees in the exploited areas has been greatly reduced and the remaining trees are those of very difficult access. Increased inter-tree distances may constrain the movement of bats (and consequently pollen) between trees, reducing the reproductive capacity of the non-exploited individuals and/or increasing the proportion of selfed progeny. Furthermore, the bat populations themselves have probably been affected by the destruction of their natural habitats in várzea forest and the disturbance of their roosting and feeding sites, which may also influence the pollination success and seed output of *C. pentandra*. Thus, any management or conservation policy for *C. pentandra* in Central Amazonia should take into consideration that outcrossing, which is promoted mainly by two bat species, is probably essential for the propagation of many remaining trees in this region and for the recovery of populations from logging.

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