

FLOWERING PHENOLOGY AND ITS IMPLICATIONS FOR MANAGEMENT OF BIG-LEAF MAHOGANY *SWIETENIA* *MACROPHYLLA* IN BRAZILIAN AMAZONIA¹

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- **Premise of the study:** Flowering phenology is a crucial determinant of reproductive success and offspring genetic diversity in plants. We measure the flowering phenology of big-leaf mahogany (*Swietenia macrophylla*, Meliaceae), a widely distributed neotropical tree, and explore how disturbance from logging impacts its reproductive biology.
- **Methods:** We use a crown scoring system to estimate the timing and duration of population-level flowering at three forest sites in the Brazilian Amazon over a five-year period. We combine this information with data on population structure and spatial distribution to consider the implications of logging for population flowering patterns and reproductive success.
- **Key results:** Mahogany trees as small as 14 cm diam flowered, but only trees > 30 cm diam flowered annually or supra-annually. Mean observed flowering periods by focal trees ranged from 18–34 d, and trees flowered sequentially during 3–4 mo beginning in the dry season. Focal trees demonstrated significant interannual correlation in flowering order. Estimated population-level flowering schedules resembled that of the focal trees, with temporal isolation between early and late flowering trees. At the principal study site, conventional logging practices eliminated 87% of mahogany trees > 30 cm diam and an estimated 94% of annual pre-logging floral effort.
- **Conclusions:** Consistent interannual patterns of sequential flowering among trees create incompletely isolated subpopulations, constraining pollen flow. After harvests, surviving subcommercial trees will have fewer, more distant, and smaller potential partners, with probable consequences for post-logging regeneration. These results have important implications for the sustainability of harvesting systems for tropical timber species.

Key words: logging impacts; Meliaceae; population genetic structure; reproductive phenology; sustainable forest management; synchronous flowering; tropical trees.

Reproductive phenology, or the timing of flowering and fruiting events, is a crucial determinant of reproductive success and offspring genetic diversity in plant species (Rathcke and Lacey, 1985; Fox, 2003; Weis and Kossler, 2004; Elzinga et al., 2007). Overlap in flowering time among individuals will determine the mating opportunities available to a female and will

constrain the genetic diversity within her progeny (Loveless and Hamrick, 1984; Lyons and Mully, 1992; White and Boshier, 2000; Bawa et al., 2003; Kitamoto et al., 2006). Flowering phenology, coupled with plant density and spatial structure, will influence pollinator visitation, gene flow, and ultimately fruit production (Rathcke and Lacey, 1985; Marquis, 1988; Ollerton and Lack, 1998; Bustamante and Búrquez, 2008). Thus flowering phenology is an essential component in understanding the reproductive ecology of perennial plants.

In long-lived tropical trees, which typically occur at low densities, the interactions between reproductive phenology and population structure are particularly important in determining the ecological and genetic neighborhood of individual canopy trees (Murawski and Hamrick, 1992; Bronstein, 1995; Stacy et al., 1996; Nason and Hamrick, 1997; Loveless et al., 1998; White and Boshier, 2000; Fuchs et al., 2003). Most studies of flowering phenology in tropical trees describe onset, peak, and cessation of flowering at the population level (Gentry, 1974; Gribel et al., 1999; Lepsch-Cunha and Mori, 1999; Adler and Kielpinski, 2000; Morellato, 2004; Herrerias-Diego et al., 2006) or document community-wide flowering patterns (Frankie et al., 1974; Bawa, 1983; Newstrom et al., 1994; Bawa et al., 2003). But ecological and genetic consequences of flowering phenology depend on flowering behavior by individuals and its variation over time. Seasonal flowering is clearly initiated by environmental cues (Frankie et al., 1974; Reich and Borchert, 1984; Borchert, 1994; Lobo et al., 2003), but within that physiological context, individual flowering behavior has been shown in many species to have a strong genetic component (Pors and

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Werner, 1989; Fox, 2003; Weis and Kossler, 2004). This can lead to assortative mating based on flowering time, with subsequent impacts on recombination within apparently panmictic populations (Fox, 2003; Hendry and Day, 2005; Kitamoto et al., 2006).

Genetic structure and genotypic diversity within populations of tropical trees is a direct outcome of mating patterns (Loveless and Hamrick, 1984; Ward et al., 2005), and flowering phenology is a critical variable influencing how gametes combine. Although many studies of tropical trees note the importance of phenology for mating systems (Stacy et al., 1996; Murawski and Hamrick, 1992; Fuchs et al., 2003), few actually document this aspect of reproductive ecology. Of more general concern has been the impact of disturbance, from fragmentation or from logging pressure, on the genetic makeup of tropical tree populations. This impact comes, not in how disturbance alters breeding biology or flowering phenology, but in how it alters population density, size structure, age structure, and population connectivity (Hall et al., 1996; Nason and Hamrick, 1997; Dick et al., 2003; Fuchs et al., 2003; reviewed in Lowe et al., 2005). As Lowe et al. (2005) point out, disturbance alters ecological interactions, especially those involving pollinators, and understanding these connections would contribute to developing guidelines for extraction intensity and forest management. In contrast to habitat fragmentation, which creates small, isolated, but relatively intact forest parcels, logging strongly reduces local adult densities, dramatically alters population size structure, and disturbs habitat. Residual adults (seed trees) left in place after logging are the source of recruitment for timber production beyond the current harvest (Guariguata and Pinard, 1998). The success of this management model depends crucially on the reproductive biology of the species and the degree to which ecological processes resist logging disturbance. But detailed information on age at reproductive maturity, age- (or size-) specific flowering effort, and annual patterns of flower production are unavailable for most important tropical timber trees, limiting our ability to make management decisions that take into account a species' reproductive biology.

Big-leaf mahogany, *Swietenia macrophylla* King (Meliaceae), is the most valuable widely traded neotropical timber species. It has been heavily logged in primary forests throughout its natural range from Bolivia to the Yucatan Peninsula of Mexico (Lamb, 1966; Veríssimo et al., 1995; Grogan et al., 2002, 2010a; Kometter et al., 2004). Future harvests of mahogany from managed forests will depend on post-logging stand regeneration. Since 2002 mahogany has been listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This listing requires verification that timber traded internationally has been harvested legally and in a manner nondetrimental to the species' role in the ecosystems where it occurs (Blundell, 2004; Grogan and Barreto, 2005). Thus local growth and regeneration should balance extraction within forests containing mahogany. Making this determination requires an understanding of how logging affects the reproductive ecology of the post-logged population.

We investigated individual-based flowering phenology in three mahogany populations in southeastern Amazonia to examine the potential implications of flowering behavior for sustainable forest management for this economically important timber species. Based on quantitative data from leaf and flower traps at 23 focal trees at one site, we describe the timing of events from dry season leaf-drop through flowering and canopy reflush, and examine variation in individual flowering patterns within and among years over a 5-yr period. Detailed data on crown phenology allow us to infer individual flowering patterns

in a large, multi-aged population of 266 trees of all size classes. We documented flowering patterns from two additional populations to provide a robust description of mahogany flowering phenology within this region. We use these phenological data to estimate pre- and post-logging flowering neighborhoods based on predicted synchrony of individual flowering periods within the population. Finally, we evaluate current forest management protocols within the context of these findings.

MATERIALS AND METHODS

Floral biology—Mahogany is monoecious, with pale yellow flowers that are approximately 0.5 cm diam, actinomorphic, and functionally either male or female (Lee, 1967). Flowering occurs immediately following crown renewal each dry season after a brief deciduous period. Each flushing stem may produce up to 12 inflorescences, and individual inflorescences can mature up to 100 flowers. The flowers have a citrusy fragrance and are visited by small butterflies, moths, and bees.

Study region and sites—The study region, at the eastern edge of mahogany's natural range in Amazonia, is 650–750 km south of Belém in the state of Pará. The primary study site is a 2050-ha forest industry-owned management area called Marajoara (7°50'S, 50°16'W), located 34 km northwest of Redenção. Annual precipitation during 1995–2001 at Marajoara ranged from 1636–2170 mm, with > 90% falling between November and May (Grogan and Galvão, 2006). The forest is evergreen with a deciduous component. Topographic relief is slight; all streams within the research area are seasonal. Mahogany occurs in low-density aggregations along or near the banks of seasonal streams (Grogan et al., 2003). Mahogany is also common on scattered boulder outcrops, especially where these occur with streambeds, and, within the region, at low densities on steep inselberg slopes. Marajoara was selectively logged for mahogany between 1992–1994, removing an estimated 3 m³ ha⁻¹. Pre- and post-logging densities of mahogany were 65.0 and 19.4 trees > 20 cm diam per 100 ha, respectively (Grogan et al., 2008). This logging intensity represented < 50 trees per 100 ha at the landscape scale, leaving forest canopy structure generally intact. Because of Marajoara's role as a model industry management area, logging was slightly less intense than would have occurred under the conventional or 'predatory' logging scenario (Veríssimo et al., 1995; Grogan et al., 2008). As a result, some larger trees persisted at the site. At the time of logging, the minimum legal cutting diameter was 45 cm diam, but that minimum was raised to 60 cm diam in 2003 (Grogan and Barreto, 2005). Observations from two additional 600-ha sites, similar physiographically and floristically to Marajoara, supplement data reported here: Corral Redondo (7°42'S, 50°12'W) located 15 km northeast of Marajoara, and Agua Azul (6°51'S, 50°31'W) located 115 km north. Both sites were heavily logged in the early 1990s.

Sampling design—Within the 2050-ha study area, we located 352 mahogany trees > 10 cm diam which remained following logging (Fig. 1). Flowering status as described below could be confirmed during each year of the study period for a subset of 266 of these trees, representing the sample for which our population-level phenology data are estimated. Of this subset, 49 trees (18.4%) were > 60 cm diam. Detailed measurements at 23 focal trees, chosen based on proximity to our field camp, crown visibility, and variation in stem size, tracked variation in yearly flowering behavior. Population structure is represented by mahogany's stem size-class frequency distribution derived from a 100%-area inventory of trees and logged stumps > 20 cm diam in a 204-ha permanent plot within the larger study area (Fig. 1).

Flowering status by diameter size class—Mahogany trees > 10 cm diam were monitored for flowering activity during the dry season. For the 266 trees in our phenology study, flowering was confirmed each year by one or more of the following methods: (1) direct observation of open flowers on the crown; (2) observation of flower buds on flushing crowns, or of fallen flowers or flower stalks beneath trees; (3) evidence from fruit capsule production. Tree crowns were scored by two observers for phenological phase during dry season censuses. Scoring was recalibrated weekly among observers for consistency. At Marajoara, where trees could be revisited, flowering onset for trees without traps was estimated based on observed crown phase on two or more dates per tree during each dry season, at least one of these during bare-crown or crown

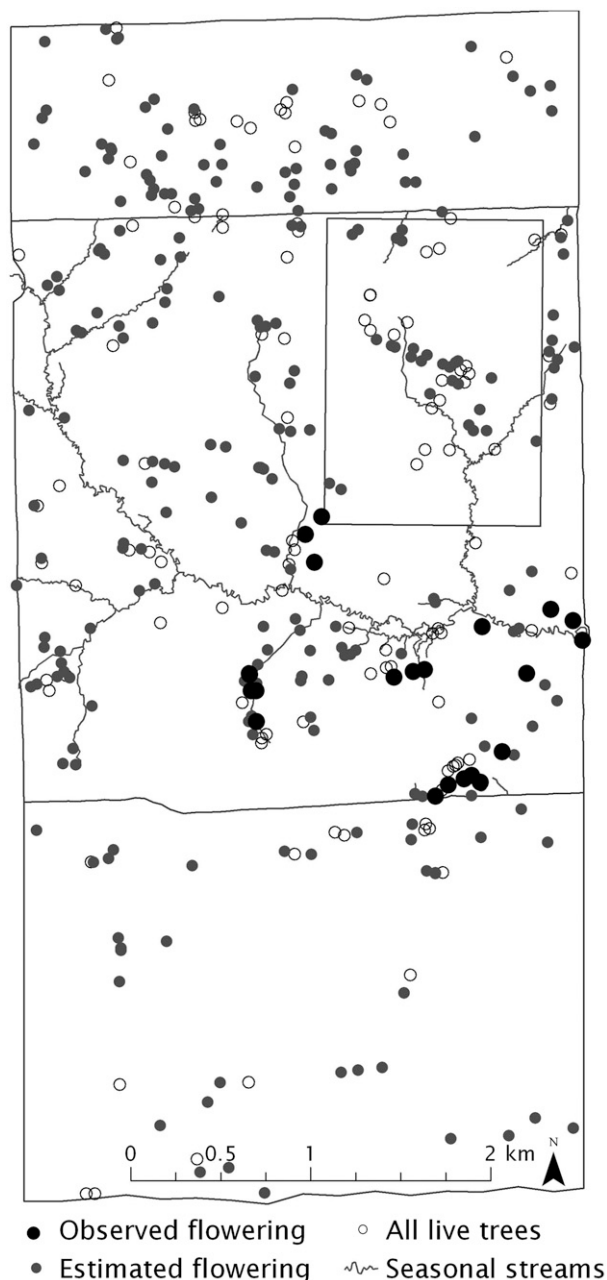


Fig. 1. Map of the 2050-ha study area at Marajoara showing sampling design. The 23-tree focal sample is shown in large black circles, including one tree located east of the main study area. The 266-tree phenology sample is shown in small gray circles and includes the 23-tree focal sample. Additional trees that survived logging are shown in open circles (total $N = 352$). The interior square indicates a 1035-ha area within which seasonal streams and an estimated 85% of surviving and logged mahogany trees are located (stumps not shown). The smallest rectangle outlines the 204-ha plot within which 100% of mahogany trees > 20 cm diam were mapped (stumps not shown; see Figs. 2 and 3).

reflush phases. We returned to trees at intervals until flowering status could be definitively determined. In 1997, when the crown scoring system was being developed and calibrated, flowering onset could be estimated for 147 of 266 trees; all trees were scored from 1998–2001.

At Corral Redondo and Agua Azul, estimated flowering onset dates were derived from a single observation date during each dry season because of difficult access. At Corral Redondo, 66 trees > 10 cm diam were observed annually from

1998–2000, 14 (21%) of these > 60 cm diam. At Agua Azul, 93 trees were observed annually during this period, only four of these > 60 cm diam. (At both secondary sites the recensus in 2001 occurred too late in the dry season to describe flowering schedules from crown scores.) Fifty-two trees at Agua Azul stood exposed to full sunlight after extensive clearing (Grogan et al., 2010b). Because a single observation missed direct evidence of flowering by some trees, data on flowering events from these sites rely more on inferential evidence, especially fruiting, than data from Marajoara.

Flowering onset, duration, synchrony, and production—To quantify flower production by individual trees, a 1.75×1.75 m plastic trap, elevated 1 m above the ground, was placed beneath the crown of 23 trees to collect fallen flowers during the annual flowering period from 1997–2001. Sample trees ranged from 26–146 cm diam, and were divided approximately equally among 10-cm diam classes. Flower traps were placed in the same positions each year. Flowers were collected, oven-dried and weighed at 3-d intervals. The relationship between stem diameter and tree crown area was determined by mapping crown perimeter along vectors (5–14 per tree) radiating from the stem base for 52 trees across a range of stem diameters, including the 23 focal trees with flower traps. While crown volume cannot be inferred from projected surface area, mahogany's shade intolerance translates into a shell-like crown with minimal interior leaf area.

Vegetative phenology—To determine the relationship between vegetative and flowering phenology, 19 trees from the flower production study were monitored throughout the 1997 calendar year for leaf-fall and leaf-flush. The timing and rate of leaf loss were quantified in greater detail during the 1997 and 1998 dry seasons for all 23 trees, using plastic traps (as above) to the windward (west) side of each tree from the end of the rainy season (early May) until complete crown loss. Leaves were collected and counted at 2-wk intervals.

Extrapolating flowering phenology to the population—Leaf and flower trap data from 1997 and 1998 were used to refine a scoring system for crown phenology. Crown shedding and reflush were each divided into four phases bridged by a bare-crown phase. During reflush, flowerbuds were observable from the second phase forward. Observations were pooled to estimate the mean number of days to flowering onset represented by successive crown phases. The date of flowering onset by trees without flower traps was then predicted based on observed crown phenology on a given calendar date.

Because duration of the flowering period for trees without flower traps could not be precisely determined, annual means from the 23 trees with flower traps were assigned to trees without flower traps at Marajoara to construct estimated population-wide flowering schedules for 1997–2001. The 5-yr mean annual value at Marajoara was assigned to trees at the two other sites from 1998–2000.

RESULTS

Logging effects on population size and spatial structure—Logging at Marajoara produced a dramatic reduction in density and proximity of mahogany trees (Figs. 2 and 3). Conventional logging at this site resulted in removal of 91.4% of mahogany trees > 45 cm diam (96 of 105)—the legal minimum diameter cutting limit in the early 1990s in Brazil—plus more than half of trees 30–45 cm diam (9 of 16; Fig. 3).

Flowering by tree size (stem diameter)—The smallest tree observed to flower at any site was 13.8 cm diam growing in closed forest at Marajoara. The smallest trees flowering at Corral Redondo and Agua Azul were 17.9 and 15.1 cm diam in heavily logged forest and in full sunlight, respectively. At Marajoara, 72% of 47 trees 10–30 cm diam flowered at least once during 5 yr, and only 1.4% of trees > 30 cm diam did not flower during this period (3 of 219 trees; Fig. 4). At Corral Redondo and Agua Azul, 50% and 75% of trees 10–30 cm diam flowered at least once during 5 yr, respectively. Flowering could not be confirmed on 3.9% (Corral Redondo) and 2.5% (Agua Azul) of trees > 30 cm diam. At all three sites, annual or nearly annual flowering became common only as trees exceeded 30 cm diam.

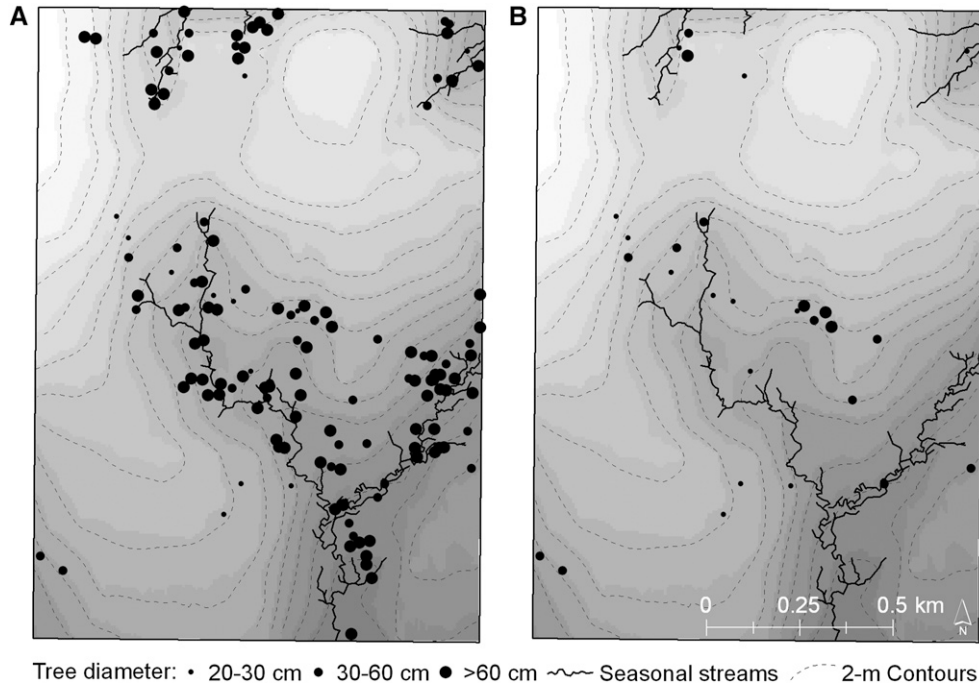


Fig. 2. Pre-logging (A) and post-logging (B) mahogany populations in 204 ha at Marajoara, showing distributions relative to topography (contours) and seasonal streams. The post-logging map (B) presents the conventional or predatory logging model (Veríssimo et al., 1995) prevalent in Brazil until 2003, under which all trees located by woodsmen were felled. The actual post-logging population is larger by 11 trees (8.3%) because some located trees were retained for management purposes. Data are from a 100%-area inventory for trees > 20 cm diam (Grogan et al., 2008).

At Marajoara, only trees > 70 cm diam flowered during every year of observation ($N = 29$; Fig. 4).

Flower production—All 23 trees with traps flowered during every year of observation from 1997–2001. Flower production (gram dry weight) by individual trees was distributed approximately normally through time (Fig. 5). As tree stem size (diam)

increased, mean annual dry weight of flower production in single flower traps increased ($P = 0.049$, $R^2 = 0.18$, $df = 21$ excluding one tree with a broken crown). Flower production by individual trees varied up to 9-fold through 5 yr, although 14 of 23 trees varied by a factor of 4 or less. But years of high flower production were not synchronous among the 23 focal trees (Table 1). Total annual flower production (summed gram dry weight

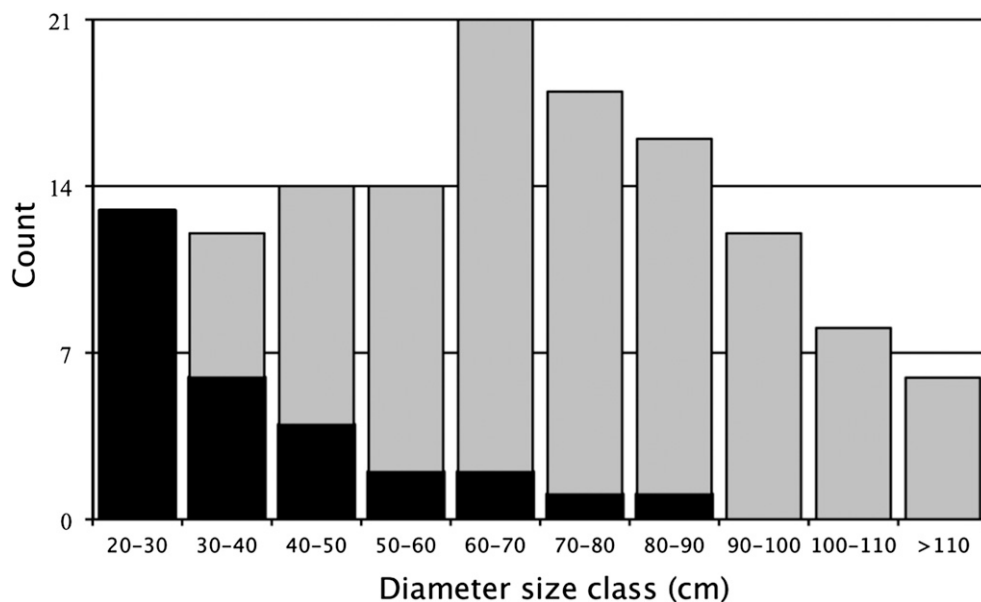


Fig. 3. Size-class frequency distribution for mahogany trees > 20 cm diam in 204 ha in Fig. 2A. Solid (black) bars show trees surviving the 1992–1994 harvest. Gray bars show logged trees.

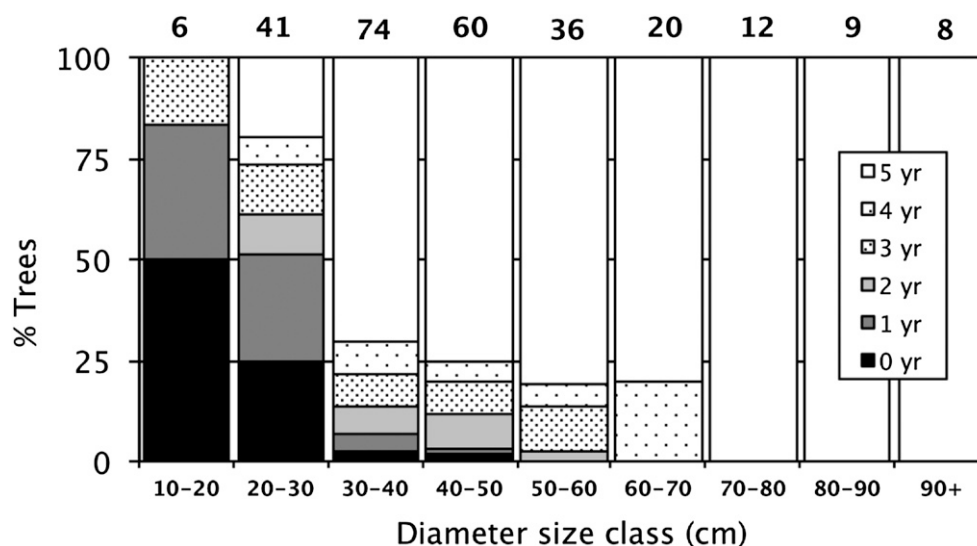


Fig. 4. Percent of trees flowering during 0–5 yr at Marajoara, 1997–2001, by 10-cm diam size class graded from black = 0 yr to white = 5 yr. Numbers in bold across the top indicate sample size by size class; total $N = 266$.

among 23 trees) varied by a factor of 2.2 through the 5-yr period.

Projected crown area demonstrated significant positive correlation with stem diameter ($P < 0.0001$, $R^2 = 0.932$, $df = 21$ as above; $P < 0.0001$, $R^2 = 0.881$, $df = 51$ including additional mapped tree crowns). Based on a mean flower dry weight of 0.00604 g and extrapolating the mean dry weight of flowers collected in traps beneath individual trees by crown area, trees with crown areas of 7 m² and 550 m² produced an estimated 30,000 and ~4.1 million flowers per year, respectively (Table 1).

Vegetative and flowering phenology—Mahogany trees shed and reflushed crowns once per year during the dry season. Fallen leaves began accumulating in traps 1–5 wk after the final wet season rainfall during 1997 and 1998. Mean number of days from the onset of leaf-fall to crown leaflessness was 42.9 ± 0.9 d ($\pm$ indicates one standard error throughout the text; Table 2). Trees

losing crowns earliest tended to be those growing on dry sites, for example, on raised boulder outcrops, or showing signs of stress associated with injury or pathogens. Mahogany trees remained leafless for less than 5 d before beginning to flush new crowns. From leaflessness to flowering onset required an additional 32.0 ± 0.8 d (Table 2).

Flowering onset, duration, and synchrony—For focal trees with flower traps at Marajoara, flowering onset ranged from July 9–August 3 during the 5-yr observation period (Table 3). On average, the first tree began flowering on July 23 ± 4.4 d. The date of latest flowering onset by any individual ranged from September 19–October 4. On average, the last tree to flower began on September 25 ± 2.5 d. The last flowers were observed in traps from October 14–27 during 5 yr. Annual periods during which one or more of the 23 focal trees were flowering ranged from 79–113 d (mean = 91 ± 5.9 d or 13 wk).

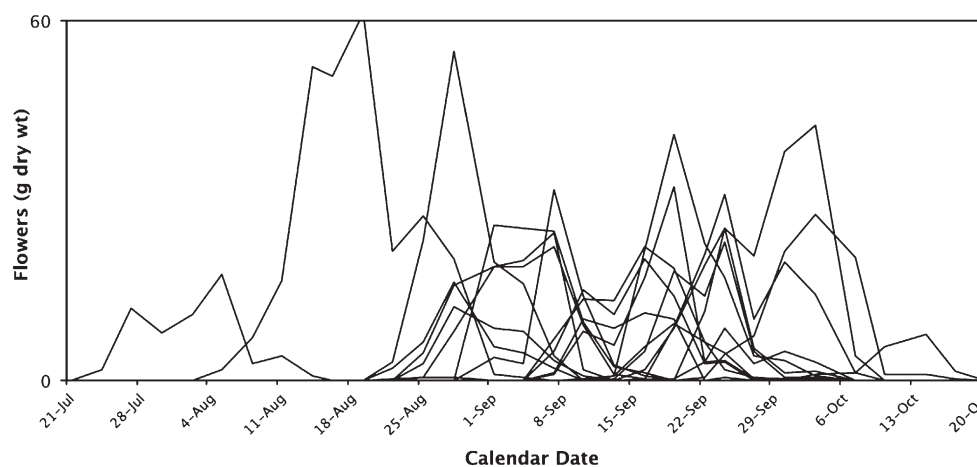


Fig. 5. Flower production cycles from onset to finish by 23 trees during 1997, by gram dry weight of flowers collected in traps. Each line represents production by a single tree at three-day intervals through its flowering period.

TABLE 1. Cumulative flower production (gram dry weight) in traps during 1997–2001 by the eight most productive trees in the 23-tree sample at Marajoara, and by the summed sample.

Tree No.	1	2	3	4	5	6	7	8	23 TREES ^a
Stem diameter (cm)	56	67	89	57	39	52	146	41	26 to 146
Crown area (m ²)	122	187	398	119	73	70	550	58	7 to 550
1997 Weight (g) ^b	261	84	112	107	143	90	84	121	1736
1998 Weight (g)	242	104	115	67	140	38	149	110	1595
1999 Weight (g)	328	123	138	141	71	147	113	170	1886
2000 Weight (g)	304	264	255	197	144	173	162	104	2817
2001 Weight (g)	125	236	186	273	233	257	185	138	3458
Ratio of max-to-min weights ^c	2.6	3.1	2.3	4.1	3.3	6.8	2.2	1.6	2.2
Mean weight (g)	252	162	161	157	146	141	138	129	2298
Mean no. flowers (1000s) ^d	41.7	26.9	26.7	25.9	24.2	23.3	22.9	21.3	16.5
Mean total flowers (1000s) ^e	1,663	1,636	3,463	1,006	576	533	4,115	404	15,691
Max total flowers (1000s) ^f	2,164	2,663	5,480	1,750	919	972	5,493	533	23,609

^a Weights, means and maximum values are summed for the 23-tree sample with flower traps.

^b Total flower production (gram dry weight) by individual trees (1–8) and summed for 23 trees.

^c Ratio of the maximum total weight (g) to the minimum total weight during 1997–2001.

^d Dry weight (g) / estimated weight of individual flower (0.00604 g).

^e Mean number of flowers * crown area.

^f Maximum total flowers among 5 yr for trees 1–8; in 2001 for 23 trees.

The mean observed flowering period for focal trees ranged from 18.4–34.0 d over 5 yr. Duration of flowering by individual trees was consistent from year to year. Interannual variation in flowering period by individuals was less than variation among trees; the largest range in difference of flowering period through 5 yr by any tree was 13 d, while 18 of 23 trees varied by 10 d or less. The shortest and longest flowering periods observed for any tree in any year were 13 and 36 d, respectively. Flowering period showed no relationship to tree stem diameter: linear regressions were not significant for any of the 5 yr, nor for the 5-yr mean of flowering period. The mean flowering period ranged from 23.0 ± 1.0 d in 1998 to 29.4 ± 0.8 d in 2000. The overall mean flowering period for individual trees across 5 yr was 26.6 ± 0.7 d.

The 23-tree sample flowered in cascading order during each year of observation. Trees flowering early in 1997 relative to others did so in successive years as well, resulting in similar flowering order during each of 5 yr (Fig. 6). Spearman's rank correlation coefficients comparing ordering in 1997 with those in 1998–2001 returned r_s values between 0.768–0.910 and P -values < 0.0001 for each comparison, indicating strong positive correlation in ranks between years. Early flowering trees had fewer potential reproductive partners than those flowering later (Fig. 7A).

Extrapolating flowering phenology to the population—Using the crown scoring system derived from flower and leaf traps (Table 2), we estimated flowering onset dates, duration, and

synchrony by trees without traps at Marajoara, Corral Redondo, and Agua Azul. Population-level results were similar in all respects to data from focal trees (Table 3). Trees in the larger population at Marajoara also flowered in cascading fashion, and early flowering trees were temporally isolated from late flowering trees (Appendices S1 and S2; see supplemental data with the online version of this article). Spearman's rank correlation comparing estimated rank ordering in 1998 with 1999–2001 gave $r_s = 0.552$ – 0.660 and P -values < 0.0001 . Viewed as proportion of trees flowering (Fig. 7B), early flowering trees had fewer potential reproductive partners than those flowering later. Similar patterns were seen at Corral Redondo ($r_s = 0.543$ – 0.739 , $P < 0.0001$) and Agua Azul ($r_s = 0.644$ – 0.763 , $P < 0.0001$).

Patterns of flowering phenology—Date of first flowering among 23 focal trees at Marajoara showed no significant relationship to either tree diameter or growth rate (mean annual diameter increment in centimeters per year over 5 yr), indicating that flowering onset is not cued by plant size or vigor. Among three trees flowering consistently early, one was in shallow soil on a boulder outcrop, while two others had suffered basal injury during logging. However, clear site-related patterns could not be discerned for habitual early and late flowerers in the larger population at Marajoara. Trees growing on or at the base of boulder outcrops initiated flowering, on average, an estimated 4.5 d earlier than trees growing within 5 m of seasonal streams, but the difference was not statistically significant (t test: $t = 0.769$, $P = 0.4486$, $df = 28$).

TABLE 2. Scoring system for estimating days to flowering onset from crown phase on a given calendar date. Data describe the mean number of days to bare crown (BC) during leaf-fall for successive subphases (O4 ... O1 for Old leaves) by 23 trees with traps; and mean number of days from BC during crown reflush until flowering onset (N1 ... N4 for New leaves). For example, a tree with $< 25\%$ of its old crown (O1) on August 1 will begin flowering an estimated 39 d later, on September 9.

	Leaves falling to BC					Leaves flushing from BC				
	O4	O3	O2	O1	BC	N1	N2	N3	N4	Onset
Days to/from BC	42.6	24.9	12.3	6.8	–	5.5	9.1	15.8	21.6	32.0
SE (days)	1.4	1.2	1.1	0.1	–	0.5	1.1	1.2	1.1	0.8
Days to flowering onset	75	57	44	39	32	27	23	16	11	–

TABLE 3. Flowering behavior at three study sites in southeast Amazonia, Brazil (MR = Marajoara, CR = Corral Redondo, AA = Agua Azul). 'First onset' indicates the first day that flowering was observed (MR focal trees) or estimated (populations) to have occurred based on crown phenology data. 'Last onset' indicates the day when the last tree observed, or estimated to flower, initiated flowering. 'Flowering period' indicates the number of days between the first and last days of flowering, observed or estimated. Standard error (SE) values in days.

	Sample <i>N</i>	Years	First onset		Last onset		Flowering period	
			Earliest	Mean (SE)	Latest	Mean (SE)	Range	Mean (SE)
MR focal trees	23	1997–2001	July 9	July 23 (4.4)	Oct 4	Sept 25 (2.5)	79–113	91 (5.9)
MR population	266	1998–2001	July 1	July 16 (5.1)	Oct 8	Oct 6 (1.2)	102–128	110 (6.1)
CR population	66	1998–2000	July 8	July 16 (5.6)	Oct 8	Sept 30 (6.0)	94–120	103 (8.4)
AA population	95	1998–2000	June 28	July 5 (4.0)	Oct 5	Oct 1 (3.2)	106–130	121 (7.4)

At Corral Redondo, mahogany trees growing on dry inselberg slopes initiated flowering, on average, an estimated 16 d earlier than trees growing along stream banks on relatively flat terrain (t test: $t = 2.460$, $P = 0.017$, $df = 52$). The overall population at Corral Redondo, however, had a mean date of first flowering identical to that of the Marajoara population (Table 3). Trees at Agua Azul began flowering, on average, an estimated 11 d earlier than those at the other two sites. This may have been due to the very open exposure at this site, with many tree crowns in full sun in pasture-like conditions. Trees growing in the large clearing at Agua Azul initiated flowering, on average, an estimated 21 d earlier than trees growing in closed (though heavily disturbed by logging) forest (t test: $t = 5.926$, $P < 0.0001$, $df = 81$; Grogan et al., 2010b).

DISCUSSION

Overall flowering pattern—Mahogany's annual flowering pattern in southeast Amazonia is linked to dry season onset and to vegetative growth cycles, as shown for trees in other seasonally dry tropical forests (Daubenmire, 1972; Frankie et al., 1974; Reich and Borchert, 1984; Borchert, 1994). In southeast Pará, mahogany flowered predictably over a period of 3–4 mo following crown leaf reflush in the mid-to-late dry season. Frankie et al. (1974) reported that dry season canopy species in Costa Rica flowered on average for 5.6 wk, but that Mexican mahogany, *Swietenia humilis*, exceeded this period, flowering for over two months during the January–April dry season. Our data on *Swietenia macrophylla* in seasonally dry Amazonian forest are consistent with these observations.

Effect of tree size on flowering—The size at which tropical trees initiate flowering is seldom reported in the literature (see Morellato (2004) and Degen et al. (2006) for examples). Size at first flowering is important for timber species because subcommercial individuals dominate the reproductive biology of post-harvest populations. At Marajoara, mahogany trees < 30 cm diam represented nearly half of the post-harvest population, but these trees flowered inconsistently and supra-annually. As tree diameter increased, annual flowering became more frequent, but even some trees that were 30–60 cm diam did not flower every year. Although analogous data for other tropical tree species are scarce, Lepsch-Cunha and Mori (1999) found that 25% of *Couratari multiflora* (Lecythidaceae) trees > 50 cm diam did not flower during the single year of their study. Lobo et al. (2003) reported that three study populations of *Ceiba pentandra* (Malvaceae) experienced irregular levels of adult flowering over three years. These data suggest that regular, annual flowering may be the case only in the largest individuals of a population.

When size class distributions are truncated by logging, mean flowering frequency of residual trees declines, reducing effective flowering density and limiting mating possibilities.

The strong relationship between stem diameter and projected crown area also meant that, despite considerable annual variation in flower production, larger trees produced much larger flower crops than subcommercial trees. These older, heavily flowering individuals make up the basic fabric of the pollination landscape in undisturbed forest (Bronstein, 1995). Large floral displays are thought to be important in attracting pollinators within a dense forest canopy (Gentry, 1974; Bawa, 1983; Rathcke and Lacey, 1985). While smaller trees may contribute to interannual variation by producing patches of floral resources that vary in time and space, large individuals exchange gametes year after year, and are likely to be the genetic and ecological mainstays of unlogged tropical tree landscapes.

Flowering onset, duration, and synchrony—Flowering onset by individual mahogany trees in southeast Pará was not synchronized, generating a complex flowering population spread over a 3- to 4-mo period. While some tropical species have short and highly synchronized flowering (e.g., *Cavanillesia platanifolia*; Murawski and Hamrick, 1992), staggered flower initiation may be typical of many tropical tree species with extended flowering periods. Potential cues for flowering onset by individuals were unclear from either the focal sample or the larger Marajoara population. In some herbaceous species, larger plants flower earlier and/or for a longer period (Schmitt, 1983; Lyons and Mully, 1992; Ollerton and Lack, 1998; McIntosh, 2002; Bustamante and Búrquez, 2008), but neither stem diameter nor individual growth rate explained date of flowering onset in mahogany. Microhabitat did not determine individual flowering schedules in any obvious way at Marajoara. Pairs of trees within 10 m of each other began flowering on very different dates, and this difference persisted from year to year. Even at Agua Azul, where heavy disturbance apparently initiated earlier population-level flowering, individual trees still showed variation in flowering schedule and correlation in flowering order between years like the Marajoara population. We hypothesize that genotype is an important factor in determining individual phenological schedules for mahogany. A strong genetic basis for flowering time has been demonstrated in several herbaceous species (Weis and Kossler, 2004; Elzinga et al., 2007). To ensure flowering overlap in the post-logged forest, loggers must leave a large enough sample of trees in adult size classes to encompass the inherent variation in flowering time within the larger population.

Date of flower initiation by individual trees was highly correlated among years, resulting in predictable cohorts of co-flowering individuals. Correlations in individual flowering time

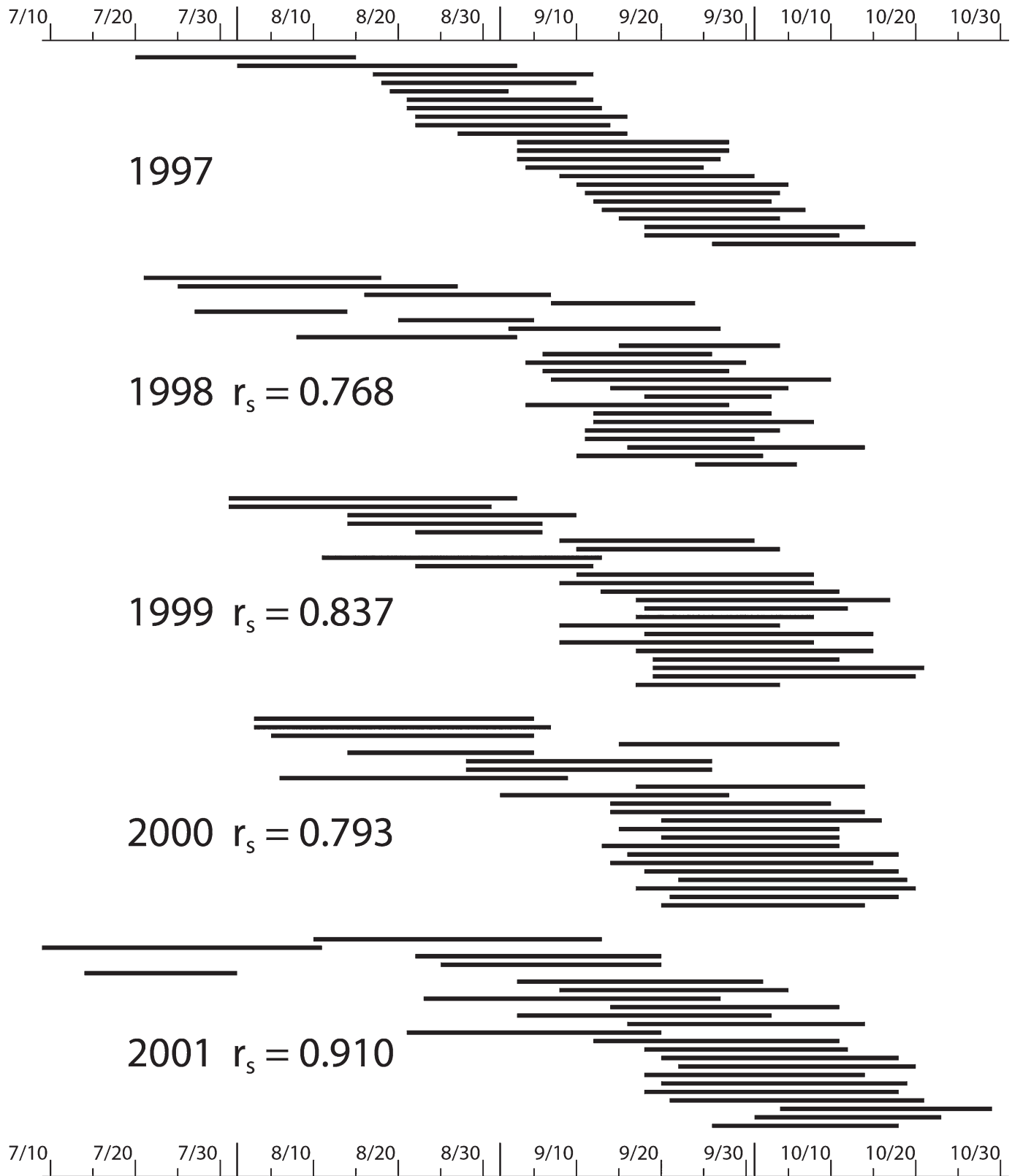


Fig. 6. Flowering schedules by 23 trees with flower traps, 1997–2001. Each tree is represented by a horizontal row spanning a year's flowering period (number of days). Tree order is the same for each year, listed from first to last flowering in 1997. Spearman's rank correlation coefficients (r_s) for comparisons with 1997 rank order are listed for years 1998–2001.

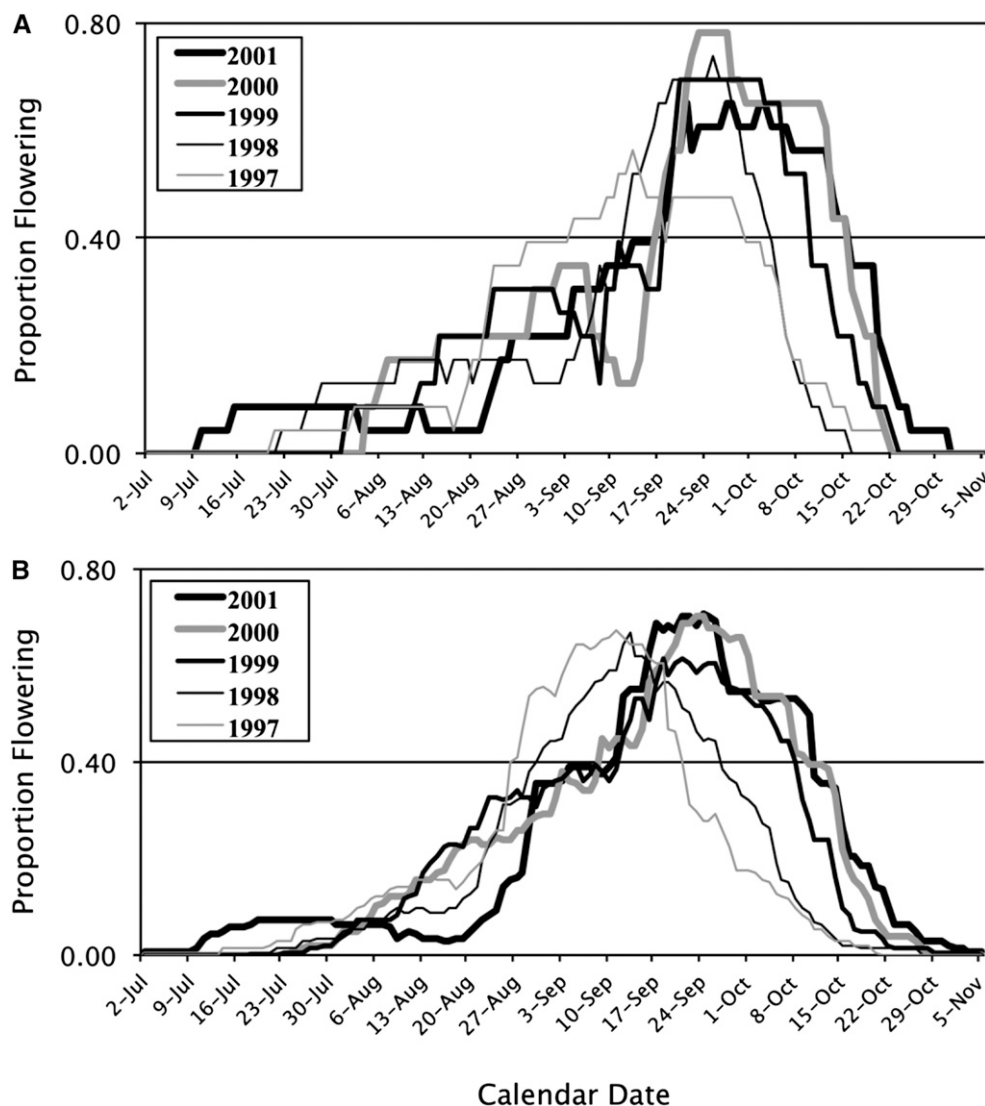


Fig. 7. (A) Observed proportion of 23 trees with flower traps flowering from early July to early November during each year from 1997–2001 at Marajoara. (B) Estimated proportion of trees in the sample population ($N = 266$) flowering as in (A), derived from crown phenology data; the line for 1997 shows a subset of the sample population during the first year when the crown scoring system was being developed ($N = 147$).

between years have been demonstrated for some temperate species (Ollerton and Lack, 1998; Buide et al., 2002; Mahoro, 2002; McIntosh, 2002), but we know of no similar data for tropical trees. To the degree that flowering order and duration result from genetic differences, trees will have reproductive access largely to mates with similar phenological genotypes. Trees flowering regularly in mid-to-late September, during the period of peak flowering, would have more potential mating partners. Conversely, early flowering individuals not only have fewer potential co-flowering mates, but they may tend to have partners drawn from the same set of individuals year after year. Under these conditions, mahogany is likely to experience assortative mating based on phenological characters (Fox, 2003; Weis and Kossler, 2004; Hendry and Day, 2005; Weis et al., 2005). Such temporal separation would generate consistent year-to-year genetic differences among progeny from adults flowering at different times. Genetic differences in time of flowering initiation could thus function as a temporal Wahlund effect in the genotypes of newly produced progeny (Loveless et al., 1998; Bawa et al., 2003).

Gene flow among individuals within any plant population depends on spatial proximity, flowering synchrony, floral attractiveness, and the behavior of the pollinator community. Many studies have shown that pollinators of tropical trees are capable of moving pollen distances of 1 km or more in undisturbed forest tracts (Murawski and Hamrick, 1992; Boshier et al., 1995; Stacy et al., 1996; Loveless et al., 1998) and even farther under conditions of fragmentation and disturbance (Nason and Hamrick, 1997; White et al., 2002; Dick et al., 2003; reviewed in Lowe et al., 2005). White et al. (2002) reported gene flow between fragmented stands and isolated individuals of *Swietenia humilis* separated by up to 4.5 km in Honduras. However, their paternity data also showed that, in the control population in a secondary forest of about 500 ha, 64% of pollinations were from within 600 m, originating within the local forest site. For *Dinizia excelsa* (Fabaceae), a canopy tree of Amazonian forests, Dick et al. (2003) reported that pollinators—Africanized honeybees—moved pollen as far as 3.2 km among isolated trees in pastures. In a highly disturbed area of

forest fragments, mean pollen movement distance for *Dinizia* was 1509 m, but in a nearby undisturbed forest location mean pollen movement distance was only 212 m. While these studies demonstrate that pollinators can move across a nonforest matrix between trees in fragmented landscapes, forest logging concessions are not usually fragmented as a result of harvest. Forest structure persists to varying degrees after logging, but population structures of harvested species are altered. In this setting, where pollinators are not confronted with sharp habitat boundaries, local pollen movement is likely to be the rule. As tree densities decline, it is unclear how far pollinators will fly between residual flowering trees, especially if those trees are small.

Gene flow and pollen movement by mobile pollinators thus generate the high outcrossing rates typical of tropical tree species (Ward et al., 2005). Decreases in adult density, whether from annual variation in flowering or from anthropogenic disturbances, predictably result in increases in selfing rates, whether in undisturbed or disturbed environments (Murawski and Hamrick, 1992; Lowe et al., 2005; Ward et al., 2005; Eckert et al., 2010). Many authors have suggested that variation in flowering phenology and reduced flowering overlap under low densities likely contribute to this process (Murawski and Hamrick, 1992; Latouche-Hallé et al., 2004). Lack of compatible mates or skewed sex ratios in dioecious species—both processes analogous to lack of flowering overlap—also have the potential to reduce both genetic diversity and fitness, including seed set (Lowe et al., 2005; Sebbenn et al., 2008). The individual flowering phenologies we describe for mahogany provide data to assess the potential effects of reduced flowering overlap on mating patterns in tropical tree populations.

At Marajoara, flowering overlap is clearly highest during peak flowering in mid-to-late September. Determining individual dates of flowering onset permits estimation of flowering overlap for any given members of the population. However, simple temporal co-flowering likely overestimates actual rates of gene flow in mahogany. Monoecious adults of some Meliaceae produce male and female flowers during different portions of their flowering period (Styles, 1972). In *Swietenia humilis* in Honduras, White and Boshier (2000) found that male flowers were produced throughout an individual tree's flowering period (averaging 31.9 ± 5.6 d), but female flowers were produced only during the middle of the flowering period. Male flowers were produced for 7.4 ± 3.9 d before female flowers became available. Female flowering lasted on average 11.4 ± 4.6 d, and the final 13.1 d of flowering again yielded male flowers only. While we lack similar data for *S. macrophylla*, our field observations from towers built into the crowns of three mahogany trees and during flower collection in traps are consistent with this pattern of differential male and female flower production within inflorescences. Apparent flowering overlap among the 23 focal trees thus probably overestimates the number of co-flowering trees with respect to pollen donation and receipt, because trees overlapping at the tails of their flowering intervals are functionally only male at these times (Bawa, 1983). In mahogany's case, simple overlap of flowering period is not a sufficient predictor of the possibility for gene flow between individuals, and the same may be true for other monoecious and dioecious tropical trees.

Management implications of flowering phenology—Logging removes a large fraction of commercial-sized trees in a forest and changes both the spatial configuration and size distribution of remaining trees from which any new, post-logging recruitment must be produced. Our data suggest that the potential for

reduced flowering synchrony among residual trees will be high, especially given the temporal constraint on female flower production. In addition, total flower production by the surviving population of generally small trees will be sharply reduced.

An estimated 65% of mahogany's historic range in Brazil had been harvested by 2001 using conventional or 'predatory' logging practices (Veríssimo et al., 1995; Grogan et al., 2010a), typically removing up to 95% of commercial trees (45 cm diam before 2003), illegally eliminating up to 47% of submerchantable trees, and targeting trees as small as 20 cm diam (Grogan et al., 2008). At Marajoara, subcommercial trees that flower annually or supra-annually (30–60 cm diam under new forest management regulations in effect since 2003) represented 32.5% of the pre-logging mahogany population > 30 cm diam but contributed only an estimated 12% of annual population-level flower production based on flower trap and crown area data from this study (Table 4). Under the typical conventional logging scenario that characterized mahogany logging operations across the Brazilian Amazon before 2003, 87% of the reproductive population (trees > 30 cm diam) would have been logged, eliminating an estimated 94% of pre-logging flower production. Where mahogany persists in logged forests in Brazil, this is the reproductive landscape it now experiences.

Temporal differences in flowering phenology by individual trees further restrict reproductive opportunities and genetic exchange after logging. To illustrate this, we examined pre- and post-logging reproductive neighborhoods (trees > 30 cm diam) within 1000 m (314 ha) of paired subcommercial trees located in separate microwatersheds at Marajoara. Within pairs, these trees flowered on completely nonoverlapping schedules in 2000 (Table 5) and, despite their proximity, had very different reproductive neighborhoods. Including stumps (not shown in Fig. 1) and live trees mapped in 1035 ha, we found that each of these four trees had 131–172 potential reproductive neighbors > 30 cm diam within 1000 m before logging. After conventional logging, reproductive neighborhood densities fell precipitously, to 10–21% of pre-logging densities. Within this radius, > 92% of surviving mahogany trees were subcommercial in size. The number of potential reproductive partners dropped still further when we restricted flowering overlap to account for limited female flower duration. Based on estimated flowering schedules in 2000, the reproductive neighborhood densities for trees with temporal overlap fell to 1–12% of pre-logging densities. Two of the four trees had no potential post-harvest reproductive partners > 60 cm diam within 1000 m under the conventional logging scenario (Table 5). Most remaining potential mates were subcommercial survivors with small crowns and low overall flower production, trees that might not be easily located by pollinators. Furthermore, the restricted number of potential pollen donors resulting from logging may dramatically reduce genetic variability in the pollen available to residual trees.

TABLE 4. Impact of conventional logging practices on mahogany population structures and estimated population-level flower production in southeast Amazonia, for trees > 30 cm diam in 204 ha at Marajoara. Post-logging figures represent percent of estimated pre-logging population ($N = 121$ trees, see Fig. 2A).

Diam size class:	Pre-logging forest		Post-logging forest	
	30–60 cm	> 60 cm	30–60 cm	> 60 cm
% Trees	32.5	67.5	9.2	3.3
% Flowers	11.9	88.1	2.8	3.2

TABLE 5. Impact of logging and sequential flowering on estimated effective breeding populations for two pairs (A, B) of surviving mahogany trees with disjunct flowering periods. Tree pairs are from 23 trees with flower traps, located in separate aggregations. Pre- and post-logging neighbors within 1000 m distance (314 ha) are divided into subcommercial and commercial size classes (30–60 cm diam, > 60 cm diam, respectively). Post-logging trees with temporal overlap are those survivors whose estimated total flowering period (male flowers available) overlaps with the target tree's projected female flowering period by one or more days.

Distance between trees within pairs:		(A) 260 m		(B) 110 m				
Focal Trees:								
Diameter	54 cm		59 cm		57 cm		55 cm	
Flowering period ^a	Aug 7–Sept 10		Sept 19–Oct 19		Aug 4–Sept 6		Sept 18–Oct 15	
Female flowering period ^b	Aug 14–Aug 25		Sept 26–Oct 7		Aug 11–Aug 22		Sept 25–Oct 6	
Neighbor diameter size class:	30–60 cm	> 60 cm	30–60 cm	> 60 cm	30–60 cm	> 60 cm	30–60 cm	> 60 cm
Pre-logging # trees	75	75	77	95	70	65	69	62
Post-logging # trees	24	3	16	2	26	2	26	2
Post-logging # trees w/ temporal overlap	5	0	6	2	1	0	14	2
Post-logging nearest potential mate (m)	395	–	190	350	820	–	175	795

^a From year 2000 flower trap data.

^b Estimated from data in White and Boshier (2000) for *Swietenia humilis*: female flowers receptive 1 wk after flowering onset, continuing for 11–12 d.

Pre-logging data on mahogany outcrossing rates and genetic diversity at Marajoara are not available. Lemes et al. (2007) showed that outcrossing rates were high ($t_m = 0.938 \pm 0.009$) even after logging at Marajoara, but the degree to which genotypic arrays of those seeds were altered as a result of timber extraction is unknown. It is noteworthy that two trees in that study produced fruits with high levels of inbreeding. This demonstrates that the paternal mating pool at Marajoara varies among different maternal trees, reinforcing the role that local pollen neighborhoods are likely to play in mating patterns. The genetic impacts of logging may thus be evident in the genotypes of post-logging regeneration (André et al., 2008). While mahogany can tolerate some level of inbreeding, a study in Bolivia in unlogged forest yielded measures of t_m close to 1.00 (Loveless and Gullison, 2003). Data from Marajoara (Lemes et al., 2007) are consistent with other studies showing increased inbreeding with declining adult population densities (Ward et al., 2005).

Robust knowledge of flowering phenology suggests several ways that forest management practices in effect for mahogany in Brazil since 2003 could be adjusted to promote pollen (genetic) exchange, fruit production, and natural regeneration. The current minimum diameter cutting limit of 60 cm (raised from 45 cm before 2003) protects subadult trees from harvest. The minimum density retention rate of 20% (raised from 10%) should additionally require that roughly equivalent numbers of trees be retained among size classes > 60 cm diam, however defined; this is because the largest trees contribute disproportionately to population-level flowering effort, and may serve as attractors for increased pollinator attention. Retained trees should be spread as evenly as possible through the management area to avoid 'pollinator isolation' by individual trees and to encourage multi-directional pollen movement among remnant trees on the landscape. Finally, annual harvests should be delayed until seeds have dispersed (mid dry season), to reap the full benefits of pollen and genetic exchange that occurred during the previous year's reproductive season.

Phenological studies of the scale we report here are time- and labor-intensive, and are not feasible as a precursor to logging management for every tropical timber species. Yet a growing body of evidence points to the fact that current logging regimes are unsustainable, both demographically and genetically (Sebbenn et al., 2008; Schulze et al., 2008a, b), leading many authors to recommend forest management practices that account

for differing life history traits of different timber species. Where phenological information is available, it should be considered along with other life history and community attributes in developing appropriate management guidelines.

When demographic changes in size class and adult density are integrated with an understanding of flowering behavior in mahogany populations, we begin to appreciate the profound changes in genetic makeup, and the substantive changes in genotypic diversity, that are likely to prevail in forests after logging. Such is the genetic landscape that mahogany must adapt to and evolve in from this generation forward across much of Brazil and South America.

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