

PHENOLOGY AND FECUNDITY IN 11 SYMPATRIC PIONEER SPECIES OF *MACARANGA* (EUPHORBIACEAE) IN BORNEO¹

STUART J. DAVIES^{2,3,4} AND PETER S. ASHTON²

²Harvard University Herbaria, Cambridge, Massachusetts 02138; and

³Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Malaysia

Reproductive traits of tropical tree species vary predictably in relation to successional stage, but this variation may be due to the species' phylogenetic histories rather than selective pressures imposed by regeneration requirements. Reproductive phenology, tree size at the onset of reproduction, and fecundity of 11 sympatric, closely related *Macaranga* species were studied to investigate within-species variation in reproductive traits in relation to resource availability, and among-species variation in relation to other life-history traits (shade tolerance, seed size and maximum tree size, H_{\max}) and consequently the requirements for forest-gap colonization. Nine species reproduced in synchronous episodes, and two species reproduced continuously over 32 mo. Episodic reproduction was most intense in 1992 following a severe drought. For several species, reproductive trees had greater light availability, lower fecundity in lower light levels, and lower growth rates than nonreproductive trees, reflecting resource-limited reproduction. Among species, H_{\max} was negatively correlated with shade tolerance and seed size. Tree size at the onset of reproduction and fecundity was strongly linked to this axis of life-history variation, but phenological pattern was not. Absolute tree size at the onset of reproduction was positively correlated with H_{\max} and negatively correlated with shade tolerance. Relative size at reproductive onset was not correlated with shade tolerance or H_{\max} . Fecundity ranged four orders of magnitude among species and was correlated positively with H_{\max} and negatively with seed size and shade tolerance. The interrelationships among these reproductive and other life-history traits are strongly correlated with the species' requirements for gap colonization.

Key words: early-successional trees; Euphorbiaceae; *Macaranga*; Malaysia; onset of reproduction; seed size; shade tolerance; succession; tree height; tropical rain forest.

The reproductive traits of tropical rain forest trees are usually considered to vary predictably in relation to the time that species appear in forest succession after disturbance (Bazzaz and Pickett, 1980; Whitmore, 1983; Denslow, 1987; Schupp et al., 1989). For example, pioneer species are often characterized as having early and frequent flowering and the copious production of small and easily dispersed seeds (Swaine and Whitmore, 1988). However, studies of pioneer species have found a wide range of variation in reproductive traits that may influence the ability of the species to colonize spatially and temporally unpredictable forest gaps. Flowering phenology (Opler, Baker, and Frankie, 1975; Lambert and Marshall, 1991; Milton, 1991), seed size (Fleming et al., 1985; Foster and Janson, 1985; Metcalfe and Grubb, 1995; Grubb, 1996), dispersal modes (Augspurger, 1986;

Augspurger and Franson, 1988), dormancy (Dalling, Swaine, and Garwood, 1997), and fecundity (Fleming, 1985; Alvarez-Buylla and Martinez-Ramos, 1992) vary substantially among pioneer trees. This is not surprising since pioneer species have evolved in a wide range of tropical tree lineages, and variation in their functional characteristics may in part depend on the characteristics of the lineage from which species evolved (Kochmer and Handel, 1986; Harvey and Pagel, 1991; Wright and Calderon, 1995). Furthermore, no single functional trait defines any grouping of tropical rain forest trees; pioneer species vary in a wide range of ecophysiological and demographic traits, yet many species successfully colonize and co-occur in forest gaps (Ackerly, 1996; Strauss-Denedetti and Bazzaz, 1996; Davies, 1998).

A suite of interrelated traits enables species to colonize particular microsites, but may simultaneously limit their ability to colonize and survive in other sites. For example, the production of large, well-defended seeds may inevitably result in a reduction in fecundity (Fleming, 1981; Grubb, 1998) and hence reduced ability to colonize spatially scattered and ephemeral forest gaps. Studies of factors influencing the ability of tropical pioneer trees to colonize forest gaps have often focused on either individual species or individual reproductive traits (e.g., Foster and Janson, 1985; Alvarez-Buylla and Martinez-Ramos, 1992). However, this approach does not provide a basis to investigate potential trade-offs in reproductive traits among tropical tree species and may not account for the importance of phylogeny in influencing the reproductive life-history traits of species (Barrett, Harder and Worley, 1996).

¹ Manuscript received 3 December 1998; revision accepted 22 April 1999.

The authors thank the Government of Sarawak, and the Sarawak National Parks and Forest Departments for permission to work at Lambir. The 52-ha Long Term Ecological Research plot was established as a collaborative project of the Sarawak Forest Department, Malaysia, Harvard University, USA (NSF award DEB 9107247 to PSA) and Osaka City University, Japan. The staff of the Sarawak Forest Department and the people of Rumah Ajai Longhouse greatly assisted with the field work. SJD was supported by a graduate student fellowship from the Department of Organismic and Evolutionary Biology and a Deland Award to the Arnold Arboretum at Harvard University. Sean Thomas, Peter Wayne, Fakhri Bazzaz, Tristram Seidler, Peter Stevens and Joe Wright made constructive comments on early versions of the paper.

⁴ Author for correspondence: Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia. (e-mail correspondence: sjdavies@mailhost.unimas.my).

TABLE 1. Life history traits for 11 species of *Macaranga*. Reproductive size threshold (RST, dbh in cm), and minimum observed reproductive size (R_{\min} , dbh in cm) from this paper, and H_{\max} (estimated maximum tree height), shade tolerance (estimated from mean crown illumination index, where lower values indicate greater tolerance) and seed mass from Davies et al. (1998). Values in parentheses are species' relative reproductive sizes (as a percentage of maximum tree dbh). N_r is the number of reproductive individuals, N_t is the total sample size. Species arranged as in Fig. 1.

Macaranga species	H_{\max} (m)	Shade tolerance (mean CI)	Seed mass (mg)	Reproductive size		N_r	N_t
				RST (cm, %)	R_{\min} (cm, %)		
Episodic reproduction							
<i>gigantea</i> (Reichb. f. & Zoll.) Muell. Arg.	29.3	4.2	13.7	12.2 (29)	9.7 (23)	2	38
<i>hosei</i> King ex Hook. f.	31.3	4.0	5.1	18.8 (34)	7.6 (14)	3	104
<i>hypoleuca</i> (Reichb. f. & Zoll.) Muell. Arg.	22.5	3.6	22.4	9.4 (26)	3.8 (11)	5	36
<i>triloba</i> (Bl.) Muell. Arg.	22.4	3.4	17.0	3.6 (24)	1.4 (9)	68	190
<i>beccariana</i> Merr.	17.2	3.4	15.2	5.3 (37)	2.6 (18)	37	255
<i>trachyphylla</i> Airy Shaw	21.5	3.2	22.7	7.3 (31)	4.8 (21)	34	233
<i>hullettii</i> King ex Hook. f.	17.9	2.6	28.3	4.6 (34)	4.4 (32)	13	33
<i>lamellata</i> Whitmore	15.0	2.1	64.0	3.7 (40)	1.2 (13)	13	52
<i>kingii</i> Hook. f. var. <i>platyphylla</i> Airy Shaw	14.9	2.0	64.2	2.2 (30)	1.2 (16)	23	53
Continuous reproduction							
<i>winkleri</i> Pax & Hoffm.	21.5	4.0	1.7	5.5 (37)	2.8 (19)	33	98
<i>havilandii</i> Airy Shaw	5.6	2.8	23.5	1.1 (44)	0.6 (24)	38	99

In this study, we use a comparative approach to investigate variation in patterns of reproductive onset, phenology, and fecundity among 11 sympatric species of *Macaranga* (Euphorbiaceae) in Borneo. The species range from very high-light demanding to moderately shade-tolerant trees (Davies, 1998; Davies et al., 1998) and vary in other life-history traits such as maximum tree size and seed mass. We test the hypothesis that the more high-light demanding *Macaranga* species have earlier and more frequent reproduction and greater fecundity than the more shade-tolerant species. First, we test for significant differences in tree size at the onset of reproduction, phenology, and fecundity among the species and assess possible environmental and allocational causes of within-species variation in reproductive activity. We then investigate the interrelationships among reproductive and other life-history traits for the species. In general, fecundity may be positively correlated with maximum tree size among species due to architectural and allocational constraints on seed production, however, seed size variation and the requirements for high-light microsites may affect this relationship (Fleming, 1985). We investigate potential trade-offs among reproductive and life-history characteristics in relation to differences in microsite preferences among the species. We also consider how this range of life-history traits influences the coexistence of this diverse group of sympatric, closely related species.

MATERIALS AND METHODS

Study species—*Macaranga* includes ~300 species of tropical trees distributed between west Africa and the south Pacific Islands (Whitmore, 1981). In Borneo there are ~50 species, many of which are high-light demanding pioneer trees. Eleven sympatric pioneer *Macaranga* species, in or closely related to section *Pachystemon*, were chosen for this study (Table 1). All Bornean species of *Macaranga* are dioecious. In the species included in this study, leaves are clustered toward the ends of orthotropic shoots and the inflorescences, borne in each of the leaf axils, are either developed with or just below the leaves (here referred to as "reproductive shoot clusters"). Staminate inflorescences are panicles with tiny (~0.5–1 mm) apetalous flowers. Small clusters of 5–

25 flowers are subtended by green or pale-brown small leafy bracteoles that are sometimes glandular. Pistillate inflorescences differ from staminate inflorescences in being stouter, less branched, and with fewer flowers. The mechanism of insect attraction to the pistillate flowers is unknown. Pistillate flowers are apetalous, 2–6 carpellate, with a single ovule per carpel, and with prominent stigmas that protrude from the calyx. Inflorescences are commonly visited by trigonid bees and thrips (Taylor, 1982; Momose et al., 1998), although how pollination occurs is unclear. Pollen is dehiscid through the apex of the tubular calyx and collects in and around the flower clusters. The fruits dehisce at maturity exposing small (1–6 mm diameter, 2–64 mg), arillate seeds that are dispersed by a wide variety of small birds and mammals (Taylor, 1982; Mitchell, 1994; Davies, personal observation).

Study site and surveys of reproduction—This study was conducted in Lambir Hills National Park (Lambir, 4°20' N, 113°50' E), Sarawak, Malaysia. The climate of Lambir is aseasonal with ~3000 mm rain per year, and average rainfall is >100 mm for all months (Watson, 1985). Daily mean maximum temperatures are ~32°C. The vegetation of Lambir is lowland mixed dipterocarp rain forest of exceptional tree species diversity (LaFrankie, Tan, and Ashton, 1995; Davies and Becker, 1996).

The phenological study involved monitoring 1191 trees in two non-contiguous 4-ha subplots of a recently established 52-ha long-term ecological research plot and in seven smaller forest plots in Lambir National Park over ~32 mo, from November 1991 to August 1994. All *Macaranga* trees in each plot were visited approximately once every 5 wk and scored as reproductive or not. Since pistillate flowers are apetalous and there is no externally obvious distinction between flowering and fruiting stages of reproduction, description of pistillate phenological patterns in this paper includes anthesis to fruit set. Trees across all size classes were monitored to enable estimates of species' size at the onset of reproduction, using both the size of the smallest reproductive individual and the size threshold above which the majority of individuals reproduce. The reproductive size threshold (RST) was estimated for the heavy flowering period in 1992, using the logistic regression model of Thomas (1996b). Occasional censuses were missed; for analysis, missed censuses for a tree were counted as reproductive if the census periods on either side of the missed census were both scored as reproductive. For *M. havilandii*, four censuses were missed in the middle of the survey period, and analyses did not include this period for this species.

Fecundity was estimated for all reproductive trees in the plots, as well as for extra trees of less common species from outside the plots.

Counts were made of the total number of reproductive shoot clusters on each tree, and the number of inflorescences on five (or all if there were fewer than five) reproductive shoot clusters. Flower number and seed production per inflorescence were counted on one inflorescence or infructescence from 3–12 different trees for each species. Fecundity for each tree was then estimated as the product of the number of reproductive shoot clusters, the mean number of inflorescences per reproductive shoot cluster, and the mean number of flowers/seeds per inflorescence/infructescence.

For analysis of within-species variation in reproductive traits, individual tree diameters at the time of reproductive activity were interpolated based on individual growth rates over the 32-mo study period (Davies, unpublished data). Tree canopy light environment was assessed using a crown illumination (CI) index on a scale of 5 (high-light) to 1 (low light), following Clark and Clark (1992), and calibrated against hemispherical fish-eye photographs (see Davies et al., 1998). Mean CI index, based on a large number of individuals for each species, is used as an ecological estimate of species' shade tolerance (5, very intolerant to 1, shade tolerant). Maximum tree size (H_{\max}) was estimated as asymptotic maximum height following Thomas (1996a), and described fully in Davies et al. (1998). Standard nonparametric tests were used for statistical comparisons of growth between reproductive and nonreproductive trees, because of the nonnormality of these data (Sokal and Rohlf, 1981).

Phenology analysis—Phenological patterns of reproductive activity were analyzed using circular statistics (Batschelet, 1981; Milton, 1991). The dates of phenological events were converted to angles between 0° and 360° . The mean angle, $\bar{\theta}$, and vector length, r , were then calculated as:

$$\bar{\theta} = \arctan(y/x) \quad \text{if } x > 0$$

$$\bar{\theta} = 180 + \arctan(y/x) \quad \text{if } x < 0$$

where,

$$x = \frac{1}{n} \sum \cos \theta_i \quad \text{and} \quad y = \frac{1}{n} \sum \sin \theta_i$$

then,

$$r = \sqrt{(x^2 + y^2)}$$

where n is the number of dates of phenological activity, and θ_i is the angle for phenological event i . The mean angle was then back-converted to a mean calendar date representing the average date of phenological activity. The length of the mean vector, r , varies between 0 and 1 and is a measure of the temporal concentration of phenological activity. Although high r values generally indicate aggregated phenological behavior, Rayleigh's test was used to determine whether the distribution of phenological activity was significantly nonrandom (Batschelet, 1981).

Reproductive phenology was analyzed at both individual and population levels for each species for 1992 and 1993, and for the sexes separately. For each reproductive individual, the mean angle and vector length were calculated. For each species, individual vector lengths were averaged (r_{ind}). r_{ind} indicates the average degree of individual temporal aggregation of reproductive activity, for example, a high r_{ind} indicates that individuals typically reproduce for a short period at one time of the year even though the date may differ among individuals (assuming no bimodality); alternatively a small r_{ind} indicates that individuals typically reproduce in a larger proportion of censuses in one or more episodes. At the population level, the mean angles for all individuals of a species were then analyzed together, resulting in a population vector length (r_{pop}) and mean angle. The mean angle for the population indicates the average date of peak reproductive activity among the individuals. r_{pop} indicates the degree of among-individual aggregation or synchrony of reproductive activity.

RESULTS

Size at reproductive onset—Tree size at the onset of reproduction varied dramatically among the 11 *Macaranga* species (Table 1). Reproductive size threshold (RST) ranged from 1.1 (*M. havilandii*) to 18.8 (*M. hosei*) cm dbh (diameter at breast height), and the minimum reproductive size observed (R_{\min}) ranged from 0.6 to 9.7 cm dbh. Among species, RST was 24–44% of H_{\max} , and R_{\min} was 9–32% of H_{\max} . RST for *M. hosei* was probably an overestimate as reproductive trees of 10–12 cm dbh were frequently observed outside the study plots (Davies, personal observation). There were no significant between-sex differences in size at the onset of reproduction (Kolmogorov-Smirnov two-sample tests, $P > 0.2$ for all species).

Reproductive phenology—Nine of the 11 *Macaranga* species (*M. gigantea*, *M. hosei*, *M. hypoleuca*, *M. triloba*, *M. beccariana*, *M. trachyphylla*, *M. hullettii*, *M. lamellata*, and *M. kingii*) reproduced in synchronous episodes twice during the study period (“episodic”), with a third episode starting as the study was terminated in 1994 (Fig. 1). Large population vector lengths, r_{pop} , in these species (range: 0.59–1.00, mean: 0.92, $N = 30$, with years and sexes separate; Table 2) indicated a high degree of intraspecific reproductive synchrony, and high means of the individual vector lengths, r_{ind} (range: 0.68–1.00, mean: 0.93, $N = 30$), reflected relatively short reproductive duration. In contrast, *M. winkleri* and *M. havilandii* reproduced continuously at the population level throughout the study period (“continuous”), although several censuses were missed for *M. havilandii* (Fig. 1). r_{pop} values were lower (range: 0.28–0.77, mean: 0.55, $N = 6$), indicating less synchronized within-species reproduction. r_{ind} values were also lower, as individuals reproduced in a large proportion of months (range: 0.20–0.69, mean: 0.47, $N = 6$; Table 2).

The timing and intensity of reproduction differed significantly between years and sexes for the episodic species (Table 2). Reproduction peaked between February and May in 1992 and between May and August in 1993. All six episodic species with sufficient sample sizes had a greater proportion of reproductive individuals in 1992 than in 1993 (G tests: four species $P < 0.02$, two species $P < 0.20$). In continuous species, the proportion of individuals flowering did not differ between 1992 and 1993 ($P > 0.55$, G test).

Reproductive frequency varied within all species (Table 3). Trees of episodic species reproduced up to three times, yet 21–68% of trees $> R_{\min}$ (0–25% of trees $> RST$) did not reproduce during the study period. In several species (*M. beccariana*, *M. trachyphylla*, and *M. kingii*) pistillate trees tended to flower more frequently than staminate trees (Table 3). Individual trees of both continuous species were reproductive for, on average, 49–66% of the censuses, with no differences between the sexes (Table 4). Although some trees were reproductively active throughout the 32-mo period, 17–37% of trees with dbh $> RST$ failed to reproduce.

Crown light availability (mean CI index) was higher in reproductive than nonreproductive trees in seven out of eight species (excluding species with small samples

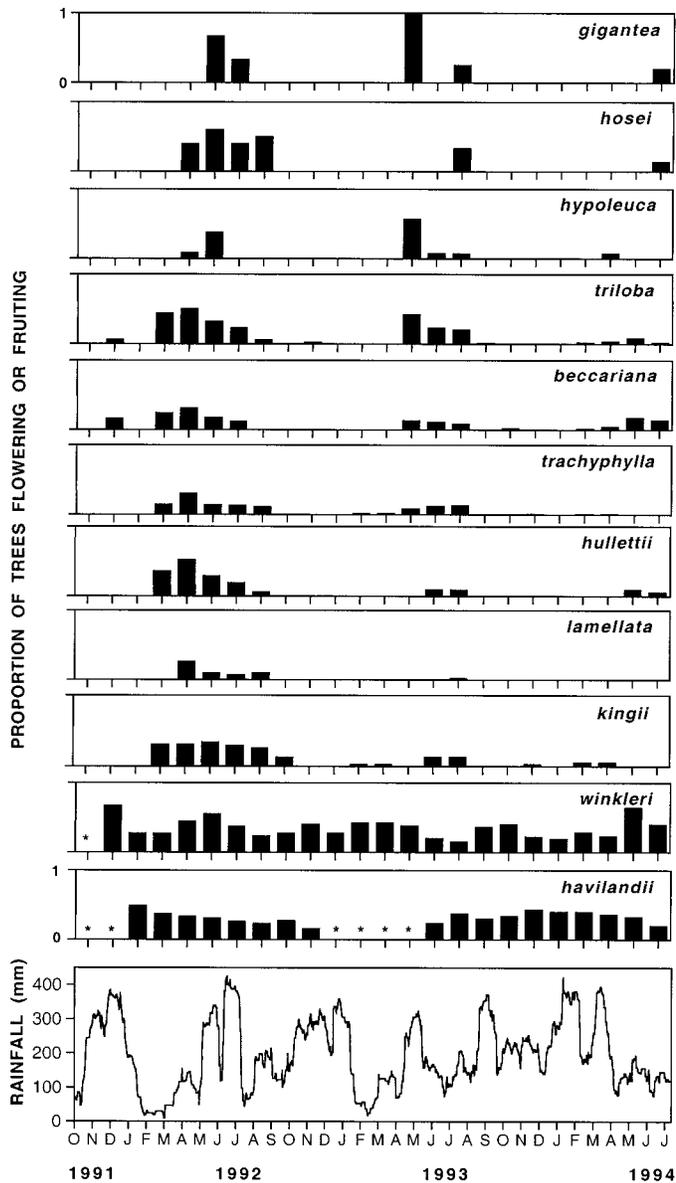


Fig. 1. Reproductive phenology of 11 species of *Macaranga* in Lambir Hills National Park from 1991 to 1994, as the proportion of trees $>R_{min}$. Running 30-d average rainfall (from records of the Lambir Hills Microwave Station) is included for comparison. Asterisks indicate missed censuses. Within episodic (top nine species) and continuous (bottom two species) reproducers, species are arranged in order of increasing shade tolerance.

sizes; $P < 0.01$ in five species; Fig. 2). For both continuous species, reproductive frequency (excluding nonreproductives) was significantly positively correlated with CI index (*M. winkleri*: $r_s = 0.49$, $P < 0.01$; *M. havilandii*: $r_s = 0.63$, $P < 0.01$). Mean CI index was marginally significantly higher for trees that reproduced two or three times than for trees that reproduced only once for *M. triloba* ($P = 0.03$), but not for other episodic species.

Diameter growth rates differed significantly between reproductive and nonreproductive trees in three species (Fig. 2). In *M. winkleri* and *M. trachyphylla*, growth rates were significantly lower for reproductive than nonrepro-

ductive trees, whereas reproductive trees had significantly higher growth rates in *M. triloba*. Diameter growth was also negatively correlated with the frequency of reproduction in *M. winkleri* ($r_s = -0.49$, $P < 0.01$), but not in other species. There were no significant between-sex differences in diameter growth rates for any species ($P > 0.1$, data not shown).

Fecundity—Flower and fruit production varied enormously among *Macaranga* species (Fig. 3). Trees produced from 10^3 (*M. havilandii*) to 10^7 (*M. gigantea*, *M. hosei*, *M. hypoleuca*, and *M. winkleri*) staminate flowers or from 10^2 to $>10^5$ seeds per reproductive episode. For continuous reproducers, annual fecundity was approximately three times the values for a single reproductive episode (Davies, personal observation). Species differed significantly in the production of both inflorescences per tree and flowers per inflorescence (Table 5). Differences in staminate and pistillate fecundity were primarily due to differences in flowers per inflorescence; inflorescence production per tree did not differ significantly between the sexes in any species.

Within species, fecundity was positively correlated with tree size, but only weakly related to crown light availability (CI index). For staminate plants, eight of ten species had significantly size-dependent fecundity ($r^2 = 0.04$ – 0.93), whereas pistillate fecundity was significantly size dependent in only five species ($r^2 = 0.10$ – 0.40 , *M. kingii* $r^2 = 0.74$). No species had significant differences in staminate fecundity among light levels ($P > 0.1$, Kruskal-Wallis tests, data not shown), and only *M. triloba* ($P = 0.05$) and *M. winkleri* ($P = 0.01$) had significantly lower pistillate fecundity in intermediate (CI class = 3) than in higher light levels (CI classes = 5 and 4).

Reproduction and other life-history traits—All measures of phenological pattern (r_{ind} , r_{pop} , reproductive frequency, and mean date of reproduction) among the 11 *Macaranga* species were not significantly correlated with other reproductive traits (tree size at the onset of reproduction or fecundity) or with other life-history traits (H_{max} , estimated shade tolerance, or seed mass) ($P > 0.05$ in all cases). In contrast, tree size at the onset of reproduction and mean annual fecundity were strongly correlated with other life-history traits. Tree size at the onset of reproduction was positively correlated with H_{max} (RST: $r_s = 0.91$, R_{min} : $r_s = 0.85$, both $P < 0.01$), negatively correlated with seed mass ($r_s = -0.66$, $P = 0.04$), and positively correlated with species' mean CI index (for RST, $r_s = 0.77$, $P = 0.01$) and therefore negatively correlated with estimated shade tolerance. However, relative size at the onset of reproduction was not significantly correlated with H_{max} , seed mass, or estimated shade tolerance (all $P > 0.1$). Among species, mean annual fecundity was positively correlated with H_{max} and negatively correlated with shade tolerance and seed mass (Fig. 3). The mean number of inflorescences per tree (δ : $r_s = 0.77$, ♀ : $r_s = 0.88$) and the mean number of flowers per inflorescence (δ : $r_s = 0.91$, ♀ : $r_s = 0.79$) were significantly positively correlated with H_{max} (all $P < 0.02$). The number of pistillate flowers per inflorescence was negatively correlated with mean seed size ($r_s = -0.87$).

TABLE 2. Summary of analyses of the phenology of staminate (δ) and pistillate (♀) reproduction in 11 *Macaranga* species over 2 yr (1992, 1993) in Lambir, Sarawak, Malaysia. r_{ind} is the average of individual vector lengths within species (the average degree of individual temporal aggregation of reproduction). r_{pop} is the population vector length (degree of phenological aggregation among individuals) for the mean peak flowering date, $\bar{\phi}$, and N is the number of reproductive trees. P is the significance of Rayleigh's test for deviation from random temporal distribution of flowering. Due to missing data for *M. havilandii*, phenology for this species was analyzed for the whole census period (1991–1994) and for the year June 1993 to July 1994. Species are arranged as in Fig. 1.

Species	Year	Sex	Individual r_{ind} (mean \pm SE)	Population r_{pop}	Population $\bar{\phi}$ (date)	N	P
Episodic reproduction							
<i>gigantea</i>	92	δ	1.00 \pm 0.00	1.00	7 May	1	—
		♀	0.94 \pm 0.00	0.94	26 May	1	—
	93	δ	1.00 \pm 0.00	1.00	15 May	1	—
		♀	1.00 \pm 0.00	1.00	5 Aug	1	—
<i>hosei</i>	92	δ	— —	—	—	0	—
		♀	0.82 \pm 0.09	0.99	21 May	3	—
	93	δ	— —	—	—	0	—
<i>hypoleuca</i>	92	δ	1.00 \pm 0.00	0.98	1 Aug	3	—
		♀	0.98 \pm 0.02	0.98	1 May	3	—
	93	δ	— —	—	—	0	—
		♀	1.00 \pm 0.00	1.00	19 May	4	—
<i>triloba</i>	92	δ	0.92 \pm 0.02	0.96	16 Mar	34	<0.001
		♀	0.72 \pm 0.03	0.87	20 Apr	30	<0.001
	93	δ	0.99 \pm 0.01	0.98	19 May	20	<0.001
		♀	0.89 \pm 0.01	0.95	28 Jun	26	<0.001
<i>beccariana</i>	92	δ	0.98 \pm 0.02	0.93	10 Mar	23	<0.001
		♀	0.80 \pm 0.04	0.84	20 Apr	14	<0.001
	93	δ	0.98 \pm 0.02	0.61	3 Jun	6	0.10
		♀	0.96 \pm 0.01	0.76	7 Jul	9	0.003
<i>trachyphylla</i>	92	δ	0.99 \pm 0.01	0.97	15 Mar	10	<0.001
		♀	0.82 \pm 0.03	0.87	29 Apr	20	<0.001
	93	δ	0.92 \pm 0.00	1.00	21 Feb	1	—
		♀	0.89 \pm 0.05	0.91	10 Jul	12	<0.001
<i>hullettii</i>	92	δ	0.99 \pm 0.02	0.93	27 Feb	3	—
		♀	0.86 \pm 0.03	0.91	26 Apr	7	<0.001
	93	δ	— —	—	—	0	—
		♀	0.92 \pm 0.00	1.00	9 Jul	2	—
<i>lamellata</i>	92	δ	1.00 \pm 0.00	1.00	27 Mar	6	<0.001
		♀	0.91 \pm 0.02	0.83	3 Jun	6	0.09
	93	δ	— —	—	—	0	—
		♀	1.00 \pm 0.00	1.00	2 Aug	1	—
<i>kingii</i>	92	δ	1.00 \pm 0.00	0.98	26 Feb	10	<0.001
		♀	0.68 \pm 0.03	0.94	27 May	14	<0.001
	93	δ	— —	—	—	0	—
		♀	0.87 \pm 0.08	0.59	25 Jun	7	0.08
Continuous reproduction							
<i>winkleri</i>	92	δ	0.34 \pm 0.05	0.56	8 Apr	16	0.007
		♀	0.51 \pm 0.09	0.77	24 May	16	<0.001
	93	δ	0.69 \pm 0.10	0.40	23 Jan	13	0.13
		♀	0.68 \pm 0.08	0.69	15 Jan	18	<0.001
<i>havilandii</i>	91–94	δ	0.20 \pm 0.04	0.52	11 Apr	33	<0.001
		♀	0.35 \pm 0.11	0.57	30 May	10	0.04
	93–94	δ	0.20 \pm 0.04	0.60	9 Jan	30	<0.001
		♀	0.42 \pm 0.12	0.28	26 Jul	8	0.55

DISCUSSION

The phenological patterns found in the 11 *Macaranga* species are consistent with patterns reported for *Macaranga* elsewhere in southeast Asia (Taylor, 1982; van Schaik, 1986; Corlett, 1990). The 5-wk census interval used and the difficulty of identifying the exact flowering time in pistillate plants may limit our ability to detect finer scale temporal differences in flowering activity, par-

ticularly among the episodic species. However, field observations suggested that flowering was concurrent among species, as anthesis occurs acropetally within and among inflorescences on a reproductive shoot, and inflorescences expand over 3–6 wk (Davies, personal observation). When closely related species are truly sympatric, they often flower at different times or have different flower morphologies and pollinators (Hurlbert, 1970; Stiles, 1975; Fleming, 1985; Ashton, Givnish, and Appanah,

TABLE 3. Reproductive frequency of staminate (♂) and pistillate (♀) trees of nine episodic reproducing species of *Macaranga* over 32 mo. For each species and sex the percentage of individuals reproducing once, twice, and three times is listed. N_{rep} is the number of plants that reproduced. P is the significance level for the test of between-sex differences in the frequency of reproduction (G test or Fisher's Exact test). The asterisk indicates that only *M. kingii* had significant differences with Bonferroni adjusted P values. The number (N) and percentage (%) of alive and undamaged nonreproductive trees are listed.

Species	Sex	Reproductive episodes			N_{rep}	P	Nonreproductive			
		1	2	3			$\geq R_{min}$		$\geq RST$	
							N	%	N	%
<i>gigantea</i>	♂	0	100	0	1	ns	1	33	0	0
	♀	0	0	100	1					
<i>hosei</i>	♂	0	0	0	0	ns	1	25	0	0
	♀	50	50	0	4					
<i>hypoleuca</i>	♂	60	40	0	5	ns	4	36	0	0
	♀	100	0	0	2					
<i>triloba</i>	♂	49	49	2	39	ns	27	27	7	9
	♀	27	70	3	33					
<i>beccariana</i>	♂	79	13	8	24	0.06	27	40	4	9
	♀	44	25	31	16					
<i>trachyphylla</i>	♂	91	9	0	11	0.05	20	38	5	13
	♀	55	45	0	22					
<i>hullettii</i>	♂	100	0	0	3	ns	3	21	2	15
	♀	88	0	12	8					
<i>lamellata</i>	♂	100	0	0	6	ns	26	68	4	25
	♀	83	17	0	6					
<i>kingii</i>	♂	100	0	0	10	0.006*	14	37	7	23
	♀	43	57	0	14					

1988; Yap and Chan, 1990; LaFrankie and Chan, 1991; Oliveira and Gibbs, 1994; but see Wright and Calderon, 1995). In these species of *Macaranga* flower morphologies are uniform, and species appear to share pollinators. Whether there are detrimental consequences to this apparent phenological overlap (Bawa, 1983) and what the reproductive isolating mechanisms in these species are require detailed study of pollinator visitation patterns, flower anthesis, and fruit maturation (Augspurger, 1981).

Community-level reproduction was synchronized, but not strictly annual among the nine episodic *Macaranga* species, suggesting that they responded to a common flowering cue. In 1992, the heaviest flowering year, there was an intense short-term drought at Lambir between January and March (Fig. 1), with cumulative 30-d rainfall <40 mm for 39 d. A general flowering of Dipterocarpaceae and other canopy species followed the drought (Davies, personal observation). The slightly later and less intense *Macaranga* flowering in 1993 was not preceded by an intense drought; cumulative 30-d rainfall from Jan-

uary to March was <40 mm for only 14 d. In 1994, flowering was initiated (although intensity was not assessed) even though cumulative rainfall in the same period was >170 mm. Our observations from 1992 to 1998 indicate that these species reproduce in all years, with considerable variation in the intensity of reproduction; species reproduce most heavily in the same years as forest-wide general flowering (see also Sakai et al., 1999). This variation may be linked to increased irradiance levels associated with drought periods as suggested by other workers (van Schaik, Terborgh, and Wright, 1993; Wright and van Schaik, 1994).

A large proportion of mature trees of most *Macaranga* species did not reproduce during the study, and there was significant variation in reproductive frequency. Much of this variation may have been due to variation in resource availability. Diameter growth in these species was shown to be strongly limited by light and soil resource availability (Davies, unpublished data). Reproductive trees in most species had their canopies in higher light levels than

TABLE 4. Reproductive frequency of staminate (♂) and pistillate (♀) trees of two continuously reproducing *Macaranga* species over 32 mo. For each species and sex the mean percentage of possible censuses in which individuals were reproductive is listed (accounting for deaths and missed censuses). The percentage of individuals reproductive for 0–25, 26–50, 51–75, and 76–100% of possible censuses is also listed. N_{rep} is the number of reproductive trees. The number and percentage of alive and undamaged nonreproductive trees are listed.

Species	Sex	Mean % censuses	% of trees reproductive				N_{rep}	Nonreproductive			
			0–25	26–50	51–75	76–100		$\geq R_{min}$		$\geq RST$	
								N	%	N	%
<i>winkleri</i>	♂	57	16	32	21	32	19	8	17	1	2
	♀	55	19	33	14	33					
<i>havilandii</i>	♂	66	12	15	21	52	33	25	37	5	10
	♀	49	30	20	20	30					

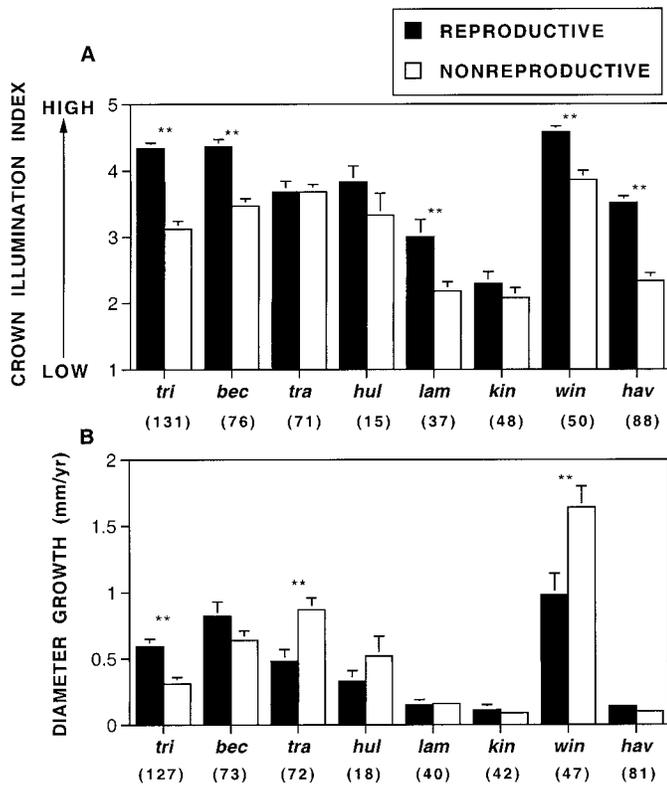


Fig. 2. Mean (+1 SE) crown illumination index (A) and median diameter growth rates (B) for reproductive and nonreproductive trees ($\geq R_{min}$) in eight *Macaranga* species. Species listed by their first three letters (see Fig. 1 for complete spelling). Sample sizes are listed below three-letter codes for each species. Significant differences between reproductive and nonreproductive trees are indicated by double asterisks from Mann-Whitney *U* tests ($P \leq 0.01$ in all cases). Three species were excluded from analyses due to limited sample sizes.

nonreproductive trees, and several species had greater reproductive frequency in higher light or reduced pistillate fecundity in lower light, suggesting that reproduction was strongly influenced by resource availability. Fecundity in pistillate plants may have been particularly sensitive to resource limitation, as tree size accounted for less of the variation in pistillate than staminate fecundity in most species (see also Melampy and Howe, 1977; Bullock and Bawa, 1981; Bullock, 1982; Bullock, Beach, and Bawa, 1983; Clark and Clark, 1987; Armstrong and Irvine, 1989; Thomas and LaFrankie, 1993; Thomas, 1996c). However, pistillate trees in several species flowered more frequently than staminate trees. A consequence of resource-limited reproduction may be reduced growth rates in reproductive trees (Bazzaz and Reekie, 1985). Reproductive trees had lower diameter growth rates in two species, and for *M. winkleri* reproductive frequency was negatively correlated with growth rate. However, if reproductive and nonreproductive trees are differentially distributed on a fine scale with respect to resource availability, reproductive trees may grow as fast or faster than nonreproductive trees. For *M. triloba*, growth rates were higher in reproductive than nonreproductive trees, but nonreproductive trees of this species were in particularly unfavorable microsites, their canopies had much

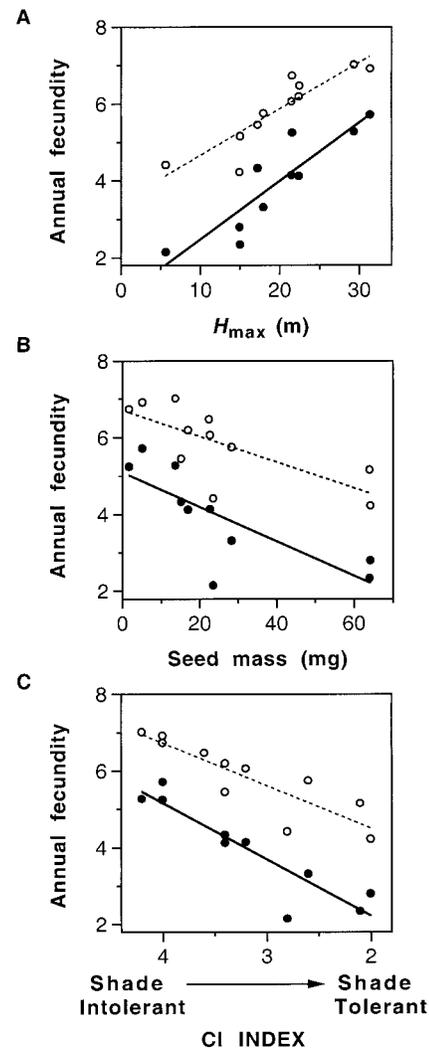


Fig. 3. Relationships between mean annual staminate (open circles) and pistillate (shaded circles) fecundity and life-history traits for the 11 *Macaranga* species. Fecundity is on a log₁₀ scale. (A) Maximum tree height, H_{max} : $\delta r^2 = 0.80$, $\eta r^2 = 0.80$; (B) seed mass: $\delta r^2 = 0.53$, $\eta r^2 = 0.61$; and (C) estimated shade tolerance: $\delta r^2 = 0.76$, $\eta r^2 = 0.84$. $P \leq 0.01$ in all cases. No estimate of seed production for *M. hypoleuca* ($N = 10$ for pistillate relationships).

lower light levels (Fig. 2), and they had higher mortality rates (Davies, 1996).

Reproduction and life history—Reproductive phenology was not correlated with other life-history traits among the 11 *Macaranga* species. The continuous reproducers, *M. winkleri* and *M. havilandii*, have extremely different life histories (Davies, 1998; Davies, unpublished data). *Macaranga winkleri* is a high-light-demanding tree of 15–20 m tall, restricted to nutrient-rich soils. Trees grow rapidly to reproductive maturity, produce a huge number of tiny seeds, incurring an indirect cost in reduced growth rates, and then continue to reproduce for several years before dying. *Macaranga havilandii* is relatively shade tolerant and occurs on nutrient-poor soils often associated with small landslips. It grows slowly to 5–6 m tall and produces a small number of relatively

TABLE 5. Flower production per inflorescence and inflorescence production per tree for staminate and pistillate plants in 11 *Macaranga* species. *P* refers to significance of between-sex differences in flower and inflorescence production based on post-hoc tests following two-factor ANOVAs. Flower numbers were log₁₀ transformed before analysis.

Species	Flowers per inflorescence							Inflorescences per tree						
	Staminate			Pistillate			<i>P</i>	Staminate			Pistillate			<i>P</i>
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>		Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
Episodic flowering species														
<i>gigantea</i>	53 010	12 580	5	617	101	3	<0.01	200	57	5	308	55	5	ns
<i>hosei</i>	22 000	3759	6	1350	575	3	<0.01	382	95	5	392	66	14	ns
<i>hypoleuca</i>	20 625	5200	4	—	—	—		146	61	7	—	—	—	
<i>triloba</i>	9775	1208	6	66	15	5	<0.01	162	21	58	204	26	57	ns
<i>beccariana</i>	4286	999	7	197	17	3	<0.01	67	11	37	110	10	49	ns
<i>trachyphylla</i>	9240	1250	5	158	30	5	<0.01	127	48	11	89	25	24	ns
<i>hullettii</i>	2768	131	8	28	4	3	<0.01	206	66	4	75	20	10	ns
<i>lamellata</i>	1963	99	4	37	3	3	<0.01	74	32	2	6	2	7	ns
<i>kingii</i>	2133	318	3	29	4	5	<0.01	8	5	5	22	7	12	ns
Continuous flowering species														
<i>winkleri</i>	36 275	19 428	8	831	130	4	<0.01	51	4	113	72	5	140	ns
<i>havilandii</i>	1575	85	4	17	2	4	<0.01	5.6	0.4	81	2.8	0.2	53	ns

large seeds. Continuous seed production in *M. havilandii* may ensure seed availability in the unpredictable event of a small landslip, in which seed would not be available in the soil. The episodic species also vary in life-history traits, with species ranging from relatively shade tolerant (e.g., *M. kingii*) to very high-light-demanding (e.g., *M. gigantea*), and differing in fecundity, H_{max} , and seed size (Davies et al., 1998).

Pioneer tree species are usually considered to initiate reproduction earlier than shade-tolerant species (Bazzaz, 1984; Swaine and Whitmore, 1988). Given that pioneers typically access higher resource levels and grow faster, they not surprisingly reach reproductive size sooner than other species. However, we found no evidence for a relationship between successional status and relative size at the onset of reproduction among the 11 *Macaranga* species. Furthermore, Thomas (1996b) reported a range of 20–75% for the relative size at the onset of reproduction among 36 shade-tolerant tree species in a peninsular Malaysian rain forest. These values completely overlap the *Macaranga* values and suggest that the life history of pioneer species, although accelerated, shows no consistent differences from nonpioneer species with regard to relative tree size at the onset of reproduction (see also Brzeziecki and Kienast, 1994, for temperate trees).

Greater fecundity in more high-light-demanding than shade-tolerant species conforms to the general expectation for tropical trees (Swaine and Whitmore, 1988; Primack and Lee, 1991). However, the more high-light demanding species were also larger trees and produced smaller seeds, so differences in fecundity may or may not represent relative differences in biomass allocation to reproduction. Among *Macaranga* species, tree size determined the potential number of sites for inflorescence production as was found for the Neotropical pioneer, *Cecropia obtusifolia* (Alvarez-Buylla and Martinez-Ramos, 1992). Larger *Macaranga* species also had more elaborately branched inflorescences bearing more flowers. The direct reason for this is unclear, but seed size was negatively correlated with the number of pistillate flowers per inflorescence and may constrain potential flower production per inflorescence. The selective advantage of smaller

seeds in more high-light-demanding *Macaranga* species may be related to a range of factors, including increased dispersal ability to access high-light microsites, lower unit energy costs, and in *M. winkleri*, the species with the smallest seed, the ability to continuously reproduce and thereby increase the probability of accessing ephemeral gaps (Dalling, Swaine and Garwood, 1997). Smaller seeds may also have lower seed reserves, may be physically impeded by dense leaf litter, and may have lower persistence times in the soil due to pathogen or drought effects, thereby excluding species from establishment in light-limited microsites (Hopkins and Graham, 1987; Alvarez-Buylla and Martinez-Ramos, 1990; Molofsky and Augspurger, 1992; Grubb, 1998).

An axis of life-history variation among the 11 sympatric *Macaranga* species ranges from very high-light-demanding to moderately shade tolerant. Maximum tree size, seed size, absolute tree size at the onset of reproduction, and annual fecundity covary with the degree of shade tolerance in these species. Smaller seeds and greater fecundity may have selective advantages for more high-light-demanding species, however these traits are also strongly correlated with, and may functionally depend upon, tree size and inflorescence architecture. Assessing whether these traits have undergone correlated evolutionary changes associated with the diversification of *Macaranga* in early-successional environments will be clarified with an explicit hypothesis of phylogenetic relationships.

LITERATURE CITED

ACKERLY, D. D. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. In S. S. Mulkey, R. L. Chazdon, and A. P. Smith [eds.], *Tropical forest plant ecophysiology*, 619–658. Chapman and Hall, New York, NY.

ALVAREZ-BUYLLA, E. R., AND M. MARTINEZ-RAMOS. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84: 314–325.

—, AND —. 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree—an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology* 80: 275–290.

ARMSTRONG, J. E., AND A. K. IRVINE. 1989. Flowering, sex ratios, pol-

- len-ovule ratios, fruit set, and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rain forest communities. *American Journal of Botany* 76: 74–85.
- ASHTON, P. S., T. J. GIVNISH, AND S. APPANAH. 1988. Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132: 44–66.
- AUGSPURGER, C. K. 1981. Reproductive synchrony of tropical plants: experimental effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775–788.
- . 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353–363.
- , AND S. E. FRANSON. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. *Journal of Tropical Ecology* 4: 239–252.
- BARRETT, S. C. H., L. D. HARDER, AND A. C. WORLEY. 1996. The comparative biology of pollination and mating in flowering plants. In J. Silvertown, M. Franco, and J. L. Harper [eds.], *Plant life histories: ecology, evolution and phylogeny*, 57–76. Cambridge University Press, Cambridge.
- BATSCHLET, E. 1981. *Circular statistics in biology*. Academic Press, London.
- BAWA, K. S. 1983. Patterns of flowering in tropical plants. In C. E. Jones, and R. J. Little [eds.], *Handbook of experimental pollination biology*, 394–410. Scientific and Academic Editions, New York, NY.
- BAZZAZ, F. A. 1984. Dynamics of wet tropical forests and their species strategies. In E. Medina, H. A. Mooney, and C. Vázquez-Yanes [eds.], *Physiological ecology of plants in the wet tropics*, 233–243. Junk, The Hague.
- , AND S. T. A. PICKETT. 1980. The physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11: 287–310.
- , AND E. G. REEKIE. 1985. The meaning and measurement of reproductive effort in plants. In J. White [ed.], *Studies on plant demography: a festschrift for John L. Harper*, 373–387. Academic Press, London.
- BRZEZIECKI, B., AND F. KIENAST. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management* 69: 167–187.
- BULLOCK, S. H. 1982. Population structure and reproduction in the Neotropical dioecious tree *Compsonera sprucei*. *Oecologia* 55: 238–242.
- , AND K. S. BAWA. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology* 62: 1494–1504.
- , J. H. BEACH, AND K. S. BAWA. 1983. Episodic flowering and sexual dimorphism in *Guarea rhopalocarpa* in a Costa Rican rain forest. *Ecology* 64: 851–861.
- CLARK, D. A., AND D. B. CLARK. 1987. Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rain forest cycad. *Journal of Ecology* 75: 135–149.
- , AND ———. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62: 315–344.
- CORLETT, R. T. 1990. Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *Journal of Tropical Ecology* 6: 55–63.
- DALLING, J. W., M. D. SWAINE, AND N. C. GARWOOD. 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology* 13: 659–680.
- DAVIES, S. J. 1996. The comparative ecology of *Macaranga* (Euphorbiaceae). Ph.D. dissertation, Harvard University, Cambridge, MA.
- . 1998. Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life-history. *Ecology* 79: 2292–2308.
- , AND P. BECKER. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. *Journal of Tropical Forest Science* 8: 542–569.
- , P. PALMIOTTO, P. S. ASHTON, H. S. LEE, AND J. V. LAFRANKIE. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86: 662–673.
- DENSLAW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431–451.
- FLEMING, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia* 51: 42–46.
- . 1985. Coexistence of five sympatric *Piper* (Piperaceae) species in a dry tropical forest. *Ecology* 66: 688–700.
- , C. F. WILLIAMS, F. J. BONACCORSO, AND L. H. HERBST. 1985. Phenology, seed dispersal, and colonization in *Muntingia calabura*, a neotropical pioneer tree. *American Journal of Botany* 72: 383–391.
- FOSTER, S. A., AND C. H. JANSON. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66: 773–780.
- GRUBB, P. J. 1996. Rainforest dynamics: the need for new paradigms. In S. C. Choy, D. S. Edwards, and W. E. Booth [eds.], *Tropical rainforest research—current issues*, 215–233. Kluwer, The Netherlands.
- . 1998. Seeds and fruits of tropical rainforest plants: interpretation of the range in seed size, degree of defence and flesh/seed quotients. In D. M. Newbery, H. H. T. Prins, and N. D. Brown [eds.], *Dynamics of tropical communities*, 1–24. Blackwell Science, Oxford.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- HOPKINS, M. S., AND A. W. GRAHAM. 1987. The viability of seeds of rain forest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* 12: 97–108.
- HURLBERT, S. H. 1970. Flower number, flowering time, and reproductive isolation among ten species of *Solidago* (Compositae). *Bulletin of the Torrey Botanical Club* 97: 189–195.
- KOCHMER, J. P., AND S. N. HANDEL. 1986. Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* 56: 303–325.
- LAFRANKIE, J. V., AND H. T. CHAN. 1991. Confirmation of sequential flowering in *Shorea* (Dipterocarpaceae). *Biotropica* 23: 200–203.
- , S. TAN, AND P. S. ASHTON. 1995. Species list for the 52-ha forest dynamics research plot: Lambir Hills National Park, Sarawak, Malaysia. Miscellaneous Internal Report. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Singapore.
- LAMBERT, F. R., AND A. G. MARSHALL. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rainforest. *Journal of Ecology* 79: 793–809.
- MELAMPY, M. N., AND H. F. HOWE. 1977. Sex ratio in the tropical tree *Triplaris americana* (Polygonaceae). *Evolution* 31: 867–872.
- METCALFE, D. J., AND P. J. GRUBB. 1995. Seed mass and light requirements for regeneration in southeast Asian rain forest. *Canadian Journal of Botany* 73: 817–826.
- MILTON, K. 1991. Leaf change and fruit production in six neotropical Moraceae species. *Journal of Ecology* 79: 1–26.
- MITCHELL, T. C. 1994. The ecology of *Macaranga* (Euphorbiaceae) trees in primary lowland mixed dipterocarp forest, Brunei. Ph.D. dissertation, Cambridge University, Cambridge.
- MOLOFSKY, J., AND C. AUGSPURGER. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68–77.
- MOMOSE, K., T. YUMOTO, T. NAGAMITSU, M. KATO, H. NAGAMASU, S. SAKAI, R. D. HARRISON, T. ITIOKA, A. A. HAMID, AND T. INOUE. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85: 1477–1501.
- OLIVEIRA, P., AND P. GIBBS. 1994. Pollination biology and breeding systems of six *Vochysia* species (Vochysiaceae) in Central Brazil. *Journal of Tropical Ecology* 10: 509–522.
- OPLER, P. A., H. G. BAKER, AND G. W. FRANKIE. 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* 7: 234–247.
- PRIMACK, R. B., AND H. S. LEE. 1991. Population dynamics of pioneer trees (*Macaranga*) and understorey trees (*Mallotus*) belonging to the Euphorbiaceae in primary and selectively logged Bornean rainforests. *Journal of Tropical Ecology* 7: 439–458.

- SAKAI, S., K. MOMOSE, T. YUMOTO, T. NAGAMITSU, H. NAGAMASU, A. A. HAMID, T. NAKASHIZUKA, AND T. INOUE. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany*, in press.
- SCHUPP, E. W., H. F. HOWE, C. K. AUGSPURGER, AND D. J. LEVEY. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70: 562–564.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, New York, NY.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56: 285–301.
- STRAUSS-DEBENEDETTI, S., AND F. A. BAZZAZ. 1996. Photosynthetic characteristics of tropical trees along successional gradients. In S. Mulkey, R. L. Chazdon, and A. P. Smith [eds.], *Tropical forest ecophysiology*, 162–186. Chapman and Hall, New York, NY.
- SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rainforests. *Vegetatio* 75: 81–86.
- TAYLOR, C. E. 1982. Reproductive biology and ecology of some tropical pioneer trees. Ph.D. dissertation, University of Aberdeen, Scotland, UK.
- THOMAS, S. C. 1996a. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany* 83: 556–566.
- . 1996b. Relative size at the onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos* 76: 145–154.
- . 1996c. Reproductive allometry in Malaysian rain forest trees: biomechanics vs. optimal allocation. *Evolutionary Ecology* 10: 517–530.
- , AND J. V. LAFRANKIE. 1993. Sex, size, and inter-year variation in flowering among dioecious trees of the rain forest understorey. *Ecology* 74: 1529–1537.
- VAN SCHAIK, C. P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* 2: 327–347.
- , J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353–377.
- WATSON, H. 1985. Lambir Hills National Park: Resource inventory with management recommendations. National Parks and Wildlife Office, Forest Department, Kuching, Sarawak, Malaysia.
- WHITMORE, T. C. 1981. *Macaranga* in New Guinea and the Bismarck Archipelago. *Kew Bulletin* 34: 599–606.
- . 1983. Secondary succession from seed in tropical rainforests. *Forestry Abstracts* 44: 767–779.
- WRIGHT, S. J., AND O. CALDERON. 1995. Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology* 83: 937–948.
- , AND C. P. VAN SCHAIK. 1994. Light and the phenology of tropical trees. *American Naturalist* 143: 192–199.
- YAP, S. K., AND H. T. CHAN. 1990. Phenological behaviour of some *Shorea* species in peninsular Malaysia. In K. S. Bawa and M. Hadley [eds.], *Reproductive ecology of tropical forest plants*, 21–35. UNESCO & Parthenon Publishing Group, Paris.