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Systematic Botany, Volume 8, Issue 4 (Oct. - Dec., 1983), 354-368.

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Systematic Botany

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Flowering Phenology and Floral Biology of *Inga* (Fabaceae: Mimosoideae)

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ABSTRACT. Seven *Inga* species that occur in three adjacent forest types in cloud forest in Costa Rica have similar floral morphology. A comparative study of flowering phenology, floral biology, and visitor activity revealed that there is substantial overlap in flowering times of many species, and simultaneously blooming species attract the same pollinators, largely regardless of flower size. Principal pollinators are hummingbirds (Trochilidae), hawkmoths (Sphingidae), and other Lepidoptera (skippers, butterflies, and settling moths). Pollinator sharing is not absolute: differences in floral behavior (different flower opening times and different patterns of flower opening) result in some separation between co-occurring species and reduce the negative consequences of pollinator sharing. Multiple flower opening times in some species increases pollination opportunities in an unpredictable climate and reduces interspecific competition for pollinators. That total nectar production per flower is greater in flowers sampled repeatedly than in those sampled only once indicates that trees may respond to greater levels of visitation by increased nectar production.

Phenological studies of tropical forest species have been done for entire communities in order to look at community patterns of flowering and fruiting (Frankie et al. 1974; Frankie 1975; Hilty 1980; Opler et al. 1980). Other studies have been done on groups of similar species, either taxonomically related (Gentry 1974a, b; Opler et al. 1975; Stiles, 1975, 1977), having similar pollinators or dispersers (Feinsinger 1976; Milton et al. 1982), or morphologically similar (some of the above). When observations are made on a finer scale it is possible to ask more specific questions about the extent of similarities and interactions between the species studied.

In montane Costa Rica, many species of *Inga* occur more or less sympatrically and have flowers that are quite similar in structure and appearance (figs. 1–7). A comparative study was undertaken to determine and describe the extent of similarity in flowering phenology, floral morphology, behavior, and visitors in sympatric *Inga* species. Information of this kind can be used to evaluate two ecological hypotheses that have received much attention in recent pollination studies: plants compete for pollinators and/or plants share pollinators.

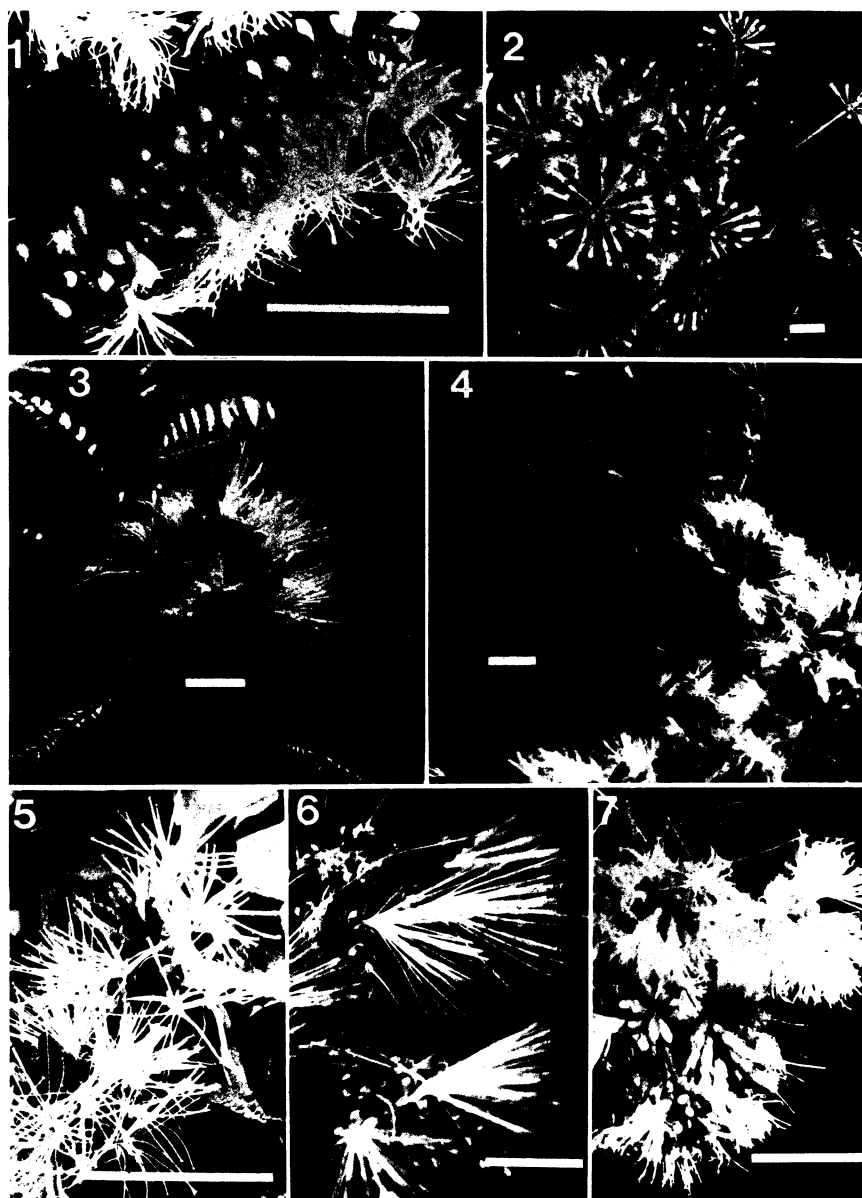
Upon first impression, the flowers of these *Inga* species appear to be so similar that it seems unlikely that they are specialized for pollination by different agents. Simultaneous flowering could result in competition for pollinators

(Ågren and Fagerström 1980; Anderson and Schelfhout 1980; Lack 1976; Levin and Anderson 1970; Mosquin 1971; Pleasants 1980; Reader 1975; Robertson 1895; Stiles 1977; Waser 1978a), and some studies have suggested that divergence of flowering times reduces competition for pollinators (Gentry 1974a; Lack 1976; Ranta et al. 1981; Stiles 1977). The possible negative consequences of overlap in flowering time and pollinator fauna are many. Energy is wasted in a species that produces numerous flowers that get little visitation; interspecific pollen may interfere with intraspecific fertilization of a given species (Waser 1978b; Wiens 1978) or lead to hybridization in closely related taxa that can interbreed.

Alternatively, pollinator sharing has been found in some plant communities where there is natural selection in favor of similar floral characteristics (Brown and Kodric-Brown 1979; Heinrich 1975; Macior 1971; Schemske 1981). The negative consequences of pollinator sharing, including stigma clogging, pollen load dilution on pollinators, and pollen wastage by plants, may be outweighed by benefits of greater pollinator attraction and more intraspecific transfer of pollen.

MATERIALS AND METHODS

Study sites. The study area is situated between 1320 and 1600 m in the Cordillera de Tilaran, Puntarenas Prov. Costa Rica, and in-



FIGS. 1-7. Flowers of *Inga* spp. 1. *I. longispica*. 2. *I. quaternata*. 3. *I. brenesii*. 4. *I. mortoniana*. 5. *I. densiflora*. 6. *I. oerstediana*. 7. *I. punctata*. Scales = 2 cm.

cludes Premontane Wet Forest, Lower Montane Wet Forest, and Premontane-Lower Montane Wet Forest Transition (Holdridge 1967). The lower areas may be considered part of the Lower Montane Moist Forest-Wet Forest Transition, as in Feinsinger (1976). The lower areas consist largely of forest remnants bordering

cleared pastures in the villages of Santa Elena and Monteverde. The transition area is included in a large tract of forest contiguous with the Monteverde Cloud Forest Biological Reserve, as well as in lower areas of the reserve itself. The uppermost locations are in the reserve, which is a large area of pristine forest. The for-

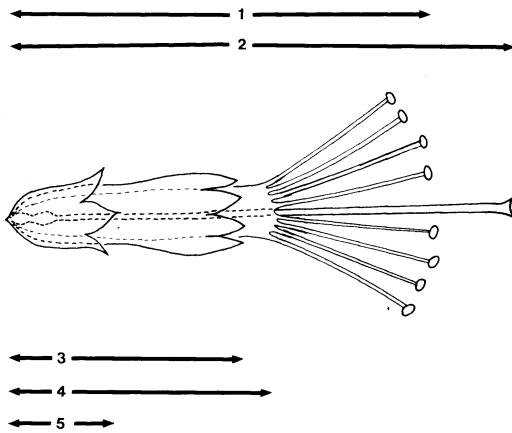


FIG. 8. Diagram of *Inga* flower. Numbered arrows refer to measurements in table 1. Nectar is contained in tube formed by monadelphous staminal filaments (measurement 4). Flowers have five connate sepals, five connate petals, and numerous stamens.

ests of each of these areas are quite different in composition, as might be expected from the elevational gradient, differential exposure, and rainfall. These sites have been described in detail (Buskirk and Buskirk 1976; Feinsinger 1976, 1978; Powell 1979; Lawton and Dryer 1980).

Study organisms. *Inga* comprises ca. 400 species of Neotropical trees, of which ca. 30 occur in Costa Rica (León 1966). This study included the seven most abundant species of *Inga* that occur in and around cloud forest at Monteverde, Costa Rica. All of these forest species are sub-canopy or canopy trees. *Inga* is the major genus of legume tree in these forests; legumes comprise a lesser component of the forest than in some lowland areas. Flowers of these *Inga* species have reduced perianth parts, numerous white stamens that provide the main pollinator visual attraction, and nectar in the floral tube. The nectar is accessible to a wide variety of floral visitors. Frankie (in Croat 1978) reported bees visiting *Inga* flowers; Salas (1974) described bat and hawkmoth pollination of *Inga vera* subsp. *spuria* (Willd.) J. León; and Feinsinger (1976, 1978) found that *Inga brenesii* Standley and *I. punctata* Willd. are important nectar resources for the hummingbirds around Monteverde.

The seven species of *Inga* studied (vouchers in CR, MO, and UC, all from Monteverde) differ in their geographic and elevational distri-

butions. *Inga brenesii* (Koptur 54 and 420) is known only from the wet highlands of Costa Rica and may be endemic to the Cordillera de Tilaran. *Inga densiflora* Benth. (Koptur 115 and 145) is found in northern South America and from Costa Rica to Panama, from low to high elevations. *Inga longispica* Standley (Koptur 217) is found only in Costa Rica, from low and high elevations. *Inga mortoniana* J. León (Koptur 418) is known only in wet highlands of Costa Rica. *Inga oerstediana* Benth. ex Seemann (Koptur 53 and 76) is known from Mexico to Panama, the West Indies, and South America (Venezuela to Ecuador) from sea level to 1800 m. *Inga punctata* (Koptur 417) is known from Mexico to Panama, Trinidad and Tobago, and northern South America, from sea level to wet highlands. *Inga quaternata* Poeppig (Haber 175; Koptur 416 and 419) is known from Mexico to Panama, and South America, from wet lowlands and wet highlands.

Flower morphological measurements. Flowers were measured fresh (except *I. punctata*, which were preserved in FAA); 25–40 flowers from 3–5 individuals of each species were measured. The parameters measured are shown in figure 8.

Phenology of flowering and fruiting. Seasonal phenology of flowering and fruiting was monitored monthly on tagged individuals, Oct 1978–Jun 1980. The level of flowering and fruiting was qualitatively assessed for each individual each month. The total flowering effort was rated low, medium, or high compared with maximum possible flowering for the species and subdivided into the proportion of buds and the proportion of open flowers. The total fruiting effort was rated low, medium, or high and subdivided into proportion of immature fruit and proportion of mature fruit. Only open flowers and mature fruit are represented in the results, as the percentage of tagged individuals having open flowers or mature fruit. Fruit were counted as immature until the pods had swelled with seeds; *Inga* pods develop before the seeds inside begin to grow.

Flower anthesis and phenology. Floral behavior (i.e., the timing and sequence of floral events) was studied on 30–50 tagged inflorescences on 1–5 trees for each species, during a peak flowering period. Trees used in the study were growing at the forest's edge, or in open pastureland, because such individuals had more

easily reachable flowers. Flowers were reached by tree climbing, using a ladder, or occasionally from the ground. At the initial tagging, open flowers were removed from inflorescences under study. To monitor anthesis, inflorescences were inspected every 2 hours, and subsequently opening flowers were followed until the flowers were "spent" (i.e., nectar production ceased, flowers wilted), 24–36 hours from initial tagging. Pattern of flower opening was assessed by recording the number of new flowers fully open in each 2-hour interval.

Anther dehiscence was determined with a magnifying lens to see if anther thecae were closed or had dehisced, exposing polyads. Stigmatic receptivity was also noted visually: *Inga* stigmata are cup-shaped, slightly spread, and become wet and shiny when they are receptive. Stigmatic receptivity was also determined using a method devised by touching the stigmata to tiny papers of Peroxtesmo K O (Machery-Nagel & Co.) to detect peroxidase, which is present at the surface of a receptive stigma (I. Baker unpubl.). Hand-pollinations were done at different periods of time after flower opening to determine the duration of stigma receptivity.

Floral odor was checked and noted over time.

Nectar production. Nectar flow was monitored on bagged (and therefore non-visited) and unbagged (open to visitors) inflorescences approximately every 2 hours from flower opening through wilting. Inflorescences were tagged and bagged with heavy paper (Pollen-Tector) bags prior to flower opening. Nectar volumes were measured by emptying the flowers with precalibrated capillary tubes (Drummond Microcaps) or, for species with very small flowers, finely drawn micropipettes were employed to extract the nectar and to spot it on strips of chromatography paper. The spot diameters were measured and converted to volumes (I. Baker 1979).

In order to determine whether nectar removal affects nectar flow in different species, some inflorescences were bagged at the same initial time as the others but were not emptied until the end of the study period.

Nectar sugar concentrations were measured with a Bellingham and Stanley pocket refractometer, which reads % sugar on a weight/weight basis (Bolten et al. 1979).

Pollinator activity. Undisturbed flowers were

observed between flower monitoring times to assess variety, abundance, and pollinator efficacy of flower visitors. Flowers were observed for two 15-minute periods every sampling interval (every 2 hr). The number of visits made by each pollinator species, the number of flowers visited by each individual, and the time spent at the tree were recorded. Pollinator efficacy was evaluated subjectively by noting the size of visitors, their behavior at flowers, and their tendency to move between trees. At night, a headlamp with a red filter or a night-viewing device (Smith and Weston Startron Scope) was employed to observe visitors. Visitors (except hummingbirds) were caught for identification.

Insect voucher specimens are in the author's collection, in the U.S. National Museum (with D. H. Janzen's general Monteverde collection), and in W. A. Haber's sphingid collection.

RESULTS

Occurrence of Inga species at the study sites. The distributions of many of the *Inga* species studied are largely overlapping, but some overlap very little in the study area (fig. 9). The *Inga* component of the lowest forest is dominated by *I. brenesii* and *I. punctata*. Several other species are somewhat less frequent but well-represented (*I. mortoniana*, *I. quaternata*, *I. oerstediana*). The remaining two species, *I. longispica* and *I. densiflora*, occur only rarely in the lowest forest.

In the middle forest, *I. densiflora* and *I. mortoniana* are abundant. *I. quaternata* is somewhat less frequent, but well-represented. *Inga brenesii*, *I. punctata*, and *I. longispica* occur only rarely at the middle site.

In the highest forest, *I. longispica* and *I. densiflora* are the predominant *Inga* species. *Inga mortoniana* is less frequent but well represented. The other species (*I. brenesii*, *I. oerstediana*, *I. punctata*, *I. quaternata*) are absent from the highest forest.

Several other *Inga* species are also known to occur in these areas but were not included in this study because they occurred too rarely and/or were thought to be introduced (*I. tonduzii* J. D. Smith; *I. coruscans* Willd.). Other genera with similar flowers also occur in these areas, including *Pithecellobium brenesii* Standley and *P. costaricense* (Britton & Rose) Standley (Fabaceae: Mimosoideae) and *Roupala montana* Aublet (Proteaceae).

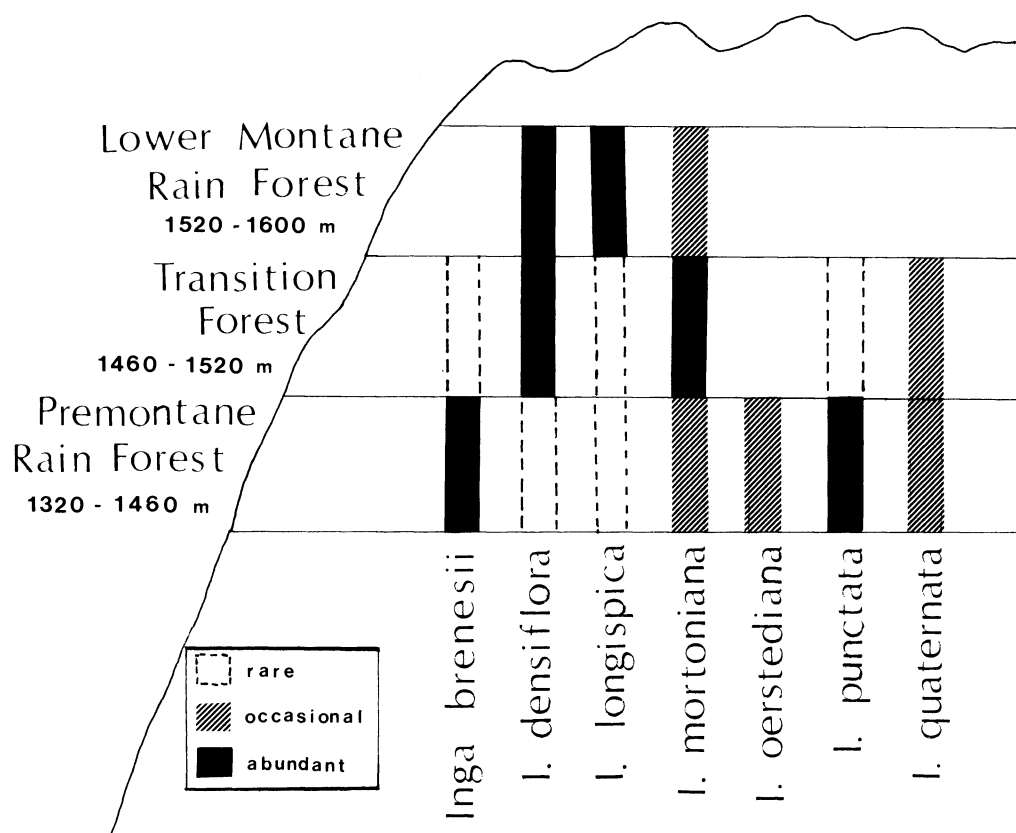


FIG. 9. Elevational occurrence of *Inga* species in the three forest types of the study area at Monteverde, Costa Rica.

Flower size. The *Inga* species fall into three groups according to flower size (table 1; fig. 8): large (3.5–4.5 cm; *I. brenesii*, *I. oerstediana*); medium (1.9–2.8 cm: *I. mortoniana*, *I. quaternata*); and small (1.4–1.6 cm; *I. densiflora*, *I. longispica*, *I. punctata*). Floral nectar in *Inga* is relatively accessible to a wide array of visitors, all of which can take nectar from the tubular flowers, while transferring pollen between the brush-like sexual organs.

Seasonal phenology of flowering and fruiting. In the low area, all species are present (*I. densiflora* and *I. longispica* are very rare). *Inga brenesii*, *I. densiflora*, and *I. oerstediana* bloomed massively toward the end of the wet season (Sep–Oct; fig. 10) during each year of the study. *Inga brenesii* bloomed for a prolonged period (3–4 months with greater than 50% of the individuals in bloom, and some individuals with flowers every month of the year). *Inga oerstediana* had discrete

blooming times of 3–4 months, 2–3 months with more than 50% of the individuals in bloom. *Inga densiflora* had two peaks within each massive bloom, 1 month apart (a total of 3 months with greater than 50% of the individuals in bloom, the entire flowering period being 4–5 months). *Inga punctata* also bloomed massively, and the peak bloom was slightly later than the other three species in this area. The blooming period extended 4 to 6 months, much longer than *I. oerstediana* and longer than *I. densiflora*. *Inga quaternata* had two blooming peaks during the wet season. The first peak at the beginning of the wet season (May–Jul) did not overlap with many other species (only *I. mortoniana* during 1979; *I. brenesii* and *I. punctata* during 1980). Individual trees bloomed twice a year. The second peak was at the same time that five other species were in bloom. *Inga longispica* bloomed massively, with two peaks during the

TABLE 1. Floral measurements (all cm) for *Inga* spp. at Monteverde, Costa Rica. Numbers given are sample mean (\bar{x}) \pm standard deviation (SD). Flowers from at least three individuals were measured. *N* = number of flowers measured. Numbered columns refer to measurements in diagram of figure 8.

	1. Stamen length	2. Pistil length	3. Corolla length	4. Tube length	5. Calyx length
<i>I. brenesii</i> <i>N</i> = 50	4.02 \pm 0.19	4.34 \pm 0.34	2.10 \pm 0.28	2.32 \pm 0.29	0.89 \pm 0.10
<i>I. densiflora</i> <i>N</i> = 20	1.58 \pm 0.13	1.54 \pm 0.13	0.77 \pm 0.06	0.94 \pm 0.80	0.30 \pm 0.01
<i>I. longispica</i> <i>N</i> = 15	1.49 \pm 0.14	1.60 \pm 0.17	0.71 \pm 0.02	0.85 \pm 0.12	0.20 \pm 0
<i>I. mortoniana</i> <i>N</i> = 20	1.99 \pm 0.11	1.92 \pm 0.11	1.09 \pm 0.11	1.42 \pm 0.12	0.79 \pm 0.06
<i>I. oerstediana</i> <i>N</i> = 36	3.62 \pm 0.59	3.77 \pm 0.48	1.53 \pm 0.21	1.78 \pm 0.29	0.47 \pm 0.10
<i>I. punctata</i> <i>N</i> = 25	1.46 \pm 0.06	1.62 \pm 0.06	0.71 \pm 0.05	0.92 \pm 0.12	0.32 \pm 0.04
<i>I. quaternata</i> <i>N</i> = 20	2.34 \pm 0.23	2.77 \pm 0.19	1.10 \pm 0.07	1.10 \pm 0.07	0.75 \pm 0.09

wet season, but each individual bloomed only once a year. The first year a few of the trees flowered for 1 month at the beginning of the dry season, but no individuals were seen flowering during the dry season of 1979–80. *Inga mortoniana* bloomed for extended periods at low levels, never more than 50% of the individuals in flower at one time. All blooming periods overlapped blooming times of many other *Inga* species, except at the middle of the wet season, when *I. quaternata* was the only other species of *Inga* in full bloom.

Three of the six species in the middle area are rare. *Inga densiflora* is more abundant, and *I. punctata* less abundant, than in the lower area. These two species have very similar-sized flowers and overlapping flowering times; the latter species predominates lower, the former higher up. *Inga mortoniana* reaches its greatest abundance in this area, and two of the other medium- or large-flowered species become less abundant (*I. brenesii*, *I. oerstediana*). *Inga quaternata* is fairly abundant here, and its flowering peaks coincide with the extended blooming period of *I. mortoniana*.

In the high area, *I. mortoniana* is still abundant, and its extended blooming period is overlapped by *I. densiflora* and *I. longispica*. One blooming peak of *Inga longispica* is early in the wet season and does not coincide with the other *Inga* species.

More *Inga* species bloom during the wet/dry season interface and dry season than during the wet season (fig. 10). During this period, sphingids and other lepidopteran pollinators are more abundant (W. A. Haber pers. comm.), and visitation is less likely to be hindered because of bad weather.

There is even greater overlap in fruiting times than flowering times (fig. 10). Six of the seven species have mature fruit during the dry/wet interface and into the wet season.

Flower anthesis and phenology. Flowers of three species (*I. mortoniana*, *I. oerstediana*, *I. quaternata*) open at only one time of day (table 2). Inflorescences of four species (*I. brenesii*, *I. densiflora*, *I. longispica*, *I. punctata*) are composed of cohorts of flowers that open at different times during the day. The two large-flowered species exhibit different patterns: the flowers of *I. oerstediana* open only in the late afternoon, whereas those of *I. brenesii* open continuously (at all times of day and night). Among the small-flowered species, most of the flowers of *I. densiflora* open in the morning at 0600, with a few opening in the late afternoon at 1600, whereas most of the flowers of *I. punctata* open at 1600, and only a few open at 0800. The flowers of *Inga longispica* open mostly at 1400 and 1700, with some opening pre-dawn at 0400.

The two middle-sized species are quite different from each other: *Inga quaternata* flowers

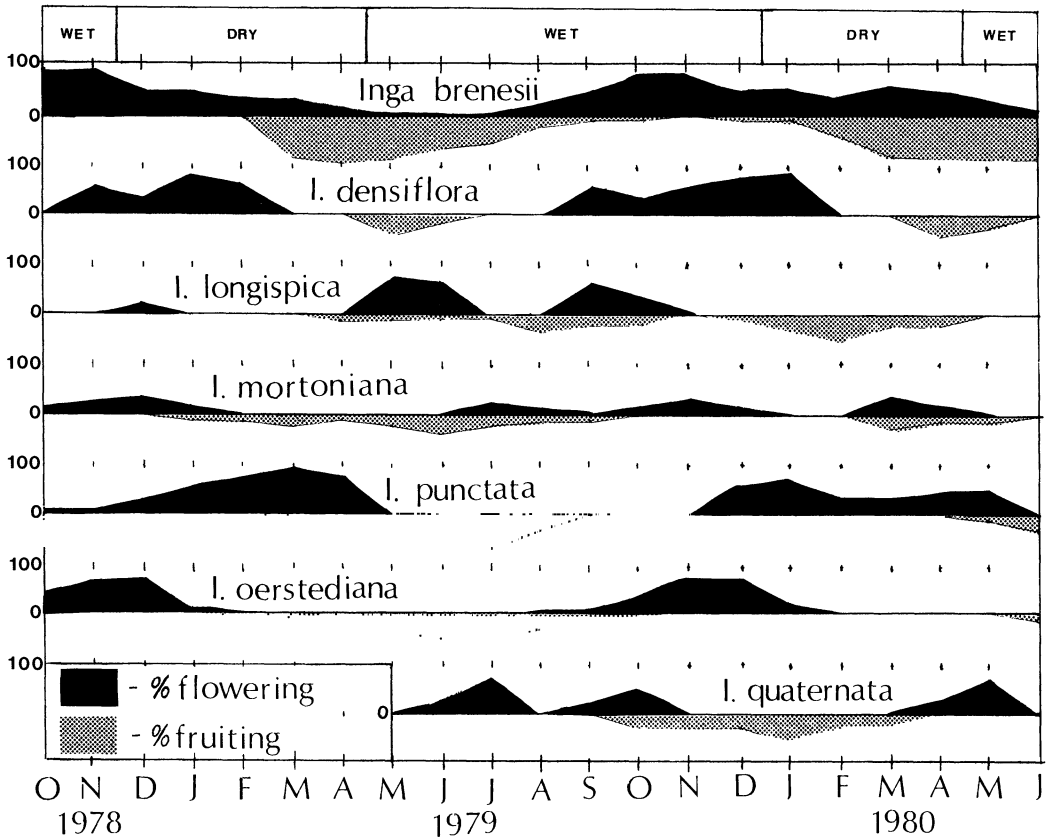


FIG. 10. Seasonal flowering and fruiting phenology of *Inga* species. The percentage of individuals flowering (i.e., with open flowers, not just buds) is represented above the zero-line for each species; the percentage of individuals fruiting (i.e., with mature fruit) is represented below the zero-line for each species. Wet and dry seasons are indicated across the top and are not exactly the same each year. Observations on *I. quaternata* did not begin until May 1979. Sample sizes were: *I. brenesii*, 35; *I. densiflora*, 10; *I. longispica*, 19; *I. mertoniana*, 9; *I. oerstediana*, 11; *I. punctata*, 21; *I. quaternata*, 4.

open early (0400) and are active through the morning and again in the evening. The flowers of *I. mertoniana* open initially between 1000 and 1200, and continue to be active for 22–26 hours, not having receptive stigmata the entire time, but continuing to produce nectar and potentially donate pollen for the duration.

The anthers of all species do not dehisce in bud. After flower opening, most of the anthers (50–100%) dehisce within 30–90 minutes. Stigmatic receptivity occurs after anther dehiscence (slight protandry) in all species except *I. longispica*.

Six of the seven species have predominantly sweet odors (table 3). Only *I. brenesii* has a non-

sweet odor that is described as “yeasty,” or even odorless by some observers.

Nectar production. Very little to no nectar is produced before anthesis. For all species, nectar flow starts after staminal filaments are fully extended. Nectar flow patterns, concentrations, and volumes are presented in table 4. Nectar volumes correlate with flower size (cf. table 1). Nectar concentrations differed within a species in day and night samples, with the concentrations higher in daytime samples. All nectars are relatively dilute and correspond with the nectar concentrations characteristic of flowers pollinated by hummingbirds (H. Baker 1975) and various moths (Percival 1965). Of these two

TABLE 2. Sequence and timing of floral events in *Inga* spp. Dawn occurs between 0500 and 0530, and dusk between 1745 and 1815.

	Time buds crack	Time flowers open (and hours after buds crack)	Minutes to anther dehiscence after flower opening	Minutes to (and hours of) stigmatic receptivity after (or before) flower opening
<i>I. brenesii</i>	0000-2400	Continuously; (8-10)	30-90	90-150, after (3-5)
<i>I. densiflora</i>	0900-1100; 1500-1800	Most at 0600, few at 1600 (12-20)	15-30	90-120, after (3-4)
<i>I. longispica</i>	930-1130; 1430-1630; 2330-0230	Most at 1400 and 1700; few at 0400 (8-12)	30-60	30-60, before (duration not determined)
<i>I. mertoniana</i>	1500-1600	Most at 1000-1200, some from 0600-1600 (19-21)	90-150	180-360, after (4-6)
<i>I. oerstediana</i>	0930-1130	Most at 1600, from 1500-1630 (5-7)	60-90	180-360, after (6-8)
<i>I. punctata</i>	0900-1100; 1730-2030	Most at 1600; few at 0800; (7-12)	60-180	120-240, after (4-6)
<i>I. quaternata</i>	1630-2030	Most at 0400, from 0200-0600 (9-12)	60-120	180-360, after (8-10)

pollinator groups, the more dilute nectar would be more suitable for crepuscular and nocturnal moths (especially hawkmoths). Nectar production continues in most species from 6-10 hours after the flowers open, with only one peak (i.e., maximum). Flowers of *I. quaternata* exhibit two peaks, morning and evening. The long-lasting flowers of *I. mertoniana* exhibit two peaks on two successive mornings, and the same flowers can be visited for 2 days.

Total nectar volumes in bagged flowers sampled repeatedly over their activity period were compared with other flowers bagged and sampled only at the end of that period (table 5). In three of the four species studied, flowers that were repeatedly sampled produced substantially greater total nectar volumes than flowers that were sampled only once (Student's *t*-test, $P < 0.001$).

Floral visitors. Abundance and pollinatory efficacy of visitors to flowers of the different *Inga* species indicate their likeliness as pollinators (table 6). Probable pollinators are those visitors with a pollinator efficacy rating of 1 or 2. Pollinator efficacy was decided on the basis of visitor size (must be large enough to touch anthers and stigmata when taking nectar), foraging behavior, and tendency for inter-tree movements (because these *Inga* are all self-incompatible; Koptur 1982).

Hawkmoths (Sphingidae) are important pollinators of all the *Inga* species. However, species with diurnally active flowers appear also to be pollinated by skippers (Hesperiidae), butterflies (Pieridae and Ithomiidae), and hummingbirds (Trochilidae). Specific identities and activity periods of visitors are provided in table 7.

DISCUSSION

Sympatric *Inga* species with different-sized flowers are visited by the same pollinators.

TABLE 3. Description, time of production, and duration of floral odor of *Inga* spp. at Monteverde, Costa Rica.

<i>I. brenesii</i> :	faint, yeasty; all the time (as flowers open continuously).
<i>I. densiflora</i> :	sweet, heady; especially strong from 0630-1000; also from 1630-1900.
<i>I. longispica</i> :	sweet; 0430-1000; 1430-1630; 1730-2030.
<i>I. mertoniana</i> :	sweet, heady; 0700 (day 1)-0900 (day 2); especially strong early morning.
<i>I. oerstediana</i> :	sweet; 1630-0630; continues faintly until 1000.
<i>I. punctata</i> :	sweet; 1630-0200; also from 0830-1200; odor in evening is more intense.
<i>I. quaternata</i> :	sweet, yeasty; 0430-2000; strong throughout.

TABLE 4. Nectar flow patterns, volumes, and concentrations for *Inga* spp. Numbers given are $\bar{x} \pm SD$ (N ; range). N = number of flowers followed.

	Time and duration of nectar production for individual flowers	Total volume (μ l) per flower (bagged and sampled once)	% sugar concentration (wt./wt.)
<i>I. brenesii</i>	peak: from opening, for 2-3 hr; continues for 6-10 hr	8.10 \pm 2.28 (39; 4-15)	morning: 18.3 \pm 3.18 (30; 13-24%) afternoon: 14.33 \pm 2.01 (43; 10-17.5%) night: 11.78 \pm 2.98 (30; 6-19%)
<i>I. densiflora</i>	peak: 0630-0930; continues for 8-10 hr; peak for few flowers 1600-1800	0.72 \pm 0.46 (30; 0.2-3.0)	day: 19.10 \pm 1.05 (10; 16-22%) night: 12.41 \pm 0.91 (10; 9.5-14.5%)
<i>I. longispica</i>	peaks: 1400-1500, 1700-1800, 0400-0500; each continues for 1-2 hr	0.37 \pm 0.38 (30; 0.1-0.9)	day: 27.7 \pm 3.01 (30; 21-31%) night: 11.82 \pm 2.54 (30; 5-18%)
<i>I. mortoniana</i>	the same flowers have 2 peaks over 22-26 hr: 0600-0800	0.75 \pm 0.60 (35; 0.1-2.2)	day: 21.5 \pm 2.01 (10; 16-23%) night: 9.29 \pm 1.11 (7; 8-11%)
<i>I. oerstediana</i>	peak: 1800-1900; continues at low rate for 12 hr	1.70 \pm 0.60 (30; 0.1-2.8)	19.00: 20.50 \pm 1.07 (44; 18-22.5%) 03.00: 13.50 \pm 3.28 (8; 10-16.5%)
<i>I. punctata</i>	peak: 1730-1930; continues for 8-10 hr; peak for few flowers 0800-1000	0.64 \pm 0.40 (41; 0.2-1.6)	day: 15.5 \pm 1.60 (12; 13.5-18%) night: 11.63 \pm 0.88 (12; 10-13%)
<i>I. quaternata</i>	same flowers have 2 peaks 0600-0700, 1700-1800, continuing for 15-16 hr	1.2 \pm 0.71 (30; 0.1-2.3)	day: 22.2 \pm 2.80 (10; 19-26%) night: 10.32 \pm 2.21 (10; 8-14%)

However, there are several factors that reduce the amount of overlap in pollination activity among the *Inga* species: elevational separation, differences in flowering seasons, and differences in floral behavior.

Some species of *Inga* are abundant in adjacent but different forest types (e.g., *I. brenesii* and *I. densiflora*). That the forest communities are compositionally quite different may restrict

interspecific pollinator movements between these species. However, some recent evidence (Haber pers. comm.) indicates that sphingid moths may move considerable distances over wide elevational ranges, so this sort of separation may not be absolute.

Differences in seasonal flowering phenology separate some species (e.g., *I. quaternata* from most of the other species, and *I. mortoniana* from

TABLE 5. Comparisons of nectar volumes secreted by *Inga* flowers sampled repeatedly over their activity period versus those sampled only once at the end of the same period. Numbers given are \bar{x} total volume (μ l) per flower \pm SD (N ; range). N = number of flowers followed. † = accept H_0 of equality (volumes from numerous samplings = volumes from once-sampled) with Student's t-test ($P > 0.05$); * = reject H_0 ($P < 0.001$).

	Sampling regime	Flowers sampled repeatedly	Flowers sampled once
<i>I. brenesii</i>	Bagged at 0730 and sampled every 2 hr, 0830-1900	14.69 \pm 4.30 (28; 1.7-22.1)	8.10 \pm 2.28* (39; 4-15)
<i>I. punctata</i>	Bagged at 1500 and sampled at 1545, 1700, 1930, and 0600	2.37 \pm 0.65 (35; 0.8-3.4)	0.64 \pm 0.40* (41; 0.2-1.6)
<i>I. mortoniana</i>	Bagged one evening and sampled 11 times over 36 hrs	2.21 \pm 1.08 (35; 0.2-4.5)	0.75 \pm 0.60* (35; 0.1-2.2)
<i>I. oerstediana</i>	Bagged at 1600 and sampled every 2 hr for 14 hrs	2.12 \pm 1.05 (41; 0-5.5)	1.70 \pm 0.69† (30; 0.1-2.8)

TABLE 6. Composition, abundance, and pollinatory efficacy (derived subjectively by evaluating size of visitors, their behavior at flowers, and their tendency to move between trees) of *Inga* flower visitors. Visitor abundance: A = abundant, C = common, U = uncommon, R = rare. Pollinatory efficacy: 1 = very good, 2 = good, 3 = fair, 4 = poor. *Inga* spp. are designated by first three letters of specific epithet.

	BRE	DEN	LON	MOR	OER	PUN	QUA
INSECTS							
Hemiptera							
Lygaeidae	C 4					C 4	
Coleoptera							
Brentidae							C 4
Cerambycidae	R 4					R 4	
Scarabidae	A 4				A 4		A 4
Diptera							
Bibionidae		A 4					U 4
Hymenoptera							
Euglossinae	U 3				U 3		
Pompilidae	R 2					R 2	
Vespidae	C 4					U 4	
Lepidoptera							
Arctiidae	U 3				U 3		
Ctenuchidae	C 3						C 3
Geometridae			C 2	C 3		C 2	C 3
Hesperiidae	C 1	C 1		A 1			U 1
Ithomiidae		U 3		C 3			
Noctuidae			C 2			U 2	C 2
Pericopidae			C 2			U 2	
Pieridae		A 2		A 2			
Pyralidae		U 3				U 3	
Sphingidae	A 1	C 1	C 1	A 1	A 1	C 1	C 1
Uranidae				R 1			R 1
HUMMINGBIRDS							
Trochilidae	A 2	C 2		U 2	A 2	C 2	C 2
MAMMALS							
Bats	R 1			R 1			

most of the other species, at certain times of year) but by and large the species overlap considerably in blooming times.

Temporal separation in pollinator activity is also effected by daily floral phenology (floral behavior): different patterns of flower opening in simultaneously blooming *Inga* species. In all of the forest areas, more than one small-flowered species is present. While the seasonal flowering periods of these species overlap somewhat, differences in floral behavior reduce overlap in pollinator activity periods. Most flowers of *I. punctata* open in the afternoon, and those of *I. densiflora* open mainly in the morning. In contrast, flowers of *I. longispica* open earlier than flowers of *I. densiflora* (morn-

ing flowering) and later than the flowers of *I. punctata* (night flowering). A peak of flower opening at one time of the day allows that species to take advantage of pollinators active at that time. For example, night-flowering *I. punctata* is pollinated mostly by crepuscular and nocturnal moths (sphingids and others); day-flowering *I. densiflora* is pollinated mostly by diurnal skippers, butterflies, and hummingbirds; and dawn-flowering *I. longispica* is pollinated mostly by nocturnal and diurnal Lepidoptera. These species do not show complete temporal separation but overlap less than if all the flowers of all species opened at the same time.

The two species that have individual flowers

TABLE 7. Specific identities and activity periods of flower visitors to *Inga* spp. at Monteverde, Puntarenas Province, Costa Rica. Activity period indicated as D = diurnal, C = crepuscular, N = nocturnal. *Inga* species abbreviated by first three letters of specific epithet.

Visitors	Activity period	<i>Inga</i> spp. visited
Lygaeidae		
unidentified spp.	D, C, N	BRE, PUN
Brentidae		
unidentified spp.	D, C	QUA
Cerambycidae		
unidentified spp.	D	BRE, PUN
Scarabidae		
unidentified spp.	D, C, N	BRE, OER, PUN
Bibionidae		
unidentified sp.	D	DEN, QUA
Euglossinae		
<i>Eulaemma</i> sp.	D, C	BRE
unidentified sp.	D	OER
Pompilidae		
unidentified sp.	D	BRE, PUN
Vespidae		
unidentified spp.	D	BRE, PUN
Arctiidae		
unidentified spp.	C, N	BRE, OER
Ctenuchidae		
<i>Ichoria quadrigutta</i>	D	BRE
<i>Cyanopepla scintillans</i> Butler	D	QUA
Geometridae		
<i>Microgonia</i> sp. 1 (<i>Koptur</i> 206)	C	MOR
<i>Microgonia</i> sp. 2 (<i>Koptur</i> 287)	C	LON
unidentified spp.	C	PUN, QUA
Hesperiidae		
<i>Astraptes anaphus annetta</i> (Evans)	D, C	MOR
<i>A. fulgurator azul</i> (Reakirt)	D, C	MOR
<i>A. galesus cassius</i> (Evans)	D, C	MOR
<i>Ouleus cyrna</i> (Mab.)	D, C	MOR
unidentified spp.	D	BRE, DEN, QUA
Ithomiidae		
unidentified spp.	D	DEN, MOR
Noctuidae		
<i>Mocis</i> nr. <i>repanda</i>	N	LON
unidentified spp.	N	PUN, QUA
Pericopidae		
<i>Mesenchroa rogersi</i> Druce	N	LON
unidentified sp.	N	PUN
Pieridae		
<i>Actinote leucomelas</i> Bates	D	DEN
<i>Dismorphia crisia lubina</i>	D	DEN, MOR
<i>D. eunoe desine</i> Hewitson	D	MOR
Pyralidae		
<i>Herpetogramma</i> sp. (<i>Koptur</i> 246)	C	DEN
unidentified sp.	N	PUN

TABLE 7. Continued.

Visitors	Activity period	<i>Inga</i> spp. visited
Sphingidae		
<i>Aelopus titan</i>	D, C	DEN, MOR, QUA
<i>Agrius cingulatus</i>	C, N	BRE, OER
<i>Pachygonia subhamata</i>	C, N	BRE, PUN
<i>Pachylia ficus</i>	C, N	BRE, OER
<i>Perigonia lusca</i>	C, N	BRE, PUN
<i>Xylophanes chiron</i>	C, N	BRE
unidentified spp.	C, N	LON, PUN, QUA
Uranidae		
<i>Coronidia leachii</i> Latr.	D	MOR, QUA
Trochilidae		
<i>Amazilia saucerotteri</i>	D	BRE
<i>Campylopterus hemileucurus</i>	D	BRE, OER
<i>Colibri thalassinus</i>	D	BRE
<i>Eupherusa eximia</i>	D	BRE, OER, PUN
<i>Heliodoxa jacula</i>	D	BRE, OER
<i>Panterpe insignis</i>	D	BRE
<i>Philodice bryantae</i>	D	BRE, OER, PUN

active for more than one peak of activity (*I. quaternata*, *I. mortoniana*) are employing an alternative strategy to having different flowers that open at different times during the day. The flowers of *I. mortoniana* are active for the longest periods (22–26 hr); this correlates with the low-level extended flowering activity exhibited by this species. It is advantageous for the flowers to be long-lived if the floral display is not massive and the probability of pollinators discovering the flowers is therefore low.

The activity of flowers of most *Inga* species extends 6–10 hours, overlapping considerably the time that the flowers of other species are open and active. *Inga* stigmata are small, and more than one pollen polyad will fit on a stigma, though the number is limited (3–6). "Stigma clogging" by foreign pollen (Waser 1978b) might have a negative effect on fruit set and fecundity of individuals whose flowering activity precisely coincides with another species. Simultaneously blooming species of *Inga* are not cross-compatible (Koptur 1982).

The behavior of *I. brenesii*, *I. densiflora*, *I. longispica*, and *I. punctata* (opening more than one cohort of flowers a day) may not only reduce interspecific competition but may also increase pollination opportunities for the species in

question. "Bet-hedging" (Stearns 1976) of this sort could be especially important at certain times of the year when the numbers of a major pollinator group are very low (e.g., Sphingidae, which are quite scarce during certain months of the year; Haber pers. comm.). This behavior may also be an adaptation to highly unpredictable daily weather conditions (fertilization subsequent to pollination is not successful under cold, rainy, inclement conditions). There is more risk involved in synchronous flower opening: all flowers could open under conditions discouraging to pollinators and unsuitable for fertilization.

Linhart and Mendenhall (1977) found that pollen movement was greatest in sphingid-pollinated *Lindenia rivalis* on clear, warm nights. I have observed hawkmoths visiting *Inga* flowers in mist and light rain, but not in heavy rain. Cruden et al. (1976) studied pollination and distribution of moth-flowered plants and concluded that hawkmoth activities are restricted by low temperatures and high elevations. They stated that in the tropics, moth-pollinated plants at higher elevations may undergo a switch to hummingbird pollination if nectar becomes available earlier in the day. In the case of *Inga* spp. around Monteverde, rain is a more impor-

tant factor than temperature. *Inga oerstediana* (with entirely nocturnal flowers) blooms in the dry season. *Inga quaternata* (with diurnal flowers having two nectar peaks) blooms in the middle of the wet season. Other species that bloom at least partially in the wet season have more than one flower-opening time. The frequent occurrence of afternoon and evening deluges in the rainy season may have selected for trees with the option of obtaining alternative pollinator services.

Sweet, heady odors are important floral attractants for moth visitors (Yeo 1973; Baker and Hurd 1968). Butterfly flowers, too, usually have sweet odors, but hummingbird flowers are often odorless (Faegri and van der Pijl 1971). Bat-flowers are often characterized by yeasty odors, as Salas (1974) observed for *Inga vera*. The lack of sweet odor in *I. brenesii* may indicate that it is adapted for visitation by hummingbirds and bats. The large numbers of sphingids observed visiting these white flowers, however, demonstrate that not all criteria of an idealized "syndrome" must be realized for any given species to receive pollination from a certain type of visitor.

Three of the four *Inga* species studied produced more nectar when it was repeatedly extracted than when nectar was measured only once at the end of the same time period. This behavior can allow a tree to respond to periods of high pollinator activity, while economizing on nectar during times of little or no visitation. The differences in day and night nectar concentrations may be controlled by the tree but are more likely to be influenced by ambient weather conditions (relative humidity), which differ between day and night and affect relatively open, short-tubular flowers like those of *Inga* (Corbet et al. 1979).

Inga flowering phenologies are not uniformly spaced throughout the year; most species have wet/dry season interface blooming times. There is extensive "pollinator sharing" in simultaneously blooming *Inga* species, but some separation in pollinator services is provided by differences in floral behavior. The various benefits of pollinator sharing (greater pollinator attraction, more intraspecific pollen transfer than when a plant species blooms alone) are more important in plants that are rare, have few flowers, or utilize pollinators that are high-

ly vagile. The *Inga* species in this study are not rare, and most species have massive floral displays. Complete sharing of pollinators and convergence of morphology and floral behavior would not benefit *Inga* as they would species that are florally less conspicuous and have more widely dispersed individuals. More detailed study of deposition of polyads on stigmas and on visitors is needed before final conclusions can be drawn as to whether differences in floral behavior affect interference between simultaneously blooming *Inga* species.

ACKNOWLEDGMENTS. H. G. Baker, G. W. Frankie, I. Baker, W. A. Haber, J. León, S. Salas, P. Feinsinger, and C. Lumer provided helpful discussion during the course of this work. Field assistance was provided by N. Murray, L. Westley, T. Szaro, B. S. Yandell, and C. Guindon. Many residents of Monteverde and Santa Elena gave their kind permission for me to study trees on their land. J. León identified the *Inga* species, and the Lepidoptera were identified by W. A. Haber, D. H. Janzen, and P. deVries. Helpful comments on earlier drafts of the manuscript were made by H. G. Baker, A. Cockburn, D. Costich, P. Davidar, G. W. Frankie, K. Grove, J. L. Hayes, S. Hendrix, H. Howe, W. J. Kress, D. A. Levin, C. Lumer, T. P. Spira, K. E. Steiner, C. E. Turner, L. K. Wagner, N. M. Waser, J. O. Washburn, M. A. Whalen, N. Wheelright, and J. Wright. The research was supported by a grant from the Center for Latin American Studies of the University of California, Berkeley, an N.S.F. dissertation improvement grant, N.S.F. grant DEB 78-11728 to G. W. Frankie and H. G. Baker, and a fellowship from the American Association of University Women.

This paper is part of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. at University of California, Berkeley.

LITERATURE CITED

- ÅGREN, G. I. and T. FAGERSTRÖM. 1980. Increased or decreased separation of flowering times? The joint effect of competition for space and pollination in plants. *Oikos* 35:161-164.
- ANDERSON, R. C. and S. SCHELFHOUT. 1980. Phenological patterns among tallgrass prairie plants and their implications for pollinator competition. *Amer. Midl. Naturalist* 104:253-263.
- BAKER, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7:37-41.
- and P. D. HURD JR. 1968. Intrafloral ecology. *Annual Rev. Entomol.* 13:385-414.
- BAKER, I. 1979. Methods for the determination of volumes and sugar concentrations from nectar spots on paper. *Phytochem. Bull.* 12:40-42.
- BOLTEN, A. B., P. FEINSINGER, H. G. BAKER, and I. BA-

- KER. 1979. On the calculation of sugar concentration in flower nectar. *Oecologia (Berl.)* 41:301-304.
- BROWN, J. H. and A. KODRIC-BROWN. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* 60:1022-1035.
- BUSKIRK, R. E. and W. H. BUSKIRK. 1976. Changes in arthropod abundance in a highland Costa Rican forest. *Amer. Midl. Naturalist* 95:288-298.
- CORBET, S. A., P. G. WILLMER, J. W. BEAMENT, D. M. UNWIN, and O. E. PRŶS-JONES. 1979. Post-secretory determinants of sugar concentration in nectar. *Plant Cell and Environment* 2:293-308.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford, California: Stanford Univ. Press.
- CRUDEN, R. W., S. KINSMAN, R. E. STOCKHOUSE II, and Y. LINHART. 1976. Pollination, fecundity, and the distribution of moth-flowered plants. *Biotropica* 8:204-210.
- FAEGRI, K. and L. VAN DER PIJL. 1971. *The principles of pollination ecology*, 2nd ed. Oxford and New York: Pergamon Press.
- FEINSINGER, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* 46:257-291.
- . 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* 48:269-287.
- FRANKIE, G. W. 1975. Tropical forest phenology and pollinator plant coevolution. Pp. 192-209 in *Coevolution of animals and plants*, eds. L. E. Gilbert and P. H. Raven. Austin: Univ. Texas Press.
- , H. G. BAKER, and P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62:881-919.
- GENTRY, A. H. 1974a. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6:64-68.
- . 1974b. Coevolutionary patterns in Central American Bignoniaceae. *Ann. Missouri Bot. Gard.* 61:728-759.
- HEINRICH, B. 1975. Bee flowers: A hypothesis on flower variety and blooming times. *Evolution* 29:325-334.
- . 1976. Flowering phenologies: Bog, woodland, and disturbed habitats. *Ecology* 57:890-899.
- HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12:292-306.
- HOLDRIDGE, L. R. 1967. *Life zone ecology*. San Jose, Costa Rica: Tropical Science Center.
- KOPTUR, S. 1982. Biotic interactions of Costa Rican *Inga* spp.: Pollination ecology and antiherbivore defense. Ph.D. thesis, Univ. California, Berkeley.
- LACK, A. 1976. Competition for pollinators and evolution in *Centaurea*. *New Phytol.* 77:541-545.
- LAWTON, R. and V. DRYER. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18:101-116.
- LEÓN, J. 1966. Central American and West Indian species of *Inga* (Leguminosae). *Ann. Missouri Bot. Gard.* 53:365-459.
- LEVIN, D. A. and W. W. ANDERSON. 1970. Competition for pollinators between simultaneously flowering species. *Amer. Naturalist* 104:455-467.
- LINHART, Y. B. and J. A. MENDENHALL. 1977. Pollen dispersal by hawkmoths in a *Lindenia rivalis* Benth. population in Belize. *Biotropica* 9:143.
- MACIOR, L. W. 1971. Coevolution of plants and animals—systematic insights from plant-insect interactions. *Taxon* 20:17-28.
- MILTON, K., D. M. WINDSOR, D. W. MORRISON, and M. A. ESTRIBI. 1982. Fruiting phenologies of two Neotropical *Ficus* species. *Ecology* 63:752-762.
- MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22:398-402.
- OPLER, P. A., H. G. BAKER, and G. W. FRANKIE. 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* 7:234-247.
- , G. W. FRANKIE, and H. G. BAKER. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 68:167-188.
- PERCIVAL, M. S. 1965. *Floral biology*. Oxford: Pergamon Press.
- PLEASANTS, J. M. 1980. Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* 61:1446-1459.
- POWELL, G. V. N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. *The Auk* 96:375-390.
- RANTA, E., I. TERAS, and H. LUNDBERG. 1981. Phenological spread in flowering of bumblebee-pollinated plants. *Ann. Bot. Fennici* 18:229-236.
- READER, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. *Canad. J. Bot.* 53:1300-1305.
- ROBERTSON, C. 1895. The philosophy of flower seasons, and the phenological relations of the entomophilous flora and the anthophilous insect fauna. *Amer. Naturalist* 29:97-117.
- SALAS, D. S. 1974. Analisis del sistema de polinización de *Inga vera* subespecie *spuria*. Thesis, Univ. Costa Rica.
- SCHEMSKE, D. W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* 62:946-954.
- STEARNS, S. C. 1976. Life-history tactics: A review of the ideas. *Quart. Rev. Biol.* 51(1):3-47.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285-301.

- . 1977. Coadapted competitors: The flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198:1177-1178.
- WASER, N. M. 1978a. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934-944.
- . 1978b. Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* 36:223-236.
- WIENS, D. 1978. Mimicry in plants. *Evolutionary Biol.* 11:365-403.
- YEO, P. F. 1973. Floral allurements for pollinating insects. Pp. 51-58 in *Insect/plant relationships*, ed. H. F. Van Emden. [Symposium #6, Roy. Entomol. Soc. London] New York: John Wiley and Sons.