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Phenological studies of shrub and treelet species in tropical cloud forests of Costa Rica

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ABSTRACT. (1) During 1978-1981, marked individuals of 107 species of treelets and shrubs in three forest types between 1300-1650 m elevation at Monteverde, Costa Rica, were monitored at monthly intervals for behaviour of leafing, flowering, and fruiting.

(2) Although there was not a pronounced seasonal pattern of leafing activity, more species produced new leaves in the dry season. Species that flush large quantities of new leaves do so more commonly in the drier months. Leaf loss was gradual and unobtrusive in species observed.

(3) Flowering activity was greatest in the late dry season and early wet season. Most species exhibited extended flowering; only 15% of the species were massively flowering. Massive flowerers showed less seasonality than extended flowerers.

(4) Of the species studied, the majority had relatively unspecialized flowers which were visited by a variety of insects; small bee-pollination was the next most common, followed by hummingbird, beetle, settling moth, sphingid, butterfly, large bee and fly pollination (the pollination system of 18 species was unknown). Hummingbird pollinated species showed little seasonality of flowering when compared with species exhibiting small moth, and beetle pollination syndromes, as well as those with unspecialized flowers.

(5) The vast majority of species studied have fleshy fruits (sarcochores). Fruiting activity was less markedly seasonal than flowering. Species with fruit are more numerous in the second half of the year (the wet season and early dry season). The second year of the study saw substantially fewer species in fruit than the first year; this is attributed to the greater than usual rainfall and inclement weather during the peak flowering season.

(6) Cloud forest shrub and treelet phenology is compared with patterns of other forests that have been studied. In general, the greater the rainfall, the less seasonality of flowering and fruiting is seen. Although Monteverde is very wet, rainfall is intermediate between that of lowland dry and lowland wet forest in Costa Rica. Seasonality of flowering and fruiting at Monteverde is more pronounced than at La Selva (wet) and less obvious than in Guanacaste (dry).

KEY WORDS: Costa Rica, flowering, fruiting, leafing, phenology, pollination, shrubs, treelets, tropical.

INTRODUCTION

Tropical cloud forest communities have not received the amount of careful study that lowland wet and dry forests have been granted (but see Tanner

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1982). Many environmental changes accompany an increase in elevation, and among these, differences in rainfall, temperature, and exposure can certainly be expected to have an impact not only on species distribution, but on overall and individual seasonal patterns of leafing, flowering, and fruiting in tropical cloud forest. We report here our findings from phenological investigations in Costa Rican cloud forest from December 1978 to March 1981, part of a larger study of plant/animal interactions involved in plant reproductive biology of cloud forest trees and shrubs. The phenological aspects of this study complement the phenological studies of Frankie, Baker & Opler (1974) and Opler, Frankie & Baker (1980) on lowland wet and dry forests of Costa Rica. In this paper we describe the pertinent aspects of the habitats, and describe and analyse patterns of leafing, flowering, and fruiting of shrubs and treelets in cloud forest at Monteverde. In addition to simple seasonality, we consider flowering and fruiting strategies, pollinator types, average plant size, and population size for the different species studied. We compare cloud forest patterns with those described from other forests, both lowland and montane.

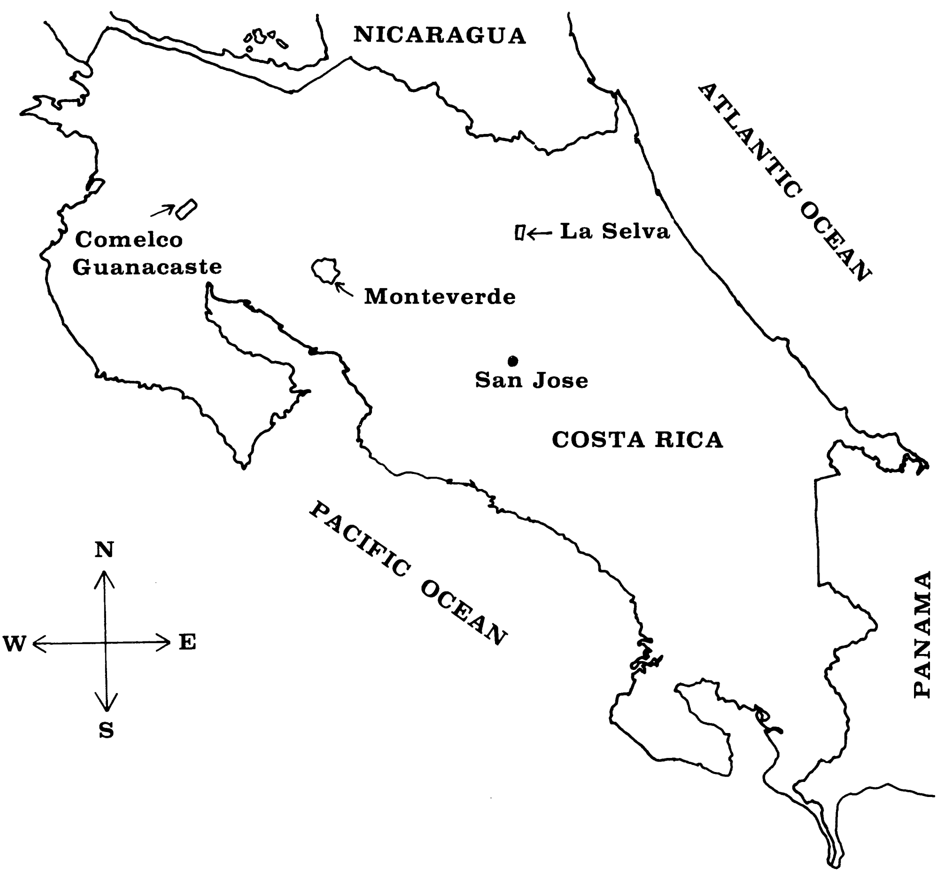

Figure 1. The location of the study site at Monteverde in Costa Rica; the sites for previous studies of lowland wet and dry forests (La Selva, and Comelco) are also shown.

METHODS

A. Study sites

The study area, Monteverde, is in Puntarenas Province (Figure 1), situated between 1320 m and 1600 m elevation, including three forest types (according to the Holdridge (1967) system of life zones, two forest types and the transition zone in between). The lowest area (Lower Montane Wet Forest, *sensu* Holdridge) is in woods on farms in the community of Monteverde (elevation 1320–1460 m above sea level). The middle area (Lower Montane Wet Forest/ Rain Forest Transition) is a large tract of privately owned forest (elevation 1480–1520 m) continguous with the highest area, the Monteverde Cloud Forest Biological Reserve (Lower Montane Rain Forest *sensu* Holdridge, or 'Cloud Forest', elevation 1550–1650 m), a large area of pristine forest managed by the Tropical Science Center, San Jose, Costa Rica. Other descriptions of these sites have been given by Buskirk & Buskirk (1976), Feinsinger (1976), Powell (1979), Lawton & Dryer (1981), and Hartshorn (in Janzen 1983).

Substantial rainfall occurs in these forests every month. The mean annual precipitation measured at the middle elevation (about 1500 m above sea level) for the period 1978–1981 was 2916 mm, ranging from 2429 to 3234 mm. The 21-year average for annual precipitation (1956–1976) was 2485 mm. The drier months are December through May (Figure 2); rainy months are generally June through November.

The second year of the study had a wet season extending for 7–8 months, longer than the first wet season in 1979 which extended only 6 months. Monthly mean temperature ranged from 24 to 27°C (high) and from 12 to 15°C (low); there is a fluctuation in temperature maxima and minima with season, dry season temperatures being 2–3°C lower than those in the wet season.

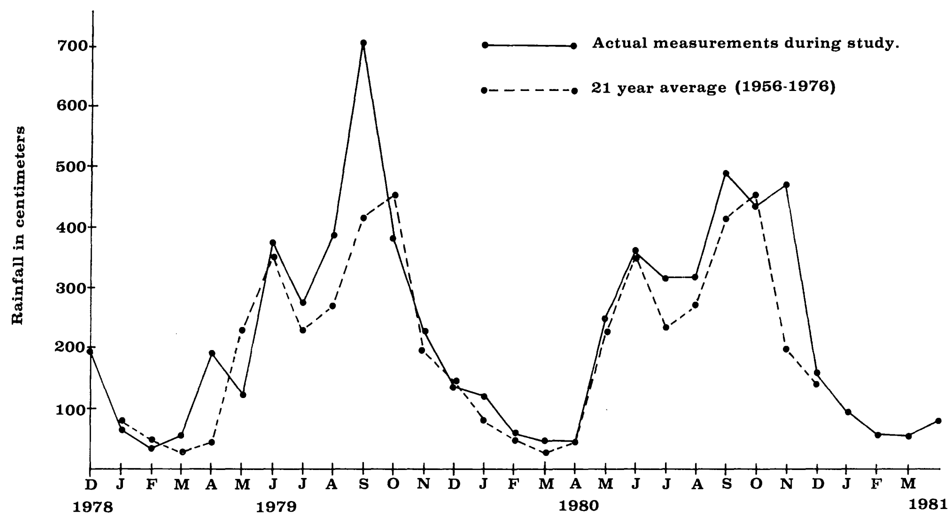

Figure 2. Mean monthly rainfall for the months of the study (solid line) and the 21-year average plotted over the same months (average from 1956–1976; dashed line).

B. Procedure

We divided the taxa into three life-form categories: treelets (with one main woody trunk, branching at a height greater than 1 m above the ground; 28 spp.), shrubs (with woody stems either multiple or branching less than 1 m above the ground; 59 spp.), and subshrubs (with greenish but woody stems, of smaller stature; 3 spp.). The casual observations reported here (indicated in the Appendix by an asterisk *) include a number of species that are more aptly classified as herbs; these were included for a more complete picture of understorey plant reproductive biology, but were not tallied up with the carefully monitored species for the various compilations.

Shrubs, subshrubs, and treelets were tagged with formica tags, which were attached with plastic-coated copper wire and numbered with indelible markers. Observations were made every month on a total of 350–470 tagged plants of 107 species, and additional notes were made on unmarked individuals of these and other species seen flowering or fruiting. Numbers varied from month to month because some individuals were added, and others died, during the course of the study.

At the lower elevation we had three transects (with 27, 38 and 76 marked individuals), at mid-elevation two transects (78 and 79 individuals), and at the upper elevation five transects (32, 31, 30, 52 and 28 individuals).

For each tagged individual, records were made of leaf flushing, leaf fall, flowering, and fruiting.

1. Leafing - Leafing activity was estimated as percentage of leaves on an individual plant that were new (increments of 5%). Leaves were not marked, and in some species we may have underestimated new leaf production, particularly in 'leaf exchangers'.

2. Leaf drop - Leaf drop was similarly noted (percentage of leaves lost, as evidenced by bare branches or leaves on the ground). The reliability of these data may be doubtful, and leaf loss again underestimated because leaves were not tagged.

3. Flowering - Flowering activity was subdivided into production of buds and open flowers; each of these two states were designated as no activity, few, intermediate, or many. For determining overall flowering activity patterns, only the open flower scores were used. Bud information gave indication of flowering episodes we might have otherwise missed; for some species, flowering time was extrapolated from observing large buds one month, and no buds the next month.

4. Fruiting - Fruiting activity was divided into the presence of immature and mature fruit. For most species it was easy to reach and examine the fruit to assess its maturity; for certain species, however, the removal of fruit was the only indication that the fruit was mature. Admittedly, some animals remove unripe fruit, so this was not absolute evidence.

5. Pollination system - For each species, observations on flower visitors and floral morphology were used to classify the species as to pollinator type. We classified any species about which we were uncertain as 'unknown'.

6. Fruit type - Diaspores were categorized by their morphology according to the classification of Dansereau & Lems (1957).

7. Population size - Relative population densities (rare, occasional, common) were estimated subjectively, as we got a general indication of the abundance of species when looking for individuals to tag.

8. Specimens - Voucher specimens of all species have been deposited in the herbaria of Missouri Botanical Garden, the Field Museum (Chicago), and the Universidad de Costa Rica. Vouchers of most species have also been deposited in the herbaria of the Museo Nacional de Costa Rica and the University of California, Berkeley.

RESULTS

A. Leafing activity

There is no pronounced seasonal pattern of leafing activity (Figure 3). Each month, the vast majority of the species had new leaves being produced. Fewer species produced new leaves in the later part of the wet season (August-December in 1979; August-February in 1980, when the wet season lasted well into the typically drier months).

We can consider leafing activity of species using different leaf flush level percentages (Figure 3); in this figure the number of species with at least one individual showing leafing activity above the cut-off indicated on the curve are totalled for each month of the study. The higher level of leafing (i.e. species with at least one individual with activity greater than 10%) showed more pronounced peaks in the dry season (January, February - June, July), suggesting that species which flush larger percentages of new leaves tend to do so in the dry season.

For species with individuals that flush larger (>10%) quantities of new leaves, the seasonality of leafing shifts with elevation (Figure 4). The peak activity for the 1300 m site is confined to the dry season (February-April), while at the middle forest site peak activity extends further into the wet season (August); the peaks are even more extended in the highest forest (from January or February to August or September). If all leafing activity greater than 0% is considered, no clear seasonal pattern with forest type is seen.

Most shrub and treelet species produced new leaves at a fairly constant, low rate. Several species had discrete, widely-spaced leafing periods. Some Solanaceae, for example *Solanum* sp. (WAH 34, 35, 36), had two main leafing periods (see Appendix); *Tabernaemontana chrysocarpa* (Apocynaceae) had leafing episodes separated by several months; *Crossopetalum eucymosum* (Celastraceae) had one leafing episode per year.

B. Leaf drop

Leaf drop occurs at a relatively constant, low rate for most species (Figure 5). There are a small proportion of the total species that lose a large quantity of leaves in any given month. One pronounced peak in leaf drop occurred in

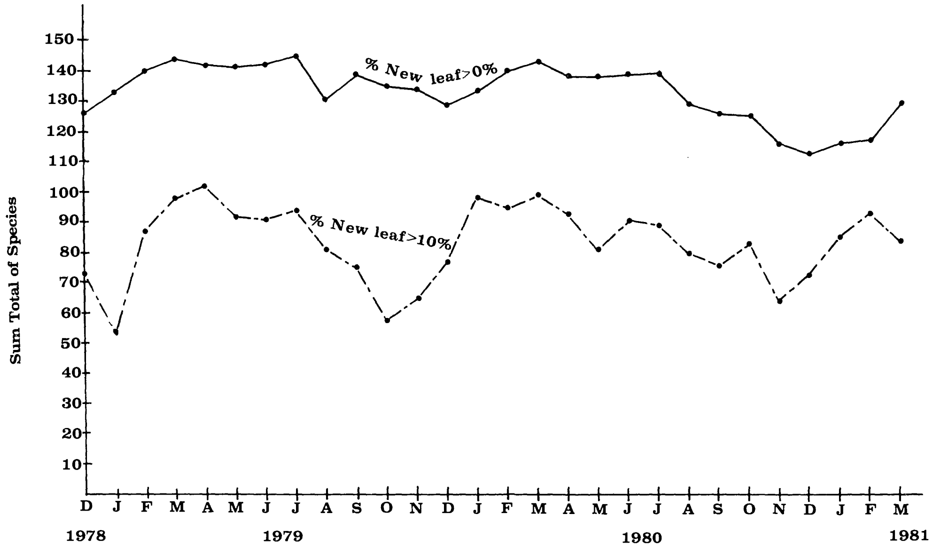

Figure 3. Leaf flushing periodicity of shrubs and treelets at Monteverde, all forest types combined. Different cutoff percentages are illustrated.

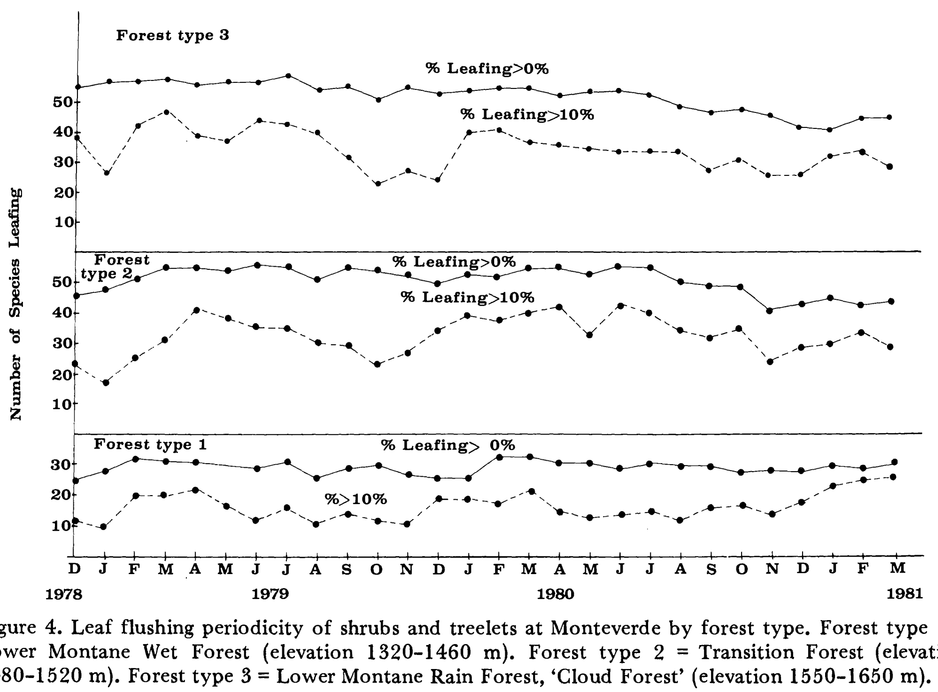

Figure 4. Leaf flushing periodicity of shrubs and treelets at Monteverde by forest type. Forest type 1 = Lower Montane Wet Forest (elevation 1320-1460 m). Forest type 2 = Transition Forest (elevation 1480-1520 m). Forest type 3 = Lower Montane Rain Forest, 'Cloud Forest' (elevation 1550-1650 m).

September of 1979, a month in which the rainfall was unusually high. The only leaf drop actually seen was in the palms (Arecaceae), which hold their senescent leaves for a long enough time to be readily observed. Leaf drop in palms took place over most of the year, with perhaps slightly less in the late dry season. Most other species lost leaves in a gradual manner; substantial leaf losses ob-

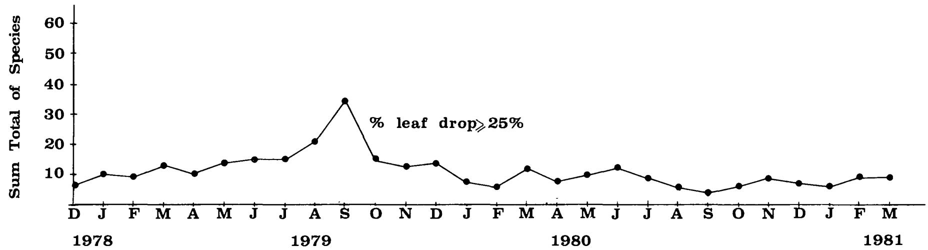

Figure 5. Leaf fall periodicity of shrubs and treelets at Monteverde in all forest types.

served were infrequent and usually associated with ill health and subsequent death of particular individuals.

C. Flowering

Peaks in flowering occur during the dry/wet season interface (April–June) (Figure 6). The peaks become less pronounced as we consider only species in which larger percentages (10% to 25%, and 50%) of the individuals of the species are flowering, but the peaks remain at the same times of year. The patterns are similar in the three forest types (Figure 7).

Gentry (1974) categorized patterns of flowering for species based upon duration: a synchronous display of many flowers (mass flowering) is common in species with short durations; whereas species with extended durations often produce only a few flowers a day over long periods (he called this 'steady-state flowering'). In our data, we defined massively flowering species as species with individuals that produced many flowers within a one-to-two month period (individuals, however, flower for shorter periods); extended flowering species were defined as species with individuals that produced fewer numbers of flowers for five months or more; and intermediate species were the rest. Massive flowerers show less seasonality than extended flowerers and species classified as

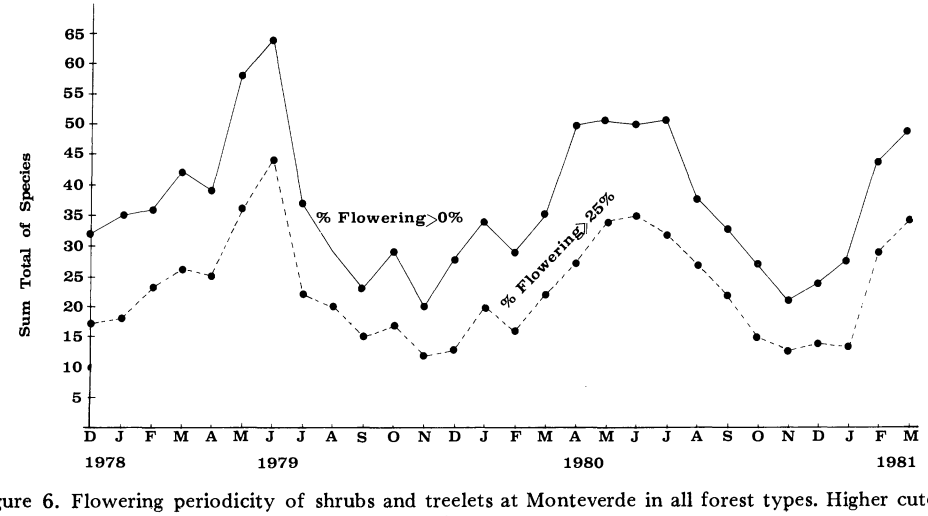

Figure 6. Flowering periodicity of shrubs and treelets at Monteverde in all forest types. Higher cutoffs are for species with ≥x% of marked individuals in flower.

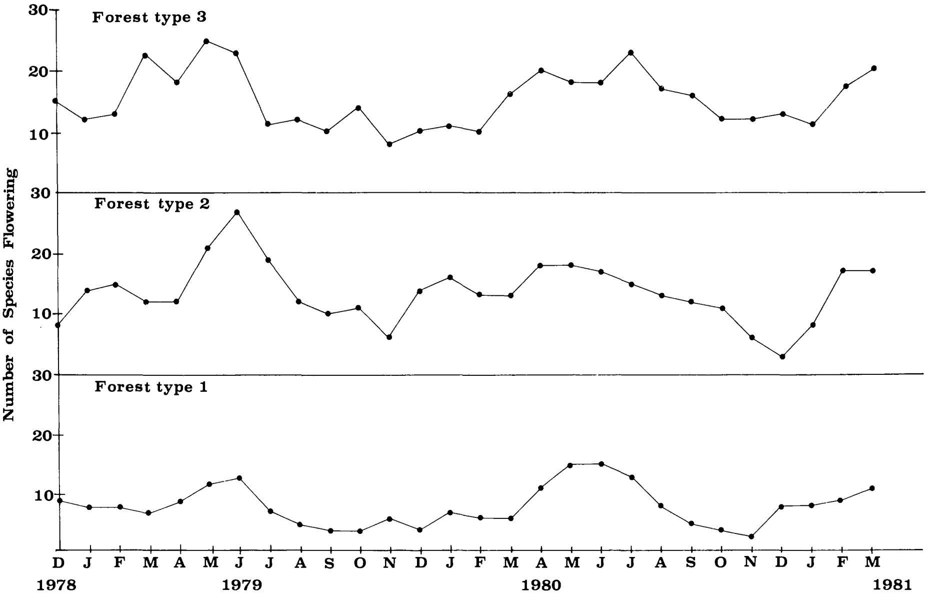

Figure 7. Flowering periodicity of shrubs and treelets at Monteverde by forest type.

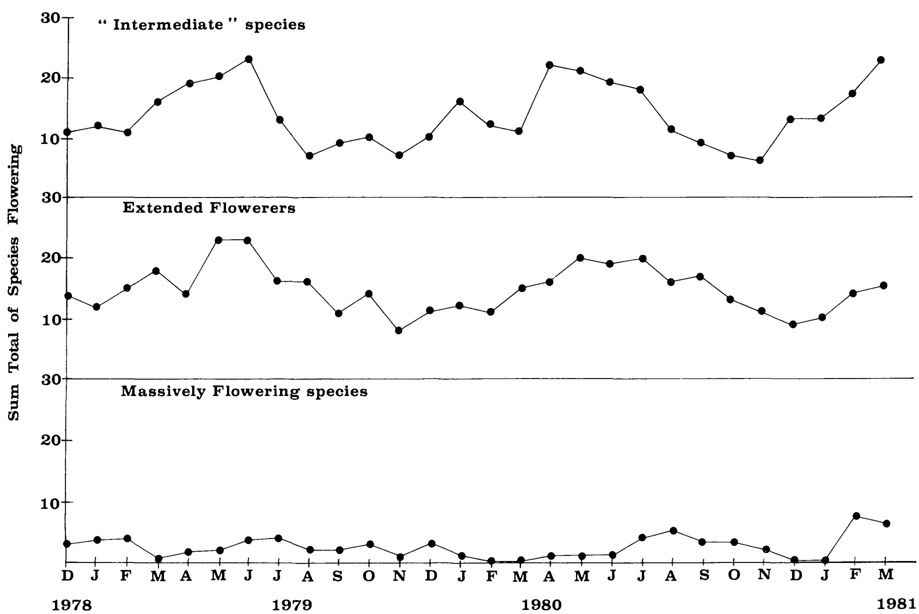

Figure 8. Flowering periodicity of shrubs and treelets at Monteverde by flowering pattern.

'intermediate' (Figure 8). A smaller proportion of the shrub and treelet species are massively flowering (16 species or 15%) than are extended flowering (35 species or 33%). This differs substantially from the Monteverde trees, where a large proportion of species was classified as massively flowering (69%) (Haber *et al.*, in preparation).

D. Pollination

Shrubs and treelets with flowers pollinated by small bees such as Halictidae (23 species of the shrub and treelet species tagged and monitored) show activity throughout the year, with a greater number of species blooming in the early wet season than at other times of the year (Figure 9). Plants (34 species) with flowers visited by a variety of insects including small Hymenoptera, Diptera, and Lepidoptera ('generalists') show a high degree of seasonality in flowering time. Peak activity is during the last few months of the dry season through the beginning of the wet season. Hummingbird pollinated species (12 species) show little seasonality of flowering, while the four small moth-pollinated

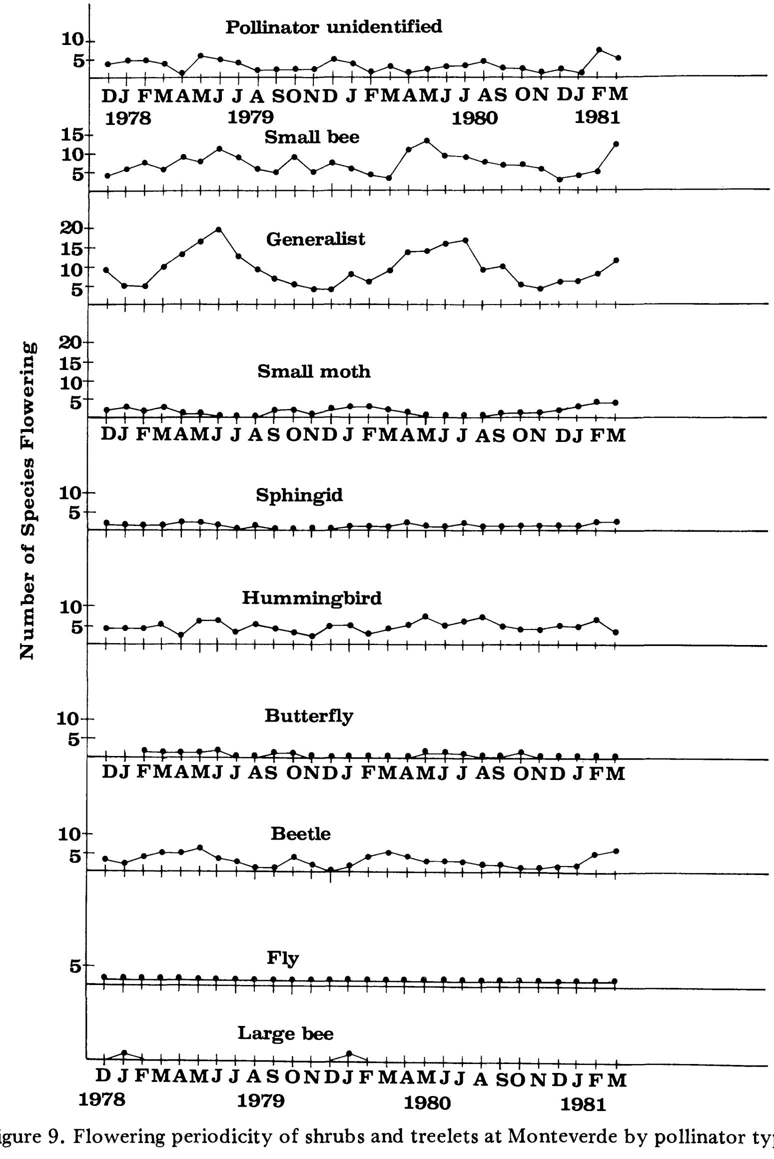

Figure 9. Flowering periodicity of shrubs and treelets at Monteverde by pollinator type.

species ('settling moths' in families such as Geometridae, Noctuidae, Ctenuchidae, Arctiidae, etc.) flower in all months except the beginning of the dry season. The four species pollinated by hawkmoths (family Sphingidae) show flowering activity spanning the entire year, except for an absence of activity from September to December of the first wet season monitored. Eight species were beetle pollinated, and flowered more in the dry season than the wet season. The other pollination categories are too poorly represented among the tagged shrubs to display any patterns, but the activity of these few species is shown for completeness (Figure 9). There were 18 species with pollination type unknown, one species pollinated by large bees (Xylocopidae), two species of butterfly pollinated shrubs (butterfly families Pieridae, Ithomiidae, etc. and Hesperiidae), and one species pollinated by flies. In addition to the tagged species, observations on pollinators were made on many other species, and are included in the Appendix.

E. Fruiting

Peaks of mature fruit production (Figure 10) were less distinct than flowering peaks. This may be because species take varying amounts of time to develop their fruit after flowers are pollinated, and mature fruit may remain on some plants for many months. Members of the Araliaceae form fruit within one month after flowering, and fruit ripens quickly. Celastraceae (*Crossopetalum eucymosum*) do not have mature fruit for 3 months after they flower, but then ripe fruit remains on the plants for 5 months. *Meliosma subcordata* (Sabiaceae) is a good example of extremely uniform flowering (April) but extended fruit development and maturation (over most of the following year the fruits were large, and every month a few would disappear). In addition, species with extended flowering times subsequently have extended periods of fruit develop-

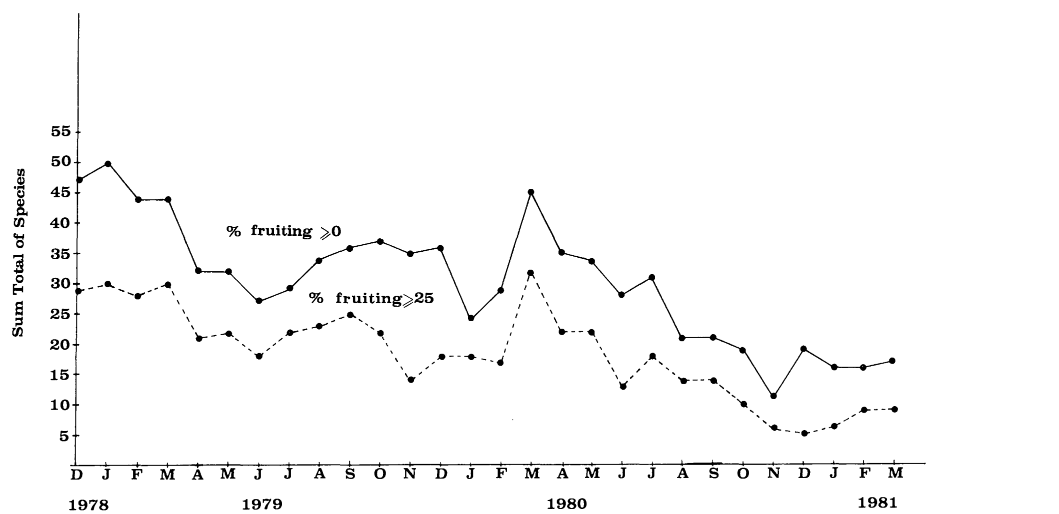

Figure 10. Fruiting periodicity of shrubs and treelets at Monteverde in all forest types. Cutoffs as in Figure 6.

ment and maturation, with fruit of many ages on an individual at one time (e.g. Apocynaceae, Annonaceae, Arecaceae, Gesneriaceae, Malvaceae, Melastomataceae, Piperaceae, Rubiaceae).

After flowering peak in May and June of 1979, the number of species with fruit increases from July until December 1979 with another peak in March of 1980. Following the second flowering peak from April to July of 1980, there was much less fruit production than in the previous year. This was probably due to the unusual long-lasting, heavy rains that fell through much of the 1979-1980 dry season and major flowering season, inhibiting both visits to flowers by pollinators and fertilization and fruit maturation subsequent to pollination (seen in hand-pollination experiments done during those times, e.g. Koptur 1983). The fruiting patterns differ somewhat between the three forest types (Figure 11), with the earliest increase in fruiting activity at the lowest site, progressing upward. The peak in fruiting seen in March of 1980 was due to fruiting activity in the upper two forests only.

F. Fruit dispersal types

The vast majority of species studied (94 out of 107) have sarcochores (i.e. fleshy fruits, or seeds with fleshy coverings inside the fruit; using the classification of dispersal units of Dansereau & Lems 1957). The overall fruiting pattern of species with sarcochores shows greater activity in the wet season than the dry season (Figure 12). Species with this fruit type were profoundly affected by heavy rains during the last year of the study which caused flowers to rot. Few shrub species (7 out of 107) have desmochores (having hooks or sticky hairs

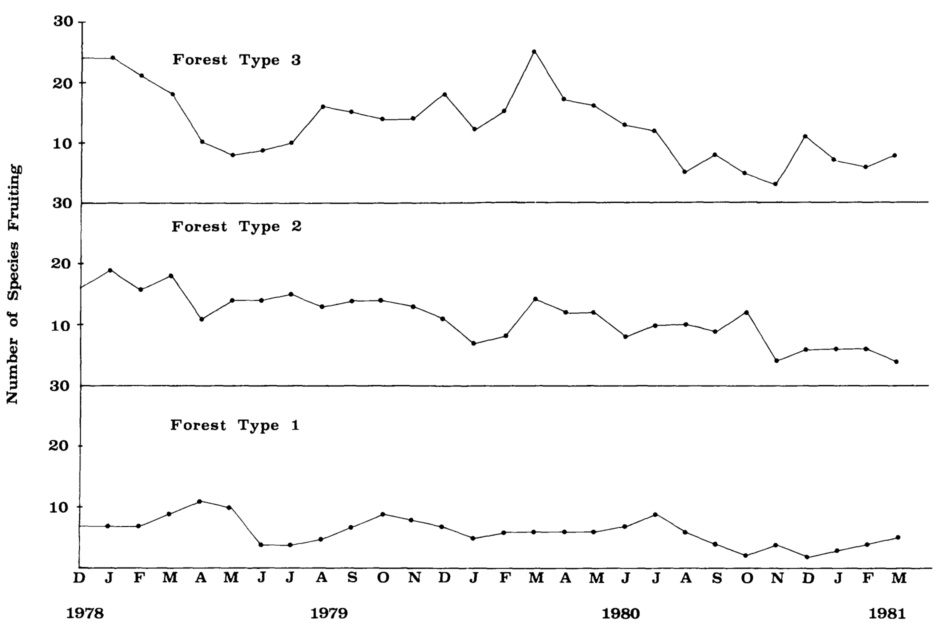

Figure 11. Fruiting periodicity of shrubs and treelets at Monteverde by forest type.

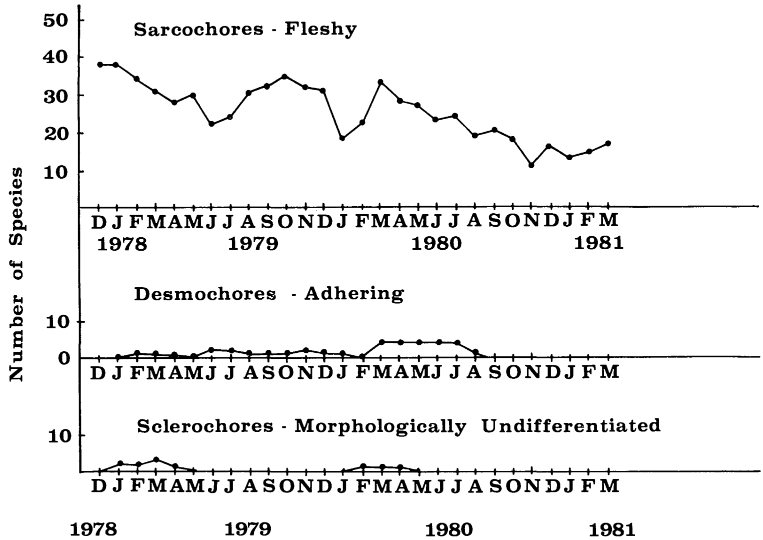

Figure 12. Fruiting periodicity of shrubs and treelets at Monteverde by fruit type.

which facilitate external dispersal on animals), but those that do tend to fruit in an extended fashion from the dry season to well into the wet season. The few species (4 out of 107) with morphologically undifferentiated sclerochores fruited in the dry season only and did not form fruit in the early dry season of 1981.

G. Patterns of abundance

Of the 107 species studied, 35 were common in occurrence, 11 were rare, and 61 were occasional. Only a small proportion of the massively flowering shrubs can be described as common in the sites studied; more often, massively flowering species are rare (6 out of 16 massively flowering species) or occasional (7 out of 16). The same pattern is seen in trees (Haber *et al.*, in preparation).

H. Vicariant species

At least 16 of the species monitored occur both in La Selva and Monteverde (Table 1). For a few of these species, the flowering period was more discrete at La Selva (e.g. *Faramea occidentalis, Piper aequale, Cephaelis elata*). For others, the flowering period extended over more months in the lowlands (*Besleria columneoides, Neea amplifolia, Psychotria tonduzii*). *Justicia aurea* flowered but did not set fruit during the course of the lowland study (Opler *et al.* 1980); this species did set fruit at Monteverde, but there were many species that did not set fruit (or set very little) during the second (rainier) year of the study.

I. Comparison of cloud forest with lowland wet forest patterns

Many lowland wet forest tree and shrub species produced leaves at a low but constant rate throughout the year (Frankie *et al.* 1974, Opler *et al.* 1980), simi-

Table 1. Species in common between Monteverde and La Selva

	Months of flowering	
	At Monteverde	At La Selva
Justicia aurea Schlecht.	2–7	1–5, 9
Razisea spicata Oerst.	12–2	1–12
Besleria columneoides Hanst.	1–10	1–12
Spigelia humboldtiana Cham & Schlect.	4–5	3–11
Mollinedia costaricensis Donn. Smith	3	3–7
Siparuna nicaraguensis Hemsl.	12–8	12–4, 6–7, 9–10
Neea aff. *amplifolia* Donn. Sm.	6–8, 12–3, 5–11	2–10
Piper aequale Vahl.	1–7, 12–11	4
P. phytolaccaefolium Opiz in Presl.	2–5, 10, 1–3	5–1
Cephaelis elata Sw.	3–12	2, 6–9
Faramea occidentalis (L.) Rich.	1–2, 2–3, 5	6
Faramea talamancarum Standl.	5–7	6
Hamelia patens Jacq.	1–12	1–12
Psychotria gracilis Benth.	3, 6–9	4–5
P. tonduzii Standl.	12, 3, 5–8	2–8

lar to cloud forest patterns. Some lowland species produced large numbers of new leaves during the drier season (this was more pronounced in trees than shrubs), also similar to cloud forest patterns.

Among wet forest shrubs and treelets, flowering lacked any distinct seasonal pattern, although the highest flowering levels occurred in the first half of the year (Opler *et al.* 1980). Rainfall patterns differ between the La Selva site and the Monteverde sites, and rainfall is a factor in the timing of flowering in tropical plants (Opler *et al.* 1976). The lowland forest has greater overall precipitation, and more wet months (notably two wet seasons: a long one from May to November, and a shorter one in January–February, separated from each other by the veranillo, or little dry season). There is no detectable seasonal pattern of fruiting of shrubs and treelets in lowland wet forest, but more pronounced fruiting seasonality is seen in cloud forests (with less rainfall and greater seasonality of flowering).

DISCUSSION

Phenological studies of tropical forests have shown the greatest seasonality in leafing and flowering in lowland dry forests (Frankie *et al.* 1976, Opler *et al.* 1980, Lieberman 1982, Rathcke & Lacey 1985). These activities may be controlled in some species by the highly seasonal pattern of rainfall; there is a correlation between rainfall and flowering, although cause and effect have not been demonstrated for all species observed to respond in this way (Opler *et al.* 1976). Floral initiation frequently occurs at the end of vegetative growth, and floral anthesis occurs some time after (usually triggered by rehydration of previously water-stressed trees (Borchert 1983, Reich & Borchert 1984). Plants of wet forests show less synchrony of leafing and flowering overall (Frankie *et* *al.* 1974, Hilty 1980, Milton *et al.* 1982, Opler *et al.* 1980), but synchrony within some wet forest species may also be proximally determined by rainfall after sufficient water stress (Augspurger 1982). The ultimate implications of synchronous flowering are biotic (Rathcke & Lacey 1985), including better pollinator attraction (Augspurger 1980, 1981), seed disperser attraction, and seed predator satiation (Augspurger 1981).

The overall amount of rainfall in a given habitat plays a role in determining the extent to which various species rely on rainfall as a flowering cue. Opler *et al.* (1980) point out that lowland wet forest on Barro Colorado Island, Panama (BCI), has rainfall (2800 mm per year) intermediate between lowland wet forest at La Selva (4000 mm) and dry forest in Guanacaste (1800 mm). Monteverde rainfall is approximately that of BCI (2900 mm). Croat (1975) found an early wet season overall flowering peak (May–July) on BCI, not unlike the peak in flowering we find for Monteverde shrubs and treelets (April–July). Flowering in both these places was more strongly seasonal than flowering of shrubs and treelets at La Selva, but less distinct than the earlier, sharper flowering peak at Guanacaste. Hilty (1980) found even less flowering seasonality in premontane rain forest in Alto Yunda, Colombia (elevation 1050 m) where average total rainfall is greater (about 5530 mm) than even at La Selva.

Cloud forests are not only wet and misty, but cooler and windier than lowland forests. The extreme and rather unpredictable fluctuations in prevailing weather conditions may have selected for reproductive characteristics that differ from those of plants in gentler climates (Baker *et al.* 1983, Bawa 1974, 1979, Frankie *et al.* 1974, Opler *et al.* 1980). The vast majority of shrubs and treelets at Monteverde have flowers pollinated by a variety of insects; lack of specialization could increase pollination opportunities, and may have resulted from conditions more harsh and unpredictable than lowland areas. Tanner (1982) found generalized insect pollination to be by far the most common syndrome for trees in the Blue Mountains of Jamaica, a cloud forest of similar elevation to Monteverde. Sobrevila & Arroyo (1978) studied the breeding systems of plants in Venezuelan cloud forests, finding a high level of dioecy, and a surprisingly low level of self-incompatibility in hermaphrodites, reflecting, perhaps, the unpredictable pollination due to the unpredictable climate. Extreme weather conditions may make unusual pollinators more likely; Lumer (1980) found several species of mice visiting flowers and pollinating *Blakea chlorantha* (Melastomataceae), a shrubby epiphyte in high elevation, exposed areas of the Monteverde cloud forest where tightly grasping rodents may have an advantage over bats (the presumed former pollinators). Misty air and very high humidity much of the year make flora nectars more dilute on average than in lowland areas (H. G. Baker & I. Baker, in prep.).

Extended flowering is more common in aseasonal environments and understorey species (Rathcke & Lacey 1985). Extended flowering may spread the risk of uncertain pollination, or reflect sparse or unpredictable resources in the wet forest understorey. Unpredictable, inclement weather, as experienced in cloud forests at Monteverde, may select for extended flowering periods in some species, as well as multiple flower opening times within a 24-hour period (Koptur 1983).

The largest family represented in this study is the Rubiaceae. Flowering and fruiting among individuals of a species in this family was almost always synchronous (i.e. more than 50% of the individuals flowered in any flowering month). Synchrony in flowering is advantageous for pollinator attraction and increases the number of potential mates (and therefore outbreeding) within a species (Rathcke & Lacey 1985). Synchronous fruiting may be of value in seed predator satiation (Augspurger 1981) and enhanced attractiveness to dispersers within a species, though synchrony with other species can detract (Wheelwright 1985). In a study of lowland wet forest Rubiaceae, Bawa & Beach (1983) found all hermaphroditic species investigated save one to be self-incompatible.

Many cloud forest shrub and treelet species hold immature fruit for an extended time (more than 4 months). The substantial decrease in the number of species fruiting in the second year of our study may have been due in part to aborted maturation of fruit during the many cool and rainy days during and following flowering. Herrera (1984) suggests that unripe fruits are more heavily attacked by insects than are ripe fruits, thus avoiding predation of the insects by dispersers. If conditions prevent fruit from maturing at its usual pace, the unripe fruit may experience more damage from fruit and seed consumers and pathogens; this may be an additional explanation for the paucity of ripe fruit produced by some species. Of species that matured fruit successfully, some retained their ripe fruit by extended periods (more than 2 months in many cases). Dispersers may have missed these individuals, and fruit removal rates appear to be very low and patchy in understorey plants. Extended fruiting is more common in the understorey than the canopy (Opler *et al.* 1974, Rathcke & Lacey 1985).

Summary

In Costa Rican cloud forests, the seasonality of rainfall is intermediate between that of lowland wet and lowland dry forests. Flowering of shrubs and treelets at Monteverde was more strongly seasonal than flowering in lowland wet forests at La Selva, but less seasonal than in dry forests in Guanacaste. The flowering peak occurs from April through July; fruiting occurred over a more extended period of each year. The majority of shrub and treelet species were found to have 'generalist' pollination systems (as Tanner (1982) found for trees in cloud forests in Jamaica), but others were specialized for certain visitors (small bees, sphingids, beetles, butterflies, settling moths, large bees). Most species had fleshy fruits, indicating the predominance of animal dispersal, commonly found in tropical wet forests. Temperature, rainfall, and exposure all contribute to distinguishing the plant reproductive interactions in Costa Rican cloud forests from those in lower elevation forests.

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Appendix. List of species recorded and their phenological behaviour. Abbreviations used in the lists are: * - casual observations on unmarked individuals; 1-12 - January through December; NLD - no leaf drop detected; DL - discontinuous leafing; CL - continuous leafing; DP - different annual periodicity; US - unsynchronized individuals within a species.

Pollinator types (primary): beetle = btl; butterfly = but; bat; fly; generalist = gen; hummingbird = hum; large bee = lb; small bee = sb; settling moth = set; sphingid moth = sph; wasp = wsp; wind = win; unknown = unk.

Individual size: treelet = treel; shrub; subshrub = subsh.

Population size: rare = rar; occasional = occ; common = com.

Flowering pattern: massive = mas; extended = ext; intermediate = int.

Fruit types (Dispersal units): pterochores (winged) = ptero; pogonochores (with long hairs) = pogon; desmochores (adhere) = desmo; sarcochores (fleshy) = sarco; sporochores (tiny) = sporo; sclerochores (moderate size) = sclero; barrochores (very large) = barro; ballochores (explosive) = ballo.

Forest types: 1 - Lower Montane Wet Forest (elevation 1320–1460 m); 2 - Lower Montane Wet Forest/Rain Forest Transition (1480–1520 m); 3 - Lower Montane Rain Forest (1550–1650 m).

Species name/authority/ voucher number	No. of indivs	Leaf drop	Leaf flush	Flowering	Fruiting	Poll. type	Indiv. size	Pop. size	Flower pattern	Fruit type	Forest type(s)
FAMILY: ACANTHACEAE											
Aphelandra aurantiaca (Scheider) Lindl.	*			8		hum	subsh	occ	int	sclero	2, 3
Dicliptera iopus Lindau	*			1		but	subsh	com	int	sclero	2, 3
Hansteinia blepharorachis (Leonard) Durkee	3	NLD	2–10	12–3	2–4	hum	subsh	com	int	sclero	2, 3
Hansteinia reflexiflora Leonard	*			1–2		hum	subsh	unk	int	sclero	1
Justicia aurea Schlecht.	1	NLD	2–7	2–7	1	hum	shrub	occ	ext	sclero	2
Justicia costaricana Leonard	*			2		sb	shrub	com	int	sclero	2, 3
Justicia oerstedii Leonard	*			1–2		hum	subsh	occ	int	sclero	1
Justicia parvibracteata Leonard	*			12		sb	subsh	occ	int	sclero	2
Justicia valerii Leonard	*			1		sb	subsh	com	ext	sclero	2
Poikilocanthus macranthus	4	NLD	12–1	2–4, 6, 9–10	3	but	shrub	com	ext	sclero	2
Razisea spicata Oerst.	4	NLD	3–6	12.2	1–3	hum	shrub	com	ext	sclero	2, 3
AMARANTHACEAE											
Iresine diffusa Humb. & Bonpl.	*			1		unk	subsh	occ	mas	sclero	3
ANNONACEAE											
Desmopsis bibracteata (Robinson) Safford	7	9–3	7–5 (DL)	4–7, 10	10, 7	btl	treel	occ	ext	sarco	1
APOCYNACEAE											
Tabernaemontana chrysocarpa Blake var. *costaricensis* L. Allorge (WAH-123)	7	NLD	1–4, 7, 12–5, 7–10	4–7	4–5, 8, 11, 7–8, (DP)	sph	treel	occ	ext	sarco	1, 3

ARALIACEAE											
Dendropanax querceti (WAH 200, and 334)	5	NLD	CL	12-1, 7, 9-12, 2-3 (DP)	1-2, 11-3	gen	treel	occ	mas	sarco	2, 3
Dendropanax albertii-smithii Nevl. (SK-263)	2	NLD	12-1, 3-4, 6-10, 11-3	6-7, 7-8	7-10	gen	treel	rar	mas	sarco	2, 3
ARECACEAE (PALMAE)											
Bactris divisiculpula (VJD-1415)	8	1-12	1-12 (CL)	9-11	12-1	unk	treel	com	ext	sarco	1, 2
Chamaedorea sp. (SK-273)	1	1-12	1-12 (CL)	7-8 (DP)	6-7	unk	shrub	com	int	sarco	2
Calyptrogyne brachystachys H. Wendl. ex Burret	7	1-12	1-12 (CL)	12-3, 5, 10-11, 1-3, 7-3 (US, DP)	8-12	btl	shrub	com	ext	sarco	2, 3
Geonoma gracilis H. Wendl. ex Spruce	8	1-12	1-12 (CL)	1-12 (US, DP)	3-8	fly	shrub	occ	ext	sarco	1, 2, 3
Chamaedorea sp. 2	2	3-11, 1-8	1-12	12, 2-3	12, 6-8, 3	unk	shrub	occ	int	sarco	3
Small sp. (SK-278)	4	1-12	1-12 (CL)	12-2, 5, 2 (DP, US)	none	unk	shrub	com	mas	sarco	1
Tall sp. (SK-274)	8	1-12	1-12 (CL)	12-1, 1, 2 (DP, US)	12-3, 5-9, 11, 5-6	unk	treel	occ	int	sarco	2, 3
Geonoma seleri Burret	8	1-12	1-12 (CL)	2, 5-7, 10, 12, 6-10, 2-3 (DP, US)	12, 2-8	unk	treel	com	mas	sarco	2, 3
Wide sp. (SK-332)	3	1-12	1-12 (CL)	5-7, 9, 1, 8, 2-3 (DP, US)	6-9, 4-5, 8	unk	shrub	occ	int	sarco	2
BORAGINACEAE											
Tournefortia bicolor Swartz.	*			4		set	shrub	occ	ext	sarco	2, 3
Tournefortia glabra L.	*			4		set	shrub	occ	ext	sarco	2, 3
BROMELIACEAE											
Pitcairnia brittoniana Mez.	*			3		hum	subsh	occ	ext	sarco	3
CAPRIFOLIACEAE											
Viburnum costaricanum (Oerst.) Hemsl.	2	NLD	1-12	2-4	3-6	gen	treel	com	int	sarco	2
CELASTRACEAE											
Crossopetalum eucymosum (Loes. & Pit.) Lundell	2	NLD	2-3, 5, 1-3	3, 2-3	5-11	unk	treel	rar	mas	sarco	1
COMPOSITAE											
Clibadium asperum (Aubl.) D.C.	*			8-9		gen	shrub	com	int	sarco	2, 3
Neomirandia biflora K & R	*			8-9		gen	shrub	com	unk	pogon	2, 3
DILLENIACEAE											
Saurauia veraguensis Seem.	*			8-9		gen	treel	com	int	sarco	3
ERICACEAE											
Vaccinium poacetum Donn. Sm.	1	NLD	3-5, 11-3	1, 3	5, 6	lb?	shrub	occ	mas	sarco	2

Appendix - *continued*

Species name/authority/ voucher number	No. of indivs	Leaf drop	Leaf flush	Flowering	Fruiting	Poll. type	Indiv. size	Pop. size	Flower pattern	Fruit type	Forest type(s)
ERYTHROXYLACEAE											
Erythroxylum amplum (WAH-304)	4	NLD	2–7	2–4	3–7	gen	treel	occ	int	sarco	1
FLACOURTIACEAE											
Hasseltia sp. (VJD-1656, and 715)	2	NLD	3–4, 6, 8–3	1	1–12 galled?	gen	treel	occ	mas	sarco	3
Xylosma quichense (WAH 311 and 291)	2	NLD	8–3	none	none	gen	treel	rar	int	sarco	3
GENTIANACEAE											
Symbolanthus pulcherrimus Gilg.	*			6		hum	shrub	occ	ext	sarco	3
GESNERIACEAE											
Besleria notabilis Morton	*			7		hum	subsh	com	int	sarco	3
Besleria princeps Hanst.	*			9		hum	subsh	occ	int	sarco	3
Besleria solanoides Kunth.	*			1–2		hum	shrub	occ	int	sarco	1
Besleria triflora (Oerst.) Hanst. (SK-71 and 116)	6	NLD	1–12 CL	2–8, 1–10	1–3, 6–9, 1–10	hum	shrub	com	ext	sarco	3
Capanea grandiflora (Kunth.) Decne. ex. Planc.	*			4		bat?	subsh	occ	int	sarco	3
Drymonia lanceolata (Hast.) Morton	*			4–5		hum	subsh	occ	ext	sarco	3
Kohleria spicata (Kunth.) Oerst.	*			1–2		hum	subsh	occ	int	sarco	1
GUTTIFERAE											
Symphonia globulifera L.f.	2	NLD	11–5, 9–10	12–1, 9–11 US	9–11	hum	treel	occ	int	sarco	1
Tovomitopsis glauca Pl. & Tr.	3	NLD	1–12 DL	3, 4–7	4–7	sb	shrub	occ	int	sarco	1
LOBELIOIDEAE (CAMPANULACEAE)											
Burmeistera cyclostigmata Donn. Sm.	*			10–11		fly	subsh	occ	int	sarco	3
Burmeistera parviflora Wimer ex. Standl.	*			11–12		unk	subsh	occ	int	sarco	3
Burmeistera vulgaris F. E. Wimer	*			11–12		unk	subsh	occ	int	sarco	3
Lobelia xalapensis H.B.K.	*			11		unk	unk	unk	unk	unk	unk
LOGANIACEAE											
Spigelia humboldtiana Cham. & Schlech.	*			4–5		sb	subsh	occ	ext	sarco	3
LYTHRACEAE											
Cuphea infundibulum Kochne	*			1–2		hum	shrub	occ	int	unk	1
MALPIGHIACEAE											
Bunchosia pilosa H.B.K.	7	8, 10, 12–1	5, 11–12, 1–9, 3 (DL)	4–7, 12–5, 7–8, 3 (US)	12–3, 7, 9–3	sb	treel	occ	int	sarco	2, 3

Glabrous yellow-flr (SK-210)	7	7–11, 8–3	1–12 DL	9–11	12, 3–5	sb	shrub	occ	int	sarco	3
Malpighia glabra (WAH-231)	1	NLD	1–2, 4, 12–1, 6–8 (DL)	3 (DP)	6–8	sb	shrub	rar	int	sarco	1
Bunchosia ternata (WAH-216)	7	NLD	1–12 DL	none	11–1, 7	unk	treel	rar	int	sarco	3
Malpig. unknown	2	NLD	1–12 DL	2–3, 5, 11 (DP)	12, 11	unk	treel	rar	unk	unk	3
MALVACEAE											
Malvaviscus arboreus Cav.	5	3–4, 8–9	1–12 DL	12–1, 5–12 (US)	10	hum	shrub	com	ext	sarco	2
MARCGRAVIACEAE											
Norantea sp.	*			3		bat?	shrub	occ	unk	unk	2, 3
MELASTOMATACEAE											
Miconia brenesii Standl.	7	NLD	1–12 DL	2–12, 3–1 US	12–5, 7–11	gen	treel	com	ext	sarco	3
Clidemia costaricensis Cogn. & Gleason	1	9, 12	1–12 DL	7–9	12	sb	shrub	occ	mas	sarco	3
Ossaea micrantha (VJD 226, 723, 859C 180)	1	NLD	1–12 DL	2 (DP)	none	sb	shrub	occ	mas	sarco	2
Miconia tonduzii Cogn. var. *serrulata* Cogn.	2	NLD	1–12 DL	12–2, 4–6, 10, 2–3 (DP)	12–5, 8, 2	sb	treel	rar	mas	sarco	2, 3
MONIMIACEAE											
Mollinedia aff. *pinchotiana* Perk. (SK-310, WAH-220, 359)	3	NLD	2–5, 9–12 (DL)	3	none	unk	shrub	rar	mas	sarco	1
Siparuna tonduziana Perk.	8	5–6, 8–9	1–12 CL	11–7	12–8	unk	shrub	com	ext	sarco	2, 3
MYRSINACEAE											
Rapanea juergensenii (VJD-1385)	2	NLD	2–5, 12–10, 1–3 DL	none	none	unk	treel	rar	mas	sarco	2
MYRTACEAE											
Eugenia oerstediana Berg.	2	NLD	2–5, 7, 1–3, 7–3 (DL)	7, 10, 3 (DP, US)	none	sb	treel	occ	int	sarco	1
NYCTAGINACEAE											
Neea amplifolia Donn. Sm.	10	NLD	1–12 DL	peak 6–8, 12–3, 5–11, 1	12–2, 9, 11–12, 2–6, 12–1	sb	shrub	com	ext	sarco	1, 2
Neea psychotrioides Donn. Sm.	8	NLD	1–12 DL	12–4, 11–2, 9–1 (DP)	2–3	sb	shrub	occ	ext	sarco	2, 3
Pisonia silvatica Standl.	13	NLD	1–12 DL	12, 2, 4, 11–2, 9–1 DP, US	2–3	gen	shrub	com	int	desmo	1
Torrubia costaricana Standl.	6	NLD	peak 3–5; 1–12	5–6, 4–7, 3	7–8	sb	shrub	occ	ext	sarco	1

Appendix – *continued*

Species name/authority/ voucher number	No. of indivs	Leaf drop	Leaf flush	Flowering	Fruiting	Poll. type	Indiv. size	Pop. size	Flower pattern	Fruit type	Forest type(s)
OLACACAE											
Heisteria acuminata (H. & B.) Engler	9	8–9	7–8, 4–6, 12–2	peak 7–10; 5–1	peak 12–4; 9–5	unk	shrub	com	ext	sarco	1
PASSIFLORACEAE											
Passiflora adenopoda DC.	*			9		lb	subsh	occ	ext	sarco	1
Passiflora biflora Lam.	*			5		lb	subsh	occ	ext	sarco	1
Passiflora capsularis L.	*			9	9	wsp	subsh	occ	ext	sarco	2
Passiflora dioscoreifolia	*			9		unk	subsh	occ	ext	sarco	2
Passiflora ligularis Juss.	*			8–9	8–9	unk	subsh	occ	ext	sarco	2, 3
Passiflora sexflora Juss.	*			7–9		unk	subsh	occ	ext	sarco	2
PHYTOLACCACEAE											
Phytolacca rivinoides Kunth et Bouche	2	NLD	1–12 DL	2, 6–7, 10, 1	12–2, 5–12, 8–10	sb	subsh	occ	int	sarco	2
Phytolacca rugosa Braun et Bouche	*			11	11–12	sb	subsh	com	int	sarco	2, 3
PIPERACEAE											
Piper aequale Vahl. (SK-145)	6	NLD	7–3 DL	peak 1–7; 12–11	9–1, 2–7	btl	shrub	com	ext	desmo	1
Piper epigynium C. DC.	3	NLD	9–11 DL	2–7	3–7	btl	shrub	com	ext	desmo	3
Piper gibbosum C. DC.	2	NLD	7–9, 12–4	3–6, 3–4, 2–3	7–8, 3–5	btl	shrub	occ	ext	desmo	2
Piper hispidum Swartz	8	NLD	1–12	3–6	6	btl	shrub	occ	ext	desmo	2, 3
Piper phytolaccaefolium Opiz in Presl.	4	NLD	1–12 DL	2–5, 10, 1–2, 3 (DP)	3–7	btl	shrub	occ	ext	desmo	2
Piper poasanum C. DC.	1	NLD	9–11 DL	12	none	btl	shrub	occ	ext	desmo	1
ROSACEAE											
Prunus? (SK-311)	3	NLD	1–12 DL	3–6, 12–3 (US, DP)	1–2, 6, 8, 12–1	gen	shrub	occ	int	sarco	3
RUBIACEAE											
Cephaelis elata Swartz.	4	NLD	1–12 DL	peaks 3, 5–6, 7–9; 3–12	1–5, 6–11	hum	shrub	com	ext	sarco	3
Cephaelis chlorochlamys Standl.	2	NLD	1–12 DL	5–6, 8, 4–9, 11	12–5, 7, 10–11, 9–12	hum	shrub	occ	ext	sarco	3
Chiococca alba (L.) Hitch	*			8–9		sph	treel	unk	mas	sarco	3
Faramea occidentalis (L.) Rich.	10	NLD	peak 2–4; 1–12 (DL)	1–2, 5, 2–3	4–8	gen	shrub	com	int	sarco	1

Faramea talamancarum Standl.	4	NLD	1-12 DL	5-6, 5-7	1, 3-6, 10, 12-6	but	shrub	occ	int	sarco	1, 2
Hamelia patens Jacq.	*			1-12		hum	shrub	com	ext	sarco	1
Hoffmannia areolata Standl.	*			4-5		gen	shrub	occ	ext	sarco	3
Hoffmannia sp. (SK-140)	4	NLD	1-12 DL	4-6, 9, 5-7	12-3, 5, 10-3	gen	shrub	occ	ext	sarco	2, 3
Hoffmannia leucocarpa Standl. (WAH-516)	1	NLD	1-12 DL	5-9, 12-9	3, 6, 9, 5, 10	gen	subsh	occ	int	sarco	2
Hoffmannia viridis Rusby	2	NLD	12-3, 5-10	12, 3, 5-8	12-1, 11-12	gen	shrub	occ	ext	sarco	3
Palicourea galeottiana Martens	5	NLD	1-12 DL	4-8, 1-2	11-5, 7	hum	shrub	com	int	sarco	1, 2, 3
Palicourea grandicarpa Standl. (SK-244)	3	NLD	1-12 DL	11-12, 12-3	none	hum	shrub	occ	int	sarco	3
Palicourea macrosepala Krause (SK-203)	3	NLD	1-12 DL	9, 2-3	3-8, 10	gen	treel	occ	int	sarco	2, 3
Palicourea fine-leaf (SK-98)	5	NLD	1-12 DL	12-6, 1-5	9-10, 6-7	gen	treel	occ	int	sarco	3
Palicourea oblong-blue berry (Willow)	2	NLD	1-12 DL	3, 6-8	12-3, 7-3	gen	shrub	occ	int	sarco	3
Palicourea spear-leaf	3	NLD	1-12 DL	12, 3, 10	3-6, 1-7	gen	treel	rar	int	sarco	3
Palicourea yw-yw (SK-138)	3	NLD	1-12 DL	5-6	9-10, 9-12	hum	shrub	com	ext	sarco	2, 3
Psychotria acuminata Benth. (SK-142)	13	NLD	12-5	peak 5-7; 5-1	12-4, 11-5	gen	shrub	com	int	sarco	1, 2, 3
Psychotria brenesii Standl.	5	NLD	6-3 (DL)	2-6, 9-10, 12-5, 7-3	1-3, 7-11, 3-6	hum	treel	com	int	sarco	3
Psychotria carthagenensis Jacq.	6	NLD	1-12 DL	4-6	12-4, 9-3, 7-8	gen	treel	occ	int	sarco	2, 3
Psychotria gracilis Benth.	5	NLD	1-12 DL	3, 7-8, 6-9	12-4	gen	shrub	com	ext	sarco	3
Psychotria grandistipula Standl.	3	NLD	1-12 DL	6, 8	1-2, 3-5	gen	treel	occ	int	sarco	2
Psychotria horizontalis Sw.	8	NLD	1-12 CL	3-7	10-4	gen	shrub	occ	int	sarco	2, 3
Psychotria jimenezii Standl.	5	NLD	1-12 DL	3-5, 10, 4-7	12-3, 9-12, 2-3	gen	treel	occ	int	sarco	3
Psychotria macrophylla R & P	7	NLD	2-12 DL	12, 4-6, 3	12, 4, 8-11, 9-10	gen	shrub	com	ext	sarco	2, 3
Psychotria microdon (DC) Urban	7	NLD	1-12 DL	6-7	12-5, 9-10	gen	shrub	com	int	sarco	1
Psychotria obtuse-leaf (WAH-)	7	NLD	1-12 DL	12-8, 1-7	12-5, 9-1, 3-6, 9-3	gen	shrub	occ	int	sarco	1
Psychotria prob. sp. nov. (SK-329) J. Dwyer	3	1-12	1-12 DL	5-6, 2-4, 6-9	6-12	gen	shrub	occ	int	sarco	2
Psychotria torresiana Standl.	*			9		gen	shrub	occ	unk	sarco	3
Psychotria uliginosa Sw.	1	NLD	1-12 DL	5-7, 9-11, 1-3	12-1, 10-5, 8-11	gen	subsh	occ	int	sarco	2
Ravnea triflora Oerst.	*			9		hum	subsh	unk	int	sarco	3
Rondeletia buddleoides Benth.	2	NLD	1-12 DL	8, 7-11	1-3	sph	treel	com	mas	sarco	2
Rondeletia torresii Standl.	5	NLD	1-12 CL	12-5, 1-4	6-10, 4-9	sph	treel	com	int	sarco	3
Xerococcus congestus Oerst.	3	NLD	6-9, 12-1, 4	6-7, 4, 9	12-2, 6, 10, 1-3	gen	subsh	com	int	sarco	2, 3
RUTACEAE											
Zanthoxylum procerum Donn. Sm.	2	NLD	2-3, 6-8, 12-2	2-3, 6-8, 12-3	1-5, 10	gen	treel	rar	mas	sarco	3
SABIACEAE											
Meliosma subcordata Standl.	4	NLD	3-8, 5-6	6	1-10, 4-5	wsp	treel	occ	mas	sarco	2

Appendix – *continued*

Species name/authority/ voucher number	No. of indivs	Leaf drop	Leaf flush	Flowering	Fruiting	Poll. type	Indiv. size	Pop. size	Flower pattern	Fruit type	Forest type(s)
SIMAROUBACEAE											
Picramnea carpenterae Polak.	9	NLD	1-12 DL	3, 5, 8, 10, 12-1, 4-5, 10-1	12-5, 10, 2	sb	shrub	com	ext	sarco	1
Picramnea latifolia Tulasne	6	4-12	1-12 DL	1-2. 6-8, 10-12, 5-11	12, 9-12, 10-1	sb	shrub	occ	ext	sarco	2, 3
SOLANACEAE											
Cestrum button-berry (WAH 52, 53, 54, 55)	5	9	1-12 DL	1, 3-5, 12-2, 4	12-2, 6, 11	set	shrub	occ	int	sarco	2, 3
Cestrum megalophyllum Dun. in DC.	2	NLD	2-3, 7-8, 11, 2-6 (DL)	10, 2-3	none	set	shrub	occ	int	sarco	2, 3
Cestrum racemosum R. & P.	6	NLD	12-8 DL	12-3; peaks 9, 1, 3	4-5, 6-10	set	shrub	com	int	sarco	1, 2, 3
Solanum arboreum H. &. B. *ex* Dun.	3	NLD	1-12	4	none	sb	shrub	com	int	sarco	2
Solanum cordovense Sesse & Moc.	3	NLD	1-12 DL	12-4, 9, 11-2, 4-6, 8-9, 12-3	4-5, 12-6, 3	sb	shrub	occ	int	sarco	1
Solanum sp. (WAH-10-111)	4	1-12	1-12	3-5	12-1, 4, 8-10, 3, 7, 9	sb	shrub	occ	int	sarco	2, 3
Solanum sp. (WAH 56-60)	7	NLD	1-12	6-8, 4-10	11	sb	shrub	occ	int	sarco	2
Solanum pertenue Standl. & Mort.	4	NLD	12-7, 1-2, 10, 2-3	2-5, 4-5, 3-5	none	sb	shrub	occ	int	sarco	3
Solanum sp. (WAH-34-36)	8	9	12-4, 6-7	4, 6, 10, 4-7, 3	10, 6-7	sb	shrub	occ	int	sarco	1
Solanum ramonense Mort. & Standl. (WAH-103-105)	10	NLD	1-12 DL	12-3, 9-2, 7-3	5, 12	sb	shrub	occ	int	sarco	2, 3
Witheringia riparia Kunth in H. & B.	7	NLD	1-12 DL	12-3, 9-3	10, 12, 5	set	shrub	com	ext	sarco	2, 3
Witheringia solanacea L. Her.	1	NLD	3-6, 10	1, 4-7, 10-1, 5-6, 11	12, 7-9, 12-1, 3-10	sb	shrub	com	int	sarco	2
URTICACEAE											
Pilea pittieri Killip	*			4		unk	subsh	com	int	sclero	2, 3