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Plant Phenology in a Cloud Forest on the Island of Maui, Hawaii¹

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ABSTRACT

We recorded the times of flowering, fruiting, and leafing for ten native canopy and subcanopy trees and shrubs (monthly from December 1994 through December 1997) in a montane cloud forest with relatively aseasonal rainfall on the island of Maui, Hawaii. These species represented the great majority of individual woody plants at the site. Flowers and fruits were available in the community year-round; however, all species exhibited annual patterns of flowering, and four species showed annual patterns of fruiting while the rest fruited in supra-annual patterns. Many species had protracted flowering or fruiting peaks, and some bore small numbers of flowers or fruit year-round. Most species flowered in a monthly peak mainly between May and August, corresponding to the period of greatest solar irradiance and marginally higher temperatures. Fruit ripening followed at varying intervals. In contrast, the heaviest flowering occurred between November and March, resulting from bloom of the dominant tree, *Metrosideros polymorpha*. At the highest elevations, *Metrosideros* flowering was heaviest during September, but peak flowering of lower elevation trees occurred in late fall and winter. Two forms of this species differed in their temporal and spatial patterns of flowering. For *M. polymorpha* var. *polymorpha* and var. *incana*, bloom peaked annually between November and January; however, for *M. polymorpha* var. *glaberrima*, flowering peaked from April through July, with an earlier secondary peak in January.

Key words: cloud forest; flowering seasonality; Hawaii; Hawaiian Honeycreeper; Maui; *Metrosideros polymorpha*; *Ohia*; phenology.

THE SEASONAL RHYTHMS OF FLOWERING, FRUITING, LEAFFALL, AND VEGETATIVE FLUSH in tropical forest plants often are associated with seasonal patterns in climate, or the interaction with animal pollinators and seed dispersers (Snow 1966, Frankie *et al.* 1974, Croat 1975, Opler *et al.* 1976, Stiles 1978, Foster 1982, Augspurger 1982, Rathcke & Lacey 1985, van Schaik *et al.* 1993, Wright 1996). Solar irradiance and rainfall appear to be the main seasonal, abiotic variables influencing phenology of tropical plants (Wright & van Schaik 1994, Wright 1996). For example, most tropical plants produce leaf flush and flowers during peaks in irradiance, except when water stress prevents this, and ripen fruits during the end of the dry or in the rainy season to reduce seedling mortality (Janzen 1967, Smythe 1970, Frankie *et al.* 1974, Croat 1975,

Foster 1982, van Schaik *et al.* 1993). Flowering and fruiting peaks in the tropics, where climate is relatively aseasonal and animal pollinators and seed dispersers are present year-round, are less pronounced overall and may occur multiple times or continually throughout the year (Putz 1979, Hilty 1980, Opler *et al.* 1980, Koptur *et al.* 1988; Newstrom, Frankie, Baker, and Colwell 1994). Our study site on Maui was characteristic of the latter scenario, with a perennially wet climate in which rainfall exceeded that of many tropical forests and the major bird pollinators were available year-round. Nevertheless, in Hawaiian rain forests, flowering and fruiting of many native trees and shrubs do show seasonal patterns, and these may vary along elevational gradients (Baldwin 1953, Porter 1973, Bridges *et al.* 1981).

We present phenological patterns over three years for the most abundant native trees and shrubs from a montane cloud forest with relatively aseasonal rainfall on the windward slope of Maui island, Hawaii. We attempt to explain the temporal abundance of flowers, especially in reference to the ecology of nectarivorous Hawaiian Honeycreepers (the main focus of our project; Berlin *et al.* in press). We compare results from our site with other

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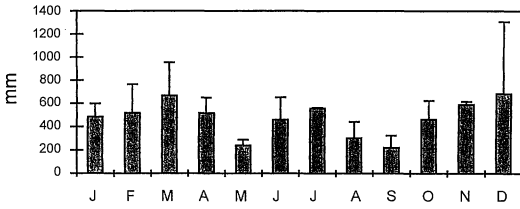


FIGURE 1. Mean monthly rainfall (mm) \pm SE from 2100 m elevation in the Hanawi Natural Area Reserve, Maui, Hawaii.

sites, although few other studies have addressed the phenology of tropical forests with aseasonal rainfall, and no others have reported the phenology of an aseasonally rainy cloud forest.

METHODS

STUDY AREA AND CLIMATE.—The study site was located in a montane cloud forest on steep, dissected, north-facing terrain between the east and west forks of Hanawi Stream at 1567 to 2128 m elevation on the windward slope of Haleakala Volcano on east Maui, Hawaii (20°45'N, 156°8'W; Jacobi 1989, Wagner *et al.* 1990). Lying within the Hanawi Natural Area Reserve, the site is protected from damage by feral ungulates and incursion by non-native weeds. The large tree Ohia lehua (*Metrosideros polymorpha*, Myrtaceae) dominates a native woody flora of low diversity.

The cloud forest physiognomy results from a climate characterized by frequent mist, heavy rainfall, wind, and cool to moderate temperatures throughout the year. Northeasterly tradewinds prevail, although occasional storms from the south bring downpours and wind more commonly between October and April. A tradewind inversion prevents upslope movement of clouds above *ca* 2000 m elevation. Two standard rain gauges in a forest opening at 1700 m elevation and at treeline (2115 m) measured annual average rainfalls of 5154 and 5114 mm, respectively, during the three-year study. Precipitation was not seasonal, although monthly and year-to-year fluctuations were high (Fig. 1). Highest monthly rainfall averages occurred in March and December, and lowest rainfall in May and September. The average monthly precipitation never fell below 200 mm, indicating perennially moist soil conditions, except during rare, brief droughts. Nighttime frost developed, especially from November through March, in grassy meadows near timberline at the upper elevational limit of our study site, but not in the forest. A few

kilometers to the east at Horseshoe Puu (1960 m) a meteorological station of the HaleNet II system in an environment similar to our site measured mean air temperatures as coolest from December through April and warmest from July through October, ranging monthly from 9.90 to 13.37°C (Loope & Giambelluca 1998, pers. comm.). At this station, average monthly solar radiation (W/m^2) peaked from May to August, with the maximum June value 71 percent greater than the November minimum (L. Loope & T. Giambelluca, pers. comm.). Thus, fluctuations in temperature and solar radiation at our site followed northern temperate seasonality, although with less amplitude. Consequently, we use the terms winter, spring, summer, and fall to refer to the north temperate seasons December–February, March–May, June–August, and September–November, respectively.

PLANT PHENOLOGY.—We selected ten native species that were the most abundant woody plants in the community and which constituted the vast majority of tree and shrub individuals at our study site. Native Hawaiian Honeycreepers exploited the flowers of all species for nectar. We also monitored a few individuals of rare native lobelias (Campanulaceae) and mints (Lamiaceae) important to birds, but will report those data separately (Pacific Island Ecosystems Science Center [PIERC] unpubl. data).

We established four transects along an elevational gradient from 1560 to 2125 m elevation, which ran parallel along ridges to avoid difficult terrain off the ridge trails. Along each transect, we established ten stations at 150-m intervals. Phenological data were taken on tagged individuals at each station. We selected *Metrosideros* based on lateral visibility of the canopy from the ground. Shrubs and subcanopy trees were visible from all sides and were selected based on the criteria of being: (1) of minimum size large enough to flower or fruit; (2) closest to the station; and (3) off the trail to avoid trampling. All species were represented on all four transects and across elevations. Two *Metrosideros* individuals were represented at all stations because of the species' dominant presence and importance to nectarivorous Hawaiian Honeycreepers (Berlin *et al.* in press). Two forms of the taxonomically complex *M. polymorpha* were present: the predominant and pubescent *M. polymorpha* varieties *polymorpha* and *incana* and the much rarer glabrous *M. polymorpha* var. *glaberrima*. We refer to these as pubescent and glabrous forms. In August 1995, we added an additional 13 individ-

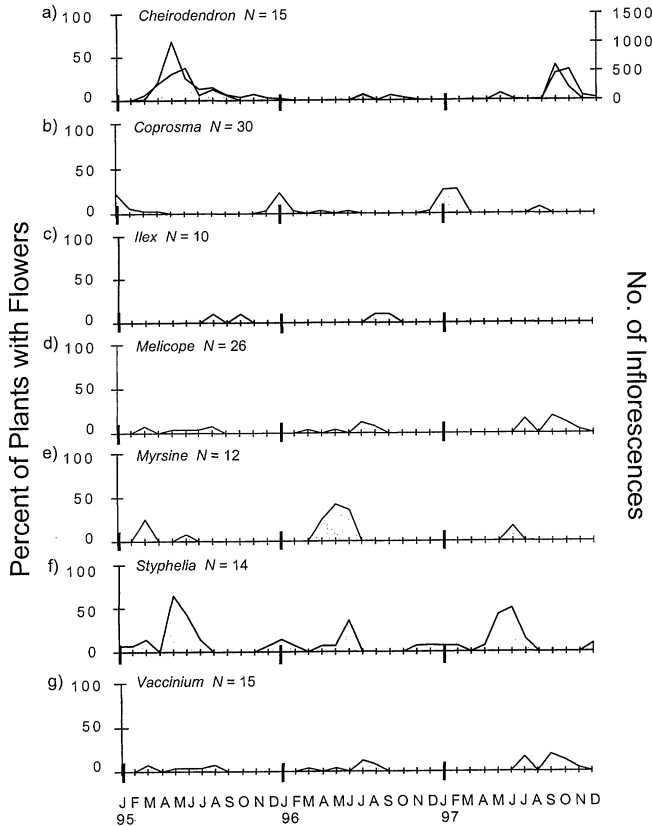


FIGURE 2. Monthly percentage of plants in good flower condition (categories 3–5, *i.e.*, >25% stems with flowers; area graph), and total number of flowers recorded (line graph) for: (a) *Cheirodendron trigynum*, (b) *Coprosma ochracea*, (c) *Ilex anomala*, (d) *Melicope clusiifolia*, (e) *Myrsine lessertiana*, (f) *Styphelia tameiameia*, and (g) *Vaccinium calycinum*.

uals of *glaberrima* to boost the sample size of this variety to 23.

We took data on the phenology of these individual plants during the first or second week of every month from December 1994 to December 1997. With the aid of binoculars, we counted or estimated the number of flowers, ripening fruits, and ripe fruits, examined leaf production and condition, and estimated the percentage of stems with flowers, ripening fruits, and ripe fruits for 275 tagged individuals. The parameters recorded for each species varied depending upon its morphology. We counted inflorescences (referred to as “flowers”) for *M. polymorpha*, *Broussaisia arguta* (Hydrangeaceae), and *Cheirodendron trigynum* (Araliaceae) and flowers for *Rubus hawaiiensis* (Rosaceae). For *Coprosma ochracea* (Rubiaceae), *Ilex anomala* (Aquifoliaceae), *Melicope clusiifolia* (Rutaceae), *Myrsine lessertiana* (Myrsinaceae), *Styphelia tameiameia* (Epacridaceae), and *Vaccinium calycinum*

(Ericaceae), we estimated the percentage of stems with flowers, unripe fruit, and ripe fruit by categories (0 = none, 1 = 1–5 percent, 2 = 6–25 percent, 3 = 26–50 percent, 4 = 51–75 percent, and 5 = 76–100 percent). We also counted or estimated the number of unripe fruit and ripe fruit for *B. arguta*, *C. trigynum*, *R. hawaiiensis*, and *S. tameiameia*. For *C. ochracea*, *I. anomala*, *M. lessertiana*, and *V. calycinum*, we counted or estimated only ripe fruit. For leafing activity of the two deciduous species, *R. hawaiiensis* and *V. calycinum*, we recorded plants as having leaves flush, vegetated, dying, or none.

We followed the classification for phenological patterns by Newstrom, Frankie, and Baker (1994): **continual** (flowering with sporadic brief breaks); **sub-annual** (flowering in more than one cycle per year); **annual** (only one major cycle per year); and **supra-annual** (one cycle over more than one year). Patterns for all species were summarized graphically

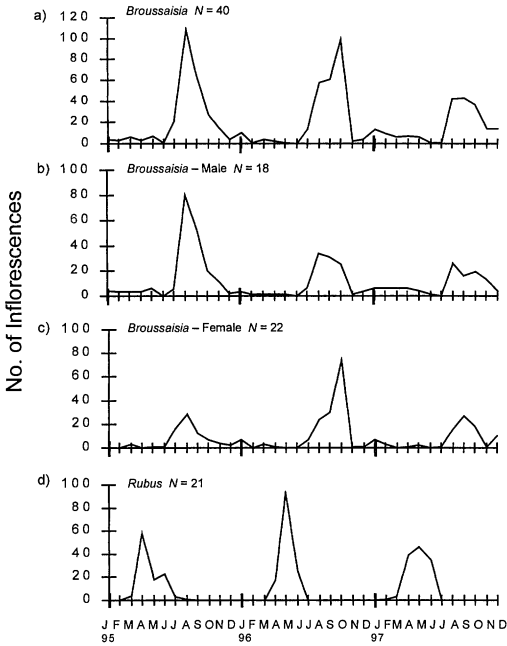


FIGURE 3. Monthly total number of flowers for: (a) *Broussaisia arguta*, (b) *Broussaisia arguta* (male), (c) *Broussaisia arguta* (female), and (d) *Rubus hawaiiensis*.

by month showing the total number of flowers and fruits, or the percentage of individuals in heavy flowering or fruiting condition (categories 3–5).

Our statistical analyses were restricted to *M. polymorpha*, the principal source of nectar for native birds (Berlin *et al.* in press). The yearly flowering cycle of *M. polymorpha* began in August and ended in July. *M. polymorpha* data were analyzed using ANOVA (SAS 1987) to compare variation in flower abundance (1) among months, (2) among the three calendar years, (3) along an elevational gradient, and (4) between pubescent and glabrous forms of *M. polymorpha*. To include elevation of the stations as a factor in the analyses, we categorized elevation into three levels: low (1567–1733 m, *N* = 12 stations, mean elevation = 1659 m); medium (1750–2030 m, *N* = 20 stations, \bar{x} = 1897 m), and high (2044–2128 m, *N* = 8 stations, \bar{x} = 2092). We performed three-way and four-way repeated measures ANOVAs using the mixed-models procedure in SAS (version 6.12, PROC MIXED). The 40 stations were considered the random subject factor nested within elevation categories (Littell *et al.* 1996). For the three-way design, the main effects were elevation category, month, and year, along with the various two-way

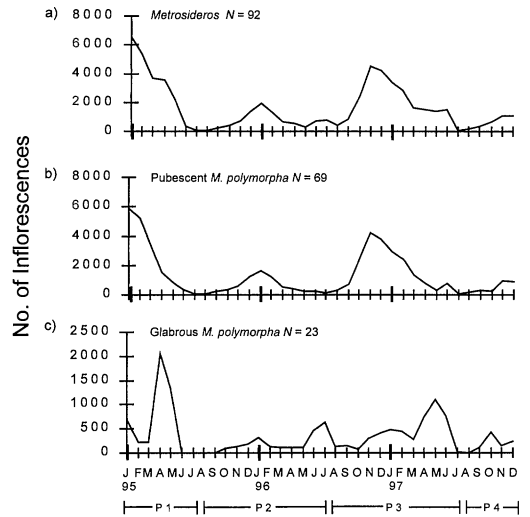


FIGURE 4. Monthly total number of flowers for: (a) *Metrosideros polymorpha* and two forms, (b) pubescent and (c) glabrous. Annual August to July flowering periods, P1–P4.

and three-way interactions of these variables. In the four-way design, the two forms of *M. polymorpha*, pubescent and glabrous, were added to the analysis as another main effect variable (form), along with the associated interactions of form with elevation category, month, and year. We assumed a compound symmetry, homogeneous variance model for the variance–covariance structure of the repeated measures (Littell *et al.* 1996). The dependent variable was the average number of inflorescences counted per tree at each station during a given visit, averaged over all trees at each station for the three-

TABLE 1. Flowering patterns of *Metrosideros polymorpha* trees. The common, annual pattern of flowering peaked in winter months from November to February. Annual asynchronous trees peaked between April and July. Some trees produced no or too few flowers for meaningful evaluation and could not be classified. *N* = number of trees.

Pattern	All trees (%) <i>N</i> = 92	Pubescent (%) <i>N</i> = 69	Glabrous (%) <i>N</i> = 23
Annual—synchronous	65	77	30
Annual—asynchronous	7	0	26
Sub-annual	5	4	9
Supra-annual	13	9	26
Continual	5	6	4
Too few flowers to classify	5	4	5

TABLE 2. ANOVA table for three-way and four-way repeated measures analyses, comparing the average abundance of inflorescences of *Metrosideros polymorpha* among elevation categories, months, and years (three-way design), and these factors along with form (pubescent and glabrous; four-way design).

Term	df	F	P
Three-way design:			
Month	11, 1293	13.89	<0.0001
Year	2, 1293	8.33	0.0003
Elevation	2, 37	1.27	0.2919
Month * Year	22, 1293	7.15	<0.0001
Month * Elevation	22, 1293	2.30	0.0006
Year * Elevation	4, 1293	2.19	0.0685
Month * Year * Elevation	44, 1293	1.36	0.0589
Four-way design:			
Month	11, 1639	6.85	<0.0001
Year	2, 1639	5.04	0.0066
Elevation	2, 37	2.42	0.1032
Month * Year	22, 1639	8.05	<0.0001
Month * Elevation	22, 1639	5.13	<0.0001
Year * Elevation	4, 1639	4.26	0.0020
Month * Year * Elevation	44, 1639	4.27	<0.0001
Form	1, 1639	0.37	0.5446
Month * Form	11, 1639	9.27	<0.0001
Year * Form	2, 1639	1.44	0.2376
Elevation * Form	2, 1639	4.38	0.0127
Month * Year * Form	22, 1639	6.38	<0.0001
Month * Elevation * Form	22, 1639	3.47	<0.0001
Year * Elevation * Form	4, 1639	4.88	0.0007
Month * Year * Elevation * Form	36, 1639	3.48	<0.0001

way ANOVA, and averaged separately for each of the two forms of *M. polymorpha* for the four-way ANOVA. Missing values occurred occasionally because trees were not visible due to weather conditions during a particular visit, resulting in two stations having no *M. polymorpha* data in one month for each station and a total sample size of 1438 observations instead of 1440 in the three-way ANOVA. The four-way ANOVA had more missing values, due primarily to stations with only one form of *M. polymorpha* present, but the theory on which PROC MIXED is based is relatively unaffected by missing values; thus conclusions are robust regarding these issues (Littell *et al.* 1996).

RESULTS

PATTERNS OF FLOWERING.—Annual flowering patterns were exhibited at the population level by all species (Figs. 2–4), except possibly for *I. anomala* and *M. clusiifolia*, which had low levels of flowering (categories 1 and 2; not shown in Fig. 2) and a continual flowering pattern throughout the year. Several species that had annual flowering patterns produced flowers year-round at low levels (*e.g.*, *B. arguta* [Fig. 3] and both forms of *M. polymorpha*

[Fig. 4]). For some species, there was moderate to high variation in year-to-year abundance (*e.g.*, *C. trigynum* and *M. polymorpha*) and in the timing of peak bloom (*e.g.*, *V. calycinum*).

Most species exhibited annual peaks distributed over several months (Figs. 2–4); however, during the May through August period of increased temperatures and solar irradiance, significantly more annual flowering peaks occurred (18 of 32 peaks compared to an expected value of 10.7 if flowering peaks had been distributed randomly throughout the year; $\chi^2 = 7.56$, $P = 0.006$). These calculations treat pubescent and glabrous *M. polymorpha* as separate populations. Flowering for *C. ochracea* and pubescent *M. polymorpha* peaked between November and February during most years, coinciding with the wettest, coolest months, which had the least solar irradiance. *B. arguta* flowering peaked somewhat later than the rest of the community (Fig. 3). *B. arguta*, a dioecious subcanopy shrub, did not display the gender differences in its flowering pattern or duration that are found in some other tropical species (Bullock 1982, Bullock *et al.* 1983, Newstrom, Frankie, & Baker 1994).

METROSIDEROS FLOWERING.—Sixty-five percent of

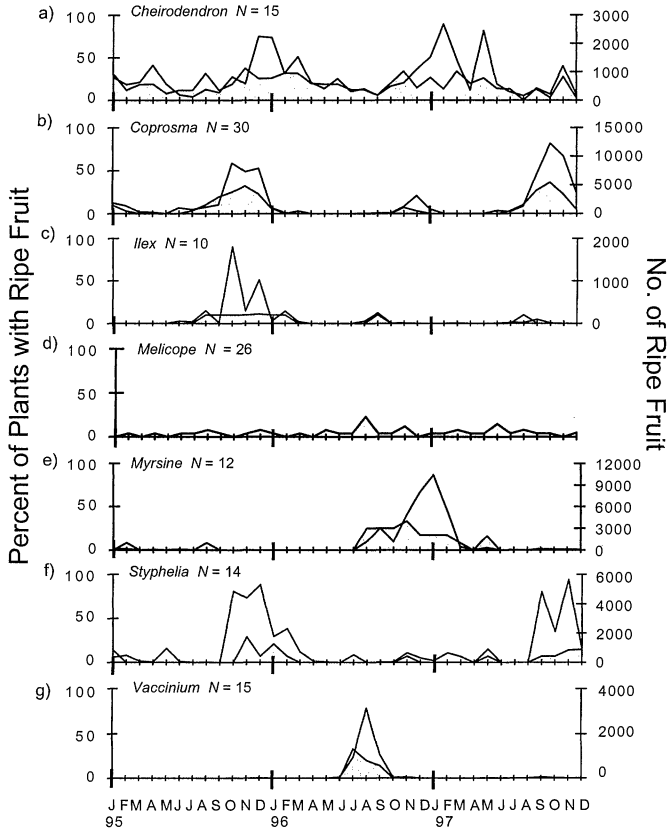


FIGURE 5. Monthly percentage of plants with ripe fruit (categories 3–5, *i.e.*, >25% stems with ripe fruit; area graph), and total number of ripe fruit recorded (line graph) for: (a) *Cheirodendron triginum*, (b) *Coprosma ochracea*, (c) *Ilex anomala*, (d) *Melicope clusiiifolia*, (e) *Myrsine lessertiana*, (f) *Styphelia tameiameia*, and (g) *Vaccinium calycinum*.

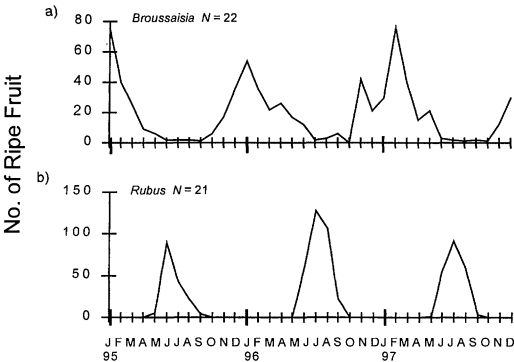


FIGURE 6. Monthly total number of ripe fruit for: (a) *Broussaisia arguta* and (b) *Rubus hawaiiensis*.

the *M. polymorpha* sampled (with pubescent and glabrous forms pooled) followed an annual flowering pattern (Table 1, annual synchronous; Fig. 4, periods P1–P4). Production of inflorescences increased gradually beginning in August, peaked between November and January, and tapered off toward July (Fig. 4a). Thus, mean flower abundance varied significantly over the 12 months each year (Table 2; three-way repeated measures ANOVA: $P < 0.0001$). Flower abundance also varied among years (Table 2; $P = 0.0003$), with the highest yield produced in 1995 ($\bar{x} = 26.06$) and the lowest abundance in 1997 ($\bar{x} = 14.33$ flowers/tree; Fig. 4a).

Although there were no significant differences among the elevation categories (Table 2; $P = 0.2919$), our data showed a significant interaction of month and elevation category (Table 2; $P = 0.0006$), because flowers were more abundant at higher elevations in fall and at lower elevations in

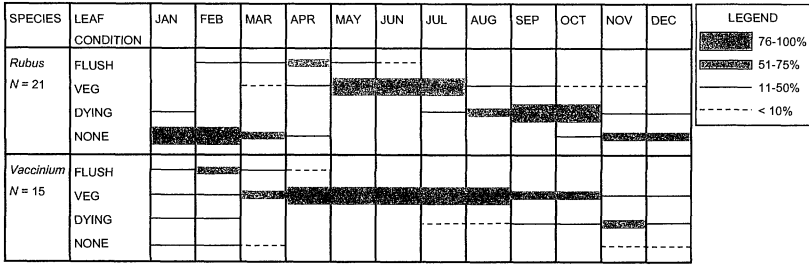


FIGURE 7. Average monthly percentage of leaves (in flush, vegetated, dying, and none) for *Rubus hawaiensis* and *Vaccinium calycinum*.

winter. In spring months, the distribution across elevations was more uniform. In summer, flowers were less abundant overall and found mostly at lower elevations. The summer bloom, however, was primarily from glabrous *M. polymorpha*.

Mean abundance of flowers between the two forms of *M. polymorpha* was not significantly different (Table 2; four-way repeated measures ANOVA: $P = 0.5446$), but there were significant two-way, three-way, and four-way interactions with month, year, and elevation category (Table 2). This implies that the two forms of *M. polymorpha* bloom in different months at different elevations. Pubescent *M. polymorpha* flowered annually (Fig. 4b), peaking in fall and winter, and because of its relative abundance, determined the overall pattern for the species (Fig. 4a; three-way ANOVA). The less abundant glabrous *M. polymorpha* produced an apparently bimodal distribution with a low peak from November through January and a high peak from April through June (Fig. 4c). At the form level, all annually flowering pubescent *M. polymorpha* trees peaked synchronously. Thirty-five percent of glabrous *M. polymorpha* flowered synchronously with peak bloom of pubescent *M. polymorpha*; another 35 percent of glabrous trees peaked between April and June; and finally, 13 percent flowered in both periods, either within or among years. The glabrous form also had a higher percentage of supra-annual flowering trees. These patterns undoubtedly resulted in the very significant higher-order interactions of the four-way ANOVA.

PATTERNS OF FRUITING.—Annual fruiting patterns were exhibited in four species: *B. arguta*, *C. trigynum*, *C. ochracea*, and *R. hawaiensis* (Figs. 5–6). The other species showed supra-annual patterns, with one or two years of major fruit production during the three-year study (Figs. 5–6). Many species had fruit available year-round at low levels (e.g., *B. ar-*

guta, *C. trigynum*, *C. ochracea*, *I. anomala*, *M. clusifolia*, and *S. tameiameiae*), mainly because of variance in fruiting times among individuals. In some species (e.g., *C. trigynum*, *I. anomala*, and *M. lesertiana*), the percentage of plants in ripe fruit did not correspond to the number of fruit counted, because a few individuals produced the peak in fruit numbers. In addition, fruiting patterns may differ from what we recorded for *M. clusifolia*, because this species bears capsules that dehisce to display seeds that are difficult to count. During the May–August period of increased temperatures and solar irradiance, fruit ripening did not peak for the community of species sampled. Thirteen of 28 annual peaks of ripening occurred during this period compared to the 9.3 peaks expected if fruit ripening had been distributed randomly among months ($\chi^2 = 2.16$, $P = 0.1415$). While two species bore ripe fruit mostly during the May–August period, all others produced ripe fruit later, mainly from September to February.

PATTERNS OF LEAFING.—The community maintained an evergreen appearance throughout the year with only two deciduous species, *R. hawaiensis* and *V. calycinum*, losing leaves on an annual basis (Fig. 7). For both species, leaves flushed, grew, then fell, as temperature and solar irradiance increased, peaked, then decreased, respectively.

DISCUSSION

OVERALL PATTERNS.—Seasonal patterns of flowering and fruiting events were found among all species in the community, although some species bore small numbers of flowers or fruit year-round. Some species had protracted flowering peaks that extended for many months, as has been shown for woody plants in aseasonal environments and understory species (Rathcke & Lacey 1985), and as docu-

mented for cloud forest shrubs and treelets in Costa Rica (Koptur *et al.* 1988). For the flora overall, flowering was more synchronized than fruiting. Excluding, for the time being, the critically important pubescent varieties of *M. polymorpha*, flowering peaks for the majority of species corresponded to the period of greatest solar irradiance and marginally higher temperatures from May through August, while peaks of fruiting followed at varying intervals. Comparable studies in aseasonally rainy, high elevation cloud forests are lacking (*c.f.* Koptur *et al.* 1988 for a seasonally rainy cloud forest). Phenology of the majority of species at our Maui site, however, showed the seasonality expected for perennially wet tropical sites at lower elevations (van Schaik *et al.* 1993). Contrary to the expected seasonality, overall flower availability to birds peaked from November to March, because of the abundant *Metrosideros* bloom.

FLOWERING OF *METROSIDEROS* VARIETIES.—As the largest and most abundant tree at our site, flowering *M. polymorpha* in all months received the heaviest visitation by nectarivorous Hawaiian Honeycreepers (Berlin *et al.* in press). Yet contrary to phenological trends within the flora and with related glabrous *M. polymorpha*, the predominating pubescent varieties of *M. polymorpha* flowered most abundantly when irradiance and temperature were lowest and average monthly precipitation was highest. The flowering phenologies we observed for pubescent versus glabrous forms of *M. polymorpha* are difficult to compare to other studies of this species because of differences among sites in climate, elevation, and substrate. Nevertheless, these previous studies demonstrated wide variance in site-specific timing of flowering peaks (Baldwin 1953, Porter 1973, Ralph & Fancy 1994) and differences in flowering peaks between pubescent and glabrous forms, with glabrous forms flowering later and longer on average (Porter 1973). Two sites are most directly comparable to ours in their environments and overlapping, although somewhat lower, elevations. Keauhou on Hawaii island (Ralph & Fancy 1994) and Waikamoi on Maui (VanGelder & Smith in press) showed peak flowering from February through August, roughly four to five months later than our site and when irradiance and temperature were greatest. While pubescent *M. polymorpha* dominated the Keauhou site, they were apparently absent at the Waikamoi site (K. Kitayama, pers. comm.), where glabrous trees accounted for a later flowering peak as in our study. Determining what ultimate and proximate factors caused the

dominant tree at our site to bloom at presumably the least favorable time of year awaits further study. Future research also should investigate if the synchronized annual pattern of pubescent *M. polymorpha* allows for reproductive isolation from glabrous varieties, and why flowering among glabrous *M. polymorpha* is less synchronized.

HAWAIIAN HONEYCREEPERS AND FLOWER PHENOLOGY.—Hawaiian Honeycreepers are important pollinators of forest plants (Carpenter & MacMillen 1980); in cloud forest at our Maui site, they foraged at most species of flowers (Berlin *et al.* in press). Two Hawaiian Honeycreepers, Apapane (*Himatione sanguinea*) and Iwi (*Vestiaria coccinea*), make daily long-distance foraging flights and seasonal, elevational migrations on the island of Hawaii in response to fluctuations in bloom (Baldwin 1953, MacMillen & Carpenter 1980, Ralph & Fancy 1995). We documented the egress of Honeycreepers from our site in July, when pubescent *M. polymorpha* and other bloom reached their nadir (Berlin *et al.* in press). These observations recall seasonal movement by nectarivorous birds along elevational gradients in other tropical regions (Stiles 1985, Stiles 1988). The delayed flowering of glabrous versus pubescent *M. polymorpha* may have implications for nectarivorous birds that rely heavily upon this important food source, since the glabrous variety blooms when flowers in the high-elevation community overall are not plentiful. With glabrous *M. polymorpha* more abundant below 1800 m, Honeycreepers from higher elevations may follow this food source downslope. For nectarivorous Honeycreepers, the low point of *M. polymorpha* flowering was bridged each year by flowers of several other species: *S. tameiameia* and *R. hawaiiensis* from April to June; and *B. arguta* from August to October. Evidence, however, is equivocal for the selection of staggered flowering times among plant species sharing the same pollinators (Stiles 1978, van Schaik *et al.* 1993).

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