NOTE:

Table 2 of P. D. Heideman's paper 'Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest' (*Journal of Ecology* (1989), **77**, 1072) was incorrectly reproduced without error bars. The correct version is shown below. The publishers apologize to Dr Heideman for this error.
    THE CORRECT VERSION HAS BEEN INSERTED IN THE TEXT.

TEMPORAL AND SPATIAL VARIATION IN THE PHENOLOGY OF FLOWERING AND FRUITING IN A TROPICAL RAINFOREST

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SUMMARY

(1) The phenology of flowering and fruiting of forest plants was studied at the community level for one year and three months in submontane rainforest on Negros Island in the Central Philippines.

(2) Temporal variation in the percentage of plants in flower or fruit was generally less than twofold. Temporal variation in abundance of flowers or fruits was higher, up to fourfold among some months. A new statistical test for comparing proportional phenological data is described.

(3) A peak in flowering during the dry season and early part of the wet season was statistically significant; this was due to temporal variation in flowering patterns of trees and palms, but not vines. A minor peak in fruiting during the first half of the wet season was not statistically significant. The long-term relationship of rainfall to phenological patterns remains uncertain.

(4) Limited comparisons were possible between the two months sampled in both 1983 and 1984. Both flowering and fruiting levels were reduced by one-half in these months in 1984 compared to the same months in 1983, indicating a difference between years in either the timing or magnitude of peaks.

(5) Peaks in numbers and an index of volume of flowers or fruit corresponded roughly to peaks in the proportion of plants in flower or fruit, but at some times the proportion of plants flowering or fruiting was a poor predictor of abundance.

(6) One of three understorey plots was significantly different from the others, with ten-fold differences in proportion of plants flowering or fruiting, and up to 100-fold differences in abundance or volume of flowers or fruits. Lower plant density, markedly different edaphic conditions at one plot and/or differential response to drought may account for these differences.

(7) Some large temporal differences in flowering and fruiting were not statistically significant, and larger sample sizes would have been necessary to determine if those differences were real. This highlights the importance of statistical treatment of data and of a concern for sample size in studies such as this.

INTRODUCTION

Food resource quality and abundance strongly affect the life histories of tropical animals (Smythe, Glanz & Leigh 1982; Worthington 1982; Dinerstein 1983; Terborgh 1983). For animals that depend upon flowers or fruits, the timing of periods of high metabolic demand may be strongly influenced by temporal variation in flowering and fruiting of the plant community. In some tropical environments, patterns of flowering and fruiting are clearly correlated with annual variation in temperature or rainfall (Janzen 1967; Smythe 1970; Frankie, Baker & Opler 1974a; Humphrey & Bonaccorso 1979; Raemaekers,

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Aldrich-Blake & Payne 1980; Foster 1982a, 1985). The relationship between climate and plant reproduction is variable in less seasonal climates, however, with different authors emphasizing seasonal components (Baker & Baker 1936; Medway 1972; Leighton & Leighton 1983), aseasonal components (Putz 1979; Opler, Frankie & Baker 1980; Wong 1983), both (Start 1974; Croat 1975; Hilty 1980), or neither (Yap 1982). Interpretation has been hampered by difficulties in adequate statistical testing of phenological data; peaks in flowering or fruiting have usually been identified by eye, without statistical tests of significance. In addition, the relationship between peaks in the number of flowering or fruiting individuals and the quantity of flowers or fruits available is often unclear. Perhaps equally troubling, the extent of microgeographic variation in abundance is generally unknown, despite the high microgeographic variation in species composition and abundance typical of many rainforests (e.g. Hubbell 1979; Whitmore 1984). Because of these problems, the sample size necessary for the documentation of meaningful community patterns is usually unclear (discussed by Frankie, Baker & Opler 1974b).

In this paper, some of these problems are addressed for flower and fruit abundance in six categories of forest plants in a weakly seasonal climate in a submontane forest in the mountains of southern Negros Island, Philippines, using a variety of statistical tests, including a new method for comparing proportional data from two sets of months. The specific questions are: (i) Is there a community-wide pattern of temporal variation in flower and fruit abundance? (ii) How great are the differences among survey areas at the study site? (iii) Do different growth forms of plants (e.g. understorey and canopy forms— trees, vines and palms) have different temporal patterns of flowering and fruiting? Much of the variation is discussed in relation to the wet and dry seasons, but it is important to recognize that the sampling period was much too short to establish long-term phenological patterns or their relationship to rainfall patterns; the focus is on short-term temporal variation and on microgeographic variation. The data on the timing of flowering and fruiting were gathered in two years, with monthly sampling in the first year and samples from three months in the second.

METHODS

The forest and the study plots

The study was conducted in a 302-ha valley at 830–1100 m elevation surrounding Lake Balinsasayao in the mountains of southern Negros Island, Philippines (9°22′N, 123°11′E) (Fig. 1). There were two distinct primary forest vegetation types within the valley, the first occurring over the ridge system that made up most of the valley and the second found only on the slopes of Mt Guintabon on the east side of the lake (Fig. 1). The ridge system included about 85% of the valley, and Mt Guintabon made up the remainder. The vegetation of the first, more abundant type was submontane dipterocarp forest, with the ridgetops grading into oak/laurel forest. The canopy was at 18–30 m, with emergents to 60 m. When the site was sampled by Antone (1983), the dominant tree species (dbh > 10 cm) in primary forest plots in this first area were *Shorea polysperma* (Blanco) Merrill (Dipterocarpaceae) (19%), *Agathis dammara* (Lamb.) L. C. Rich. (Araucariaceae) (14%), *Cinnamomum mercadoi* Vid. (Lauraceae) (11%), *Canarium asperum* Benth. (Burseraceae) (8%), and *Syzygium nitidum* Benth. (Myrtaceae) (6%). Trees in the families Alangiaceae, Myrsinaceae, Anacardiaceae, Euphorbiaceae, Guttiferae, Lauraceae, Meliaceae, Mora- ceae and Sapotaceae were also prominent canopy and subcanopy trees; oaks (Fagaceae) were present but rare. There were approximately twenty-seven species of *Ficus* within the
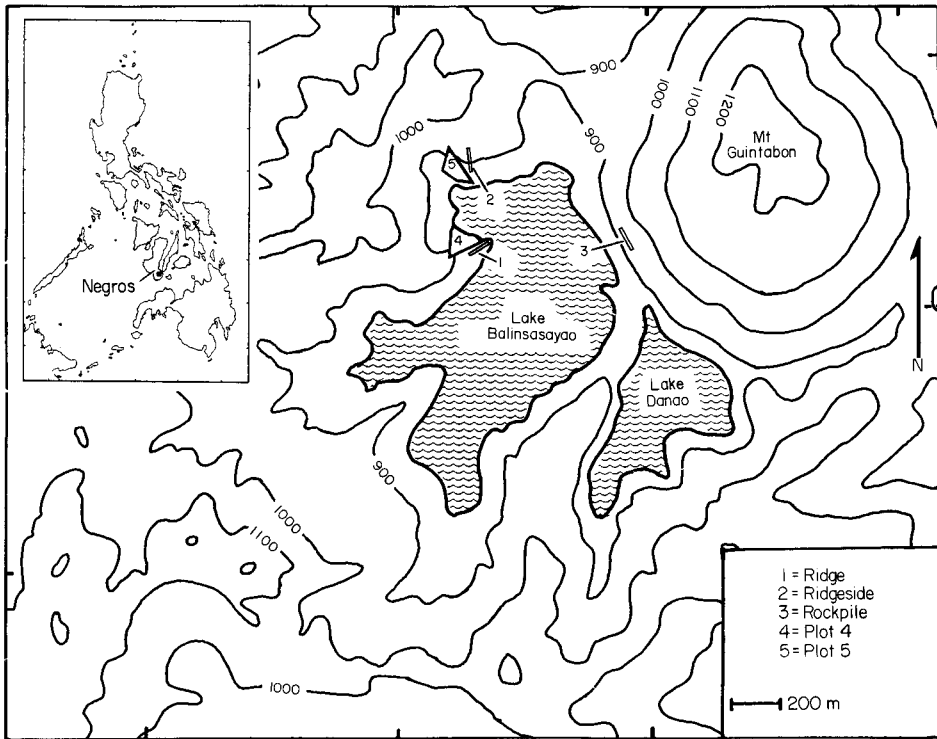
FIG. 1. Map of the study area, the Lake Balinsasayao watershed, southern Negros Island,
Philippines, with the locations of survey plots marked. The inset shows a map of the Philippines
with a circle marking the location of the study site on Negros Island.

area (Utzurrum 1984), growing as vines, shrubs and free or strangling trees, including
some prominent emergent trees. Four species of non-spiny palms were prominent in the
understorey and subcanopy; climbing spiny rattan palms (*Calamus* spp. and other genera)
were common in the understorey, but were harvested by local settlers too frequently to
attain lengths greater than a few metres. Tree ferns (*Cyathea* spp.) and several species of
Musa (Musaceae) were also common. Common woody and herbaceous vines were
climbing bamboo (*Schizostachyum* sp.) and members of the Araceae, Asclepiadaceae,
Pandanaceae (*Freycinetia* spp.), Moraceae (including *Ficus* spp.) and Piperaceae (*Piper*
spp.). Two species of *Piper* were the most abundant vines, constituting 24% of the
understorey and subcanopy vines in the survey transect plots (see below). No other
species of vine made up more than 10% of the total.

The forest profile on Mt Guintabon differed from that of the rest of the study area in
having a much lower canopy (12–15 m), smaller diameter boles, and a several-fold lower
density of trees and shrubs. The species composition on Mt Guintabon also differed from
the other portion of the study area, most notably in the near absence of dipterocarps
(*Shorea*; 1% vs. 19% elsewhere) and *Agathis dammara* (< 1% vs. 14% elsewhere) (Antone
1983). The most abundant tree species (dbh > 10 cm) in primary forest in this area were
Alangium meyeri Merrill (Alangiaceae) (15%), *Memecylon lanceolatum* Blanco (Memecy-
laceae) (10%), *Cratoxylum formosum* (Jack) Dyer (Hypericaceae) (8%) and *Epicharis
cumingiana* (C.D.C.) Harms. (Meliaceae) (6%) (Antone 1983). The same two *Piper* spp.
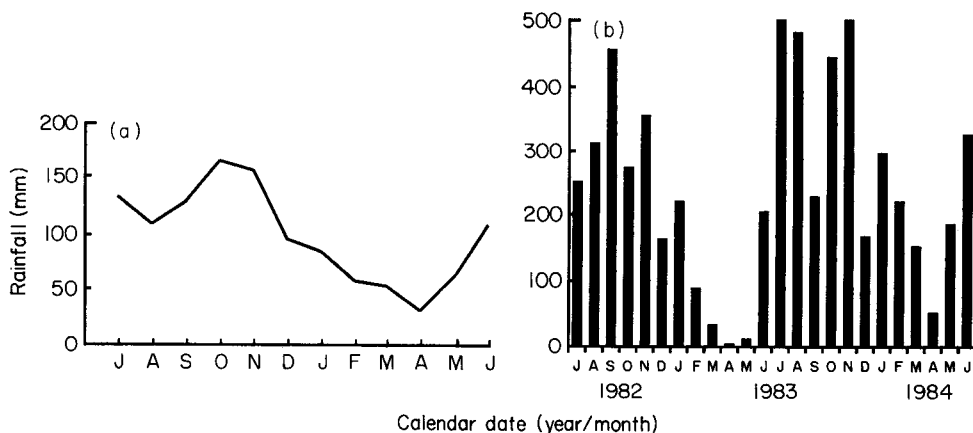
FIG. 2. Rainfall on southern Negros Island. (a) Mean monthly rainfall at Dumaguete City, 1958–83 (source: Dumaguete City Weather Station). (b) Monthly rainfall at Lake Balinsasayao during the period of study, July 1982–June 1984 (source for July 1982–June 1983: Heideman & Erickson 1987; source for July 1983–June 1984: B. Maata and R. V. Cadeliña, unpublished data).

were the most abundant understorey and subcanopy vines (52%); only one other species (unidentified) made up more than 5% of the total. The floristic differences between Mt Guintabon and the other ridges may have been caused by edaphic factors. Two major soil types occur within the valley, one a moderately deep volcanic soil with moderate to high fertility (Lowrie 1983) on the steep-sided ridges that make up most of the valley, and the other a substrate of large boulders (up to 5 m diameter) with a shallow soil of unknown fertility but apparently higher humus content on the slopes of Mt Guintabon.

About 10–20% of the forest had been cut and burned for subsistence farming. The remaining forest had been disturbed by collection of rattans, selective removal of herbs and barks for folk medicines (e.g. *Cinnamomum*), collection of showy orchids for sale locally, tapping of trees for resin collection (*Agathis dammara*), occasional illegal selective cutting for canoe construction and small-scale commercial sale (primarily *Shorea polysperma* and *S. negrosensis* Foxw.), and the removal of trees and large palms for hut construction locally (several species of ironwoods for house posts, a large variety of softer woods for beams and wall posts, palms split for flooring material, and sheets of *Shorea* bark for walls). The survey plots were in areas where disturbance had been slight.

An attempt was made to collect voucher specimens of as many species represented in the plots as possible. Collections were incomplete, however, and the available reference material did not permit identification beyond the family or genus level for many species. Identifications were made by Dr Domingo Madulid and the staff of the Philippine National Museum and Dr E. J. H. Corner, University of Cambridge (for *Ficus* spp.). Voucher specimens were divided between the Philippine National Museum and the Herbarium of The University of Michigan.

Climate

A detailed description of the climate is provided elsewhere (Heideman 1987; Heideman & Erickson 1987); the following is a brief summary. Mean annual rainfall probably averages about 3100 mm at Lake Balinsasayao. Monthly rainfall is highly correlated with that of the coastal city of Dumaguete, 14 km distant, but is about 2·5-times greater (Fig. 2). Dumaguete City generally has a dry and a wet season, but the timing and severity

of the seasons are quite variable and not very predictable. The dry season most frequently occurs from February–May. Generally, the Dumaguete dry season is not severe; the wet-season months average only about two to four times as much rain as dry-season months. At Lake Balinsasayao, the dry season is shorter, beginning later and ending sooner than at Dumaguete City. The 'typical' dry season at the Lake is probably about two months long and occurs in March and April or April and May. The study began early in a rather typical wet season in 1982, but the following dry season (1983) began early and was more severe than usual (Fig. 2b) because of the effects of the El Niño southern oscillation. The period July 1983–June 1984 was wetter than usual (Cadeliña 1987; Heideman & Erickson 1987), and the dry season at the Lake in 1984 was truncated to a single month bracketed by very wet months (Fig. 2b).

Survey plots

Survey plots were scattered over the range of edaphic and exposure conditions in the study area. Two types of survey plot were assessed during each month of data collection: two hillside plots of approximately 1 ha in area and three transect plots of 100 m × 6 m. The transect plots were used primarily to obtain data on understorey plants, while the hillside plots gave a much larger sample of canopy trees. Each transect plot was divided into four subplots, and each hillside plot was divided into two subplots. Four of the five plots were located in primary forest of the dominant type having abundant *Shorea* and *Agathis*. The 'Ridge' transect plot was a moderately exposed ridgetop on the same ridge system as the 'Ridgeside' transect plot, which ran up the side of a ridge. The hillside 'Plot 4' was adjacent to the Ridge transect and hillside 'Plot 5' was adjacent to the Ridgeside transect plot. The third transect, 'Rockpile', was the only plot in the Mt Guintabon forest type (Fig. 1).

The survey areas sampled about 60–80 species of trees, about one-third of the roughly 200 identified from the valley area to date (Antone 1983; P. D. Heideman and R. C. Utzurrum, unpublished data). Seven of the twenty-seven species of *Ficus* recorded in the study area were included in the survey plots. Approximately 1014 plants were surveyed, excluding dipterocarps, *Agathis* and rattan palms (see below), including 484 trees (129 canopy/emergents), seventy palms of four species and 460 vines.

Data collection

To determine the intensity of monthly flowering and fruiting, the number of flowers and fruits on plants were counted using a method modified from Wong (1983). In each sampling period, the survey plants were examined, scored as currently bearing flowers and/or fruits, and the approximate number and size of flowers and/or fruits were assessed. Only flowers and fruits still attached to plants were included. Relative to survey methods that employ fruit traps to collect falling fruit, this had the disadvantage of including some reproductive structures that were immature and of providing only imprecise estimates of the mass of fruit, but it minimized the bias against fruits that ripen on trees and are removed from them by bats (Marshall 1983) or birds, and thus not captured by fruit traps. The method was chosen because this study was part of a broader study on fruit bat reproductive ecology (Heideman 1987, 1988, 1989; Heideman & Heaney 1989).

Surveys were conducted by the author and one assistant using 9 × 25 and 7 × 24 power binoculars. Only canopy and emergent trees on the two hillsides were surveyed; these were initially examined from a distance of 50–200 m, and then re-examined from a distance of 20–50 m. Canopy trees in the 1-ha hillside plots that were obscured by other trees were

excluded from the survey. The transect surveys were conducted by walking the midline (the trail was not included in the area of the plot) and examining plants with boles or stems within the transect area, including either (i) only understorey plants (Rockpile and Ridgeside), or (ii) all understorey, subcanopy, and canopy plants (Ridge). Each plant was assigned to one of six classes; understorey shrub/tree, understorey vine, palm, subcanopy tree, subcanopy/canopy vine or canopy/emergent tree. The understorey was arbitrarily defined as all plants 3–6 m tall, the subcanopy as plants > 6 m tall but overshadowed by other vegetation (typically 6–12 m), and the canopy/emergent zone included all plants without overshadowing vegetation. No plants < 3 m tall were included. Those few very tall plants for which flowering or fruiting status was occasionally difficult to determine (< 1% in each month) were coded as undetermined and excluded from analysis in that month.

The precise periods of anthesis, fruit ripening and seed dispersal were not determined for most plants because the monthly sampling regime usually missed these events. Therefore, although flower buds were distinguished from open flowers and unripe fruits were distinguished from ripe or mature fruits, flower buds were lumped with open flowers, and unripe fruits were lumped with ripe fruits in the analyses. This approach probably masked some temporal variation in flowering and fruiting. All seed-bearing structures were classed as 'fruits'. Because the intent was to obtain information on the availability of resources to animals, inflorescences that were composed of a large number of tightly packed flowers or fruits were defined as single flowers or fruits (e.g. *Piper* spp., *Ficus* spp.). Abundance of flowers and fruits was assessed in three ways. Plants were first scored as flowering, fruiting, both or neither. The approximate number of flowers and fruits on each plant was recorded on a categorical log_{10} scale (i.e. $1 = 1–10$, $2 = 11–100$, . . .). Maximum length of flowers and fruits for each reproductive plant was categorized as follows: 1–5 mm, 6–10 mm, 11–50 mm, 51–100 mm, or > 100 mm.

Two taxa of plants, *Agathis dammara* and *Shorea polysperma*, were excluded from the numerical analyses, but are included in the Discussion. The gymnosperm *A. dammara* was excluded because it was known that only emergent trees were reproductive and pollen dissemination and cone maturation were difficult to detect. The dipterocarp *S. polysperma* was excluded because it is a mast-fruiting species, flowering synchronously at irregular intervals of several years. Rattan palms were excluded because all mature individuals had been harvested.

The phenological data were taken at approximate monthly intervals beginning in very late July 1982 and continuing until mid-June 1983, and in April, June and July 1984. The sampling periods were 30 July–11 August, 3–10 September, 12–18 October, 16–21 November, 17–20 December, 18–22 January, 15–20 February, 14–16 March, 17–20 April, 22–24 May and 15–17 June in 1982–83; and 18–21 April, 26–28 June and 20–23 July in 1984. Sampling periods were longer in two months (August and September 1982) because frequent rain hindered data collection.

Data analysis

The mid-points of the abundance categories were used to determine the relative number of flowers and fruits in each plot and plant category. The mid-points of the size categories were used to calculate an index of flower and fruit volume: the cube of maximum length; however, members of the largest size category were relatively longer and narrower than the majority of smaller fruits, and thus a better approximation, (maximum length) $\times$ (maximum length/3)^2, was used. The volume index is only meaningful relative to the

same index in different months or in other plots, and the units of the volume index have been omitted from the Tables and Figs.

Because individual plants in flower or fruit in one month were often still in flower or fruit in the next month(s), samples from consecutive months were not fully independent; therefore, techniques accommodating repeated measures were utilized in the analysis. Three methods were used to test statistical hypotheses. Temporal variation in the proportion of plants in flower or fruit was examined using a procedure developed by W. A. Ericson of the Statistical Research Laboratory of The University of Michigan (personal communication). This technique for comparing correlated proportions obtains 95% confidence intervals for the difference between proportions in two sets of intervals. Confidence intervals are calculated using an upper bound for the variance of a linear combination of correlated proportions, using a normal approximation to the sampling distribution of a linear combination of those correlated proportions (see Appendix). Because it uses an upper bound for the variance, the procedure is conservative and is consequently of low power statistically.

Repeated measures analysis of variance (computer program BMDP2V; Dixon 1985) was used for comparisons of numbers and the volume index for flowers and fruits among plant categories and for all plants combined between months, seasons and years. Survey plots were included as a factor to remove the effects of plot differences. Because the preplanned comparisons required contrasts of equal numbers of months, the four months of the local dry season with its transition months (February–May) were compared with four mid-wet season months (September–December) in the comparison of seasons for the number and volume index variables. Comparisons using all trees and all vines were not conducted because not all plant categories were surveyed at all sites. The assumption of homogeneity of population covariance matrices was not always met (sphericity test; computer program BMDP2V; Dixon 1985); the more conservative Greenhouse–Geisser procedure for conducting F-tests at reduced degrees of freedom (Winer 1971) was followed in those cases. The distributions of the residuals for both the number and volume index variables were non-normal for all plant categories, and none of the transformations provided fully acceptable distributions. Log_{10} transformations gave the best fit to normality, and these transformed variables were used in the analyses, but the P values provided will differ unpredictably from their true values. Because of this problem, the less-powerful non-parametric Quade test (Conover 1980) was used as a check on the significance levels for some comparisons between months. The results of both analyses are presented in the text and tables.

For the repeated measures ANOVA and the Quade test, the survey subplots were treated as the sampling units from the population of all possible subplots. Thus, the data points in each test consisted of single values for each individual subplot for each month. Therefore, the sample size was the number of subplots (generally 8–12) not the number of plants. This approach allowed the determination of statistical measures of dispersion necessary for most statistical testing. Analyses were run using data standardized by number of plants (e.g. number 100 plants^{-1} for each subplot) and by area (e.g. number ha^{-1} for each subplot) in order to distinguish density effects. Low numbers of some categories in some plots made it necessary to combine some categories for most statistical tests. In most cases, the patterns found for the combined data set were also characteristic of the subsets; exceptions are noted below.

Variation between survey plots was examined by conducting separate one-way analyses of variance on a data set consisting of the mean monthly value for each subplot for the

abundance variables of each of four plant categories. Therefore, significance levels for this particular analysis apply to the individual tests, not to the entire analysis (Table 2). Falsely significant differences between pairs of transect plots are expected by chance about twice in the Table (at the 0·05 level).

RESULTS

Temporal variation in flowering and fruiting

Community patterns

The community-wide pattern of percentage of plants in flower in 1982–83 showed a peak in the early wet season of 1982 (August and September) and a second peak in the drier months of 1983 (February–May), continuing into the early wet season month of June in 1983 (Fig. 3a; only the Ridge transect plot is graphed because only in that plot were all plant categories surveyed—see the Methods). The community-wide peaks resulted from the sum of approximately coincident peaks for palms and the three categories of trees, while vines showed no peaks. A similar but more pronounced pattern can be seen in the number of flowers ha^{-1} (Fig. 3b), but the peak in number of flowers ha^{-1} in 1982 extended two months beyond the peak in percentage flowering. The pattern for the volume index ha^{-1} in 1982–83 includes only a single peak in one wet season month (Fig. 3c). The peaks for both number and volume index are due almost entirely to the contribution of subcanopy trees, although when the dipterocarps flowered in June 1983 they out-produced all other groups.

The repeated measures ANOVA revealed significant differences between months for both number of flowers and the volume index for understorey plants as a group and for canopy trees (Table 1). There were also differences between seasons (drier months of February–May vs. wet season months of September–December) and between years (April and June 1983 vs. April and June 1984), but these were significant at only $0·1 > P > 0·05$ for the two variables (Table 1). There were no statistically significant differences for any of these tests for understorey trees alone, palms alone, or understorey vines alone. The analysis could not be conducted on subcanopy trees or subcanopy and canopy vines, because an insufficient number of plots were sampled for these two categories. The results of the Quade test (Conover 1980) were similar to the results of the ANOVA, but some differences that were significant in the latter were not significant using the Quade test (Table 1).

Plant category patterns

The percentage of plants in fruit was relatively constant for most plant categories in 1982–83, both in the Ridge transect plot (Fig. 3d) and in the entire data set (Fig. 4d, j, p). There was a slight tendency toward more fruiting in the wet-season months. The number of fruits ha^{-1} peaked in the mid-wet season (Fig. 3e), about one month after the early wet season peak in number of flowers ha^{-1} (Fig. 3b). No fruiting peak followed the dry season peak in number of flowers. As with flowering, the greatest contribution was made by subcanopy trees. The fruit volume index ha^{-1} pattern showed a mid-wet-season high and a dry-season low (Fig. 3f). Each plant category contributed significant portions of the total volume index in at least one month.

There were no significant differences between months, seasons or years for number of fruits or the volume index by any test (Table 1).
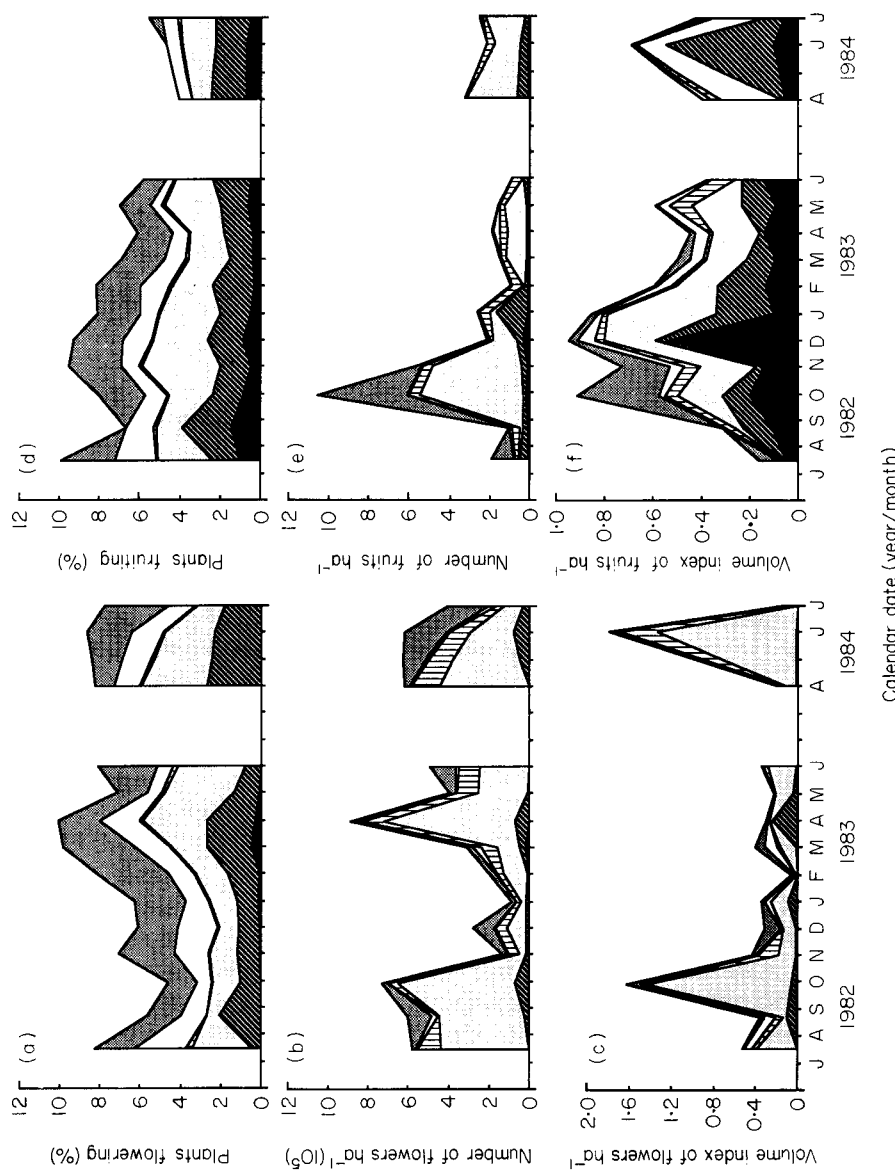
FIG. 3. Monthly values for three abundance variables for all plants in flower and fruit in the Ridge transect plot (the plot in which all plant categories were sampled; see the Methods). (Approximate monthly sample size: thirty-one canopy trees, sixty-six canopy trees, 135 understorey trees, twenty-six palms, 161 canopy and subcanopy vines and 182 understorey vines.) Each background pattern represents a separate category of plants; from lowest to highest on the figure are palms (■), understorey trees (▨), subcanopy trees (▦), canopy trees (▩), understorey vines (□), and canopy vines (▨). Each line is a cumulative total. Percentage of plants in flower (a) and fruit (d), number of flowers (b) and fruit (e) ha⁻¹ (in units of 100000) and volume index of flowers (c) and fruits (f) ha⁻¹.

TABLE 1. Comparisons of amount of flowering and fruiting between months, and between seasons and years [Months 'M': July 1982–June 1983; Seasons 'S': October 1982–January 1983 (wet) vs. February–May 1982 (dry); Years 'Y': April and June 1983 vs. April and June 1984; and interactions 'I']. Results using a repeated measures ANOVA are shown above; for the comparison of months, results using the more conservative non-parametric Quade test are shown as well (see the Methods). Attained level of significance is shown as follows: −, $P > 0.10$; +, $P < 0.10$; * $P < 0.05$; ** $P < 0.01$. Sample sizes (n) are the number of subplots, not the number of plants (see Methods).

	n	Number of flowers plant^{-1}				Volume index flowers plant^{-1}				Number of fruits plant^{-1}				Volume index fruits plant^{-1}			
Repeated measures ANOVA:		M	S	Y	I	M	S	Y	I	M	S	Y	I	M	S	Y	I
Understorey trees, palms & vines	12	*	−	+	−	*	+	−	−	−	−	−	−	−	−	−	−
Canopy trees	8	*	−	+	YM**	*	−	−	−	−	−	−	−	−	−	−	−
Quade test:		M				M				M				M			
Understorey trees	12	**				**				−				−			
Understorey palms	12	−				−				−				−			
Understorey vines	12	−				−				−				−			
Subcanopy trees	4	−				−				−				−			
Canopy trees	8	−				−				−				−			

Trees

The pattern of percentage of trees in flower in 1982–83 included peaks in the early wet season and dry season (Fig. 4a). The number of flowers plant^{-1} followed the same pattern as the percentage of trees in flower, with highs in the early wet season and dry season (Fig. 4b). The approximate volume of flowers plant^{-1} showed a different pattern, with a peak in the mid-wet season and in the dry season of 1984 (Fig. 4c).

Significantly more trees flowered in the dry season than in the wet season ($P < 0.05$; $n = 484$; correlated proportions test—see the Appendix). Significantly more subcanopy and canopy trees flowered in April and June 1983 than in those months in 1984 ($P < 0.05$; $n = 196$; correlated proportions test), but the difference for trees as a whole was not significant ($P > 0.10$; $n = 484$; correlated proportions test).

Understorey trees, subcanopy trees and canopy trees all followed the same general pattern of variation for percentage of plants flowering and number of flowers plant^{-1}. The pattern for understorey trees in 1982–83 differed slightly, however, from the pattern for trees as a whole, with the peak in flowering occurring in mid-dry season, earlier than the peak for canopy and subcanopy trees (Fig. 3a). The same general pattern was observed in each category of trees at all but one site (six of seven plant category × plot combinations).

The percentage of trees in fruit in 1982–83 was roughly constant (Fig. 4d). The average number of fruits plant^{-1} fluctuated over the period, with no evidence of statistically meaningful peaks or lows when averaged over all sites and classes (Fig. 4e). The volume of fruits ha^{-1} showed a peak in the early part of the wet season, a gradual decline continuing through the first three months of the dry season, followed by a peak in the transition months between the dry and wet seasons (Fig. 4f).

There were no statistically significant differences in the proportion of trees fruiting in the wet and dry seasons ($P > 0.10$; $n = 484$; correlated proportions test), although more understorey and subcanopy trees fruited in the wet season than the dry season. In April

and June 1983, more trees in all categories were in fruit than in those months in 1984, but these differences between years were not statistically significant ($P > 0.10$; $n = 484$; correlated proportions test).

For subcanopy and canopy trees, there were weak peaks in fruiting in the late dry season and early wet season in two of four category–plot combinations. In the other two cases, however, peaks in fruiting were found in mid-wet season, and the net effect was equality between seasons. There was an early dry season peak in fruiting understorey trees in two plots, and a weak peak at the third, but no peak in the following late dry season (just after a two-month high in flowering) at two of the plots, and only a weak peak at the third.

Palms

Palms showed a single distinct peak in flowering in the dry season for all three measures of abundance in 1982–83 (Fig. 4g–i). The seasonal difference in proportion flowering was statistically significant ($P < 0.05$; $n = 70$; correlated proportions test). In the dry season of 1984, in contrast, no palms surveyed were seen in flower (Fig. 4g), and this difference between years was statistically significant ($P < 0.05$; $n = 70$; correlated proportions test). The presence of fruits in 1984 indicates that some palms must have flowered in earlier months, however. The same pattern of flowering was found at two of the transect plots; only one palm was observed in flower at the third transect plot, Rockpile.

The percentage of palms in fruit was greatest in the wet season, and was lowest in three months in the late wet season and early dry season, just before and during the peak in flowering (Fig. 4j). The patterns for number and volume index of fruits palm^{-1} were relatively constant except for a single high peak in December for both variables (Fig. 4k, l). The lack of correspondence with the pattern of percentage of palms in fruit had two causes. First, the 1982 wet-season peak in fruiting palms included many palms that had lost most, but not all, fruits. These palms were recorded as fruiting, but carried very low numbers (and thus volumes) of fruit. Second, a few individuals of a single species of large palm produced a large proportion of both the number and volume of fruits in months in which they fruited, including the December peak (Fig. 4d–f). Palms were never observed in fruit at one of the three transect plots, Rockpile.

Vines

For flowering vines, there were no consistent seasonal differences for any of the three abundance variables (Fig. 4m–o). Similarly, the proportion of vines in fruit was relatively constant through the year, with a slight decline through the dry season months (Fig. 4p). The pattern for both number and volume of fruits followed the same pattern as that of percentage of vines in fruit, except for a mid-wet season peak in number and volume index (Fig. 4q, r). There were no significant differences between seasons or years for any of the variables for either flowering or fruiting vines ($P > 0.10$; $n = 460$; correlated proportions test).

Dipterocarps

Some dipterocarps began flowering in May 1983. Buds were visible on many trees as early as April, about 1·5 months after the beginning of the dry season of that year. About 60% (19 of 33) of the canopy and emergent *Shorea polysperma* flowered. The entire crown flowered on only a few trees, and on many trees only one or two of the major branches of the crown produced flowers. During May and June, *S. polysperma* trees were producing of the order of ten times the number of flowers of all other plants combined (except on Mt
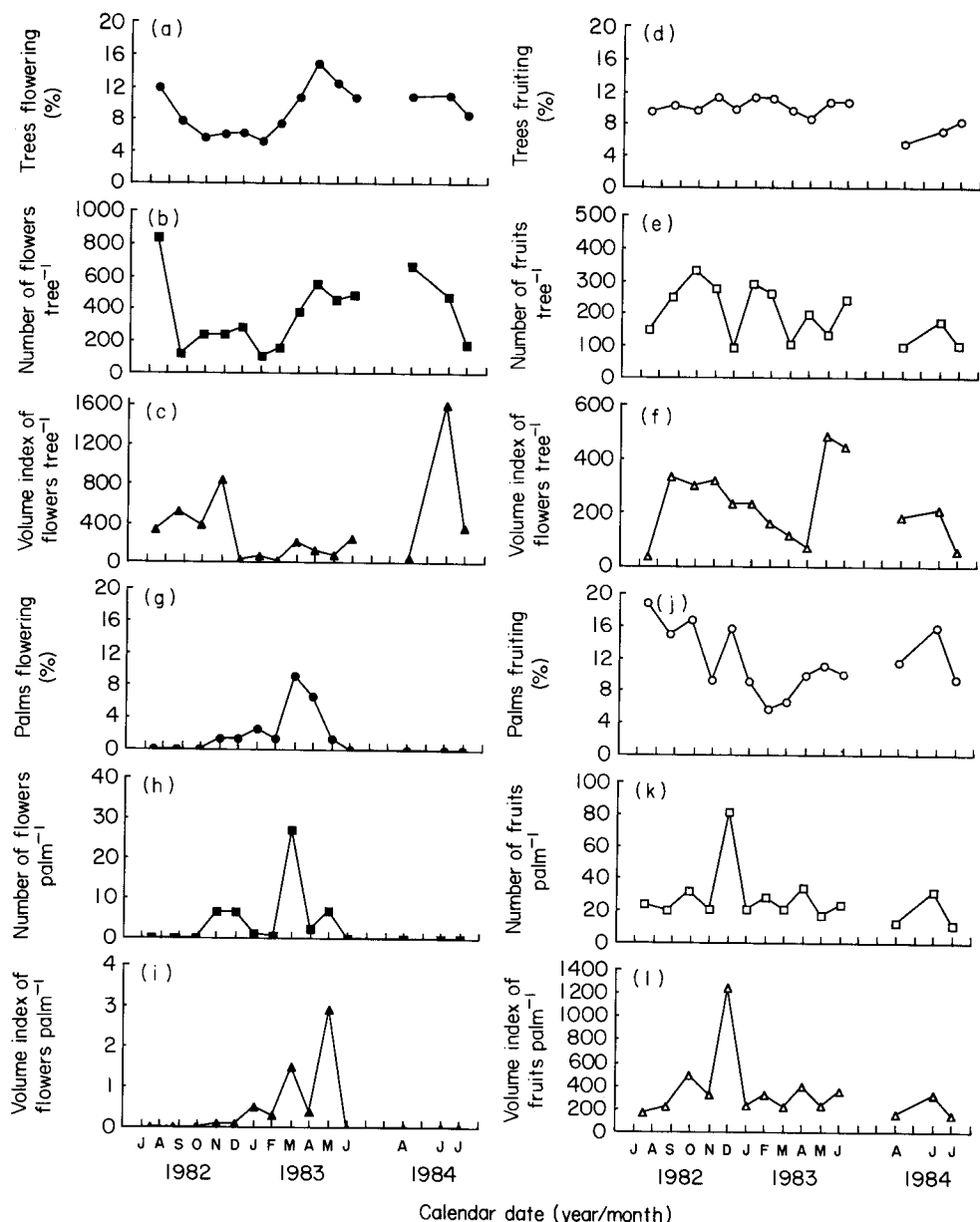
FIG. 4. Abundance of flowers and fruits in three plant categories (trees, palms and vines) during 14 months between July 1982 and July 1984. All trees (in all five plots; $n = 484$; a–f), all palms (in all three transect plots; $n = 70$; g–l) and all vines (in all three transect plots; $n = 460$; m–r) are included. Abundance is shown as percentage of plants flowering (a, g, m) or fruiting (d, j, p), number of flowers (b, h, n) or fruits (e, k, q) plant^{-1} and volume index of flowers (c, i, o) or fruits (f, l, r) plant^{-1}.

Guintabon). The only evidence of seed maturation before the end of sampling in 1983 (18 June) was a few fallen seeds found floating in the lake early in that month. There was no evidence of flowering or fruiting in the dipterocarps during sampling in 1984.
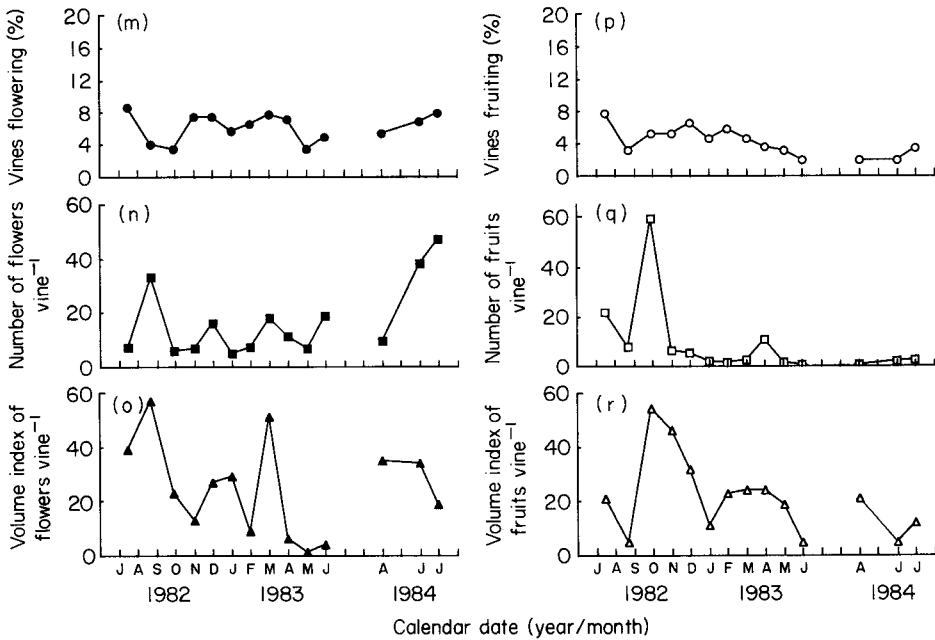
FIG. 4 (cont.)

Gymnosperms

Agathis dammara cones were over 5 cm long when first observed in July 1982. The cones grew slowly until October or November, and by mid-January 1983 the seeds had been released and the cones had fallen from the trees. Small cones were again visible on the trees in March and April. One 60 m emergent tree, the tallest in the survey, produced about 1000 cones in 1982, but in June 1983 held only about 100 young cones. Similar tenfold reductions in cone numbers in 1983 were noted on the other four mature *A. dammara* surveyed. In 1984, the large emergent held several hundred cones; the others held numbers comparable to the number they had held in 1982.

Variation between plots

Although the presence and pattern of temporal change were generally consistent between sites for each plant category, the sites differed in the magnitude of production. There were large, statistically significant differences in abundance between some transect plots for understorey trees and palms but relatively few differences for vines (Table 2). Overall, the between-plot differences in abundance plant^{-1} was rarely above tenfold for proportions of plants in flower or fruit, and ranged up to 100-fold in number or volume index ha^{-1}. For the same comparisons on the number or volume index per 100 plants (i.e. after eliminating density differences), the differences were slighter, generally on the order of tenfold. The Ridgeside and Ridge transect plots were generally statistically indistinguishable, while both differed significantly from Rockpile in many comparisons. Differences were most apparent in the abundance per unit area comparisons, because the Rockpile plot had fewer plants per unit area. Some differences remained in the abundance plant^{-1} comparisons, although in many cases these differences were not significant

TABLE 2. Differences between survey plots in number of plants flowering and fruiting and number and volume of flowers and fruits. Quantity ha^{-1} is contrasted with proportion (quantity per 100 plants). The upper portion of the table covers flowering for four categories; the lower covers fruiting. Each cell of the table includes three plots (1, Ridge; 2, Ridgeside; 3, Rockpile; 4 and 5, the two 1-ha plots); understorey plants were surveyed only in Plots 1, 2 and 3; canopy trees only in Plots 1, 4 and 5. Below the plot number is the mean for 14 months for that plot. The bars above the plot numbers join plots that are not significantly different ($P < 0.05$; one-way ANOVA; BMDP computer program; Dixon 1985). Canopy trees were not included in the ha^{-1} comparisons because some canopy trees in Plots 4 and 5 were not surveyed (see the Methods).

	Number of plants in flower						Number of flowers (in 1000s)						Volume index of flowers (in 1000s)					
	ha^{-1}			100 plants⁻¹			ha^{-1}			100 plants⁻¹			ha^{-1}			100 plants⁻¹		
Understorey trees	1	2	3	2	1	3	1	2	3	1	2	3	1	2	3	1	2	3
	140	180	20	13	6·4	1·7	40	50	2	2	3	0·2	50	80	20	2	5	2
Understorey palms	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	15	6	0	3·7	0·9	0	2	3	0	0·6	0·7	0	0·1	0·4	0	0·03	0·08	0
Understorey vines	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	160	90	50	6·5	5·8	5·3	30	20	2	1·3	1·1	0·3	70	40	20	3	3	2
Canopy trees				1	4	5				1	4	5				1	4	5
				16	10	11				100	100	100				100	200	5

	Number of plants in fruit						Number of fruits (in 1000s)						Volume index of fruits (in 1000s)					
	ha^{-1}			100 plants⁻¹			ha^{-1}			100 plants⁻¹			ha^{-1}			100 plants⁻¹		
Understorey trees	1	2	3	2	1	3	1	2	3	1	2	3	1	2	3	2	1	3
	150	160	40	11	6·8	3·6	70	40	2	3	2	0·2	200	200	20	11	9	2
Understorey palms	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	90	50	0	19	11	0	20	9	0	6	2	0	300	100	0	80	20	0
Understorey vines	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	90	70	50	3·2	4·1	6·4	10	6	5	0·5	0·4	0·5	20	20	70	1	1	8
Canopy trees				1	4	5				1	4	5				1	4	5
				22	10	10				70	40	80				160	30	40

(Table 2). Both the lower plant density and reduced abundance may be due to the shallower and rockier soil in the Rockpile plot.

For canopy trees, the two 1-ha plots were generally more similar to each other than to the Ridge transect plot, but only one difference was statistically significant (Table 2).

DISCUSSION

Three major conclusions emerge from this study. (i) At this site, where climatic seasonality relative to most tropical sites was low, within-year variation in flowering and fruiting was also low (two- to fourfold) relative to most tropical sites, but comparable to that of similar submontane rainforest elsewhere in the tropics. The comparisons of two months between years hint that the predictability of the timing or amount of seasonal variation may also be low. (ii) Microgeographic variation in flower and fruit abundance (of the order of ten- to 100-fold between some plots) was so great that it must have had a profound effect on the distribution and relative success of animals that use these resources. (iii) Some large differences at the community level were not statistically significant. Larger sample sizes might have resolved this problem, but note that sample

sizes were comparable to those in a number of other studies making inferences about community patterns. Statistical treatment of the data was essential for assessment of the significance of variation. This result highlights the importance of using statistical techniques to assess variation in phenological studies.

Temporal variation in flowering and fruiting

The intensity of both flowering and fruiting varied between months; flowering peaked in the dry and early wet season, while fruiting was highest in the first half of the wet season. These peaks and lows in the intensity of flowering and fruiting tended to occur synchronously in different plots and plant categories, indicating that the pattern was robust within these different elements of this forest. Overall abundance varied among months from less than twofold for percentage of plants in fruit to about four- or fivefold for numbers of flowers and fruits and the volume index for flowers (Fig. 3). This is generally less than has been observed at more seasonal sites, where five- to tenfold differences may be observed (Koelmeyer 1959a, b; Snow 1965; Smythe 1970; Croat 1975; Heithaus, Fleming & Opler 1975; Foster 1982a; Terborgh 1983), but similar to that at equally seasonal sites (Hilty 1980; van Schaik & van Noordwijk 1985; Gentry & Emmons 1987).

The observation of greater flowering in the drier months (February–May) and the early wet-season months (July–October) is consistent with those found elsewhere (e.g. Koelmeyer 1959a; Janzen 1967; Croat 1975; Foster 1985). This is also consistent with the observation that, in some species of tropical plants, a dry period followed by rain triggers flowering (Opler, Frankie & Baker 1976; Augspurger 1982, 1985). The tendency toward greater fruiting in the early wet season (statistically non-significant) is similar to the pattern of peaks in the late dry season or early to middle wet season noted elsewhere (Koelmeyer 1959a; Snow 1965; Janzen 1967; Smythe 1970; Heithaus, Fleming & Opler 1975; Foster 1982a, 1985).

The lack of a stronger within-year pattern of fruiting for palms and trees is surprising, given the dry season peaks in flowering. This is even more surprising given that distinctions were not made between ripe and unripe fruits, which should have had the effect of exaggerating any post-flowering fruiting peak. Some of this may be attributable to the effects of the drought and decreased cloud cover associated with the El Niño southern oscillation. In part, the evenness of fruiting was due to plants flowering but not producing fruit, particularly during the long dry season and drought in 1983. The evenness of fruiting may also reflect staminate (male) flower production, and moisture deficit during the drought may have caused some hermaphroditic plants to produce only staminate flowers in that year (e.g. Janzen 1978). The effects of the drought were most obvious for vines, many of which lost leaves or died, and this suppressed flowering and fruiting in that category. Peaks in the percentage of plants fruiting were further obscured by the tendency in some species for apparently mature fruits to be available for up to four months, and for others to flower and fruit irregularly or continuously throughout the year. The weak and extended fruiting peak may be a common feature of forests in weakly seasonal environments; Hilty (1980) also found that fruiting did not always rise following flowering peaks in a submontane rainforest with similarly mild seasonal variation in rainfall. This raises the possibility that consistently high moisture availability may increase the advantages of uncoupling flowering and fruiting periods.

The lower levels of flowering and fruiting in 1984, at times when resource levels were peaking in 1982 and 1983, suggest that resource peaks are relatively unpredictable in

timing. A plausible cause for the lower production is the unusually short dry season of 1984. A year without a dry season on Barro Colorado Island in Panama was marked by greatly reduced flower and fruit production (Foster 1982b). The dry period of 1984 at Lake Balinsasayao may have been too short to trigger flowering in a subset of the species or individuals studied, causing a mild reduction in production.

What inferences can be made about the year-to-year predictability of seasonal variation? Unfortunately, the sampling period is too short for generalizations. There might be an annual pattern of flowering and fruiting related to the timing of wet and dry seasons, as there was during 1982–83, but this is largely speculation. Two points suggest that if any such pattern exists, it is likely to be somewhat variable among years. First, the timing and strength of wet and dry seasons at the site are only mildly predictable (Heideman 1987). Second, the relationship between rainfall and the timing of flowering and fruiting was fairly weak during the sampling period. Thus, although these results are consistent with a mild seasonal pattern of flower and fruit abundance, it seems just as likely that there is much variation from year to year. Low predictability of plant phenological events is common in climates that are as seasonal or less seasonal than that of southern Negros. At such sites, minor seasonal phenological changes are found in some years, but may be slight or undetectable in others (e.g. Medway 1972; Opler, Frankie & Baker 1980; Wong 1983; van Schaik & van Noordwijk 1985).

Correspondence between measures of abundance

The percentage of plants in flower or fruit was not necessarily a good indicator of abundance of flowers and fruits. Similarly, in Terborgh's (1983) data it can be seen that highs and lows in the number of species in fruit did not always match those in the fresh mass of fruit. Hilty's (1980) data on the percentage of crown surface in flower and fruit also show some peaks out of phase with some peaks in flowering and fruiting. In contrast, Foster (1982a) found peaks in the number of species fruiting plot^{-1} that matched peaks in the number of seeds plot^{-1}, although the amplitudes of the peaks differed.

The lack of correspondence between variables in some months was to some extent the effect of flowering or fruiting by individual species. In some months, a few individuals of a single species produced, for example, a large number of very small fruits, creating a peak in fruit number without a corresponding peak in the index of volume. To the extent that such species were over- or under-represented in the sampling plots relative to the forest as a whole, this is also a problem of sample size. A second problem in this study, of uncertain significance, lies in the use of categories for number and size of flowers and fruits. This certainly decreases accuracy. In addition, a flower generally fills only a small fraction of the volume it encloses, and thus flower structure and size greatly affect the volume index. Nevertheless, this sometimes poor correspondence between percentage, total numbers, and a volume index indicates that information on resource availability based on counts of plants and species may not accurately reflect the amounts actually available to animals.

Differences between plant categories

There were some differences in phenological patterns between classes of plants. Proportionately fewer vines produced flowers or fruits, and vines accounted for a very small part of total production. Canopy and subcanopy trees displayed similar overall patterns of flower and fruit production, but understorey trees had a slightly different pattern.

One category of plants, subcanopy trees, contributed the greatest part of the total numbers and relative volume of flowers and fruit in most months (Fig. 3). The greater importance of subcanopy trees than canopy trees can be explained, at least in part, by the exclusion of the dominant species of the canopy, *S. polysperma* and *A. dammara*. These two species made up eleven of the forty-one canopy and emergent trees in the Ridge transect plot, including all five emergents. *Agathis* contributes a relatively small number and volume of flowers and fruits, and its exclusion from the analyses did not greatly affect the results. The dipterocarps, however, produce a tremendous number and volume of flowers and fruits when they do reproduce, usually at intervals of several years, but produce much less or nothing in other years. As a result, because the remaining, relatively less common dominant canopy and emergent tree species produced a relatively low number and volume of flowers and fruits, the subcanopy trees as a group contributed a greater amount of flowers and fruit. This higher production in the subcanopy must have affected the vertebrate community feeding on flowers and fruits. One important caveat here is that the analysis of relative contributions uses data from only the Ridge transect plot, and these conclusions should be treated cautiously. However, the proportion of plants flowering and fruiting and the amounts produced were largely consistent with production in the Ridgeside transect plot and hillside Plot 4 and Plot 5 (Table 2).

Plant phenology and the vertebrate community

It is frequently argued that selective pressures on nectarivore and frugivore reproduction should result in reproductive peaks coincident with those of plants. The pattern on southern Negros is consistent with this hypothesis for the period 1982–83; the community of volant vertebrates that feeds on flowers and fruits on southern Negros reaches a peak in the production of young during the late dry season and early wet season periods of higher flowering and fruiting in 1982–83 (birds: Alcala & Carumbana 1980; bats: Heideman 1987, 1988).

Microgeographic variation

It is clear that the floristic and/or edaphic differences between plots had a profound impact on production rates of flowers and fruits (Table 2), and that the differences are biologically as well as statistically significant. Microgeographic variation in species richness and abundance has been demonstrated in many tropical forests (Wong & Whitmore 1970; Hubbell 1979; Tomboc *et al.* 1980; Thorington *et al.* 1982; Whitmore 1984), but only rarely have associated differences in production of flowers and fruits been documented (Terborgh 1983). While microgeographic variation in abundance of flowers and fruits is to be expected in plots differing floristically, the magnitude of the differences found here, up to 100-fold, is surprising, and is certainly sufficient to have a high impact on the animal community.

Assessments of community patterns

The literature on tropical plant phenology is characterized by a relatively low reliance on statistical methodology to assess the validity of observed patterns. The validity of seasonal peaks is usually convincing (e.g. Snow 1965; Smythe 1970; Medway 1972; Croat 1975; Heithaus, Fleming & Opler 1975; Opler, Frankie & Baker 1980; Foster 1982a; Terborgh 1983; Wong 1983), but the general lack of statistical tests makes evaluation of the more subtle differences difficult. Particularly in sites such as this on southern Negros, where climatic seasonality and the amplitude of temporal change in flowering and fruiting

is reduced, statistical comparisons must be used to assess the potential significance of differences within and between years. While the sample size in this study was not high (about 1000 plants with only 129 canopy trees, excluding dipterocarps and *Agathis*), it was, nevertheless, comparable to a number of other studies that have made inferences about phenological patterns at the community level (e.g. Medway 1972; Putz 1979; Hilty 1980; Raemaekers, Aldrich-Blake & Payne 1980; Wong 1983). It was also apparent that, at least with these sample sizes, counts of plants or species in flower or fruit do not always correspond to estimates of numbers of volume of flowers and fruit (Hilty 1980; Terborgh 1983). It is clear that inference about community-wide abundance patterns of flowers and fruits made from counts of plants or species alone should be made cautiously, and that any phenological study would benefit from appropriate attention to statistical tests of significance.

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APPENDIX

A statistical test for the comparison of correlated proportions

A set of variable measurements taken successively on the same sample of individuals cannot be assumed to be independent. This does not create a statistical problem if only two points in time are to be compared. If, however, observations from a number of points in time are combined, the assumption of independent observations required for virtually all statistical tests has been violated, and special statistical approaches, such as repeated measures analysis of variance, are required. No such approach is available for comparing data in the form of proportions, however. As a result, in the comparison of two seasons, the inclusion of more than one observation period in a season precludes statistical comparisons, while the use of only a single observation period for each season ignores a substantial amount of relevant data. Therefore, a technique devised by William A. Ericson of the Statistical Research Laboratory of The University of Michigan was used for the comparison of correlated proportions within two seasons.

The method uses an upper bound to the covariance between observation points to determine an upper bound for the variance of a linear combination of correlated proportions, using a normal approximation to the sampling distribution of a linear combination of those correlated proportions. This upper limit of the variance is then used to calculate an approximate 95% confidence interval for the contrast of two subsets of the set of proportions. The use of this upper bound reduces the power of the test (greater chance of false acceptance of the null hypothesis). Thus, the procedure provides a conservative test, but failure to reject the null hypothesis will, in some cases, be due to its low power.

Terms

P' the estimate of the proportion from the first period or season.
P'' the estimate of the proportion from the second period or season.
C the estimate of the contrast between two sets of proportions.
n sample size at each observation point.
T_1 number of observation points in period or season 1.
T_2 number of observation points in period or season 2.
Min $(P_i P_j)$ the smaller of the two proportions.

Confidence intervals

An estimate of the contrast between the two periods or seasons is:

$$C = \frac{1}{T_1} \sum_{i=1}^{T_1} P'_i - \frac{1}{T_2} \sum_{i=1}^{T_2} P''_i.$$

A maximum value of the estimated variance of the contrast $V(C)$ can be obtained using the formula:

$$\text{Estimated } V(C) \leqslant \frac{1}{(T_1)^2} \sum_{i=1}^{T_1} \frac{P'_i(1-P'_i)}{n} + \frac{1}{(T_2)^2} \sum_{i=1}^{T_1} \frac{P''_i(1-P''_i)}{n} +$$

$$\frac{1}{(T_1)^2} \sum_{i,j=1\, i \neq j}^{T_1} \frac{\text{Min}\,(P'_i, P'_j) - P'_i P'_j}{n} + \frac{1}{(T_2)^2} \sum_{i,j=1\, i \neq j}^{T_2} \frac{\text{Min}\,(P''_i, P''_j) - P''_i P''_j}{n} +$$

$$\frac{2}{(T_1)(T_2)} \sum_{i,j=1}^{T_1,\,T_2} \frac{P'_i P''_j}{n}.$$

Finally, an approximate 95% confidence interval for the contrast is obtained from:

$$C \pm 1\cdot96 \sqrt{V_{\text{estimate}}(C)}.$$