

## A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae

NATHANIEL T. WHEELWRIGHT\*

*Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853, USA*

**Key words:** Lauraceae, seed dispersal, frugivory, tropics, masting, phenology, plant reproduction, annual variation in fruit production

**Abstract.** Fruit crop sizes varied from year to year among 22 sympatric, bird-dispersed tree species in the Lauraceae. Each species in the lower montane forests of Monteverde, Costa Rica fruited at a characteristic season, but there was wide year-to-year variability in the proportion of each population that produced fruit and in the average size of fruit crops. Over a 7-year period (1979–1985), overall fruit production was high during three nonconsecutive years and low during four years. Within genera, tree species displayed distinct fruiting schedules. Even within populations, individual trees sometimes fruited in different years or failed to fruit altogether.

Yearly rainfall and temperature patterns did not explain annual variation in fruit production. Unexpectedly, neither did previous reproductive histories: there was little correlation between an individual tree's fruit production in a given year and its fruit production the previous year. On the other hand, vegetative growth was negatively correlated with reproduction in 12 of 15 species.

Lauraceous fruits make up 60–80% of all fruits eaten by bird species such as Three-wattled Bellbirds and Resplendent Quetzals. These birds may respond to annual variation in the availability of lauraceous fruits by migrating locally, by expanding their diets to include previously ignored foods or unripe fruits, or by delaying breeding.

\* Present address: Department of Biology, Bowdoin College Brunswick, Maine 04011, USA

### Introduction

Lifetime patterns of fruit production, like other features of a plant's reproductive biology, have been molded by natural selection by seed dispersers over thousands of generations. At least, that is what most researchers interested in frugivory and seed dispersal assume. It is daunting to recognize, however, that we make such an assumption in the absence of crucial information on the heritability of reproductive traits, or on the strength of selection imposed by different kinds of interactions with seed dispersers. We know very little about the scheduling of reproduction or the magnitude of annual and individual variation in fruit production in most tropical tree species (Janzen, 1978). Seldom do we know if we are witnessing a 'normal' year, or even what a 'normal' year is in terms of plant reproduction.

The earliest systematic studies on flowering and fruiting in tropical plants were conducted only recently (McClure, 1966; Medway, 1972; Frankie *et al.*, 1974; Hilty, 1980; Opler *et al.*, 1980). The work was directed chiefly at determining broad within-year patterns such as the number of species flowering or fruiting within a given month or forest stratum. From these descriptive studies, the focus of research shifted to the question of how competition for pollinators or seed dispersers might select for staggered phenologies within years (Frankie, 1975; Stiles, 1977; for a review see Wheelwright, 1985a) or how the timing of fruit production related to the

behavior of seed dispersers (Thompson and Willson, 1979). Other studies searched for the proximate cues responsible for observed phenologies, especially in relatively aseasonal tropical forests (Alvim and Alvim, 1978; Putz, 1979). What has rarely been reported are long-term studies of marked individual plants. Janzen (1978) and Milton *et al.* (1982) presented unusually complete phenological data on individuals of four tropical tree species, and research currently in progress (G. Frankie, pers. comm.) promises to detail reproduction over more than a 10-year period for many more plant species.

This paper describes individual variation in fruit production by 22 plant species studied over a six-year period; among these species are six studied in a seventh year. I have focused on 16 of the commonest species. The plants, all sympatric bird-dispersed trees in the Lauraceae, are conspicuous members of the lower montane forests of Costa Rica. They provide fruit for at least 18 bird species, several of which depend on the Lauraceae for food (Wheelwright *et al.*, 1984). The purpose of the paper is (1) to document year-to-year variability in fruit production by a group of related plant species in a tropical forest, (2) to demonstrate between-year differences in reproductive output among individual trees of the same species, and (3) to consider some of the life history trade-offs and environmental cues that may produce community-level reproductive patterns.

## Methods

### *Study area*

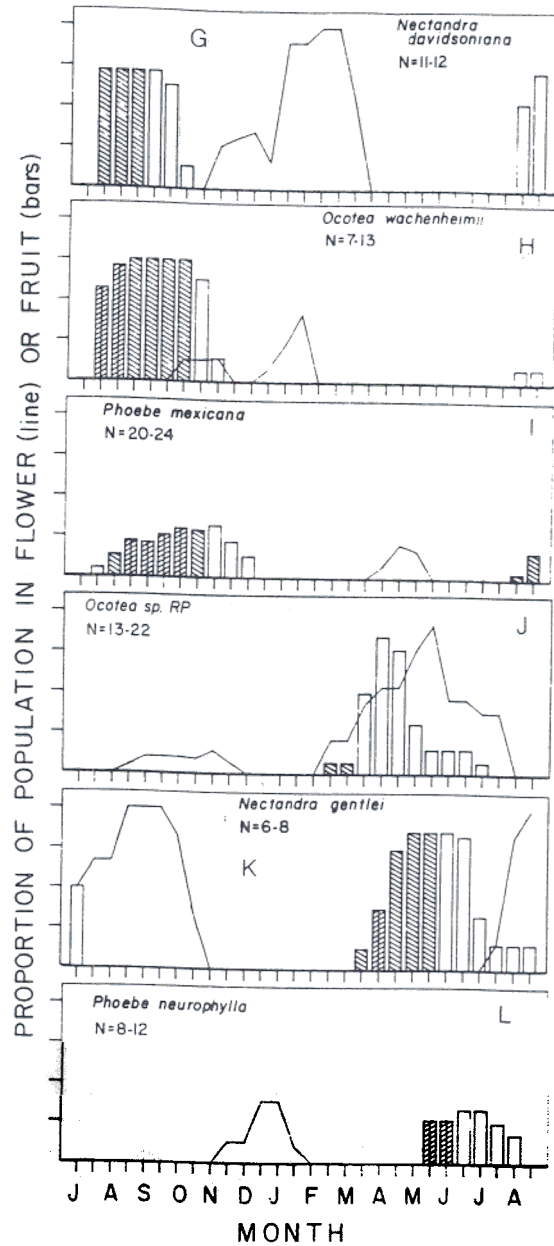
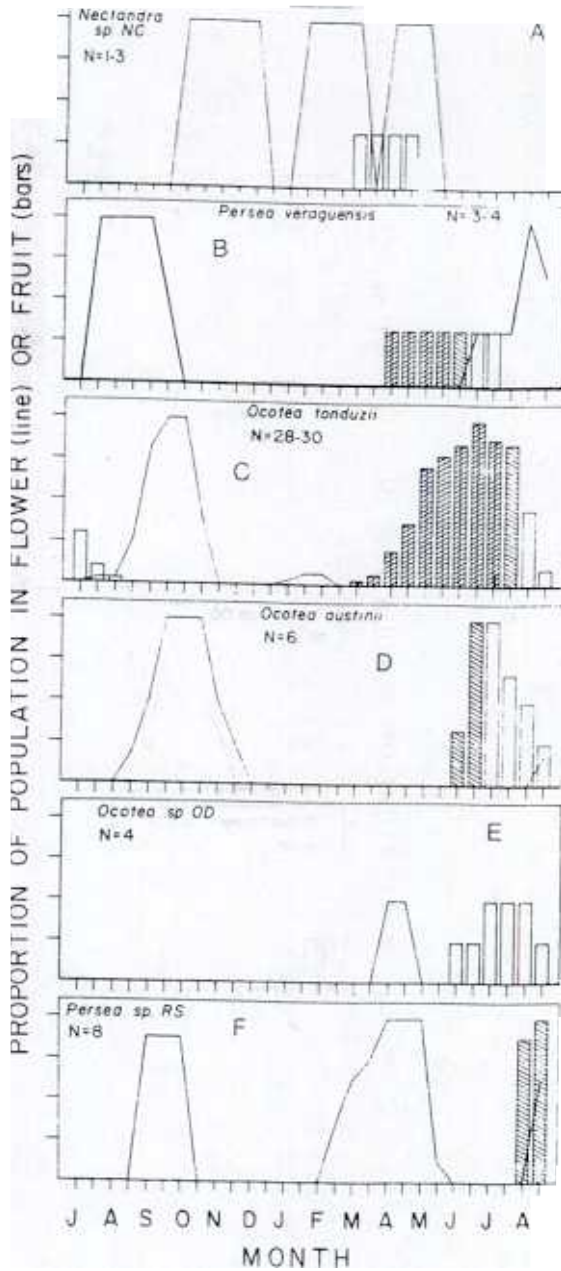
The study area covers 15 km<sup>2</sup> of lower montane wet and rain forests (Holdridge, 1967) in Monteverde, Costa Rica (10° 18' N, 84° 48' W). Monteverde lies on a plateau along the continental divide at an elevation of 1350 to 1550 m. The soils, volcanic in origin, are quite fertile. They support a diverse forest, comprising approximately 800 woody plant species, many of which are bird-dispersed (Wheelwright *et al.*, 1984). In 1980 I established a transect from the relatively dry western edge of the plateau

to the cloud forest on the divide itself, 4 km to the east. The habitat consists of undisturbed forests (including the 2700 ha Monteverde Cloud Forest Reserve, which borders the 33,000 ha Arenal Forest Preserve), small cattle pastures, and woodlots. For a more complete description of the area, see Lawton and Dryer (1980) and Wheelwright *et al.* (1984).

A mean of 2529 (SD = 394) mm of rain falls annually in Monteverde (n = 28 yrs). About 85% of the yearly precipitation comes during a distinct wet season, which typically begins in mid-May and lasts until late-December. The dry season averages 144 (SD = 21) days (n = 19 yrs). During the period of this study, rainfall averaged 2703 (SD = 469) mm. The period included one of the rainiest years (1981: 3234 mm) and one of the driest years (1983: 1971 mm) in which meteorological records have been kept. Daily minimum temperatures from 1979 to 1983 averaged 14.9° C (SD = 0.3° C); daily maximum temperatures averaged 21.9° C (SD = 0.6° C). Unlike rainfall, temperatures remain relatively constant throughout the year. Mean annual relative humidity in Monteverde is estimated to range between 85% and 90% (R. Lawton, pers. comm.). The lengths of the longest and shortest days of the year differ by only 69 min.

### *Tree species*

At least 22 bird-dispersed lauraceous tree species occur in the same or adjoining habitats at Monteverde. Their taxonomy is still being resolved (W. Burger, pers. comm.). For consistency, if not nomenclatural accuracy, this paper retains the names used in previous publications. Except for two understory species, the species are shade-tolerant canopy trees which together constitute much of the biomass of the forest. The basic reproductive pattern for most lauraceous species at Monteverde is to fruit once a year, four to 12 months after flowering (Fig. 1a-y). As this paper demonstrates, that basic pattern is commonly violated. During flowering, lauraceous species display thousands or millions of small (2-4 mm diameter) light-colored flowers in panicles. The flowers are visited (and presumably pollinated) mainly by flies, bees, and



wasps. In any month of the year, at least one lauraceous species can be found with ripe fruit at Monteverde (Wheelwright, 1985a). Two species are dioecious, including one (*Ocotea bernouliana* (= *O. tenera*: B. Hammel, pers. comm.) in which some individuals switch from the production of female flowers to the production of male flowers with age (N.T. Wheelwright, unpublished data). Lauraceous fruits are distinctive because of their

large size, high protein and lipid content, and large single seed (Snow, 1973; Wheelwright *et al.*, 1984). Because they produce 'high investment' fruits, the Lauraceae allegedly exemplifies one extreme fruiting strategy in McKey's (1975) model, in which fruit quality is predicted to be positively correlated with dispersal quality by specialized seed dispersers. The Lauraceae has accordingly played a key role in the development of the theory of coevolution be-

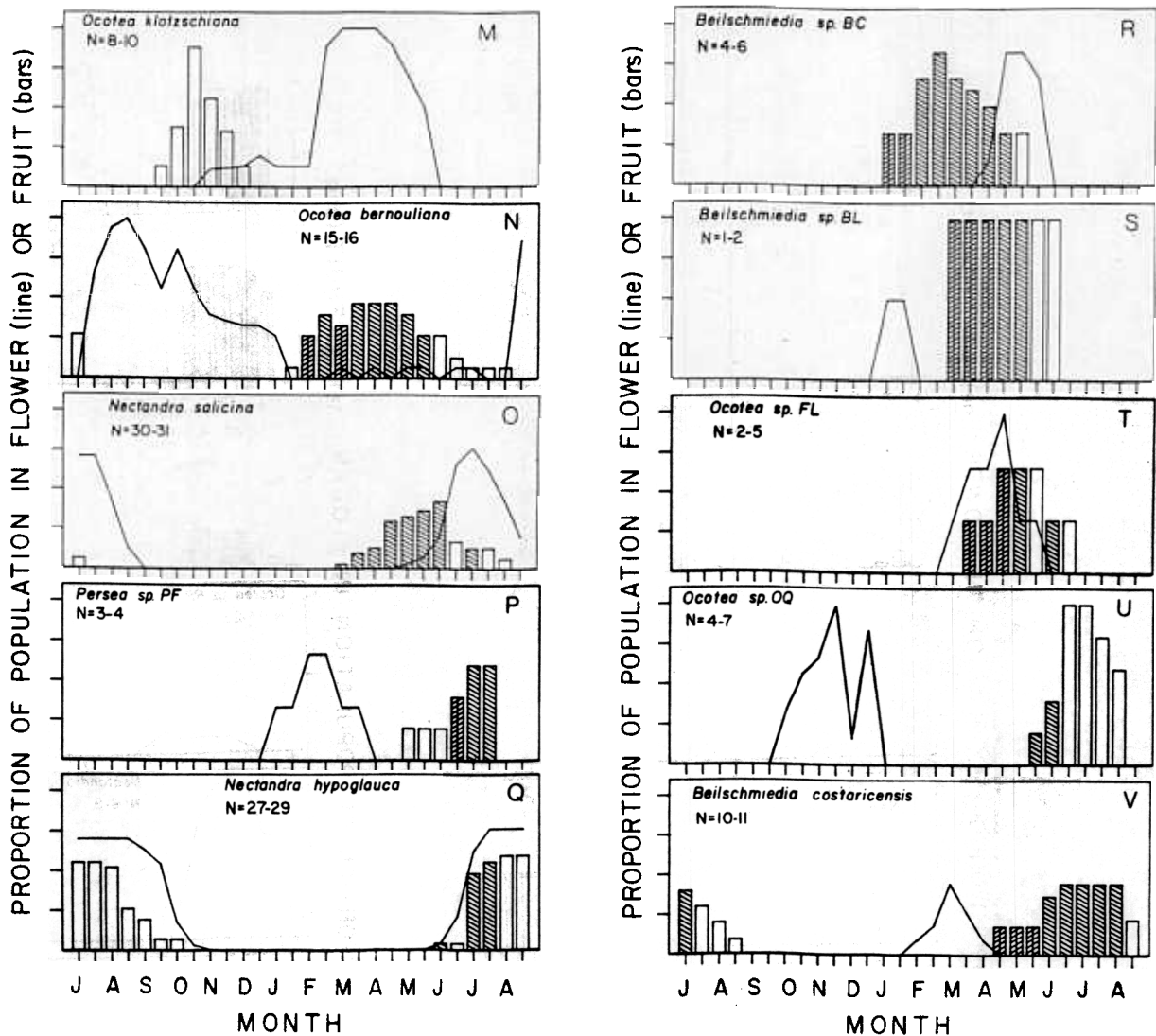


Fig. 1a-v. Seasonal flowering and fruiting phenologies of 22 bird-dispersed tree species in the Lauraceae of Monteverde, Costa Rica in 1980-1981. Solid lines = percent of population with open flowers. Bars = percent of population with ripe fruits. Shading of bars corresponds to mean level of fruit production (double-hatched = heavy; single-hatched = moderate; open = light).

tween fruiting plants and their seed dispersers (McKey, 1975; Howe and Estabrook, 1977; Wheelwright and Orians, 1982).

Annual crop sizes range from a single fruit in understory species to as many as 100,000 in fecund individuals of small-fruited species. The modal crop size among the group as a whole is about 20,000 fruits. The trees' major seed dispersers, birds such as Resplendent Quetzals (*Pharomachrus mocinno*), Three-wattled Bellbirds (*Pro-*

*nias tricarunculata*), Emerald Toucanets (*Aulacorhynchus prasinus*), and Mountain Robins (*Turdus plebejus*), swallow lauraceous fruits entire, regurgitating the seeds 15-60 min later. Only one to five fruits (depending upon fruit and bird size) are consumed per feeding bout.

#### *Quantifying reproduction in the Lauraceae*

Since June 1980 I have monitored reproduction in

286 marked trees, representing 22 species. Individual trees of six of these species were observed during 1979 as well. For the 16 commonest species, I was able to observe five or more individuals (the minimum sample size recommended by Fournier and Charpentier, 1975) over at least a six-year period (median = 10 trees/species; total = 265 trees); all but three of those species generally had developing fruits during each census period (see below). The reproduction of the other six lauraceous species, which are rarer or more local in distribution, is discussed only briefly here. A detailed analysis of seasonality in flowering and fruiting within the 'guild' of lauraceous species is presented in Wheelwright (1985a), where the methods of recording reproductive states are described in detail.

The periods of this study included June through August 1979; June 1980 through July 1981 (Fig. 1a-v); and 10-14 days in each of the following months: March 1982, February 1983, August 1983, February 1984, and March 1985. At biweekly intervals during these periods (except 1979) I censused all 286 trees along the transect. Censuses were also conducted monthly from August 1981 through July 1982 for a subsample of three trees per species.

During each census I examined every tree with binoculars or a spotting scope from a distance of five to 30 m (depending upon the height of the tree) and noted the production of new leaves, flowers, or fruits. I also recorded the developmental stage of fruits during each census. The intensity of vegetative growth, flowering, or fruiting for each individual was scored as 0, 1, 2 or 3, depending on whether 0%, 1-25%, 26-75%, or >75% of the canopy area showed activity. This method estimates total fruit availability in the forest in only a general way because trees differ in size. However, the method had several advantages over methods such as counting fruits on each tree (although the results of both methods are correlated). By being less time-consuming, it allowed me to monitor a larger proportion of the population. Additionally, it yields an estimate of reproductive effort unbiased by the size of trees: the method distinguished modestly fruiting, massive individuals from massively fruiting, modest-sized individuals, even when the two have similar fruit crop sizes.

My estimates of mature fruit crop sizes are based mainly on crop sizes of developing fruits noted at the same time each year. Observations of reproductive status in February or March give a reasonable estimate of fruit crop size at ripening for most species, irrespective of the stage of fruit development at the time of the census. Lauraceous species at Monteverde require an average of 8.6 months to develop ripe fruits following flowering (cf. Fig. 1a-v). Fruit crop sizes can be easily measured even when developing fruits are minuscule. Most species ripen their fruits within a few months of my annual censuses (Fig. 1a-v; Wheelwright, 1985a; cf. Foster, 1982a). Moreover, the majority of species bear fruits in brightly colored expanded pedicels which remain on the plant for up to several weeks after fruits have been removed, so fruit crop sizes can be estimated even for species that have already begun fruiting.

Fruit abortion (which usually takes place within several weeks of flowering) and pre-dispersal seed predation reduce absolute fruit numbers in many lauraceous species (N.T. Wheelwright, unpublished data). However, given the general scoring system used in this study, my dry season censuses accurately indicated both the proportion of the population that ultimately fruited as well the size of the ultimate fruit crop size. This was confirmed by comparing mid-February census estimates of fruit crop size with estimates when fruits of each species had matured in 1981, the year for which I have complete annual records for the entire sample of trees. Fruit crop sizes in February were strongly correlated with fruit crop sizes at ripening (mean  $r = 0.79 \pm 0.22$ , range = 0.42-1.00,  $P < 0.5$ ,  $N = 13$  species). Space constraints prevent the presentation of complete records for individual trees. Copies of the original data may be obtained by writing the author.

## Results

### *Variation in fruit production: differences between years and species*

Fruit production fluctuated annually (Fig. 2, Fig

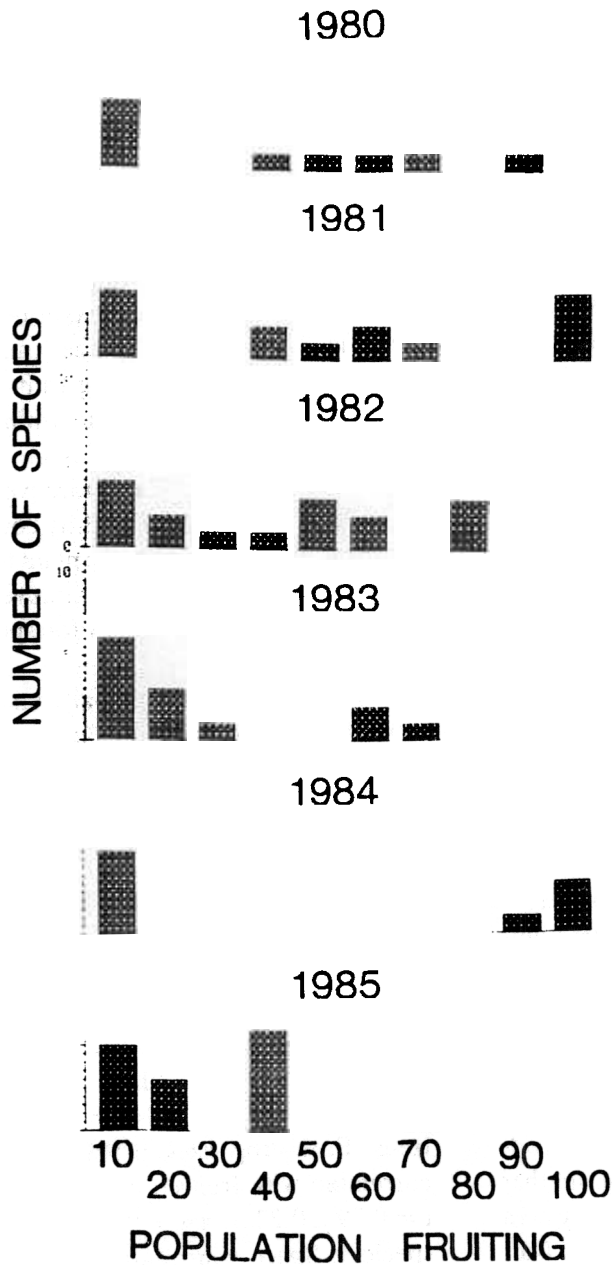
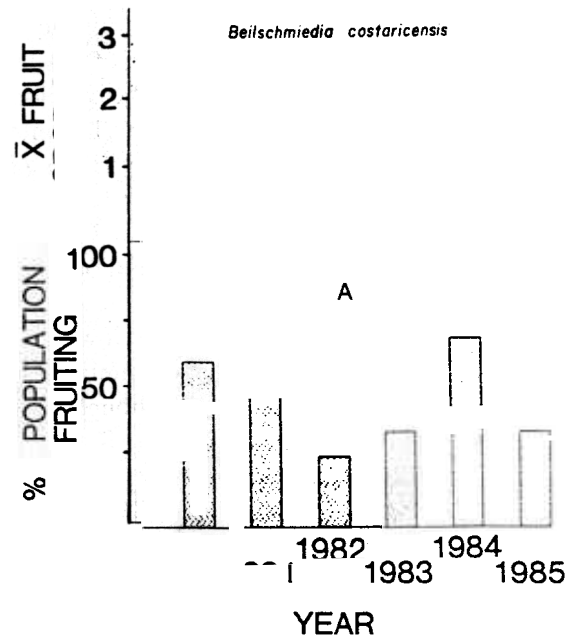
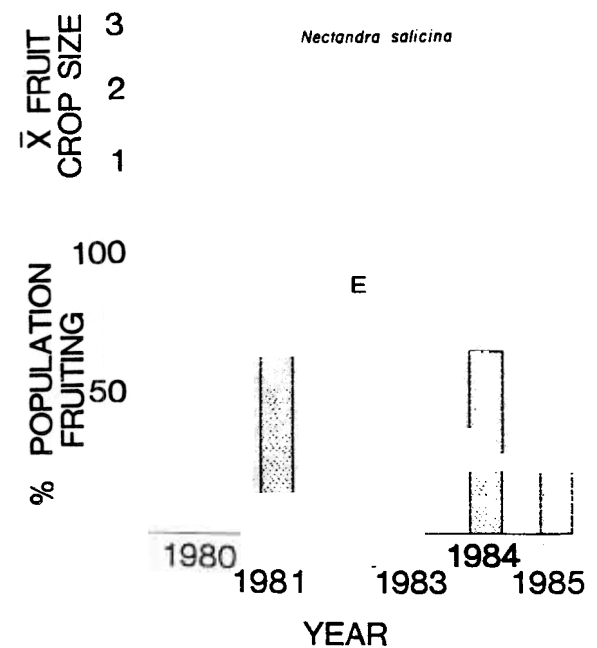
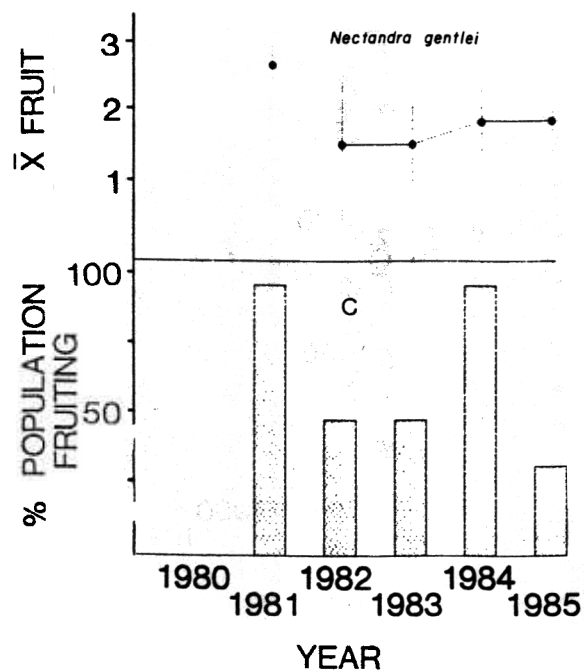
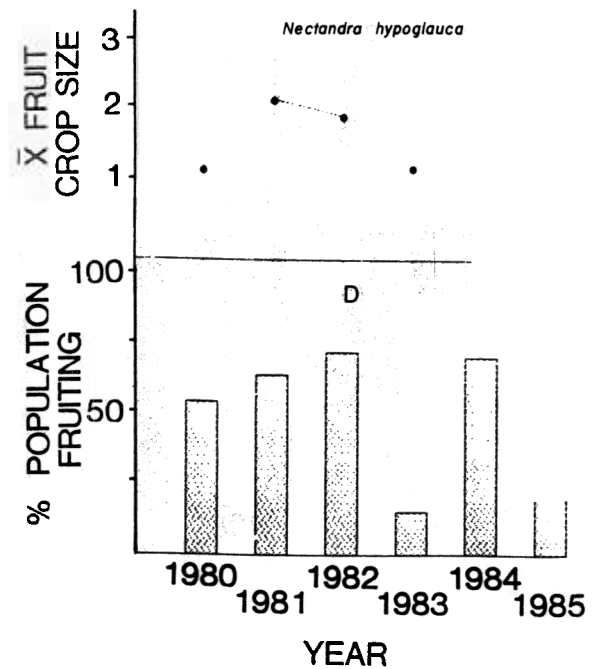
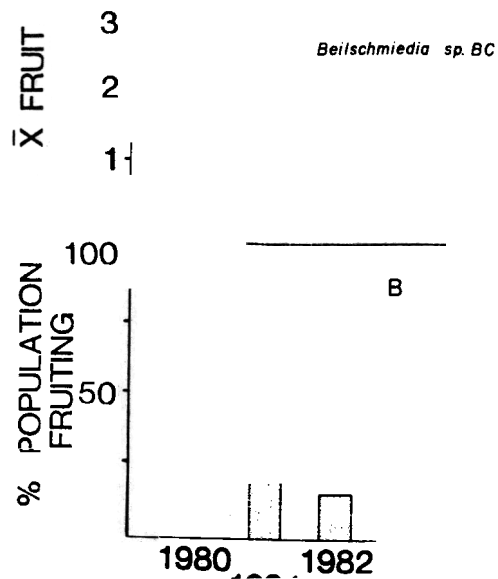


Fig. 2. Frequency distribution of the percent of the population of each of 16 lauraceous species producing fruits in different years.

year during which over 50% of the population of most species bore fruit. Both 1982 and 1983 were years of low fruit production. In 1984, as in 1979 and 1981, most trees of most species produced fruit. In 1985 fruit levels were exceedingly low: in 14 of the 16 commonest tree species, less than 40% of the population set fruit (Fig. 2). Thus, considering the Lauraceae as a whole, there were three 'boom' years and four 'bust' years over the course of this study. 'Boom' years were always separated by at least one 'bust' year.

Different tree species skipped reproduction in different years (Fig. 3a-m) - a 'boom' year for one species was not necessarily a 'boom' year for another. Even congeners varied in annual fruit production. 1980 was a prolific year for three lauraceous species favored by birds (*B. costaricensis*, *N. hypoglacua*, and *O. wachenheimii*); the same year was barren for three congeners that are also critical for birds (*B. mexicana*, *N. salicina*, and *O. tonduzii*) (Fig. 3a-m). 1985 was an unproductive year for most species, including *B. costaricensis*, but one of the most productive years for *B. mexicana*. Thus, if there were specific environmental cues responsible for between-year variation in fruit production in the Lauraceae, related tree species responded differently to them.

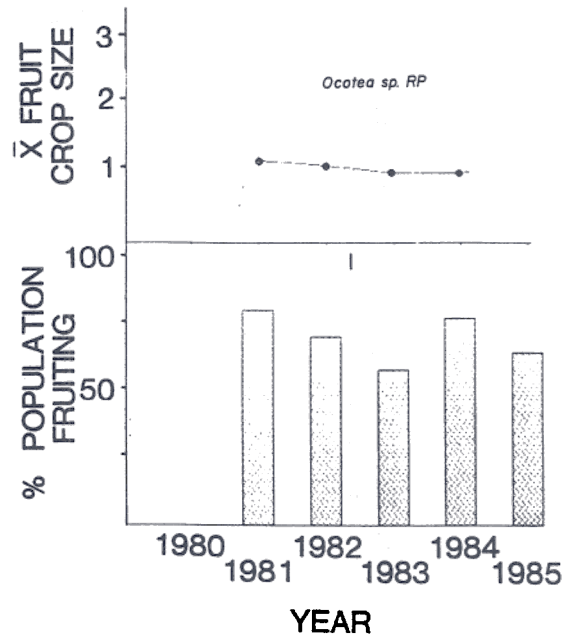
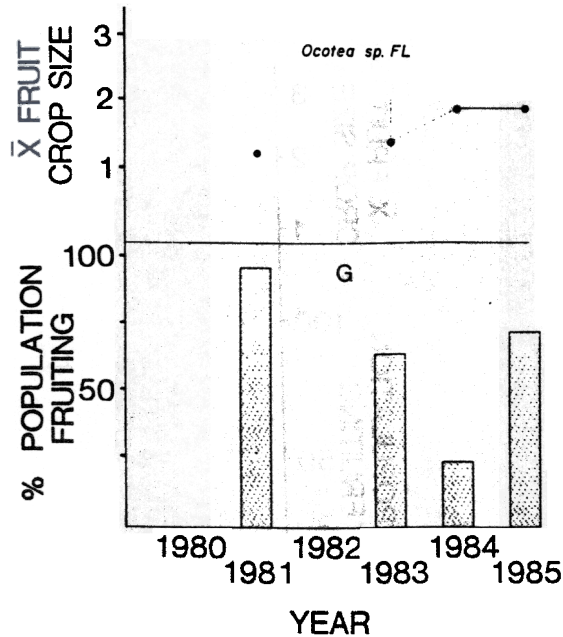
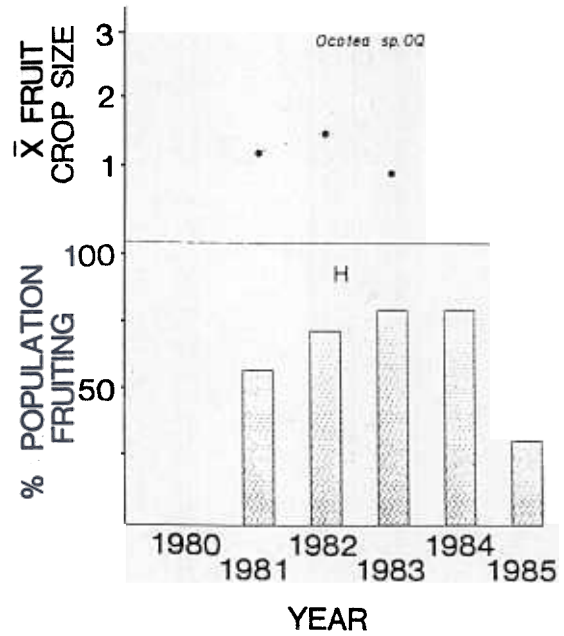
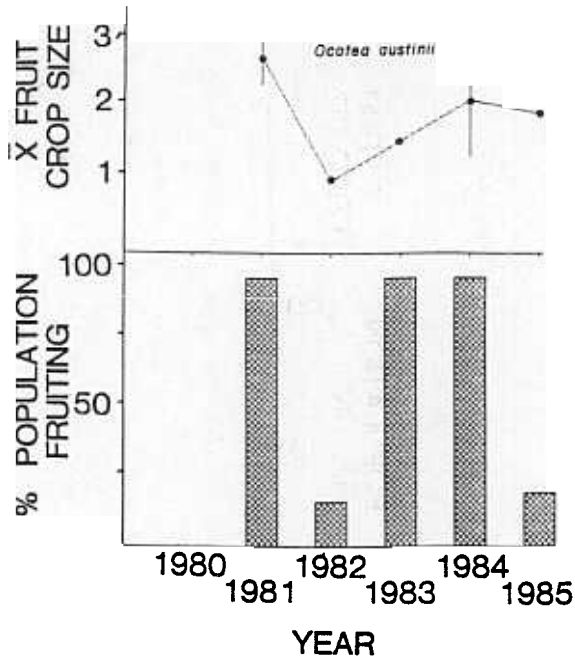




#### Annual variation in fruit production among individuals

Individual trees within species fruited in different years (Fig. 3a-m, lower graphs). Trees that did fruit also varied with respect to how much fruit they produced each year (Fig. 3a, upper graphs). Some

individuals failed to fruit during the entire study period. Fruit production within a given year was rarely uniform within a population; seldom did either 0% or 100% of a population produce fruit. More typically, an intermediate proportion (40-80%) of each population produced fruit in a given year (Fig. 3a-m). Even in 'boom' years, a portion



of the population of most species failed to fruit. Because the seasonal timing of flowering and fruiting in reproductively active individuals was quite synchronous (Fig. 1a-v), and all individuals in the study were mature trees, between-year asynchrony in fruit production did not result from individually staggered seasonal phenologies or the inclusion of reproductively immature trees in the sample.

Table 1 illustrates year-to-year variation among

individual trees of one species, *B. costaricensis*. The species bears moderate crops of bulky fruits typically produced at about two-year intervals. Yet some trees missed fruiting periods, bearing fruits only twice during six years. Other trees fruited (at low levels) during six of the seven years. Even trees with relatively regular reproductive cycles fruited asynchronously. Trees 51, 55, 61, 67, 69, 70, and 71 all occur within several hundred meters of each



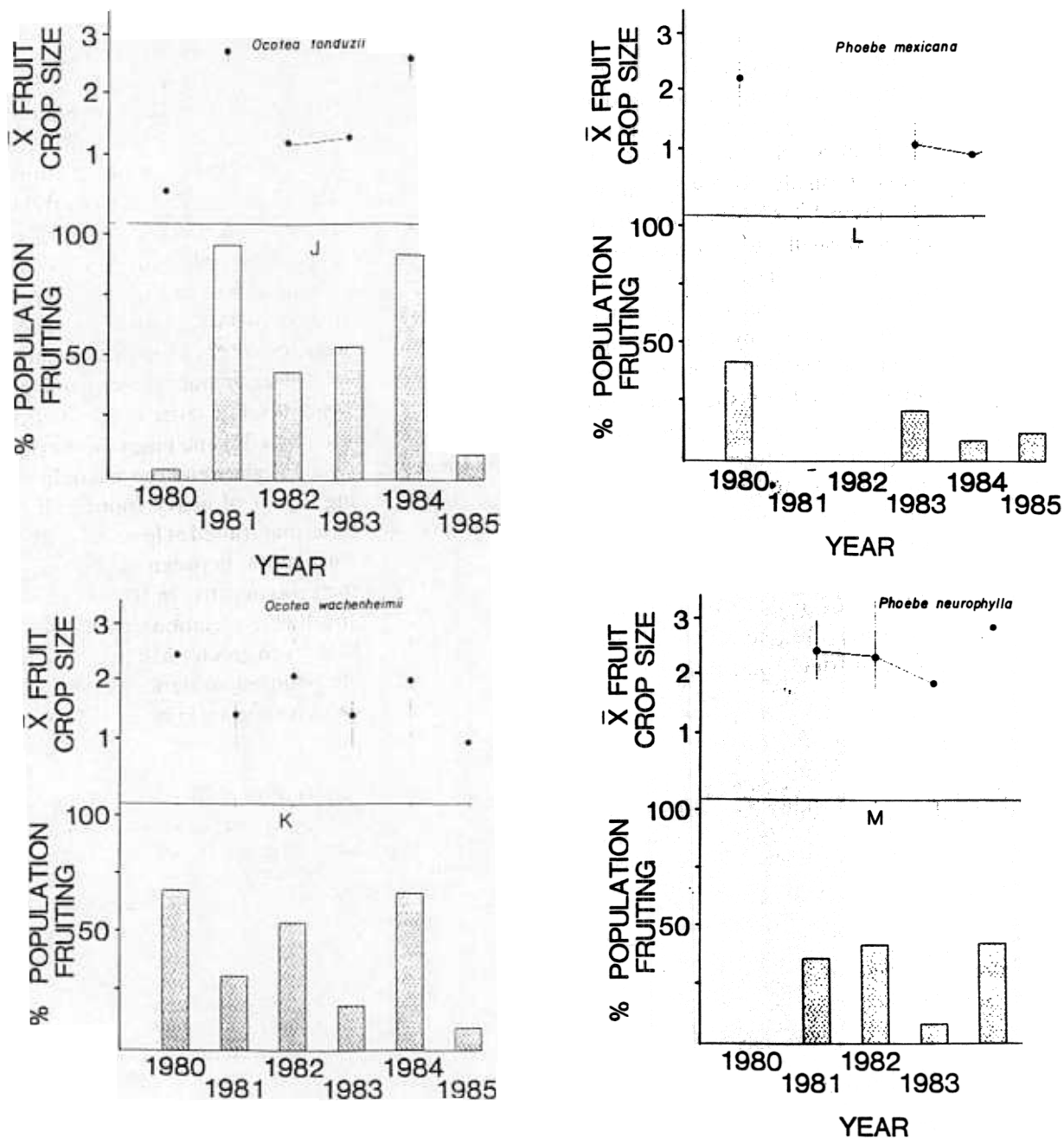


Fig. 3a-m. Above: Annual variation in mean value of index of fruit production ( $\pm 1$ SD) from 1980 through 1985 for reproductively active individuals of 13 lauraceous tree species. The index corresponds to no (0), low (1), moderate (2), and high (3) fruit production (see Methods). Below: percent of the population producing fruit in different years. Sample sizes presented in Table 2.

other, yet they showed distinct cycles (Table 1). Examples of such variability within populations could be drawn from other species. One large, vigorous individual *N. salicina*, for instance, failed to fruit from 1980 to 1984; it produced a large crop

in 1985, a year in which less than a third of the *N. salicina* population fruited. On the other hand, annually fruiting species such as *N. davidsoniana* and *O. bernouliana* (= *O. tenera*) seemed remarkably synchronous and constant in their annual fruit production (cf. Table 3).

*Year-to-year differences in climate and fruit production*

There was no straightforward relationship between fruit production and rainfall during the preceding year as might have been expected (Alvim and Alvim, 1978; Opler *et al.*, 1976). For example, 1980 was unusually wet (3051 mm of rainfall) and was followed by a year of high fruit production; 1983 was unusually dry but was also followed by a year of high fruit production. Likewise, 1982 and 1983, both years in which fruit production was quite low, were preceded by years of high (3234 mm) and average (2581 mm) rainfall, respectively. Mean annual rainfall for the years preceding the three 'boom' years was 2483 mm, only slightly below the 28-yr mean. In terms of the monthly distribution of rainfall, the three 'boom' years shared little in common except abnormally dry Aprils. Temperature extremes and average annual temperatures, which may have affected floral initiation (Buttrose and Alexander, 1978), differed little over the course of the study and indicated no correlation with subsequent fruit production.

*Previous reproductive efforts and variation in fruit production between years*

In some species, an individual tree that produced many fruits one year was likely to produce few fruits the next year (Table 2). I examined the relationship between fruiting efforts in consecutive years, and found negative correlations in nine of 15 species, suggesting the possibility of trade-offs in reproductive allocation between years. However, fruiting efforts in successive years were positively correlated in the other six species. Sample sizes were too small or seasonal phenologies inappropriate for examining the remaining species. In most cases absolute correlation coefficients were rather low ( $r < 0.30$ ) and insignificant ( $P > 0.10$ ); there was only a slight trend toward reduced fruiting following a year of heavy fruiting. If I considered only trees that fruited at least twice during the study, the correlation between successive reproductive efforts was negative in 11 of the 15 species, with larger absolute correlation coefficients. The trend may have been greater had there not been an inexplicably positive correlation between flowering levels in successive years in nine of 15 species. The relation-

*Table 1.* Reproductive records for *Beilschmiedia costaricensis* illustrating individual variability in fruit crop size and reproductive periodicity in one species in the Lauraceae. Other species show similar variability, although with less of a tendency towards biennial fruit production. Although the proportion of the population that fruited each year varied relatively little and the mean size of fruit crops was similar (Fig. 3a), individual trees fruited out of synchrony with each other and differed in the number of fruits produced in different years. 3 = heavy fruit production, 2 = moderate fruit production, 1 = light fruit production, 0 = no fruits produced, - = not observed (see Methods).

Tree No	Year							
	1979	1980	1981	1982	1983	1984	1985	1986
11		0	0		0	3	0	
32		3	0	0	0	3	0	0
38		3			0	0	3	0
						2		
55			0			2	0	
61			0	0	0	0	3	
67			2	0			3	
69				0				
		0		0	0		0	
				0	0		0	

ship between fruit production in a given year and fruit production two years later was even less clear ( $r < 0$  in seven species,  $r > 0$  in eight species). Fruit production and the production of new leaves in the same year were negatively correlated in 12 of the 15 species, with greater absolute correlation coefficients (Table 2).

#### *Reproductive patterns within the Lauraceae*

There appear to be three general reproductive patterns within the Lauraceae: erratic moderate-level fruit production, periodic prolific fruit production, and consistent low-level fruit production. Most species can be assigned to one, depending upon their average fruit crop sizes and the regularity with which they produce fruit (Table 3), although there is some overlap between the groupings. The groupings cut across generic classifications, fruit traits, seasonal phenologies, and habitats (*cf.* Monasterio and Sarmiento, 1976).

The erratic moderate-level fruiterers have fruit crops of variable sizes. What unites species in this

group is that they produced little or no fruit during most years of the study but produced substantial crops during one or two years. Individuals and populations alike were inconsistent in reproduction. The group includes all three species in the genus *Phoebe*, plus species in three other genera. Of 38 individual *Phoebe* trees, only four fruited more than twice during the study period, and none fruited more than three times, despite requiring relatively little time (four to six months) to develop their fruits (Fig. 1m, p). (Even though *Phoebe mexicana* flowers and fruits between censuses, the lack of flower primordia, empty cupules, and vegetative growth indicated no reproduction.) On average, individual trees within species in this group fruited during 18% (SD = 9%, range = 11–29%) of the years of the study. Many trees fruited only once or not at all during six years of observation. When fruit production was high, however, birds fed readily on fruits of these species.

The periodic prolific fruiterers seemed to show more regular, although supra-annual, fruiting cycles than the erratic, moderate-level fruiterers; when

Table 2. Correlation ( $r$ ) between fruit production in present vs. previous years, and between fruit production vs. vegetative growth in the same year from 1980 through 1985. There was a relatively weak trend towards reduced fruit production following a year of heavy fruit production. Vegetative growth and reproduction were more negatively correlated in most species.

Tree species	Correlation coefficient: current vs. previous fruiting	No. successive plant-years	Correlation coefficient: fruiting vs. vegetative growth	No. successive plant-years	No. individual trees
<i>B. mexicana</i>	-.22	21	-.33	27	6
<i>B. costaricensis</i>	-.44**	42	-.56	55	12
<i>N. gentlei</i>	-.07	24	-.09	31	7
<i>N. hypoglauca</i>	.00	102	-.28*	135	30
<i>N. salicina</i>	.05	104	.14	135	29
<i>O. austinii</i>	-.43	21	-.67	27	6
<i>O. bernouliana</i>	.58**	56	-.15	73	16
<i>O. sp. F1</i>	-.28	7	.09	14	5
<i>O. sp. K2</i>	-.07	20	-.06	27	6
<i>O. sp. RP</i>	.13	39	.11	52	12
<i>O. tonduzii</i>	-.42**	110	-.09	142	30
<i>O. wachenheimii</i>	-.18	34	-.31*	49	12
<i>Persea veraguensis</i>	.41	12	-.12	15	3
<i>Ph. mexicana</i>	.23*	85	-.07	113	25
<i>Ph. neurophylla</i>	-.03	39	-.16	56	14

\*  $P < .01$

$P < .05$

they did fruit, they did so abundantly. Their reproduction is reminiscent of temperate zone mast seeders (Rehfeldt *et al.*, 1971; Silvertown, 1980). The reproductive behavior of these trees strongly influenced the movements and behavior of fruit-eating birds and set the rhythm of the forest from the standpoint of birds that depend on lauraceous fruits. Yet these tree species have low constancy and only moderate consistency (*sensu* Colwell, 1974; Putz, 1979) of fruit production. On average, individual trees in this group fruited during 43–72% of the years of the study, depending upon species ( $\bar{x} = 55\%$ ,  $SD = 9\%$ ). The coefficient of variation (CV) of fruit crop size index ranged from 0.48–1.16 ( $\bar{x} = 0.64$ ,  $SD = 0.25$ ).

The consistent low-level fruiterers annually produced small crops of fruits that were removed slowly. These species are the between-year analogues of within-year 'tricklers' (Smythe, 1970). Trees of different species fruited during an average of 84% of years ( $SD = 6\%$ ), with a CV of fruit crop size index of only 0.29–0.47 ( $\bar{x} = 0.37$ ,  $SD = 0.09$ ). *N. davidsoniana*, with moderate to large fruit crops, is distinct, but like the other species in this group, its fruits are not highly favored by birds. By and large, the group is of minimal importance to fruit-eating birds. There was no correlation between fruit size and reproductive pattern (Table 3), but consistent fruiterers tended to be species of smaller stature (*cf.* Silvertown, 1980).

*Table 3.* Three general patterns of fruit production within the Lauraceae at Monteverde. Mean crop size and variability in crop size refer to annual levels in the population as a whole. Consistency of population refers to the regularity with which populations fruited during the study period; consistency of individuals reflects the mean frequency during the study period that individuals of each species produced fruit. Note that phenological patterns cut across genera. Species designated with asterisks were classified on the basis of observations during only two years (\*) or censuses of fewer than five individuals (\*\*).

Tree species	Fruit size (g)	Mean fruit crop size	Variability in crop size	Consistency of population	Consistency of individuals
<b>Erratic moderate level fruiterers</b>					
<i>Phoebe mexicana</i>	1.4	moderate	moderate	low	low
<i>Ph. neurophylla</i>	1.6	high	moderate	low	low
<i>Nectandra gentlei</i>	1.0	moderate	high	moderate	low
* <i>Persea sp. RP</i>	0.3	low	moderate	low	moderate
<i>Ocotea sp. FL</i>	9.3	low	moderate	low	moderate
** <i>N. sp. NC</i>	1.0	low	?	low	low
<b>Periodic prolific fruiterers</b>					
<i>N. salicina</i>	7.4	moderate	moderate	low	moderate
<i>O. wachenheimii</i>	2.9	high	low	moderate	
<i>O. tonduzii</i>		high	high	low	moderate
<i>O. austinii</i>	1.3	high	high	moderate	moderate
<i>Beilschmiedia mexicana</i>	12.9	moderate	moderate	low	high
<i>B. costaricensis</i>	12.4	high	high	moderate	high
<i>N. hypoglauca</i>	5.5	high	high	moderate	high
** <i>B. sp. BI</i>	15.2	moderate	?	?	high
<i>P. veraguensis</i>	0.7	high	high	low	low
** <i>P. sp. PF</i>	5.0	high	?	low	low
<b>Consistent low-level fruiterers</b>					
* <i>O. klotzschiana</i>	6.0	low	low	high	high
<i>O. sp. RP</i>	1.4	low	low	high	high
<i>O. bernouliana</i>	6.6	low	low	high	high
* <i>N. davidsoniana</i>	3.3	moderate	low	high	high
<i>O. sp. K2</i>	7.4	low	moderate	high	high
* <i>O. sp. OD</i>	0.9	low	low	high	high

*Importance of lauraceous fruits for birds*

The 'failure' of lauraceous fruit crops in certain years must affect the birds that rely on these fruits for food, just as fruit failure on Barro Colorado Island led to diet shifts and emigrations in fruit eating animals (Foster, 1982b). The diet of male Three-wattled Bellbirds consists chiefly of lauraceous fruits during the birds' breeding season (Snow, 1977; Table 4). I collected seeds from 'seed traps' (see Snow, 1970; Wheelwright, 1985b) suspended beneath the display perches of five male bellbirds from different parts of the study area. Lauraceous fruits made up the majority of fruits eaten by each bellbird (60–78%; Table 4). In terms of fruit mass or caloric content, lauraceous fruits comprised a substantially higher proportion of bellbirds' diets because of the large size and high lipid concentration of lauraceous fruits (Snow, 1971; Wheelwright *et al.*, 1984). Lauraceous fruits were clearly critical elements of bellbirds' diets, but the birds did not appear tied to any one species. Rather, lauraceous species appeared interchangeable in space and time. Bellbirds whose perches were located in different habitats consumed different fruit species (Table 4). During the course of the five-month breeding season, birds shifted in

their use of different lauraceous fruit species as some species became scarce and others abundant.

Resplendent Quetzals depended on lauraceous fruits too, both for nestlings (81% of individual fruits delivered to the nest) and adults (80% of fruits whose seeds were recovered in seed traps beneath quetzal nest-guarding perches) (Wheelwright, 1983). Many other bird species, especially toucans and thrushes, commonly ate lauraceous fruits (Wheelwright *et al.*, 1984). A preference for certain fruits is not necessarily indicative of a dependence on them, of course. But in the case of quetzals, toucanets, and bellbirds, at least, there is evidence that the birds are strongly affected by lauraceous fruit abundance. During years of low fruit production, quetzals fed on unripe or low-growing fruits of other families (e.g., *Rubus rosae-folia* (Rosaceae)) or left the area entirely (Wheelwright, 1983). Toucanets began following army ant swarms or consumed fruits that they normally ignored (e.g., *Piper* spp.). Breeding by quetzals, bellbirds, and toucanets was apparently delayed during fruit shortages in 1983 and 1985 (pers. obs.). Quetzals' seasonal migrations between forest types appear linked to the phenologies of different lauraceous species (Wheelwright, 1983), and the morphology and geographical distribution of the genus

Table 4. Relative frequency of different lauraceous fruit species eaten by, and proportion of the fruit diet made up by lauraceous fruits for five male Three-wattled Bellbirds between March and July, 1981. Frequencies were calculated on the basis of number of seeds regurgitated (corrected for number of seeds/fruit). Diets were determined by identifying seeds recovered from seed traps.

Lauraceous fruit species	Bellbird no.				
	1	2	3	4	5
<i>B. costaricensis</i>	3.9	2.0	0	0	0
<i>N. sp. NC</i>	0.5	3.3	0	2.0	0
<i>N. gentlei</i>	0	0.2	0	0	0
<i>N. hypoglauca</i>	0	0	0	0	30.0
<i>N. salicina</i>	1.1	0	72.6	0	20.0
<i>N. sp. NY</i>	1.1	0	0	0	0
<i>O. austinii</i>	2.2	3.8	0	2.0	0
<i>O. sp. RP</i>	0	0	0	0.4	0
<i>O. tonduzii</i>	91.2	90.7	27.4	95.6	50.0
% of entire diet made up of lauraceous fruits	60.2	69.8	73.7	78.3	71
No. fruits eaten	303	602	99	323	14

*Procnias* seems related to their dependence on lauraceous fruits (Snow, 1973; see also Crome, 1975). Irregular irruptions of Emerald Toucanets to the lowlands of Costa Rica (G. Stiles, pers. comm.) conceivably occur during years in which lauraceous trees fail to produce fruit in highland forests.

## Discussion

Fruit production in tropical forests is inconstant, both within years (Snow, 1965; Hilty, 1980; Foster, 1982a; Wheelwright, 1985a) and between years (Foster, 1982b; Howe, 1983). This study demonstrates that reproduction in an important group of bird-dispersed tree species varies annually. During seven years, most Lauraceae at Monteverde, Costa Rica fruited prolifically in three years and produced relatively little fruit during four years. Still, individual trees and species fruited out of phase with the broader pattern. Consistency and predictability (Colwell, 1974) were higher at the community level than at the species or individual level (Putz, 1979). Although the data suggest a two- to three-year cycle in fruit production among Monteverde's Lauraceae, seven years is too short a time to detect such periodicity. Nonetheless, supra-annual reproductive cycles are known for many temperate tree species, especially conifers, oaks and beech (Gysel, 1956, 1971; McNeill, 1954; Rehfeldt *et al.*, 1971; Silvertown, 1980; Svårdson, 1957), and are suspected for certain tropical trees (Foster, 1982b). Surprisingly, only the studies of Gysel (1956) and Janzen (1978) present long-term data on marked individuals. The dearth of such studies has permitted a misconception about mast fruiting. Defined as synchronous reproduction at irregular intervals at a periodicity characteristic of the species (Silvertown, 1980), masting is probably rarely completely synchronous or periodic, and it is perhaps characteristic only of individuals, judging from this study.

Despite the high variation observed among individuals, fruiting was not random within species. Most individuals in a population at Monteverde tended to fruit at the same time within and between years, and fruit crop sizes were grossly similar

within the population. But many individuals bypassed reproduction in a given year or fruited irregularly. Occasionally individual trees fruited heavily at a time when their conspecifics had small fruit crops. Species within a genus seemed no more synchronous in between-year fruiting than species in separate genera. The family as a whole showed little consistent synchrony, even though there were years of general fruit scarcity or abundance.

Foster (1982b), among others, has hypothesized that supra-annual reproductive rhythms in tropical forests may be caused by cycles of depletion and replenishment of energy and nutrient reserves, entrained or reset by irregular climatic events (*cf.* Eis *et al.*, 1965). Alternatively, annual variation in reproduction could be favored by the advantage of escaping seed predators in time or discouraging the buildup of large predator populations (Janzen, 1976; Silvertown, 1980), designed to minimize competition for space during vegetative growth (Janzen, 1967), or caused by annually varying pollinator limitation (Baker *et al.*, 1983), competition for dispersers (Snow, 1965; Stiles, 1977), or climatic fluctuations (Alvim and Alvim, 1978).

None of these hypotheses completely explains annual variation in fruit production within the Lauraceae of Monteverde. The 'allocation' hypothesis (Harper, 1977; Foster, 1982b) receives some support from this study. Fruit production in a given year was negatively correlated with the previous year's reproductive effort in the majority of species. Nonetheless, absolute correlation coefficients were low and mostly insignificant. More convincing is the evidence that vegetative growth and fruit production in the same year are negatively correlated in 12 of 15 species. Larger sample size and more detailed estimates of fruit crop size may clarify the relationship between fruit production and vegetative growth or previous reproduction.

The 'seed predation' hypothesis, unlike the 'allocation' hypothesis, predicts tight between-year synchrony within populations (see Augspurger 1981). Such was not the case in the Lauraceae of Monteverde. The fact that seed predation is extremely high suggests that the selection pressure for synchronous fruiting exists. Moreover, pre-dispersal predation (chiefly by weevils) was most se-

vere among the erratic and periodic fruiterers (Table 3), and rather low in most species of consistent, low-level fruiterers (although it is not obvious whether this is cause or effect of phenology). Post-dispersal seed predation rates (caused mainly by heteromyid rodents) were uniformly high (approaching 100%) except for the genus *Beilschmiedia*, whose seeds are protected by a stony endocarp (N.T. Wheelwright, unpublished data). As for the 'pollinator limitation' and 'community coadaptation' hypotheses, I have no data to test the former, and the latter is discredited on a number of grounds (Poole and Rathcke, 1979).

Annual variation in fruit production did not seem obviously related to climatic variability, but more detailed measurements of the yearly distribution of rainfall need to be made. I suspect that annual variation in fruit production results from a combination of life-history trade-offs (previous reproductive efforts, vegetative growth: cf. Bull and Shine, 1979), responses to climatic variation (Foster, 1982b), and changes in pollinator abundance and behavior.

#### *Variance in reproductive success among trees*

Several species in this study produced perplexingly few fruits over a six-year period. *Ocotea sp. RP*, a common canopy tree of the lower montane rain forest, provides one example. I systematically observed 12 individuals over the study period and casually noted fruit production in another dozen individuals. I estimated that the entire sample of 24 trees produced no more than 10,000 fruits over a six-year period. Most trees bore fewer than 100 1.4-g fruits each year, despite producing hundreds of thousands of insect-pollinated flowers yearly. This contrasts with *O. tonduzii*, a species similar in habitat, stature, and fruit size. Single *O. tonduzii* individuals bore up to 100,000 fruits in a season. Because the odds are so minimal that any fruit will be swallowed, its seed safely dispersed, and the seedling spared being shaded out, destroyed by herbivores, or buried by a treefall, it is hard to imagine that the infertile *O. sp. RP* individuals in my sample are actually replacing themselves or dispersing many successful propagules. Nothing in

their seed or seedling biology suggests unusually high survival to compensate for low fecundity. Rather, it seems probable that a fraction of the population, located in distinct habitats, may be responsible for most successful reproduction. Large portions of a forest may be suitable for a plant's growth, but only fragments of the habitat – or perhaps only other habitats – may support reproduction as well. Strong winds blow year – round across the lower montane rain forest: quite possibly, insect pollination and high seed set occur only in sheltered coves, even though seeds may be dispersed and seedlings survive in open areas. Thus, the conspicuous trees that constitute the overwhelming biomass in certain habitats may owe their presence to a constant rain of propagules from some other part of the forest where conditions favor reproduction.

The demonstration that individual trees and species vary from year to year in fruit production raises the question of how fruit-eating birds are affected. In temperate zone conifers, supra-annual cycles in reproduction lead to major movements of certain birds species (Bock and Lepthien, 1976; Svärdsön, 1957) and influence the timing of reproduction in others (Ligon, 1978). Irruptions may occur as well in tropical fruit-eating birds. Conceivably, some life history features of fruit-eating birds, such as the delay in reproductive maturity typical of many species, are related to supra-annual cycles of fruit production in a manner analogous to seed-eating insects (Kraft, 1968). Only long-term studies of both trees and birds will determine the effect on birds of annual variation in fruit production in the trees on which they depend.

#### **Conclusion**

It is commonplace to note that we need long-term studies of marked individuals to provide answers to critical ecological questions. I bother echoing this appeal in the case of studies of plant reproduction because the data are relatively effortlessly obtained. Although only a handful of such studies have been published on tropical, or even temperate zone trees, many researchers doubtless have

gathered data similar to those presented in this paper. Annual monitoring of trees bordering one's study site (or one's backyard), if carried out with careful records over several decades, would be enormously valuable. Phenological observations need be neither highly quantitative nor very frequent in order to make a contribution, given that we have so little information on lifetime patterns of reproduction in long-lived plants. Records of simple presence or absence of fruits, or, better yet, qualitative indices of fruit production such as those presented here, would be useful. The validity of infrequent phenological sampling should be checked against more frequent censuses. Sampling biases to be aware of when establishing a census transect include the non-random selection of census trees (such as trees along a path, or conspicuously fruiting trees).

Seven years is far from 'long-term,' but the results of this study illustrate that the period is long enough to show annual variation in fruit production among individuals and species, and to suggest supra-annual reproductive periodicity in tropical trees.

#### Acknowledgements

Earlier versions of this paper were improved by the comments of Alejandro Estrada, Ted Fleming, Charlie Janson, Sarah Sargent, David Snow and Mark Witmer. Bob Lawton and John Campbell graciously supplied meteorological information. Bill Haber introduced me to the Lauraceae of Monteverde. Jim Wolfe conducted most of the phenological observations for the year 1981–1982. I would like to express appreciation to the entire Monteverde community and to acknowledge support from the Organization for Tropical Studies, Sigma Xi, the National Science Foundation, a National Academy of Sciences John Henry Grant, a Carr Postdoctoral Fellowship at the University of Florida, and the Section of Ecology and Systematics, Cornell University.

#### Literature cited

- Alvim, P. de T. and R. Alvim. 1978. Relation of climate to growth periodicity in tropical trees. In: *Tropical trees as living systems* (eds. P.B. Tomlinson and M.H. Zimmermann). Cambridge Univ. Press, New York. pp. 445–464.
- Augsburger, C.K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775–788.
- Baker, H.G., K.S. Bawa, G.W. Frankie and P.A. Opler. 1983. Reproductive biology of plants in tropical forests. In: *Tropical rain forest ecosystems* (ed. Golley, F.B.). Elsevier Sci. Publ. Co., New York.
- Bock, C.E., and L.W. Lephien. 1976. Synchronous eruptions of boreal seed-eating birds. *Am. Nat.* 110: 559–571.
- Bull, J.J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* 114: 296–303.
- Buttrose, N.S. and E.D. Alexander. 1978. Promotion of floral initiation in Fuerta avocado by low temperature and short daylength. *Scientia Hort.* 8: 213–217.
- Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55: 1148–1153.
- Crome, F.H.J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Aust. Wild. Res.* 2: 155–185.
- Eis, S., E.H. Garman and L.F. Ebel. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* Dougl.), and western white pine (*Pinus monticola* Dougl.). *Can. J. Bot.* 43: 1553–1559.
- Foster, R.B. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. In: *The ecology of a tropical forest* (eds. E.G. Leigh, Jr., et al.), pp. 151–172. Smithsonian Institution Press, Washington, D.C.
- Foster, R.B. 1982b. Famine on Barro Colorado Island. In: *The ecology of a tropical forest* (eds. E.G. Leigh, Jr. et al.), pp. 201–212. Smithsonian Institution Press, Washington, D.C.
- Fournier, L.A. and C. Charpentier. 1975. El tamaño de la muestra y la frecuencia de las observaciones en el estudio de las características fenológicas de los árboles tropicales. *Turrialba* 25: 45–48.
- Frankie, G.W. 1975. Tropical forest phenology and pollinator-plant coevolution. In: *Coevolution of animals and plants* (eds. L.E. Gilbert and P.H. Raven), pp. 192–209. Univ. Texas Press, Austin, Texas.
- Frankie, G.W., H.G. Baker and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecology* 62: 881–919.
- Gysel, L.W. 1956. Measurements of acorn crops. *Forest. Sci.* 2: 305–313.
- Gysel, L.W. 1971. A 10-year analysis of beechnut production and use in Michigan. *J. Wildl. Manag.* 35: 516–519.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, New York.



- Hilty, S.L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12: 292–306.
- Holdridge, L. 1967. Life zone ecology. Tropical Science Center Publ., San José, Costa Rica.
- Howe, H.F. 1983. Annual variation in a neotropical seed-dispersal system. In: *The tropical rain forest: ecology and management* (eds. S.L. Sutton *et al.*), pp. 211–227. Blackwell Sci. Publ., Oxford.
- Howe, H.F. and G.F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111: 817–832.
- Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21: 620–637.
- Janzen, D.H. 1976. Why bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* 7: 347–391.
- Janzen, D.H. 1978. Seeding patterns of tropical trees. In: *Tropical trees as living systems* (eds. P.B. Tomlinson and M.H. Zimmerman) pp. 83–128. Cambridge Univ. Press, New York.
- Kraft, K.J. 1968. Ecology of the cone moth *Laspeyresia tortueta*, in *Pinus banksiana* stands. *Annals Ent. Soc. Amer.* 61: 1462–1465.
- Lawton, R. and V. Dryer. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101–116.
- Ligon, D.J. 1978. Reproductive interdependence of pinyon jays and pinyon pines. *Ecol. Monogr.* 48: 111–126.
- McClure, H.E. 1966. Flowering, fruiting, and animals in the canopy of a tropical rainforest. *Malay. For.* 29: 182–203.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. In: *Coevolution of animals and plants* (eds. L.E. Gilbert and P.H. Raven), pp. 159–191. Univ. Texas Press, Austin, Texas.
- McNeill, W.M. 1954. Observations on cone and seed production in plantations of Scots Pine in Scotland. *Forest.* 27: 122–133.
- Medway, L. 1972. Phenology of a tropical rainforest in Malaya. *Biol. J. Linn. Soc.* 4: 117–146.
- Milton, K., D.M. Windsor, D.W. Morrison and M.A. Estribi. 1982. Fruiting phenologies of two tropical *Ficus* species. *Ecol.* 63: 752–762.
- Monasterio, M. and G. Sarmiento. 1976. Phenological strategies of plant species in the tropical savannah and the semi-deciduous forest of the Venezuelan llanos. *J. Biogeogr.* 3: 325–356.
- Opler, P.A., G.W. Frankie and H.G. Baker. 1976. Rainfall as a factor in the synchronization, release, and timing of anthesis by tropical trees and shrubs. *J. Biogeog.* 3: 231–236.
- Opler, P.A., G.W. Frankie and H.G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecology* 68: 167–188.
- Poole, R.W. and B.J. Rathcke. 1979. Regularity, randomness and aggregation in flowering phenologies. *Science* 203: 470–471.
- Putz, F.E. 1979. Aseasonality in Malaysian tree phenology. *Malay. For.* 42: 1–24.
- Rehfeldt, G.E., A.R. Stage and R.T. Bingham. 1971. Strobili development in Western White Pine: periodicity, prediction and association with weather. *Forest Sci.* 17: 454–461.
- Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linnean Soc.* 14: 235–250.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104: 25–35.
- Snow, B.K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis* 112: 299–329.
- Snow, B.K. 1977. Territorial behavior and courtship of the male Three-wattled Bellbird. *Auk.* 94: 623–645.
- Snow, D.W. 1965. A possible selective factor in the evolution of fruiting seasons in a tropical forest. *Oikos* 15: 274–281.
- Snow, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194–202.
- Snow, D.W. 1973. Distribution, ecology and evolution of the bellbirds (*Procnias*, Cotingidae). *Bull. Brit. Mus. (Nat. Hist.) Zoology* 25: 1–14.
- Stiles, F.G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198: 1177–1178.
- Svärdson, G. 1957. The 'invasion' type of bird migration. *Brit. Birds* 50: 314–343.
- Thompson, J.N., and M.F. Willson. 1979. Evolution of temperate bird/fruit interactions. *Evolution* 33: 973–982.
- Wheelwright, N.T. 1983. Fruits and the ecology of Resplendent Quetzals. *Auk* 100: 286–301.
- Wheelwright, N.T. 1985a. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44: 465–477.
- Wheelwright, N.T. 1985b. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808–818.
- Wheelwright, N.T., W.A. Haber, K.G. Murray and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16: 173–192.
- Wheelwright, N.T. and G.H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems with terminology, and constraints on coevolution. *Am. Nat.* 119: 402–413.