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Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest

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ABSTRACT. We studied the seed dispersal ecology of the Neotropical pioneer tree *Cecropia peltata* L. (Moraceae) in tropical dry forest by documenting its (1) fruiting phenology, (2) rates of visitation by vertebrate frugivores, and (3) rate of recruitment of juveniles in different habitats at Santa Rosa National Park in northwestern Costa Rica.

At Santa Rosa, *C. peltata* is a common but patchily-distributed plant. Fruiting in females is seasonal, and fruit availability peaks in June through August (the early wet season). Females bear a few ripe fruit per day over a 4-5 month fruiting period. At least 28 vertebrate species (15 diurnal and 13 nocturnal species) eat *Cecropia* fruit; equal numbers of ripe fruit are removed during the night and day. Owing to their more gentle treatment of seeds in the gut, birds and bats probably are more effective dispersal agents than monkeys. The recruitment rate of juveniles into already established populations was about 0.8 ha^{-1} y^{-1} compared with a rate of 176 ha^{-1} y^{-1} during the colonization of a cleared roadside.

KEY WORDS: *Cecropia peltata*, Costa Rica, phenology, plant recruitment, seed dispersal.

INTRODUCTION

Despite increased interest in frugivory and seed dispersal in recent years (Howe 1986, Howe & Smallwood 1982, McKey 1975, papers in Estrada & Fleming 1986), seed dispersal ecology has been studied in detail in relatively few species of tropical plants. In this paper we provide an account of the seed dispersal ecology of the dioecious pioneer tree *Cecropia peltata* L. (Moraceae) as part of a larger study of the interactions between frugivorous bats and their food plants in Costa Rican tropical dry forest (Fleming, 1981, 1985, 1988, Fleming *et al.* 1985). We address the following questions: (1) What are the daily and seasonal patterns of fruit production and maturation in *C. peltata*, (2) What animals eat its fruit and with what potential dispersal consequences; and (3) What is the recruitment rate of new individuals into intact and disturbed habitats?

Cecropia peltata occurs in a variety of habitats from Mexico to Venezuela, Colombia, the Guianas, and the Greater and Lesser Antilles (Burger 1977). Its demography has been studied in Puerto Rico (Crow 1980, Silander 1979), and

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general aspects of its phenology in Costa Rica were described by Frankie *et al.* (1974). Cruz (1974) and Leck (1972) describe its attractiveness to a wide array of fruit-eating vertebrates. Putz (1983) and Janzen (1983) discuss the colonization of treefall gaps by *C. peltata* in Panamanian and Costa Rican forests, respectively. Species of *Cecropia* are generally thought to be 'large gap specialists' (Brokaw 1986a, b, Denslow 1980, Popma *et al.* 1988); individuals seldom reach reproductive maturity in gaps <150 m^2 in area.

STUDY AREA AND METHODS

This study was conducted between July 1979 and June 1984 at Santa Rosa National Park, Guanacaste Province, in northwestern Costa Rica. Vegetation and climate of Santa Rosa, which lies within Holdridge's (1967) Tropical Dry and Premontane Moist Tropical Forest zones, have been described elsewhere (e.g. Fleming 1985, Fleming & Heithaus 1981, Hartshorn 1983). For more than 300 years prior to becoming a national park in 1971, Santa Rosa was a cattle ranch. As a result, much of its natural vegetation has been disturbed, favouring the abundant establishment of such pioneer species as *C. peltata* (Janzen 1983), *Muntingia calabura* (Elaeocarpaceae) (Fleming *et al.* 1985), *Cochlospermum vitafolium* (Cochlospermaceae), and *Guazuma ulmifolia* (Sterculiaceae). (Unless stated, plant names follow Janzen & Liesner 1980.)

Rainfall averages 1658 ± 177 (SE, $N = 8$) mm annually. Most rain occurs between mid-May and mid-November (Figure 1). The rainy season had begun by mid-May in 1979–1982 but was delayed about 2 weeks in 1983 because of a prolonged drought associated with the El Nino southern oscillation from October 1982 until early June 1983. Rainfall in 1983 (909 mm) was far below average.

Most of our observations on phenology, vertebrate dispersers, and recruitment were made in two habitats in upland portions of the park: evergreen forest (two sites), which, at Santa Rosa, occurs in moist ravines on north- or west-facing escarpments, and deciduous forest (five sites), the most widespread habitat. Recruitment of *C. peltata* was also monitored in two transects along 4 km of the park road adjacent to evergreen and deciduous forest and grassland.

Flowering and fruiting phenology

Males and females produce axillary clusters of inflorescences (spathes) in this wind-pollinated species (Bawa & Opler 1975). Females produce fewer (ca. 4 vs. ca. 20) but larger (4–10 cm long by 10–12 mm wide vs. 3–7 cm by 2–4 mm) spadices per inflorescence than males (Burger 1977, Little & Wadsworth 1964). Female spadices contain hundreds of tiny, single-seeded fruits. Mean number of viable seeds per spadix was found to be 800 in Puerto Rico (Silander 1979); seeds are about 1.9 mm long and weigh 1.6 mg when air-dried (Perry & Fleming 1980). We will call spadices 'fruits' in discussions of fruit consumption by vertebrates.

Reproductive censuses were made at biweekly intervals from January 1980 to August 1981 and from June 1983 to July 1984. In 1980–81, the number of unopened spathes, open spathes (males only), and individual spadices (females only) on 2–3 easily-observable branches on an average of 10.1 (range 3–15) individuals of each sex were counted at two evergreen forest and three deciduous forest sites. Because the flowering and fruiting stages of female spadices could not readily be distinguished, we combined these stages in our censuses. Data from all censused branches were combined to determine seasonal reproductive trends at each site. In 1983–84, numbers of spadices were recorded on two branches on each of seven females located at one evergreen site (N = 3) or in deciduous forest along the park road (N = 4).

To determine the relationship between plant size, as measured by diameter at breast height (DBH), and female fecundity, we counted the total number of spadices borne by a randomly-selected group of individuals at one evergreen site (N = 17–24 depending on year) and at one deciduous forest site (N = 10–12) in July, the mid-point of the fruiting season. We censused these females in 1980–82 to determine annual variation in fecundity.

Because we could not visually distinguish between ripe and unripe female spadices, we used an indirect method to estimate daily rates of spadix (fruit) maturation. We counted the number of recently-stripped spadix 'cores', which remain attached to their peduncles and are highly visible because of their light colour, relative to the number of intact spadices on 22 occasions in July 1980 and June and July 1981; cores become brown and shrivelled within two days after being stripped. We expressed the number of ripe spadices as a percentage of the total spadix crop. This provides a minimum estimate of the number of ripe spadices currently on a tree because it does not include the number of untouched ripe spadices or entire spadices removed by monkeys.

Vertebrate frugivores

To determine rates of visitation and fruit consumption by vertebrates, we observed *C. peltata* trees for 91.4 h (82.8 h on 43 occasions during the day and 8.6 h on six occasions at night) between 27 June and 15 September 1980 and for 42.6 h (39.6 h during the day on 12 occasions and 3.0 h at night on two occasions) between 5 May and 23 July 1981. During the day, we watched single trees (N = 3) or one group of four trees for 1–4 h in the morning beginning at 0600 or in the afternoon beginning at 1300. We spent approximately equal amounts of time observing each tree or group of trees. At night, we watched four trees using a Ni-Tec night vision scope for 1.5–2 h each between 1830 and 2030, a peak feeding time for bats (Heithaus & Fleming 1978).

During the diurnal watches we recorded the time of arrival of each visitor, its identity, and, whenever possible, the duration of its visit and the amount of fruit consumed during the visit. We also recorded food searching and handling behaviour and social interactions. During nocturnal watches, we counted the number of bats flying past the field of view (this count sometimes included

numerous passes made by the same bat(s)) and the number of contacts bats made with spadices. We also recorded the duration of visits by other nocturnal mammals. Mist net studies (e.g. Fleming 1988, Fleming *et al.* 1977, Heithaus *et al.* 1975) provided us with information about which species of bats eat fruits of *C. peltata.* We used data published by Fleming (1988, Appendix 8) to determine the relative importance of *C. peltata* in the diets of several species of bats.

We obtained a more precise estimate of diurnal and nocturnal fruit removal rates by counting the number of spadices on 2–4 clearly visible branches on each of seven trees at dawn (0530–0600) and late in the afternoon (1730–1800) for five weeks (21 June–28 July 1981).

Recruitment rates

We used two techniques to estimate the rate of recruitment of young *C. peltata*, expressed on a ha^{-1} y^{-1} basis, into the Santa Rosa population. First, we obtained a 'static' picture of recruitment by mapping all *C. peltata* plants taller than 30 cm in five plots ranging from 0.5 to 9.8 ha in area. Fleming & Heithaus (1981) provide comparable data from two additional plots. We recognize three size classes in this paper: seedlings (height >2 cm but <1 m), juveniles (height $\geqslant 1$ m, DBH <10 cm), and adults (DBH $\geqslant 10$ cm); most plants with a DBH $\geqslant 10$ cm are sexually mature at Santa Rosa.

We obtained a 'dynamic' picture of recruitment in *C. peltata* and other vertebrate-dispersed plants by censusing two 8000 m^2 transects along a 4 km section of the park road as described by Fleming *et al.* (1985). For each seedling we recorded height (in cm); distance (to the nearest 0.1 m) from the nearest individual of any of the following five vertebrate-dispersed species: *C. peltata, Chlorophora tinctoria, Muntingia calabura, Piper amalago*, and *Solanum hazenii*; and whether it was covered by forest canopy. The first transect was recensused in the summers of 1981–1983; the second was recensused only in 1981.

RESULTS

Flowering and fruiting phenology

Frankie *et al.* (1974) reported that *C. peltata* in Guanacaste Province flowers from April through August and bears mature fruit from May through September. Our quantitative data generally support their qualitative observations (Figure 1). In 1980 male flower production began in February, peaked in mid-June, and was over by October. In 1981 male flower production peaked in early April and declined thereafter (Figure 1). In both years female flower/fruit production lagged about one month behind male flower production. Peak female reproductive output occurred in mid-June in 1980 but was later in 1981, even though the wet season began earlier that year (Figure 1). The wet season began later in 1983 than in either 1980 or 1981, and the 1983 flower/

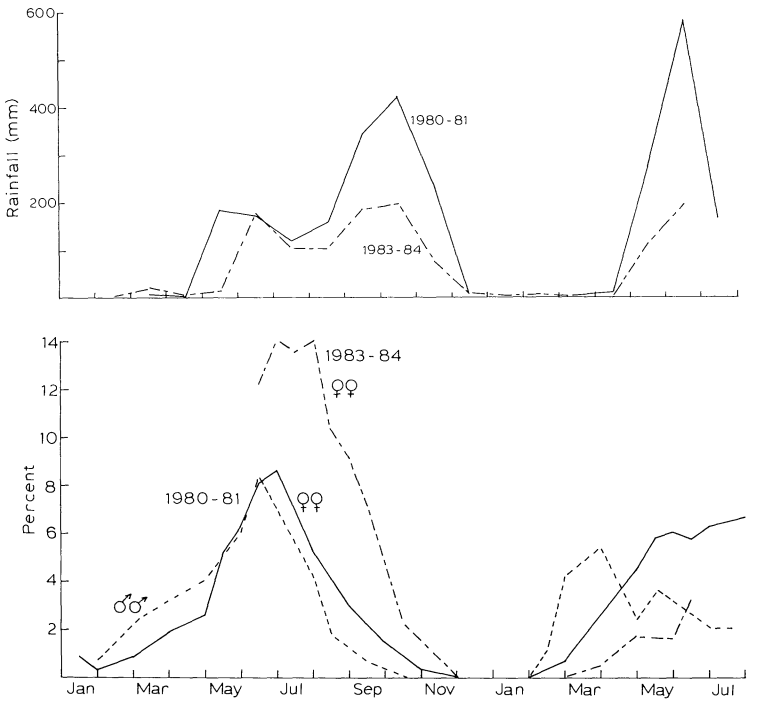


Figure 1. Distribution of monthly rainfall and flowering and fruiting curves (standardized to a total area of 1.0) for *Cecropia peltata* in 1980–81 and 1983–84. Curves represent the percentage of the total number of male inflorescences and female spadices counted in all censuses taken on a particular date. Data from 1980–81 are from one evergreen forest site (no. 1 in Table 5).

fruit peak occurred about one month later than in 1980. Within years, fruit and flower peaks occurred about two weeks earlier at evergreen (moist) sites than at deciduous (dry) sites.

Female fecundity, as measured by the size of an individual's standing crop of immature and mature spadices in July, was significantly correlated with DBH and differed between the two sites (Table 1). In a stepwise multiple regression analysis of the 1982 data, site entered the equation before DBH, but both variables contributed significantly to the regression (site, $F_{1,31} = 5.04$, $0.05 > P > 0.025$; DBH, $F_{1,31} = 4.46$, $0.05 > P > 0.025$). Results of a two-way

Table 1. Mean fruit crop size in July in females of *Cecropia peltata* at two sites. Counts represent number of spadices.

Site	Year	No. of females	$\bar{X} \pm SE$
Evergreen forest	1980	17	550.1 ± 91.2
	1981	24	601.8 ± 76.5
	1982	21	645.2 ± 90.0
Deciduous forest	1980	10	640.0 ± 119.6
	1981	12	898.7 ± 141.1
	1982	12	972.0 ± 110.6

ANOVA examining the effects of site and year on spadix crop size were significant (main effects: $F_{3,95}=4.33$, $P=0.007$), but site was the only significant variable ($F_{1,95}=9.44$, $P=0.003$). Plants at the deciduous forest site (no. 7 in Table 5) bore larger spadix crops than did those at the evergreen forest site (no. 1 in Table 5) in each of three years. Individual growth rates were also higher and adult densities and annual mortality rate were lower at the deciduous site than at the evergreen site (Table 5 and our unpublished observations).

The daily rate of fruit maturation is low in *C. peltata.* Percentages of stripped spadices averaged 2.7 ± 0.3 (SE) with a range of 0.7–4.6% in 22 censuses. On any given day, a female bears few (usually <10) ripe spadices. Because a few ripe spadices are matured per day over several months, the phenological pattern of *C. peltata* can be described as 'steady state' (*sensu* Gentry 1974). This pattern also appears to apply to wet forest *Cecropia* species (e.g. *C. obtusifolia*) (Estrada & Coates-Estrada 1984, Frankie *et al.* 1974).

Vertebrate frugivores

A total of 28 vertebrate species, including 15 diurnal and 13 nocturnal species, is known to eat the fruit of *C. peltata* at Santa Rosa (Tables 2 and 3). The diurnal species included four mammals and 11 birds; an additional three bird species visited the trees but did not eat the fruit. The nocturnal species included nine bats and four arboreal mammals. (Bird names follow American Ornithologists' Union 1983, bat names follow Jones & Carter 1976 and names of other mammals follow Hall 1981).

Three species of monkeys were the major diurnal fruit eaters (Table 2). Despite its low visitation frequency (7% of the censuses and at only one of the four sites), the howler monkey was the top fruit consumer. Because many of the spadices they ate were unripe (based on size), howler monkeys should probably be considered significant predispersal seed predators as well as potential seed dispersers. Two birds, the scrub euponia and red-legged honeycreeper, were the most frequent diurnal *Cecropia* visitors but accounted for only 3.9% of the total fruit consumption.

The three major chiropteran *Cecropia* consumers, *Carollia perspicillata, Artibeus jamaicensis,* and *Glossophaga soricina* (Table 3), are abundant and widespread at Santa Rosa (Fleming *et al.* 1977). On the four occasions that fruit removal by bats could be clearly distinguished from bat passes, removal rate averaged 0.216 min^{-1} (range 0.033–0.583). Like many birds, bats remove only a small portion of a ripe spadix in each feeding pass. Faecal data (Table 3) indicate that during its fruiting season, *C. peltata* represents one-third or more of the diets of three bat species, *Artibeus jamaicensis, A. lituratus,* and *Sturnira lilium.* Another widespread nocturnal *Cecropia* visitor was the kinkajou (*Potos flavus*), which we saw or heard at all sites. Although we were unable to quantify its fruit consumption, we suspect that the kinkajou has a significant impact on the *C. peltata* fruit crop (see below).

Visitation and fruit consumption rates were low throughout the day and

Table 2. Fruit consumption, visitation frequency, and duration of visits at *Cecropia peltata* trees by diurnal vertebrate frugivores in 1980–81. Data for all sites combined. For visitation durations, mean ± 1 SD and sample size are presented.

Species	No. of fruit eaten			Visitation frequency*	Duration of visit (min)†
	1980	1981	Total (proportion)		
Mammals:					
Spider Monkey (*Ateles geoffroyi*)	325	26	351 (0.226)	0.238	5.6 ± 5.0 (24)
Howler Monkey (*Alouatta palliata*)	808	184	992 (0.640)	0.071	12.4 ± 6.7 (13)
White-faced Monkey (*Cebus capucinus*)	34	95.5	129.5 (0.084)	0.190	3.9 ± 4.8 (21)
Variegated Squirrel (*Sciurus variegatoides*)	1.2	1.0	2.2 (0.001)	0.119	2.5 ± 2.7 (4)
Birds:					
Scrub Euphonia (*Euphonia affinis*)	10.3	12.9	23.2 (0.015)	0.548	3.7 ± 4.4 (125)
Red-legged Honeycreeper (*Cyanerpes cyaneus*)	2.7	1.0	3.7 (0.002)	0.310	3.4 ± 4.9 (82)
Long-tailed Manakin (*Chiroxiphia linearis*)	2.8	0.2	3.0 (0.002)	0.190	0.9 ± 1.0 (12)
Keel-billed Toucan (*Ramphastos sulphuratus*)	5.8	–	5.8 (0.004)	0.071	1.6 ± 1.0 (4)
Black-headed Trogon (*Trogon citreolus*)	2.2	–	2.2 (0.001)	0.143	3.0 ± 1.8 (5)
Golden-fronted Woodpecker (*Centurus aurifrons*)	1.5	–	1.5 (0.001)	0.214	8.5 ±13.6 (10)
Crested Guan (*Penelope purpurascens*)	15	1	16 (0.010)	0.167	7.7 ± 6.2 (6)
Turquoise-browed Motmot (*Eumomota superciliosus*)	1.3	–	1.3 (0.001)	0.071	3.6 ± 2.1 (4)
Magpie Jay (*Calocitta formosa*)	5.3	3.5	8.8 (0.006)	0.143	1.7 ± 1.2 (13)
Orange-chinned Parakeet (*Brotogeris jugularis*)	9.5	–	9.5 (0.006)	0.119	9.7 ± 6.4 (7)
Kiskadee (*Pitangus sulphuratus*)	–	0.5	0.5 (0.000)	0.024	1.2 (1)

* Calculated as the proportion of censuses at which a species was seen.
† These data represent means of single individuals or groups (counted once per visit).
Additional birds seen in trees but which did not eat fruit: Blue-crowned Motmot (*Momotus momota*), Yellow-green Vireo (*Vireo flavoviridis*), and Clay-coloured Robin (*Turdus grayi*).

throughout the fruiting season (Table 4). Mean visitation rates, which ranged from 0.028 to 0.332 min^{-1}, differed significantly among sites (for log-transformed data, $F_{2,38} = 6.07$, $P = 0.0053$). Similarly, rates of fruit consumption, which ranged from 0.0082 to 0.696 fruit min^{-1}, differed significantly among sites (for log-transformed data, $F_{2,35} = 6.31$, $P = 0.0048$). In both years, fruit consumption rates were highest at the evergreen site (no. 2) where the three species of monkeys were most common.

Duration of visits by frugivores usually were brief. Diurnal visits ranged from a mean of 0.9 min in the long-tailed manakin to 12.4 min in the howler monkey (Table 2). Several species, including each of the monkeys and the scrub euphonia,

Table 3. Number of faecal samples (seed loads) of *Cecropia peltata* taken from phyllostomid bats at Santa Rosa, 1974–1984. Source of data: Fleming (1988, Appendix 8).

Species	Number of *C. peltata* loads (proportion)	*C. peltata* as a proportion of a species' total seed loads (sample size)
Carollia perspicillata	232 (0.567)	0.241 (962)
C. subrufa	10 (0.024)	0.072 (139)
Artibeus jamaicensis	87 (0.213)	0.503 (173)
A. lituratus	19 (0.046)	0.487 (39)
A. phaeotis	6 (0.015)	0.231 (26)
A. toltecus	2 (0.002)	0.500 (4)
Glossophaga soricina	28 (0.068)	0.144 (195)
Sturnira lilium	26 (0.064)	0.338 (77)
Phyllostomus discolor	1 (0.002)	0.250 (4)

Additional nocturnal mammals seen in trees: *Didelphis virginiana* and *Caluromys derbianus* (Didelphidae), *Potos flavus* (Procyonidae), and *Ototylomys phyllotis* (Cricetidae).

Table 4. Summary of the diurnal visitation and fruit consumption rates at four sites. Except where indicated, data are expressed as mean ± 1 SE (no. of censuses).

Site* and habitat (no. trees observed)	Year	Visitation rate (no. arrivals min^{-1})†	Fruit consumption rate (no. eaten min^{-1})
1. Evergreen forest (4)	1980	0.317 ± 0.067 (8)	0.017 ± 0.010
	1981	0.082 (0.042–0.122)‡(2)	0.023 (0–0.46)‡
2. Evergreen forest (1)	1980	0.059 ± 0.014 (20)	0.354 ± 0.13
	1981	0.322 ± 0.26 (5)	0.696 ± 0.44
3. Riparian forest (1)	1981	0.047 (0.008–0.10)‡(3)	0.019 (0–0.057)‡
7. Deciduous forest (1)	1980	0.028 ± 0.010 (9)	0.0082 ± 0.0032

* Site numbers are the same as those in Table 5.
† Groups were counted as one arrival.
‡ Range of values.

red-legged honeycreeper, crested guan, magpie jay, and orange-chinned parakeet, visited the trees in groups of up to 12 individuals. Except for one chase of a white-faced monkey by a spider monkey, we saw no intra- or interspecific aggression in *Cecropia* trees.

Nocturnal visits by bats and arboreal mammals also were brief. Bats hovered for a few seconds and bit off chunks of fruit before flying off. On 7 July 1981, a pair of bats repeatedly visited the same cluster of spadices to feed, removing 1.5 spadices that night and a similar amount the next night. Arboreal mammals, *Didelphis virginiana* and *Potos flavus*, usually spent <15 min in a tree before moving on. One kinkajou ate two fruits during the 11 min it was in a tree.

During the five weeks that we monitored diurnal vs. nocturnal fruit removal, 224 fruits were taken; 118 (53%) disappeared during the day and 106 (47%) disappeared at night. From these observations, we conclude that diurnal and nocturnal animals consume similar amounts of *C. peltata* fruit.

Rates of recruitment

Recruitment rates of gap-dependent trees depend on rates and patterns of habitat disturbance (Martinez-Ramos & Alvarez-Buylla 1986). To judge from the population structure of *C. peltata* at Santa Rosa, recruitment has been episodic. In the absence of human disturbance, juvenile recruitment rates appear to be low.

Total density of *C. peltata* and the proportion of this density represented by juveniles at seven sites are shown in Table 5. Total density ranged from 6.4 to 159.7 stems ha^{-1} and averaged 44.0 stems ha^{-1}. At five of the seven sites, juveniles, which mature in less than five years at Santa Rosa (see below), comprised less than 10% of the total population. The two remaining sites had higher proportions of juveniles and bore evidence of extensive disturbance in the form of fire (site 5) or tree clearing (site 7). The exceptionally high density of *C. peltata* at site 1 reflects an episode of large-scale tree clearing about 25–30 years before our census, but recent recruitment in that area has been infrequent. Assuming that the observed juveniles were recruited over a period of five years, the annual juvenile recruitment rate at these sites averaged 0.83 ha^{-1} with a range of 0.12–2.74 ha^{-1}.

The 1980 survey of 1.6 ha of park roadside revealed high densities and clumped distributions of *C. peltata* seedlings. The tree-covered transect (T1) contained 191 seedlings at a density of 239 seedlings ha^{-1}. The grass-bordered transect (T2) contained 55 seedlings at a density of 69 ha^{-1}. In T1 and T2, 91% and 42% of the seedlings, respectively, were tree-covered (but were not necessarily in heavy shade). These proportions are higher than those expected if seedlings were distributed independently of tree cover (in T1, $\chi^2 = 113.6$, $P \ll 0.001$; in T2, $\chi^2 = 441.0$, $P \ll 0.001$). In contrast, seedlings of the large gap specialist *Muntingia calabura* occurred more frequently in the open than expected by chance (Fleming *et al.* 1985).

In both transects, most individuals (73% in T1 and 78% in T2) grew < 2 m from another *C. peltata* seedling in obvious clumps. Mean distance between individuals within clumps, which contained an average of 3.81 individuals (SE =

Table 5. Population density of *Cecropia peltata* at seven sites at Santa Rosa National Park.

Site, habitat, plot size and year	Density (number ha^{-1})		
	Juveniles	Adults	Total
1. Evergreen forest, 0.72 ha, 1980	5.6 (0.035)*	154.1	159.7
2. Evergreen forest, 0.47 ha, 1980	4.3 (0.084)	46.8	51.1
3. Riparian forest, 9.8 ha, 1980	0.7 (0.042)	16.1	16.8
4. Riparian forest, 1.5 ha, 1980	1.4 (0.069)	19.0	20.4
5. Deciduous forest, 2.4 ha, 1977†	2.9 (0.212)	10.8	13.7
6. Deciduous forest, 8.8 ha, 1982	0.6 (0.094)	5.8	6.4
7. Deciduous forest, 1.0 ha, 1977†	13.7 (0.343)	26.3	40.0

* Proportion of total density.
† Data from Fleming & Heithaus (1981).

0.51, range = 2–18, N = 47), was 0.56 ± 0.06 m (N = 85) compared with a mean distance of 7.76 ± 0.83 (N = 67) between clumps and single individuals. The frequency distribution of single and clumped individuals deviated significantly from a truncated Poisson distribution (Cohen 1960) owing to an excess of singles and groups containing more than five individuals ($\chi^2 = 35.4$, $P < 0.01$). Finally, 24 of the 47 *Cecropia* clumps contained other vertebrate-dispersed seedlings. Seedlings of *C. peltata* co-occurred with those of *Chlorophora tinctoria* 12 times, with *Muntingia calabura* 11 times, and with *Piper amalago* and *Solanum hazenii* three times.

Recensuses of transect T1 in 1981–1983 and T2 in 1981 revealed that little additional recruitment of *C. peltata* occurred after 1980. The number of *Cecropia* individuals in T1 declined 21% from 191 to 150 between 1980 and 1983; numbers in T2 declined 43.6% from 55 to 31 between 1980 and 1981. In 1980 in T1, 118 individuals (61.7%) were <0.5 m tall whereas only 7.5% of 186 and 0.63% of 160 were this tall in 1981 and 1982, respectively. By 1982 two females were sexually mature (at an age of $\leqslant 3$ years), and in 1983 eight females and two males were mature. These observations indicate that for *C. peltata*, the time window for colonization of this roadside disturbance was $\leqslant 2$ years. Brokaw (1986b) reported a similar situation for *C. insignis* when it establishes in gaps on Barro Colorado Island, Panama.

Recruitment rates of *C. peltata* from the seedling into the juvenile size class (i.e. plants $\geqslant 1.0$ tall and <10 cm DBH) in T1 were considerably higher than rates observed in our forest plots. In July 1980, 7.9% of 191 plants were juveniles; in July 1981, 77.0% of 183 plants were juveniles. Juvenile recruitment rates in the periods mid-1979 to mid-1980 and mid-1980 to mid-1981 were 18.8 and 176.3 ha^{-1}, respectively, compared with only 0.8 ha^{-1} y^{-1} in forests adjacent to the road.

DISCUSSION

In many respects, *Cecropia peltata* is a typical fleshy-fruited pioneer plant. It grows rapidly (in volume but not in biomass (Jordan & Farnworth 1980)), becomes sexually mature in 3–5 years, produces large seed crops annually, attracts a diverse array of frugivores, and has a lifespan of 20–30 years (Crow 1980, Putz & Holbrook 1988, Silander 1979). Because their small seeds accumulate in high densities in the soil (Bell 1970, Guevara & Gomez-Pompa 1972, Holthuijzen & Boerboom 1982, Putz 1983, Uhl & Clark 1983), various *Cecropia* species can rapidly colonize large treefall gaps and other large clearings in high numbers (de Foresta *et al.* 1984, Foster *et al.* 1986, Uhl *et al.* 1981).

Although it resembles certain other Neotropical vertebrate-dispersed pioneer plants (e.g. *Muntingia calabura*, Fleming *et al.* 1985) in a number of ecological characteristics, *C. peltata* differs in three important respects from theoretical expectations. First, its fruit (or collectively, the spadix) does not contain a watery, sugary pulp. Instead, it is rich in fibre and seed but is relatively de-

pauperate in soluble energy as well as in lipids and nitrogen (Herbst 1986). Thus, its fruit appears to be an exception to the 'opportunistic' dispersal syndrome of Snow (1971) and McKey (1975). Second, within seasonal constraints, it has a 'steady state' rather than the 'cornucopia' phenology (*sensu* Gentry 1974) predicted by Howe & Estabrook (1977).

The third deviation from theoretical expectations (Howe & Estabrook 1977, Smythe 1970) is the clumped, rather than separated, fruiting periods of *C. peltata* relative to those of other 'opportunistic' fruiting plants at Santa Rosa. As summarized in Fleming (1988), the fruiting period of *C. peltata* overlaps broadly with *Muntingia calabura, Chlorophora tinctoria*, and small-seeded *Ficus* species (e.g. *F. ovalis, F. cotinifolia*), each of which attracts a wide array of avian and mammalian frugivores. Compared with these species, *C. peltata* produces far fewer and less sugary fruits per tree per day (Fleming *et al.* 1985, Heithaus & Fleming 1978, Herbst 1986), which would seemingly put it at a competitive disadvantage in attracting frugivores. Further competition for the attention of such bats as *Carollia perspicillata, C. subrufa, Glossophaga soricina,* and *Sturnira lilium* comes from several shrubs and treelets (e.g. *Piper amalago, P. pseudo-fuligineum, P. jacquemontianum* (Piperaceae) and *Solanum hazenii* (Solanaceae)) which also fruit during the first half of the wet season (Fleming 1985, Heithaus & Fleming 1978).

Despite its high degree of phenological overlap with several other fruiting species and its relatively low nutritional reward per plant per day, *C. peltata* appears to have a very efficient seed dispersal system in at least two respects: (1) it experiences relatively low seed waste and (2), as documented by soil seed studies (cited above), its seeds are widely dispersed to a variety of habitats. Although we have not rigorously quantified seed waste in Santa Rosa plants (cf. Howe 1980, Howe & Vande Kerckhove 1979), we noted that, except where monkeys have been feeding, few ripe fruits accumulate under *C. peltata* trees compared with the hundreds to thousands of intact or partially eaten fruits that rot under trees of *Ficus* spp. and *Chlorophora tinctoria.* Because most vertebrates spend little time at *Cecropia* plants before moving away to rest or feed elsewhere, we suspect that a higher proportion of *C. peltata* seeds is removed from the vicinity of parent plants than is the case in *Ficus.* This behaviour should increase the radius of its seed shadow.

Not all vertebrates that eat fruits of *C. peltata* are likely to provide the same 'quality' of seed dispersal service in terms of treatment of the seeds in the mouth and gut and where the seeds are deposited. Olson & Blum (1968) and Fleming (1988), for example, indicated that *Cecropia* seeds have higher germination percentages when they pass through various species of birds and bats, respectively, than unpassed controls, at least under laboratory conditions. In contrast, Chapman (1989) was unable to germinate *C. peltata* seeds taken from monkey faeces at Santa Rosa, and Vásquez-Yanes & Segovia-Orozco (1986) reported that seeds of *C. obtusifolia* had lower probabilities of germinating after passing through spider monkeys than when passed by the bat *Artibeus jamaicensis.*

These results suggest that the digestive systems of birds and bats treat *Cecropia* seeds more gently than do monkeys.

Seed deposition locations are also likely to differ tremendously among different frugivore species. Seeds pass much more rapidly through bats and passerine birds (in 30 mins or less; Fleming 1988, Levey 1986, Murray 1986) than through spider or howler monkeys (about 4 and 20 h, respectively; Milton 1981). Because of this, birds and bats are probably more likely to deposit *Cecropia* seeds closer to parent plants than are monkeys, although bats can provide relatively long-distance dispersal (e.g. 0.5 to several km) when they change feeding areas or return to their day roosts (Heithaus & Fleming 1978, McCracken & Bradbury 1981). Birds and bats sometimes differ in their seed deposition patterns in that birds are more likely to defecate seeds under fruiting trees or perches than are bats (Charles-Dominique 1986, de Foresta *et al.* 1984, Thomas 1982, Thomas *et al.* 1988).

A recruitment model

Our current knowledge about seed dispersal and juvenile recruitment in *C. peltata* at Santa Rosa can be summarized in the form of a graphical model. As discussed by Janzen (1970) and Fleming & Heithaus (1981), recruitment of juveniles into a plant population involves the interaction between two probability distributions: the probability that a seed will be deposited a particular distance from the parent plant (P_d) multiplied by the probability that a seed can become established at that distance (P_{es}). The distribution of recruitment distances is the product of P_d and P_{es}.

Data on seed deposition patterns around fruiting *C. peltata* trees presented in Fleming & Heithaus (1981) and Fleming (1988), and data on distances between juveniles and the nearest adult plant gathered in this study, provide data for estimating these two probability distributions (Figure 2). It should be noted that these calculations provide only a rough indication of expected recruitment distances because they are based on distances between juveniles and any adult tree, regardless of sex. More precise predictions would result if we had considered distances between juveniles and female trees in this dioecious species. However, since the sex ratio is 1:1 in our total sample of adults (143 females, 139 males) and the sexes are not spatially segregated (our unpublished observations), fine-tuning this analysis would not appreciably change our results.

Results of these calculations are shown in Figure 2a. P_d falls off rapidly with distance, and P_{es} reaches an asymptote at about 20 m away from adult plants. The frequency distribution of recruitment distances peaks at a distance of less than 5 m, as predicted by the observed frequency distributions of juvenile-adult distances (Figure 2b). These results support Hubbell's (1979) conclusion that 'relatively simple physical and biological mechanisms govern seed dispersal' and recruitment in certain tropical plants. At Santa Rosa, young *Cecropia* plants often become established close to adult plants away from gaps. This

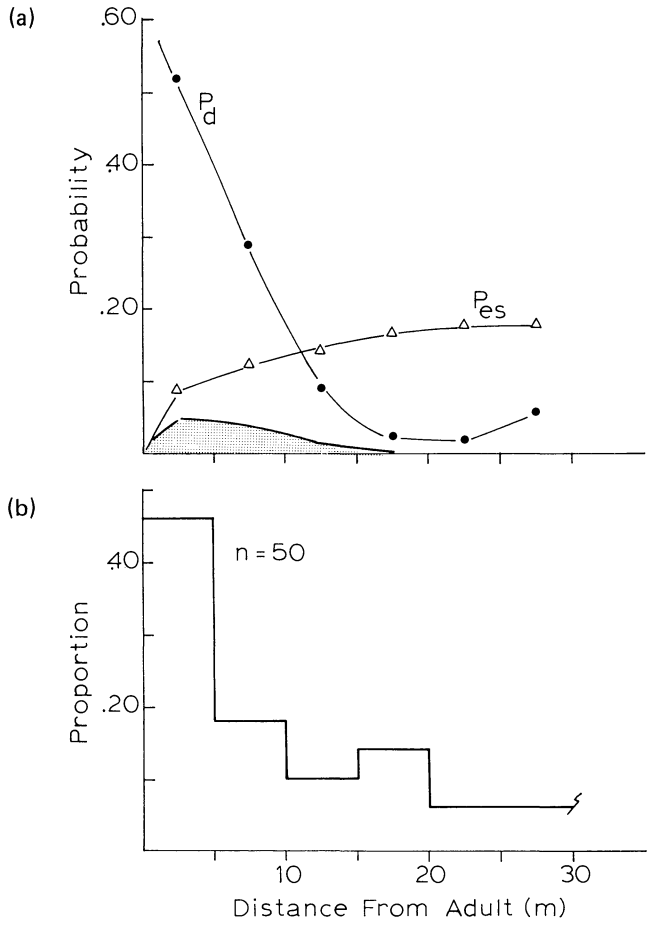


Figure 2. Recruitment of juveniles into the *C. peltata* population at Santa Rosa. (a). Probability of seed deposition (P_d) and probability of seedling establishment (P_{es}) as a function of distance from a fruiting plant. The stippled area indicates the expected distribution of juveniles. P_d is the frequency distribution of 168 seed clumps as reported in Fleming & Heithaus (1981). P_{es} represents the product of the cumulative frequency distribution of distances between juveniles and the nearest adult in distance classes of 1-5, 6-10, . . . , 45-50 m by 0.19, the probability that an adult will have a juvenile within 50 m of it. (b). The observed distribution of juvenile-adult distances in seven plots.

leads us to question whether *C. peltata* should be classified as a 'large gap specialist'.

By emphasizing the expected frequency distributions of juvenile plants close to adult plants, the model shown in Figure 2a deals with only one of the two important components of recruitment in pioneer species; i.e. it only deals with *local recruitment* into an already established population of adults. It does not deal with *distant recruitment*, which in pioneer species involves the establishment of juveniles in disturbances some distance away from adult plants. Distant recruitment in fleshy-fruited pioneer plants results from two characteristics of their seeds: (1) their high mobility resulting from being ingested by a diverse array of vertebrates and which produces a long tail on the P_d curve and (2)

their ability to remain dormant in the soil for extended periods of time (e.g. Vásquez-Yanes & Smith 1982). Distant dispersal enables pioneer plants to invade gaps in primary forests in which their adult densities are low.

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