

Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico

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ABSTRACT. Fruit production, frugivore foraging activity and seed dispersal was studied at 10 *Cymbopetalum baillonii* (Annonaceae) trees during an entire fruiting season. Fruits dehisced during the first six months of the year offer to potential dispersal agents a package of 8-24 arillate seeds. Insects and fungi, however, killed up to 14% of the seeds potentially available for dispersal before fruit dehiscence. Visitation by 24 species of birds and one mammal to the trees closely followed the availability of arillate seeds. The foraging activity of *Peromyscus* and *Heteromys* rodents accounted for >80% mortality of the seeds deposited under the crown of the parent tree. Among those seedlings that became established under the crown mortality was >90% after 12 months. Seeds dispersed under conspecific fruiting trees experienced intense predation by vertebrates. Field experiments showed that seeds and seedlings planted >30 m away from adult trees survived significantly longer than those planted under the crown and at distances <30 m. An unequivocal advantage to dispersal away from the tree and under allospecific trees was evident from the data. A very narrow range of frugivores (N=8 species) accounted for the quality component of dispersal services to the trees. The tree with the lowest animal visitation and fruit crop was the most efficient in the dispersal of its seeds.

KEY WORDS: *Cymbopetalum baillonii*, frugivory, Mexico, seed dispersal, seed predation, tropical rain forest.

RESUMEN. La producción de frutos, la actividad alimenticia de animales frugívoros y la dispersión de semillas por estos últimos fue estudiada en 10 árboles de *Cymbopetalum baillonii* (Annonaceae) durante una época completa de fructación. Las frutas capsuladas se abren durante los primeros seis meses del año ofreciendo a los dispersores un paquete de 8-24 semillas arilladas. Sin embargo, los insectos y hongos matan hasta un 14% de las semillas potencialmente disponibles para la dispersión antes de la apertura de las cápsulas. La apertura de las cápsulas resultó en la visitación de veinte y dos especies de aves y de un mamífero que siguieron muy de cerca la distribución temporal de la disponibilidad de las semillas arilladas. Las semillas dispersadas bajo la copa del árbol progenitor y de árboles conespecíficos fueron intensamente depredadas por roedores de los géneros *Peromyscus* y *Heteromys* que causaron el 80% ó más de la mortalidad observada. Entre las plántulas que se establecieron en estos sitios la mortalidad fue igual ó mayor que el 90% después de 12 meses. Experimentos con semillas y plántulas mostraron que aquellas sembradas a 30 ó más metros del árbol progenitor y bajo árboles alo-specíficos sobrevivieron significativamente más tiempo que las sembradas a distancias menores de 30 metros. Un grupo muy restringido de frugívoros (N=8 especies) trasladaron las semillas a distancias mayores de 30 m aportando así un servicio de calidad en la dispersión. El árbol con el menor número de visitas por frugívoros y con una de las cosechas más bajas de frutos fue el individuo más eficiente en la dispersión de sus semillas.

INTRODUCTION

In the reciprocal interaction between plants and frugivores, plants have their seeds dispersed and dispersers get a nutritional reward. Dispersal of seeds involves removal of the seed from the parent plant by an agent that deposits

them somewhere rather than kills them (Herrera 1985). Mutualistic and non-mutualistic frugivores are important potential selective agents on plant traits related to the dispersal process (phenology, fruit morphology, spatial display, pulp and seed traits and nutrient and toxic quality) and thus to the interaction of plants and dispersers (see Dirzo & Dominguez 1986, Herrera 1985, 1986, Howe & Smallwood 1982, Janzen 1983a, 1983b, Wheelwright & Orians 1982 for reviews). In addition, the spatial distribution (e.g. isolated vs clumped) of conspecific fruiting plants may be important in modulating frugivore responses to plant traits associated with seed dispersal and the destination of the plant's seeds (Herrera 1984, 1985, Herrera & Jordano 1981, Howe *et al.* 1985, Manassee & Howe 1983).

The seeds ingested by frugivores as contaminants of fruit flesh represent the potential fitness of the plant. It has been suggested that frugivores may raise or lower this fitness through the 'efficiency' (quantity) and/or 'quality' (favourable germination sites) components of seed dispersal (Herrera & Jordano 1981). However, it is the postdispersal fate of the seed that may be critical in determining whether the fitness of the plant has been raised or lowered by frugivore dispersal activity. The ultimate fate of the dispersed seed is often determined by factors generally unrelated to the frugivore-plant interaction such as when and where favourable germination (and growth) microsites exist and in what number, the particular characteristics of the microsite in which the seed was deposited and the local ecological context in which the microsite is found (Herrera 1985).

In general there is a paucity of quantitative information on fruit production, frugivore activity, seed dispersal and especially on the fates of the dispersed seeds for tropical trees (Clark & Clark 1981, Howe *et al.* 1985; see Dirzo & Dominguez 1986 for a review). Some of these studies suggest that escape from mortality near the parent plant or at other high density concentrations may be a selective advantage of dispersal (Connell 1971, Janzen 1970).

This paper examines, for *Cymbopetalum baillonii* R.E.Fr. (Annonaceae) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico, (a) fruit production and frugivore activity, (b) the consequences of frugivory (predispersal seed predation and seed dispersal), (c) the consequences of seed dispersal (germination potential, initial seed germination and establishment and postdispersal seed predation) and (d) dispersal efficiency of individual trees during the 1984 fruiting season.

NATURAL HISTORY BACKGROUND

Cymbopetalum baillonii is a monoecious, shade tolerant, medium-sized tree (to 20 m), that is common in the mid strata of tropical rain forests in Mexico from southern Veracruz to Chiapas (Pennington & Sarukhan 1968). The trees produce distinctive fruits on stalks bearing from eight to 17 fruits. The mean number of stalks per tree is $16.5 \pm \text{SD } 6.3$ (range 7-26; $N=22$ trees) with a mean num-

ber of 109 ± 47.2 fruits per tree ($N=22$). Each fruit, which is cylindrical, consists of a husk about 15–25 cm long and 6–10 cm wide. Mean fresh weight of fruit was 76.2 ± 27.0 g ($N=75$). The husk accounts for 85% of the wet weight of the fruit. Unripe fruits are green but acquire a lustrous yellow/red colour when mature (Figure 1).

The capsules dehisce along the distal margin, opening over a period of a few hours in the morning to a width about 9.0 cm, exposing a set of 8–24 arillate seeds ($\bar{x} = 17.57 \pm 3.85$, $N=200$). The shiny brown seeds measure 15.2 ± 1.15 mm in length ($N=200$), weigh 0.51 ± 0.1 g ($N=200$) when fresh, and are enclosed in a thin red-orange aril with a mean fresh weight of 0.12 ± 0.04 g ($N=200$). The seed is slippery and hard. A random sample of 75 fruits taken from 10 trees contained a mean of 1.15 ± 2.1 non-viable seeds per fruit. Nutritional analyses of fruit components (seed, aril and husk) were conducted at the Animal Nutrition Laboratory of UNAM using standardized techniques (Flores 1981) and were performed on freshly fallen ripe fruits dried to constant weight for 48 hours at 60°C . The extraction values given are the dry weight means of five replications from composite samples. Arils are rich in lipids and energy and the capsule is rich in carbohydrates; seeds were especially rich in protein (Table 1).

METHODS

The study site. Research was carried out from February 1984 to September 1985 at the Estación de Biología Los Tuxtlas of the Instituto de Biología, UNAM, in southern Veracruz, Mexico ($95^\circ 04' \text{W}$, $18^\circ 34' \text{N}$; elevation 150–530 m). The vegetation at the study site is tall evergreen rain forest. Mean annual rainfall is 4900 mm, but is distributed seasonally with a dry season ($\bar{x} = 111.7 \pm 11.7$ mm per month) from March to May and a wet season ($\bar{x} = 486.25 \pm 87.0$ mm per month) from June to February (Estrada & Coates-Estrada 1983).

Fruit production and phenology. Fruit production was monitored throughout the 1984 fruiting season at 10 *C. baillonii* trees. These occurred in three

Table 1. Nutritional components of *Cymbopetalum baillonii* fruit; values are proportions of dry weight (mean \pm SD).

	Ash %	Protein %	Lipid %	Soluble carbohydrates %	kJ/g
Capsule	3.5 (± 0.3)	8.8 (± 1.3)	3.6 (± 1.3)	42.2 (± 5.6)	12.1 (± 3.1)
Aril	1.5 (± 0.8)	7.2 (± 0.9)	61.2 (± 8.6)	23.6 (± 5.5)	27.6 (± 4.3)
Seed	1.7 (± 0.3)	10.9 (± 0.7)	18.5 (± 1.1)	30.2 (± 6.3)	3.5 (± 0.1)



Figure 1. Fruits of *C. baillonii* (a) stalk of undehiscent fruits (note the conspicuousness of the fruits); (b) a stalk with undehiscent (right), totally dehiscent with all seeds removed (left) and partly dehiscent (centre with some seeds removed) fruits. Note the arillate seeds in the middle fruit.

well-defined clusters in approximately 1.2 ha of primary forest. Trees varied from 5 to 17 m in height ($\bar{x} = 12.4 \pm 3.7$) and from 20 to 42 cm dbh ($\bar{x} = 31.5 \pm 8.2$ cm). The area under the crown varied from 12.5 to 60 m².

All fruits in the crown of each tree were counted twice by eye. Each count was done independently by each of us two weeks (25 Jan.–7 Feb. 1984) before the beginning of fruit dehiscence. Thereafter, every two days in the early morning (0600–0900 h) we counted the number of fruits that had dehisced on each tree. After the period of fruit dehiscence in all trees observations of flower and fruit phenology were continued until the end of December 1984. Fruit phenology and fruit dehiscence were recorded every two weeks during a four-year period (Jan. 1981–Dec. 1984) on an additional 12 *C. baillonii* trees, located about 0.5 km from the focal trees.

Frugivore activity. Every two days, during the entire period of fruit dehiscence (10 Feb.–15 June 1984), 3.5 hours in the morning (0600–0930 h) and 3.5 hours in the afternoon (1430–1800 h) were spent censusing animal visitors at each tree for 20 minutes. Censusing periods were rotated among trees so that each individual tree was included in every hour of observation. We recorded the identity of the frugivores, time spent feeding, the number of seeds removed, and the number of seeds dropped under the crown. Bird flights after fruit consumption were recorded as follows: within the crown, from 10 to 19 m, from 20 to 29 m and >30 m away from the tree. In addition, we noted if the flight terminated at *Cymbopetalum* trees in the vicinity.

Predispersal predation. To appraise predispersal damage to fruits by invertebrates we collected one sample (N=50) of undehiscent fruits from the crowns of the 10 trees studied (5 fruits/tree). Another sample (N=100) was collected from the crowns of individuals located about 0.5 km from the focal trees. For all samples, we recorded the presence of holes in the fruits and the number of damaged seeds, and collected insects or larvae found within the husk for identification.

Postdispersal fate of seeds. Every two days we censused under each tree crown the number of freshly fallen seeds and fruits in randomly located 1 m²

plots (2-3 per tree). We noted the number of seeds that had disappeared since the previous census (new seeds were colour marked with a dot of paint at each census) and also recorded the number of seeds germinating.

Seed removal by animals under the crown of each tree was experimentally assessed by placing sets of 10 seeds each as follows: with aril, without aril, enclosed in a wire mesh cage, and unprotected with aril and without aril in each 1 m² plot. The number of seeds remaining in each treatment was recorded 24 hours later. After the experiments, we placed Sherman live traps baited with *C. baillonii* seeds in the same plots and checked them 24 hours later.

We examined the effect of distance on removal of seeds by terrestrial vertebrates as follows: the area under the crown of each tree was divided into four equal sized wedges, using the trunk as a centre and randomly choosing two of the dividing lines as the origin of a 1 X 50 m long transect. At each transect at each tree, we placed seeds without arils in 1 m² plots at the following distances: under the crown, at 5 m, at 10-19 m, at 20-29 m, and at between 30-50 m. Ten seeds were placed under the crowns of each tree and subsequent plots had a lower number of seeds with the last plot having three seeds. This simulated the natural condition of high density seed clumps under the crown of the tree and low density clumps away from the tree. We counted daily the number of seeds remaining for a period of 50 days. An additional experiment in which seed density was kept constant was carried out, at a later date, in the same transects by placing sets of 10 seeds each (seeds were randomly dispersed in the 1 m² plot) at the same distance intervals. The presence of seeds was also checked daily for a period of 50 days.

Seedling mortality. We evaluated the survival of seedlings under the crown and away from the parent tree by planting, after the period of fruit dehiscence of each tree, five seedlings (\bar{x} = 13.64 \pm SD 1.94 cm in height) in 1 m² plots located at the same intervals and in the same transects used to assess seed removal by terrestrial vertebrates; seedling survival was checked monthly for 12 months and once more 24 months after planting.

Germination experiments. Individual seeds (N = 150) were planted in random locations on the forest floor under the following treatments: seeds with arils (N = 50), seeds with arils removed by us (N = 50), and seeds regurgitated by birds (N = 50). Each individual seed was protected from seed-eating vertebrates by a wire mesh cage. This experiment was replicated with the same treatments and number of seeds in a growing-house; in contrast to the seeds planted in the field, these seeds were watered daily. The number of seeds germinating was recorded every two days in both cases.

The gross impact of light and microsite conditions on germination of frugivore-dispersed seeds was evaluated by planting sets of three bird-regurgitated seeds each at every metre along a 10 m long transect starting in the middle of a tree fall gap (area = 40 m²) and ending inside the forest. This transect simulated a light continuum: high in the middle of the gap to very low several metres inside the forest. These seeds were enclosed in wire cages to protect against

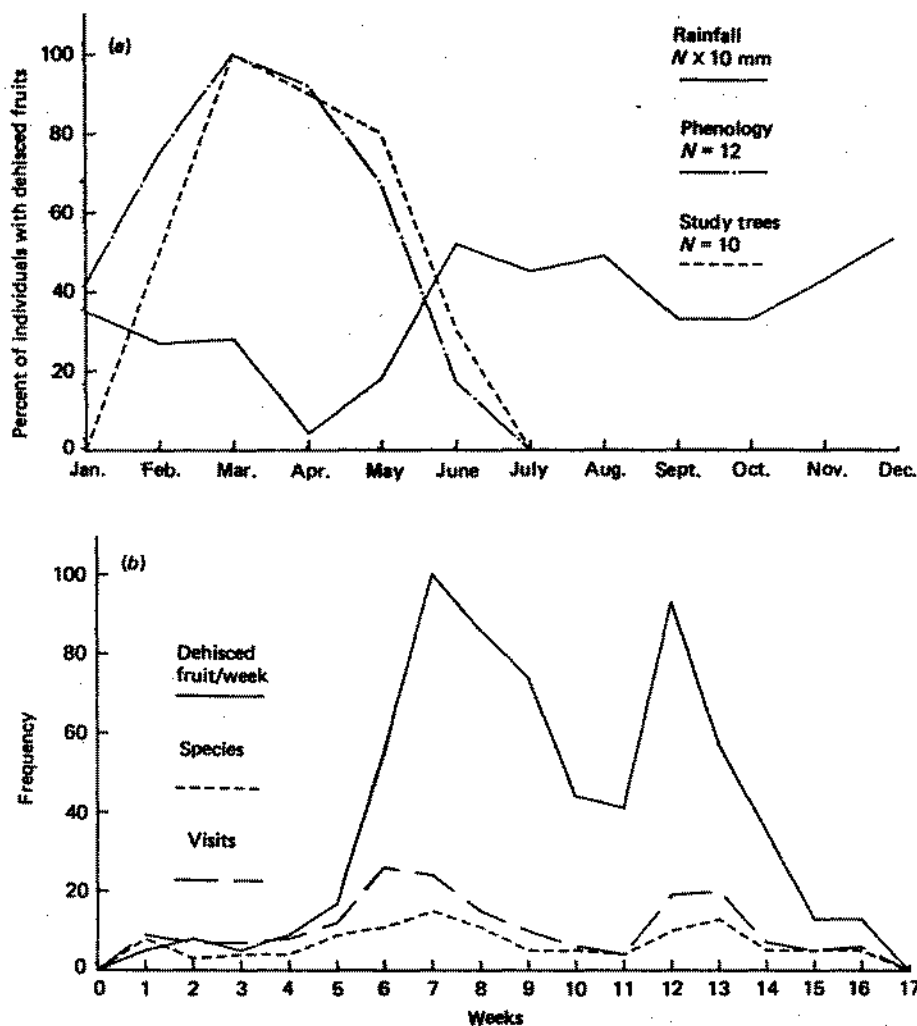


Figure 2. (a) Phenology of dehiscence fruit in study trees for 1984 and in 12 additional trees for 1981-1984. (b) Production of dehiscence fruit per week in the study trees and the associated temporal pattern of frugivore visitation.

removal by vertebrates and were not watered. Germination was checked every two days for three months and the number of surviving seedlings was monitored for 17 months after germination.

RESULTS

Fruit phenology. Dehiscence fruits were present during the first six months of the year, mainly during the dry season and until the onset of consistently high rainfall (Figure 2a). Flowers were produced between May and July, and young fruits were present as early as June. These matured very slowly and attained maximum size by December-January.

Table 2. List of frugivores at *C. baillonii* trees ranked by number of seeds taken. (Note, M = North American migrants; (I) = Seeds dispersed under non-conspecific trees.)

	Weight g ±	Feeding time (sec)	No. visits	No. seeds dropped under crown	Dispersed under <i>C.</i> <i>baillonii</i>	Dispersal distances (I) (m)			Seeds consumed
						10-19	20-29	>30	
BIRDS									
<i>Habia fuscicauda</i> (Red-throated Ant-tanager)	40	5610	45	17	13	5	31	—	—
<i>Amazona autumnalis</i> (Red-lored Parrot)	245	2160	4	16	—	—	—	—	46
<i>Hylocichla mustelina</i> (M) (Wood Thrush)	45	3840	31	10	17	10	18	—	—
<i>Cyanocorax morio</i> (Brown Jay)	285	1530	7	14	—	—	—	17	—
<i>Ramphastos sulfuratus</i> (Keel-billed Toucan)	350	1260	5	5	—	—	7	6	—
<i>Oeolus castaneus</i> (Chestnut-coloured Woodpecker)	78	2160	7	9	2	—	7	4	—
<i>Habia rubica</i> (Red-crowned Ant-tanager)	35	1710	13	10	1	1	9	—	—
<i>Catharus ustulatus</i> (M) (Swainson's Thrush)	40	900	9	2	—	5	5	—	—
<i>Melanerpes aurifrons</i> (Golden-fronted Woodpecker)	52	1080	6	4	2	—	6	1	—
<i>Turdus grayi</i> (Clay-coloured Robin)	65	720	7	2	2	1	5	—	—
<i>Trogon massena</i> (Slaty-tailed Trogon)	90	840	3	5	—	1	—	4	—
<i>Myiarchus tyrannulus</i> (Brown-crested Flycatcher)	32	520	4	2	—	4	1	—	—
<i>Attila spadiceus</i> (Bright-rumped Attila)	45	660	3	1	—	2	—	2	—
<i>Lanio aurantius</i> (Black-throated Shrike-tanager)	35	390	4	2	—	—	3	1	—
<i>Vireo olivaceus</i> (M) (Red-eyed Vireo)	19	480	1	0	1	2	1	—	—
<i>Momotus momota</i> (Blue-crowned Motmot)	140	540	1	2	—	1	4	—	—
<i>Megarhynchus pitangus</i> (Boat-billed Flycatcher)	38	240	1	2	—	—	3	—	—
<i>Trogon collaris</i> (Collared Trogon)	68	720	1	4	—	—	3	—	—
<i>Psarocolius montezuma</i> (Montezuma Oropendola)	350	120	1	0	—	—	—	2	—
<i>Piranga rubra</i> (M) (Summer Tanager)	40	240	2	2	1	—	1	—	—
<i>Campylorhynchus zonatus</i> (Band-backed Wren)	35	60	1	0	—	—	1	—	—
<i>Eucometis penicillata</i> (Gray-headed Tanager)	25	120	2	3	—	—	—	—	—
<i>Euphonia hirundinacea</i> (Yellow-throated Euphonia)	14	240	2	2	—	—	—	—	—
<i>Mionectes oleagineus</i> (Ochre-bellied Flycatcher)	15	180	2	3	—	—	—	—	—
MAMMALS									
<i>Sciurus despei</i> (Tree Squirrel)	250	1800	3	3	—	—	—	—	10

In the study trees the period of fruit dehiscence lasted 16 weeks (second week of February to first week of June) with two marked peaks between 24 March-14 April and between 5-11 May (Figure 2b). The number of dehisced fruits ranged from five to 100 per tree per week. The number of weeks trees contained dehiscent fruit ranged from four to 12 ($\bar{x} = 9.8 \pm 3.0$) and individual trees showed distinctive fruiting peaks with Kurtosis values ranging from 1.8 to 3.5 ($\bar{x} = 2.5 \pm 0.6$). The total number of undehisced fruits produced by the study trees ranged from 44 to 173 ($\bar{x} = 101.2 \pm 47.2$), with a corresponding potential seed crop per tree of 792 to 3114 ($\bar{x} = 1966 \pm 850$) seeds.

The frugivore assemblage. During the day 24 species of birds and one mammal species visited the crowns of the trees and consumed the fruit (Table 2). Censuses at each tree recorded 1-47 visits by animals of 1-18 species throughout the season (Table 3). No nocturnal visitors were detected in 40 night watches (20 minutes duration each) carried out between 1900-2400 hours and spread throughout the period of fruit dehiscence. Frugivore visitation closely followed the weekly temporal pattern of dehisced fruit production (Figure 2b). Birds ranged in size from 18 g (*Euphonia hirundinacea*) to 350 g (*Ramphastos sulfuratus*); four species were North American migrants.

Consequences of frugivory

Predispersal predation. Examination of 300 undehisced fruits about 6 months old removed directly from the crown revealed that 25% were inhabited by insect larvae (Lepidoptera - 1 species, Diptera - 3 species, Staphylinae - 1 species, Coleoptera - 1 species, Hymenoptera - 2 species), and 2% were inhabited by *Camponotus* ants. Those with beetle infestation had from 1 to 13% ($\bar{x} = 5.7 \pm 5.3\%$) of the seeds destroyed ($\geq 50\%$ of the embryo removed). Those with ants had a fungus invading about 30% of the inner tissue of the capsule and from 5 to 10% ($\bar{x} = 5.2 \pm 3.1\%$) of the seeds were destroyed.

Observation of frugivore activity detected that the Tree Squirrel (*Sciurus deppii*) and the Red-lored Parrot (*Amazona autumnalis*) consumed and crushed seeds, killing them outright in the crown. Both seed predators dropped many undamaged seeds under the tree; together they killed 14% of the seeds removed by animals in the crown (Table 3).

Seed dispersal and shape of the seed shadow. The tree's mean number of dehisced fruits available per day was positively correlated with the number of frugivore species ($r = 0.79$, $P < 0.05$) and animal visits ($r = 0.70$, $P < 0.05$) at each tree; no correlation existed between frugivore body weight and the number of seeds taken by each species ($r = 0.16$ NS, $N = 25$). Foraging time at each tree was correlated positively with the number of seeds removed ($r = 0.94$, $P < 0.01$) and with the number of seeds dropped under the crown ($r = 0.98$, $P < 0.01$) by frugivores, hence stressing the 'wasteful' nature of seed dispersal. Trees with a high mean number of dehisced fruits per day attracted a greater number of frugivores and had more seeds dispersed and more seeds dropped under the crown than trees with small numbers of dehisced fruits per day (Table 3). Of

Table 5. *C. baillonii* seeds handled by frugivores, initial fate of seeds, and dispersal efficiency ratios (seeds dispersed/seeds wasted + seeds dispersed) per tree.

Tree no.	dbh (cm)	Height (m)	Total no. fruit	Seed weight (g)*	Dehisced fruit		No. of visitor species	No. visits	Feed time (sec)	Seed waste			Seed dispersal			Total RDE	RDE >30 m	No. of conspecific neighbours 0-30 m		
					Mean no. fruits/day	No. weeks				Dropped under crown	Killed by predators	Disp. under <i>C.b.</i>	Distance (m)							
													Total	10-19	20-29				>30	
1	47	11	173	0.38±0.06	4.5±2.9	14	18	47	129	41	29	7	77	5	36	12	53	0.40	0.09	3
2	39	13	68	0.56±0.09	3.2±2.4	12	6	24	41	7	0	11	18	3	11	1	15	0.45	0.03	4
3	59	17	95	0.48±0.13	2.6±2.2	12	11	31	87	26	1	10	37	1	19	14	34	0.47	0.19	4
4	40	12	142	0.36±0.07	2.8±1.3	11	7	19	36	7	0	8	15	8	6	2	16	0.51	0.06	3
5	45	14	111	0.35±0.06	2.6±1.4	13	6	6	23	2	5	1	8	1	6	3	10	0.55	0.16	1
6	49	14	166	0.42±0.07	4.0±2.4	10	8	17	46	13	0	0	13	8	11	0	19	0.59	0	1
7	35	7	53	0.30±0.11	1.5±0.7	6	3	10	27	7	0	0	7	2	11	0	13	0.65	0	1
8	26	5	87	0.44±0.07	2.0±1.0	6	3	6	36	9	21	0	30	0	3	0	3	0.09	0	1
9	37	14	44	0.35±0.07	1.4±0.7	11	1	1	8	3	0	0	3	0	0	2	2	0.40	0.40	1
10	39	16	153	0.36±0.07	3.2±1.9	8	5	7	18	5	0	2	7	4	2	3	11	0.61	0.16	3
Total			1092							120	56	39	215	32	105	37	176			
(% = total/391)										(31)	(14)	(10)	(55)	(8)	(27)	(9)	(45)			

* F = 6.9, P < 0.005, RDE = relative dispersal efficiency (see text).

all the seeds observed to be handled by frugivores ($N=391$), 31% were dropped under the crown of the fruiting tree, 8% were dispersed to distances of 10–19 m, 27% were dispersed 20–29 m and 9% were dispersed >30 m (Table 3).

Influence of neighbours. Proximity of conspecific fruiting plants strongly influenced the destination of dispersers (and seeds) after eating fruit. Ten per cent of the seeds observed to be handled by potential dispersers were deposited under neighbouring conspecific fruiting trees. A positive correlation ($r=0.92$, $P<0.05$) was found between the number of seeds dispersed under neighbouring conspecific fruiting trees by frugivores and the number of conspecific neighbours each tree had within a 25–30 m perimeter, using the bole as the centre (Table 3).

Important dispersers. As a result of their high contribution to seed removal some bird species were pre-eminent seed dispersal agents. Thus 44% of the seeds removed by birds from the 10 trees were dispersed by the Red-throated Ant Tanager (*Habia fuscicauda*), a resident species, and by the Wood Thrush (*Hylocichla mustelina*), a North American migrant. These two birds, however, also accounted for 22% of the seeds ($N=120$; Table 3) dropped under the crown by all frugivores and for 74% of the seeds dropped ($N=39$) under neighbouring conspecific fruiting trees. However, only eight bird species displayed long distance flights (>30 m) after ingesting seeds. Of these, the Brown Jay (*Cyanocorax morio*) and the Keel-billed Toucan (*Ramphastos sulfuratus*) were the principal long distance dispersers of seeds as they accounted for 46% and 16% respectively of all the seeds ($N=37$; Table 3) dispersed at this distance.

Consequences of Dispersal

Frugivory and germination of seeds. No differences were found in the germination success or in latency of germination of seeds (without arils, with arils and regurgitated by birds; $N=50$ in each case) planted in the field ($N=150$) and in the growing-house ($N=150$). Seeds watered daily in the growing-house displayed significantly (t test $P<0.001$) higher germination numbers (80–84%) and shorter germination times (25–46 days) than seeds planted in the field (50–56% and 61–81 days respectively); water was an important factor promoting germination.

Seed germination experiments in the treefall gap to forest transect showed that 92% of the seeds planted in the forest (shaded environment) germinated compared with only 44% in the gap (unshaded environment). None of the seeds survived as seedlings in the treefall gap 17 months after planting. In contrast, 42% survived as seedlings in the forest. All of the seeds planted on the gap-edge section (a partly shaded area) of the transect germinated and 67% survived as seedlings after 17 months. Latency of germination was higher for seeds planted in the light gap ($\bar{x}=55.8 \pm 9.2$ days) than for seeds planted inside the forest ($\bar{x}=47.7 \pm 2.0$ days; $t=3.22$ $P<0.01$).

Fate of seeds dispersed under and away from the parent tree. Density of *C. baillonii* seeds dispersed under the crown of each tree ranged from 5 to 40

seeds m^{-2} ($\bar{x} = 21.3 \pm 12.5$ seeds m^{-2}). Of 536 seeds censused in $1 m^2$ plots under the crowns of the 10 trees (2–3 m^2 per tree), 85% (56 to 100% per tree) were removed mainly by rodents (see below) and only an average of 7% (0 to 26% per tree) germinated and became established as seedlings. Nine per cent of the seeds counted under the crown were not removed by vertebrates and did not germinate; the majority of these seeds were non-viable and rotted on the ground.

Exclosure experiments showed that all the unprotected seeds (with or without arils) under all trees were removed within 12 hours. In contrast, those protected by the cages remained intact; ants did not remove any seeds. Sherman live traps (baited with *C. baillonii* seeds) under the crowns of all trees captured *Heteromys desmarestianus* ($N=6$) and *Peromyscus mexicanus* ($N=10$) rodents. Only one terrestrial diurnal vertebrate, the Ruddy-Quail Dove (*Geotrygon montana*), was observed eating *Cymbopetalum* seeds under the crown of the trees.

Experiments evaluating the effect of dispersal distance on seed survival showed that all seeds located within 25 m of the tree and occurring at densities of 6–10 seeds m^{-2} , were removed by vertebrates by the fifth day after deposition. However, those located at distances $>30 m < 50 m$ from the tree and occurring at lower experimental densities (<6 seeds m^{-2}) remained longer on the ground (Figure 3a). Similar results were obtained when seed density was kept constant ($N=10$ seeds m^{-2}) at each distance interval (Figure 3b). Sherman live traps baited with *Cymbopetalum* seeds and placed at the same distance intervals from each tree for one night captured *Heteromys* ($N=6$) and *Peromyscus* ($N=10$) rodents.

Captive *Peromyscus* and *Heteromys* rodents avidly ate seeds of *Cymbopetalum* that were offered simultaneously with seeds of other fruiting species (*Pseudolmedia oxyphyllaria*, *Brosimum alicastrum* – Moraceae) known to be eaten by these rodents (Estrada & Coates-Estrada 1986). Chemical analyses showed that *Cymbopetalum* seeds had a higher protein/dry weight content ($\bar{x} = 10.9 \pm 0.7\%$) than the seeds of *B. alicastrum* ($\bar{x} = 7.8 \pm 0.6\%$) and *P. oxyphyllaria* ($\bar{x} = 6.4 \pm 0.4\%$). No evidence was found of seed damage caused by insects on the ground.

Seed dispersal and survival of seedlings. Distance from the parent tree had an important effect on seedling survivorship. At the end of the period of fruit dehiscence seedling density under the crown of each of the 10 trees ranged from zero to 2.6 seedlings m^{-2} ($\bar{x} = 1.2 \pm 1.1$). Mortality of those seedlings established under the crown and in the immediate vicinity (10–15 m) of the parent tree was 91% ($N=183$) after a 12 month period. Monthly censuses of experimental seedlings planted under the crown and at 5 m, 10–19 m, 20–29 m, and 30–50 m away from each tree showed that, after one year, on the average 80% of the seedlings planted under the crown were dead whereas only 40% of the seedlings at 50 m had the same fate. At 24 months, 40% of the seedlings survived at 30–50 m while under the crown only 10% had the same fate

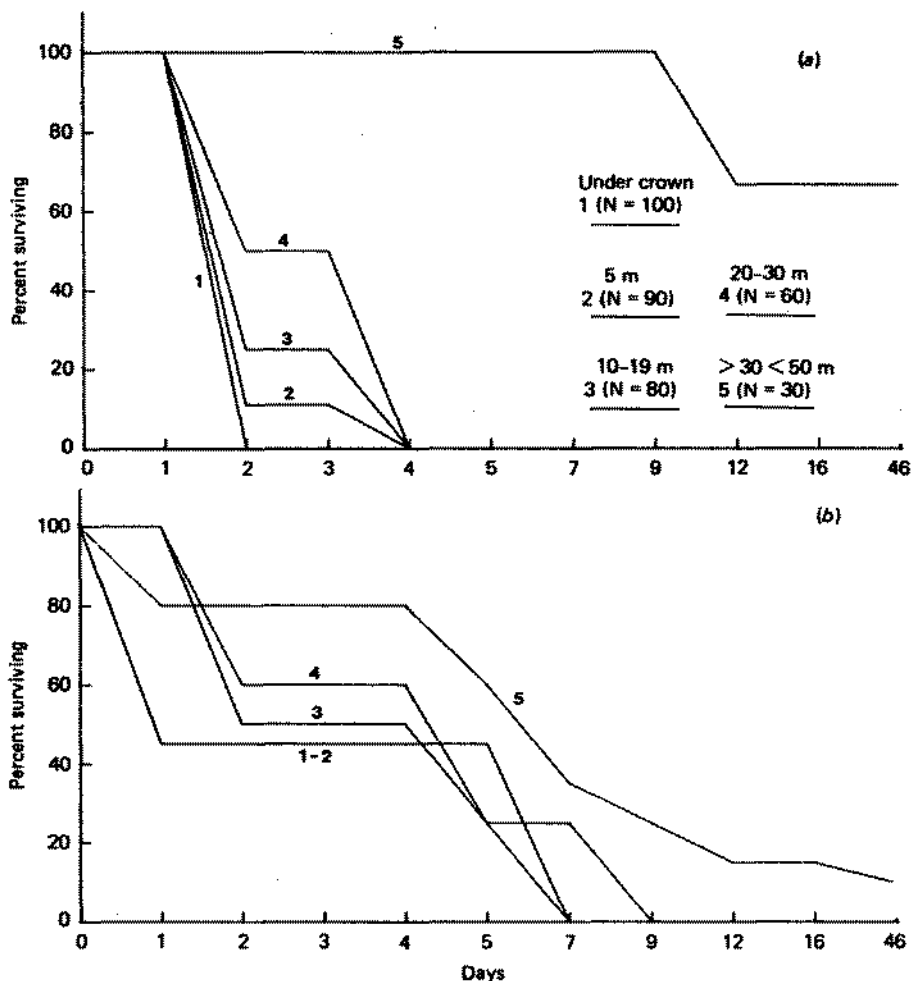


Figure 3. (a) Survival of seeds planted at various distances from the parent tree. Seed density for each tree was 10 seeds m^{-2} under the crown and 3 seeds m^{-2} at $>30 < 50$ m from the bole. (b) Survival of seeds at the same distance intervals when seed density was kept constant (10 seeds m^{-2} at each distance interval/tree).

(Figure 4). Seedlings surviving under the crown and at 50 m for 12 months did not differ significantly in total height ($\bar{x} = 16.4 \pm 1.8$ cm, $N=3$ vs $\bar{x} = 19.2 \pm 3.3$, $N=6$; $t=1.3$, $DF 7$, $P=0.10$) or in number of leaves ($\bar{x} = 5.3 \pm 1.1$ vs $\bar{x} = 7.6 \pm 4.1$; $t=0.93$, $P=0.19$).

Relative dispersal efficiency. Seeds dispersed under the parent tree and under neighbouring conspecific fruiting trees together with those killed by invertebrate and vertebrate seed predators represent the cost each tree pays to have its seeds dispersed. Relative dispersal efficiency, expressed as the number of seeds dispersed under non-conspecific trees divided by the total number of seeds wasted + total number of seeds dispersed under non-conspecifics per tree (RDE=1.0 would indicate maximization of seed survival and no waste

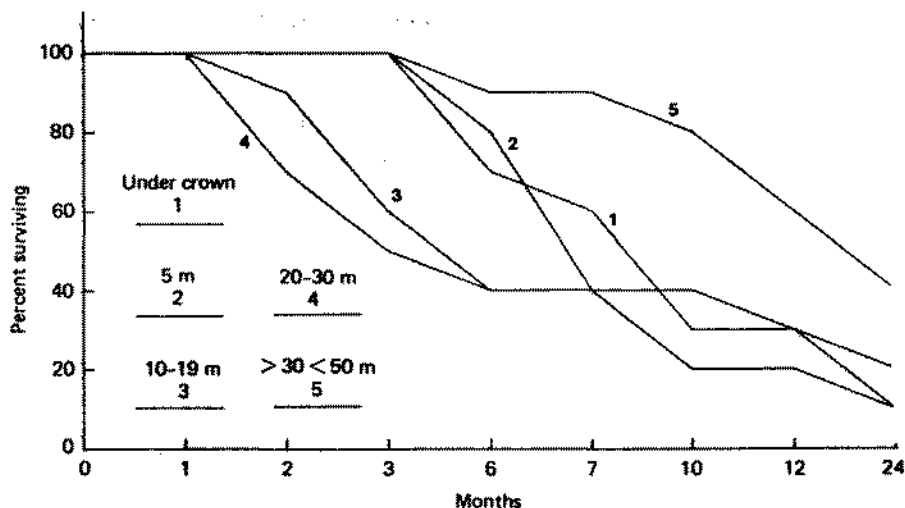


Figure 4. Survival of seedlings planted at various distances from study trees after the period of fruit dehiscence. Experimental density was 5 seedlings m^{-2} per distance interval per tree.

of maternal investment) was greatly variable among individual trees (range 0.09–0.65) (Table 3).

Efficiency was not significantly associated either with the number of frugivore visits ($r = -0.03$, NS), nor to the number of weeks of fruit dehiscence in each tree ($r = 0.15$, NS), nor to the mean seed weight of each tree ($r = -0.47$, NS). Variations in numbers of seeds dropped under the crown, in numbers of seeds killed by parrots and squirrels, and interference by neighbouring conspecific plants in fruit may have been greatly responsible for the observed variations in individual relative dispersal efficiency (Table 3). Individual trees with a high number of visits and a high number of seeds removed were not as efficient as trees with low number of visits and low numbers of seeds dispersed (Table 3). When only the total number of seeds dispersed >30 m from the parent tree (a distance at which seed and seedling mortality are significantly reduced) is considered, only four trees had relative dispersal efficiency values >0.10 . Of these, tree no. 9, with the lowest number of frugivore visits scored was the most efficient (RDE = 0.40). In contrast, tree no. 1, with the highest number of frugivore visits and largest fruit crop, was one of the less efficient according to this measure (RDE = 0.09) (Table 3).

DISCUSSION

At Los Tuxtlas, *C. baillonii* is a tree species whose oil-rich arils and protein-rich seeds are an important reward to 24 bird species and to one mammal that act as arboreal dispersers and predators of the seeds. Once on the ground, the seeds are eagerly sought and consumed by rodents.

The number of dehisced fruits available each day at each tree strongly influenced the frequency of visitation and the time spent feeding at the trees by

frugivores. Albeit seed size differences were found among individuals, trees with small seeds were not consistently depleted more than trees with large seeds as has been reported for other Neotropical tree species with arillate seeds (Howe *et al.* 1985). Instead, daily dehiscence fruit availability was a factor closely related to depletion of arillate seeds. Medium sized birds such as *H. fuscicauda* and *H. mustelina* with high visitation rates dispersed a great number of seeds but, by dropping many seeds under the crown of the parent tree and under the crowns of neighbouring conspecific fruiting trees, were also responsible for a great proportion of 'seed waste' observed.

It was noteworthy that all bird species in the disperser assemblage deposited some seeds >20 m from the parent trees. However, only eight species dispersed seeds at distances (>30 m) that enhanced initial seed survival and establishment; this suggests a narrow range of effective dispersal agents. In this view, *H. fuscicauda* and *H. mustelina* quantitatively were important removers of seeds but qualitatively were poor dispersers. The converse was true for birds such as *C. morio*, *R. sulfuratus*, and *C. castaneus* among the eight species dispersing seeds at distances >30 m.

As a result of its size and the size of the frugivore, dispersal of the seed is by regurgitation rather than defecation; since regurgitation is a faster method of voiding seeds than defecation seeds are more likely to be deposited a short distance from the parent tree (Levey 1986). Terrestrial vertebrate seed predators hence find a dense seed shadow under the crown of fruiting trees and a less dense, but localized, shadow consisting of scattered seeds within a radius of 50 m.

Recruitment of *C. baillonii* seems to be strongly reduced at the seed stage by intensive seed predation by mammals. An unequivocal initial advantage to long distance dispersal was evident for seeds deposited under non-conspecific trees and farthest from the parent tree; seed density was apparently of secondary importance relative to distance. Just how seeds escape the devastating post-dispersal predation by rodents is not entirely clear, but in some instances seeds were observed to have germinated while 'hidden' by leaf litter; random factors (environmental variance, *sensu* Herrera 1985) may play a role here.

Germination of seeds and initial establishment of seedlings under the crown and at various distances away from the parent tree also suggests that effective dispersal agents may not be indispensable for initial dispersal success. However, seedlings established under the parent tree suffered greater mortality than seedlings established away from the parent tree, reinforcing the idea of an initial advantage to dispersal away from the parent tree.

Cause of seedling mortality under the crown and in the immediate vicinity (up to 15 m) was difficult to determine. Herbivore damage by insects was observed on the leaves of 49% of the seedlings established (N=74) but we could not ascertain the impact of such damage on continued survival after 12 months. Seedlings produced new leaves despite losses of up to 70% of their leaf area. Acceptability experiments of seedlings of 40 tree species to deer

(*Odocoileus virginianus*) and peccaries (*Tayassu tajacu*) showed, however, that *Cymbopetalum* was one of a few ($N=5$) species not accepted by these two herbivores (A.E. and R.C.E. unpublished data).

It is likely that several factors contributed to mortality among seedlings. For example, density dependent mortality and distance from the parent tree were variables important in the survival of seeds, for seed predators (i.e. rodents) were seemingly density and distance responsive. Seedlings located the farthest from the parent trees and occurring at lower densities survived longer, implying that seed transportation by the frugivore away from the parent tree enhances chances of establishment and seedling longevity (Clark & Clark 1981, Dirzo & Dominguez 1986, Howe *et al.* 1985).

Cymbopetalum seeds can germinate in forest light gaps but do not become successfully established when deposited in these sites. When frugivores deposit the seeds inside the forest or at a light gap edge, where soil humidity is higher, latency of germination is reduced and seeds achieve an initial establishment. Since water is a critical factor promoting germination of the seed, those seeds released by the tree via dispersers during the dry season (March-May) had to wait longer on the ground than those released at the end of the rainy season (February) and during the onset of the rains (June). Such seed sets were eaten by rodents prior to germination. Perhaps only some of the seeds dispersed during the last month and the first month of the rainy season, and those that serendipitously remained 'hidden' in the leaf litter, were able to elude rodent predation and became established as seedlings.

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