SEED AND SEEDLING ECOLOGY OF *Carapa guianensis*[1] /

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Resumen

Carapa guianensis *(Meliaceae) es una especie arbórea sub-dominante del bosque superhúmedo maduro del noreste de Costa Rica. Los árboles florecen en setiembre y producen frutos maduros el siguiente mes de mayo. La nizaciòn fenológica de la población produce marcadas diferencias anuales en la producción de semillas.*

La semilla producida por árboles individuales varió desde 754 hasta 3 944 semillas, con un peso seco promedio de 15.6 g. La mejor germinación se obtuvo cuando la semilla estuvo en contacto directo con suelo húmedo. En suelos drenados, las semillas hundidas hasta la mitad o sobre la superficie germinaron mejor. En suelos mal drenados (suampos), las semillas sobre la superficie o enterradas hasta la mitad presentaron un 90 por ciento de germinación. Las semillas completamente enterradas en suelos mal drenados y las colocadas sobre la superficie de suelos bien drenados no germinaron.

Los frutos caen debajo de la copa del árbol y de ahí del 54 al 98 por ciento de las semillas son transportadas a otros sitios. Es probablemente un factor importante en la dispersión de las semillas y en germinación. Las larvas de Hypsipyla ferrealis *se alimentaron de las semillas de* C. guianensis. *La remoción experimental de diferentes proporciones de endosperma de las semillas, simulando el daño causado por los insectos a los roedores, causó una reducción del número de plántulas y un aumento en la mortalidad*

Se postula que una ventaja de las semillas grandes en especies del mango tropical es la producción de un talluelo largo, lo que le permite colocar sus hojas sobre las aguas caídas en forma estacional durante todo el año.

Introduction

Carapa guianensis Aubl. (Meliaceae) is an important timber tree in the lowland wet Neotropics from Belize to Amazonian Brazil and in the Antilles (18). It is predominantly a species of swampy or periodically inundated land, occasionally forming nearly pure stands (4, 6, 12, 14, 15). As part of a demographic study of a *C. guianensis* population in Costa Rica, the authors have gathered information on its seed and seedling ecology.

This study was conducted during July – September 1974 and 1975, and in August 1976 at La Selva, the Organization for Tropical Studies' field station in northeastern Costa Rica, near Puerto Viejo de Sarapiqui, Heredia Province. The vegetation is premontane wet forest, warm transition in the Holdridge life zone system (11). Elevation ranges from 35 m above sea level along the Rio Puerto Viejo to 150 m above sea level about 3 km from the river. Mean annual temperature and rainfall are 24.1°C and 3 930 mm, respectively, without an effective dry season (9)

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In the undisturbed primary forest at La Selva, *C. guianensis* is a canopy tree which attains 2 m in diameter and 45 m in height. It is a sub-dominant of the 2 ha swamp forest in Study Area II, but also occurs in much lower densities on the higher and better drained slopes and ridges (Table 1). The occurrence of swamp species on better drained sites at La Selva is probably related to the very high rainfall throughout the year (9). The swamp soils in Study Area II are poorly drained old alluvium with high organic matter and nutrient levels (3). The Study Area II swamp has a microrelief of less than one meter consisting of interspersed hammocks and sloughs.

Fecundity

Carapa guianensis at La Selva flowers in September and produces mature fruit the following May (7). The annual production of seeds is variable; in some years (e.g., 1973, 1975) very few members of the population produced seeds, whereas in other years (e.g., 1971, 1974, 1976) virtually all mature trees bore heavy fruit crops. The fruit of *C. guianensis* is a four-valved dehiscent capsule 10 – 14 cm in diameter that falls from the tree when ripe, breaking into four segments and liberating the seeds. Impressions in the valve wall indicate the number of seeds contained in that segment. Based on a sample of 2 948 valves on the ground beneath four reproductive trees, the mean number of seeds/valve was 1.67 ± 0.06 (one S.D.) or 6 – 7 seeds/fruit. This compares well with Smith's (16) report of 7 – 8 seeds/fruit for Central American trees. Estimates for populations in northern South America, however, are considerably higher with up to 16 seeds/fruit having been reported (1, 6, 15). Marshall (12) estimated that 12 seeds/fruit was average for trees in Trinidad.

We obtained a mean fresh seed weight for *C. guianensis* of 32.1 ± 10.6 g (n = 25) and have found viable seeds from the same tree ranging from 19.0 to 62.2 g fresh weight. A mean of 15.6 ± 5.0 g (n = 76) was obtained for seeds dried at 24°C for 72 h. Fanshawe (6) reported a dry seed weight of 10 – 12 g.

Fecundity estimates were obtained for three trees in August 1976 by counting the number of seed impressions in all valves collected under each tree (Table 2). Estimates for two trees were obtained in August 1974 by counting the number of valves in a 45° area out from the base of the tree, multiplying by eight for extrapolation to 360°, and multiplying by 1.67 seeds/valve for total seed production estimates (Table 2). The crowns and valve distribution under these trees were fairly uniform. All trees sampled were located in swampy areas.

Germination

The requirements for germination of *C. guianensis* seeds were determined in July and August 1974 by planting seeds in each of three habitats: (1) heavily shaded swamp, (2) moderately shaded cacao plantation, and (3) open ground. The swamp soil was wet and occasionally covered with standing water; the latter two sites were on well-drained old alluvium. Within the three habitats, 10 seeds were sown in each of three ways: (a) on the soil surface, (b) embedded in the soil to one-half the seed's diameter, and (c) buried 20 cm beneath the soil surface. Planting occurred immediately following collection of seeds from under a fruiting tree. The majority of the seeds germinated within two to four weeks after planting. In 10 weeks high germination percentages were found for the surface-sowed and embedded seeds in the

Table 1. Dominance values based on individual ≥ 10 cm dbh for the five most important tree species in the 2 ha swamp of Study Area II, La Selva. Dominance values for *C. guianensis* on slopes and ridges (Study Area III, 4 ha) are presented parenthetically for comparison.

Species	Density (stems/ha)	Frequency (% 20 m X 20 m quadrats with species)	Basal area (m^2/ha)	Importance value (%)
Pentaclethra macroloba	122	42	19.82	56
Carapa guianensis	62 (9)	27 (9)	13.16 (1.1)	34 (2)
Pterocarpus officinalis	25	18	11.27	24
Astrocaryum alatum	61	29	0.85	16
Iriartea gigantea	35	23	0.90	11
Others	401	325	21.91	159
Total (115 species)	706	464	67.91	300

Table 2. Fecundity estimates for *C. guianensis* trees in the La Selva forest. * denotes estimate obtained in August 1974 by valve counts in a 45° area out from the base of the tree extrapolated to 360°. All other trees censused in August 1976.

Tree no.	dbh (cm)	Estimated no. of seeds
4 268	19.7	754
7 154	41.5	2 171
5	64.0	2 108*
1	90.0	3 522
4	95.0	3 944*

swamp, for the embedded seeds in the cacao, and for the buried seeds in the exposed site (Table 3). It is clear that *C. guianensis* seeds will not germinate when buried in the swamp, or if they become too dry, as on the surface of the ground in full sun. These observations accord with Marshall's (12) report that poor germination is often the result of water-logging or dessication. In the course of this study we found that newly collected seeds lost their viability rapidly, and had to be protected from drying if stored for any length of time before planting.

Seed dispersal and predation

Carapa guianensis seeds float, which enhances dispersal in a swamp or riparian species. We found *C. guianensis* seeds as an occasional component of debris deposited on the Atlantic beach at Tortuguero, and in Corcovado National Park on the Pacific coast, especially near the mouths of water courses. Fanshawe (6) reported that the seeds float until they rot.

From the distribution of valves in contiguous 2 m^2 quadrats along 11 haphazardly chosen 18 m radii from the bases of 5 reproductive trees in 1974, we constructed an average expected valve shadow transect (Figure 1). A very strong concentration of seeds occurs on the ground beneath the crown because the unopened fruits fall when mature. Such a high concentration of large seeds beneath a reproductive tree, as well as in a larger area such as the swamp forest of Study Area II, should be a prime temporal food source for seed eaters. Fifty-four to 96 percent of the expected number of seeds in the 11 sampled transects had been removed from the area at the time the valve count was made.

The major vertebrate predators of *C. guianensis* are collared peccaries (*Tayassu tajacu*), white-lipped peccaries (*Tayassu pecari*), and large rodents such as agoutis (*Dasyprocta punctata*) and pacas (*Agouti paca*). On Barro Colorado Island, Panama, Smythe (17) cited the agouti as the principal dispersal agent of large seeds through its scatter hoarding behavior, the transport and burial of seeds in various sites away from the fruiting tree (see also 13). Although utilizing *C. guianensis* seeds as food, agoutis probably enhance the germination of seeds that are buried and subsequently not retrieved. Agoutis, pacas, and collared peccaries are resident components of the La Selva forest fauna, but the gregarious white-lipped peccary has been rarely seen at La Selva. According to knowledgeable local people, white-lipped peccaries are usually found in swamps feeding on *Carapa* seeds. We did not observe any sign of white-lipped peccaries in Study Area II during the summers of 1974, 1975, and 1976.

Rate and quantity of seeds transported (presumably by agoutis, as evidenced by many tracks at the study sites) were determined in 1974 by placing different quantities of freshly collected seeds at varying distances under a reproductive *C. guianenesis* and under a control tree (*Virola koschnyi* Warb.) of approximately the same size. The experimental tree was within 200 m of other reproductive *C. guianensis*, whereas the control tree was over 200 m from the nearest reproductive *C. guianensis*. There were fresh valves under the *C. guianensis* at the time, but very

Table 3. Germination percentages of *C. guianensis* seeds 10 weeks after planting under different sowing and site conditions. n = 10 for each treatment.

Sowing position	Site conditions		
	Dense shade, poorly-drained soil	Partial shade, well-drained soil	Full sun, well-drained soil
Seed buried 20 cm	0	30	90
Seed half-embedded	90	70	30
Seed on soil surface	90	10	0

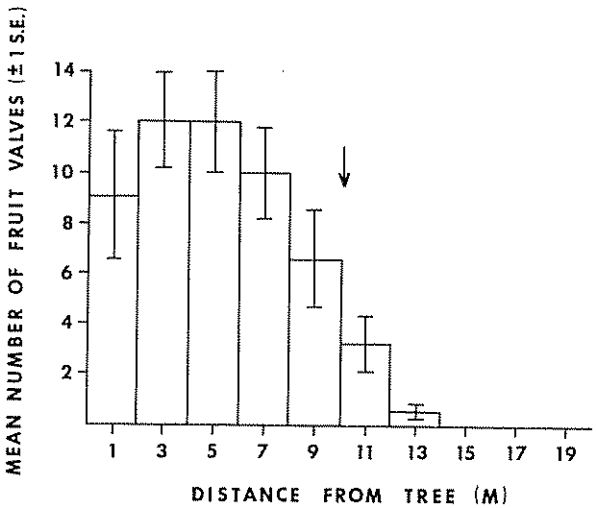

Fig 1 Average transect valve distribution based on valve counts in contiguous 2 m² quadrats from a total of 11 transects beneath five *C. guianensis*. Arrow indicates the average extent of the crowns above the transects. Bars indicate ± one S.E.

few seeds; these were removed. There were no fruits or seeds under the control tree. No precautions were taken to prevent contamination of seeds with human scent. All piles of seeds were checked daily for the first six days, then intermittently to record the number of seeds removed. The data (Table 4) show that some piles were discovered within 24 h of placement, and that seed removal was rapid. Of the piles of seeds beneath the *C. guianensis*, 45 percent of the seeds was removed in three days; 94 percent of the seeds beneath the control tree was removed in the same amount of time. Fewer sources of additional *C. guianensis* seeds near the control tree may have influenced the rapid and thorough removal of seeds. Seeds were removed from all piles except one with 5 seeds and one with 2 seeds.

In the forest we frequently found germinating *C. guianensis* seeds with the radicle missing and part of the seed chewed away through the opening made by the emerging root. Live traps baited with germinating seeds captured a porcupine rat (*Haplomys gymnurus*) that ate the radicles of the seeds in the traps and damaged them similarly to seeds we had observed.

The larvae of *Hypsipyla ferrealis* Hampson (Lepidoptera, Pyralidae, Phycitinae) are commonly found in seeds of *C. guianensis* at La Selva. Becker (2) found 36 percent of the seeds (n = 4 328) collected near Siquirres (65 km southeast of La Selva) infested with 9.3 ± 7.7 larvae/seed (n = 45). In freshly fallen seeds at La Selva we found up to 46 larvae/seed with an average of 5.1 ± 7.6 larvae/infested seed (n = 37). *Hypsipyla ferrealis* usually completes its life cycle

Table 4. Number of *C. guianensis* seeds removed between census days from different sized piles beneath a *C. guianensis* tree and a control tree (*Virola koschnyi*) in the La Selva forest. Seed removal between census days summed for all piles of the same size.

No. of piles & seeds	Time in days after seed pile placement									Total # of seeds removed	Percent seeds removed
	1	2	3	4	5	6	10	13	15		
2 piles of 25 seeds											
Carapa	2	25	0	3	0	2	5	13	0	50	100
Control	0	29	19	0	0	0	1	0	0	49	98
4 piles of 10 seeds											
Carapa	0	13	1	2	0	0	12	4	1	33	83
Control	0	26	12	0	0	0	0	0	0	38	95
6 piles of 5 seeds											
Carapa	7	8	0	4	5	0	0	0	0	24	80
Control	0	26	2	0	1	0	0	0	0	29	97
5 piles of 2 seeds											
Carapa	3	0	0	0	1	3	1	0	0	8	80
Control	0	6	2	0	0	0	0	0	0	8	80
Cumulative % removed											
Carapa	9	45	45	52	57	61	75	88	88	–	88
Control	0	67	94	94	95	95	95	95	95	–	95

within 40 days, but some larvae go into diapause for as long as five months (2). Although it is possible that the larval diapause is sufficient to delay the life cycle until the following year's young fruits are available for oviposition as suggested by Becker (2), the fact that the *Carapa* population at La Selva produces very few fruits in certain years must seriously reduce the *H. ferrealis* population if alternative food sources are not available or utilized. Entwistle (5) indicated that *Spondias mombin* L. (Anacardiaceae) and a *Rheedia* sp. (Clusiaceae) in Trinidad are attacked by *H. ferrealis*. Both of these taxa occur in the Atlantic lowlands of Costa Rica, but neither has been found to host *H. ferrealis*. It is likely that other host plants occur in Costa Rica because Becker (2) reported that adult moths can be found at Turrialba throughout the year. Predation by larvae could be a selection pressure in the evolution of the phenological pattern of "good" and "bad" seed years.

We observed no shoot-borer activity on *C. guianensis* seedlings or saplings even though the genus *Hypsipyla* is well-known for the damage it causes other members of the Meliaceae (see 8).

To simulate insect or rodent damage to a seed we removed either 50 percent, 75 percent, or nearly 100 percent (by weight) of endosperm from three groups of 25 seeds each. All treated seeds and 10 whole seeds were partially embedded in the same swamp site as that for the germination investigation. There was a significant negative correlation ($r = -.76$, $P < 0.01$) between the amount of seed removed and seedling height at six weeks (Figure 2) at which time almost all seedlings had ceased growing. By the eleventh week all plants from treated seeds were dead, whereas five of the whole-seeded seedlings still survived. The difference in seedling survival at 11 weeks between the untreated and any treated group was significant by a binomial distribution test ($P < 0.002$). Endosperm removal from the treated seeds may have exposed them to fungi, bacteria, and other soil organisms whose action could further diminish seed reserves and reduce seedling survival. One cause of mortality for several of the treated seedlings was apical meristem damage. We have observed seedlings in the forest respond with up to three successive shoots after the previous meristem was damaged. A reduction in seed reserves, however, not only reduces seedling growth, by may also lessen the seedling's ability to resprout following destruction of the growing shoot.

The large seed with its store of endosperm should be important with respect to withstanding or recuperating from herbivory, in addition to enhancing seedling establishment in other ways. For a species of

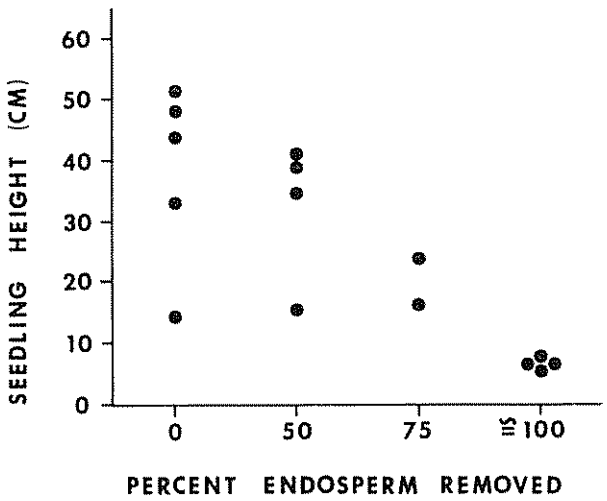

Fig 2. Heights of surviving seedlings 6 weeks after treatment and planting from seeds with different amounts of endosperm removed. n = 25 for each treated group of seeds; n = 10 for control seeds.

swamp and seasonally or occasionally inundated forests such as *Carapa guianensis*, the large seed reserves may serve to establish an extensive root system for physical support, or may be important in getting the seedling's leaves above the normal level of standing water. Flood waters have probably been a strong selective force in the evolution of very large seeds in several swamp species, e.g., *Mora oleifera* (Triana) Ducke, *Pachira aquatica* Aubl., *Prioria copaifera* Griseb. *Carapa* seedlings put up a 50 – 60 cm tall shoot before leaves are produced and upward growth slows, while producing a very limited root system. These observations suggest that for *C. guianensis* the large seed may be especially important in producing a tall shoot to raise the leaves above flood water level.

Summary

Carapa Guianensis (Meliaceae) is a sub-dominant tree species in mature swamp forest in northeastern Costa Rica. The trees flower in September and produce mature fruit the following May. Phenological synchrony of the population produces marked differences in year to year quantities of seed produced.

Seed production of individual trees ranged from 754 to 3 944 seeds having an average dry weight of 15 6 g. Seeds germinated best in contact with moist soil. In well-drained soils, half-embedded and completely buried seeds germinated best. In poorly-drained swamp soils, seeds on the surface or half-embedded had 90 percent germination. Neither buried seeds in the swamp soils nor surface-sowed seeds in the well-drained soils germinated

Fruits fall to the ground beneath the tree's crown where 54 to 98 percent of the seeds are removed. Scatter hoarding by agoutis is probably an important factor in seed dispersal and in promoting germination. Larvae of the moth *Hypsipyla ferrealis* feed on *C. guianensis* seeds. Experimental removal of different proportions of endosperm from seeds, simulating insect or rodent damage, produced smaller seedlings and increased mortality.

It is theorized that one advantage of large seeds to tropical swamp species is the ability to produce a tall shoot to raise the leaves above the normal seasonal or annual flood waters.

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