

VARIATION IN AVERAGE SEED SIZE AND FRUIT SEEDINESS IN A FRUIT CROP OF A GUANACASTE TREE (LEGUMINOSAE: ENTEROLOBIUM CYCLOCARPUM)¹

D. H. JANZEN

Biology Department, University of Pennsylvania, Philadelphia, Pennsylvania 19104-4288

ABSTRACT

A detailed examination of the ordinary 1980 fruit crop of an ordinary large adult guanacaste tree (*Enterolobium cyclocarpum*) in Guanacaste Province, Costa Rica (1980) shows that for fruits with about 6–16 seeds (range, 1–18 seeds per fruit) there is about 1 g dry weight fruit tissue per seed (seeds averaging about 820 m each). Fruits that have about 1–5 seeds on average have 1.5–3 times as much dry fruit tissue per seed as do the seed-rich fruits, and also contain seeds that weigh about 8% more on average than the seeds in the seed-rich fruits. The average seed weight per fruit was found to decrease slightly if all sizes of fruits are considered, but to remain essentially constant over the range of 7–16-seeded fruits. This category contained 78% of the fruits. These findings suggest that different parts of the seed crop may end up in different dispersers and dispersers with different preferences for fruit seediness and tolerances for seed size may remove different portions of the seed crop.

THE GUANACASTE TREE (*Enterolobium cyclocarpum*, Mimosaceae) is a rare but very large and therefore conspicuous and well-known member of the deciduous lowland forests of tropical Mexico and Central America (e.g., Pennington and Sarukhan, 1968; Standley, 1922). It also ranges well into lowland South America, and has been planted as a roadside and garden tree throughout the tropics. I am confident that its large indehiscent fruits (Fig. 1, 2) were once eaten by members of the Pleistocene herbivorous megafauna and that its seeds were dispersed by passing through them (Janzen, 1981a, b; Janzen and Martin, 1982). To understand this, I am studying the interaction between guanacaste fruits and the horses, cows, tapirs, peccaries, and rodents that eat guanacaste fruits and seeds in Santa Rosa National Park, in Guanacaste Province in northwestern Costa Rica (Janzen, 1981a–d, 1982a–e; Janzen and Higgins, 1979; Hallwachs and Janzen, 1982a, b). A description of a fruit crop and its seeds is necessary background for these studies, and in addition, the guanacaste fruit and its crop are worthy of close scrutiny as an example of the sort of reproductive structures and behavior commonly associated with seed dispersal through seed consumption by

large terrestrial herbivores. Many of the seemingly nonsensical reproductive traits of the guanacaste tree—indehiscent fruits, delayed fruit maturation, dry season fruit drop, variable seed size, variation in fruit seediness, hard seeds, etc.—take on adaptive meaning when viewed in the context of seed dispersal by extinct large mammals (or by recently introduced large mammals).

I have chosen to divide the description of the guanacaste fruit and seed crop into several portions. On the one hand, I am 6 years into a very long-term monitoring program of the fruiting of about 400 individually identified guanacaste trees in Santa Rosa National Park. In this study the focus is on variation in timing, fruit crop sizes, and seed sizes, and the results will be presented many years from now. On the other hand, I here present a detailed look at the production and traits of one large fruit and seed crop of one ordinary large adult guanacaste tree. Not only do I wish to draw the reader's attention to this interesting species of plant, but to induce others to look closely at similar tree-animal systems in the floras with which they are most intimately familiar.

THE TREE AND ITS FRUIT CROP—The fruit crop was from *E. c.* number 20, the enormous guanacaste tree (Fig. 3) growing at the west end of the camping area between the Historic Casona and the Administration Area of Santa Rosa National Park. This tree is very healthy, is probably over 200 years old, has a DBH of 114 cm and is the largest guanacaste tree in an area of about 1 km²; its crown has not been

¹ Received for publication 28 May 1981; revision accepted 2 December 1981.

This study was supported by NSF DEB 77-04889 and 80-11558, and by Servicio de Parques Nacionales de Costa Rica. R. Glass, A. Wolff, G. Stevens, and W. Hallwachs aided in data gathering and processing. The manuscript was constructively criticized by W. Hallwachs and G. Stevens.

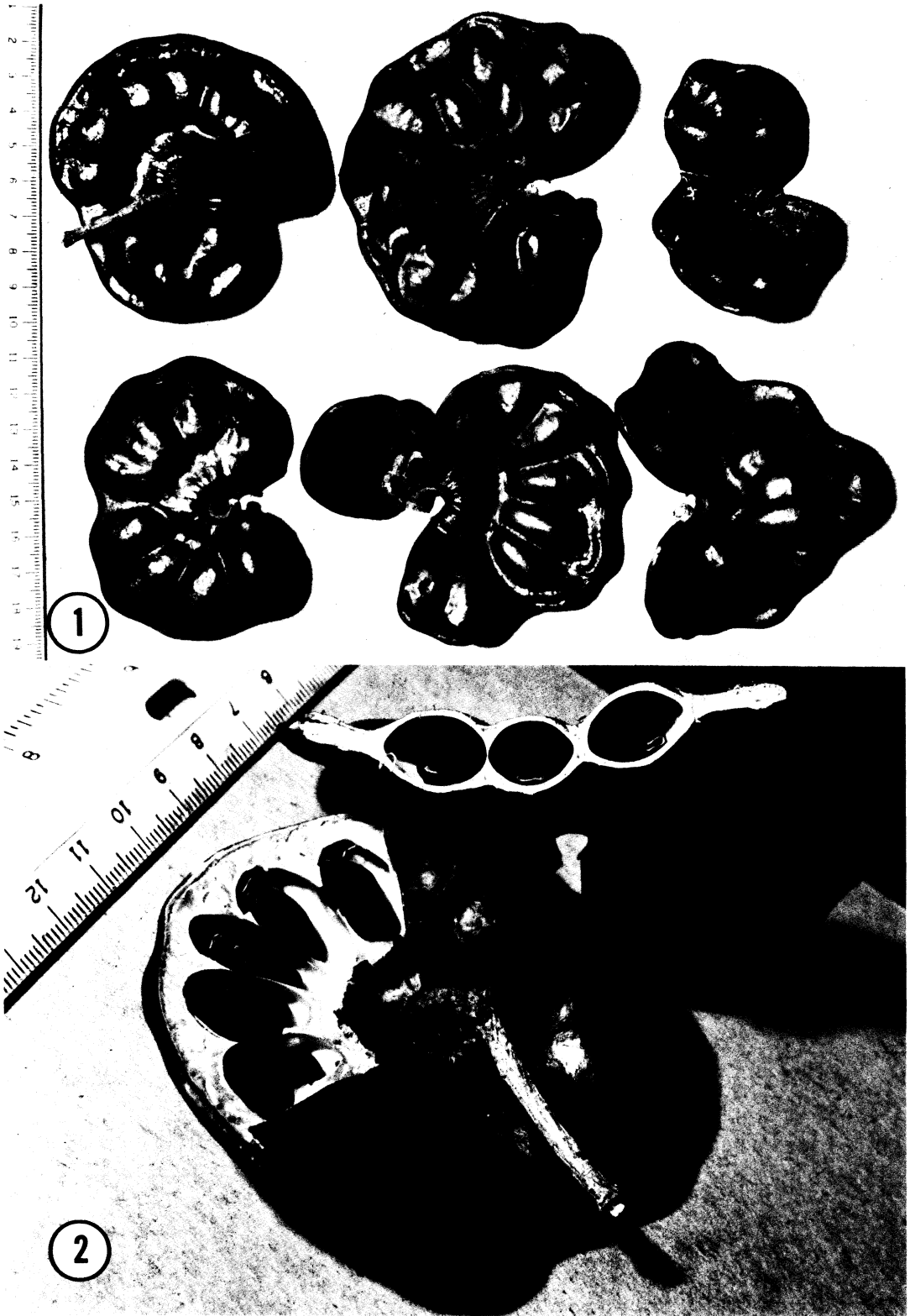


Fig. 1, 2. 1. Various-seeded fruits of *Enterolobium cyclocarpum*; fruits at upper left and top center are 'perfect' in that adjacent ovules were not aborted and therefore there is about 1 g dry weight fruit tissue per seed. 2. Longitudinal section of guanacaste fruit exposing seeds in their cavities at the end of attachment (upper); lateral section of indehiscent guanacaste fruit to expose seeds (center).

TABLE 1. *Distribution of filled living seeds among the 709 fruits (7,295 seeds) and among the fruit tissues in the 1980 crop of Enterolobium cyclocarpum number 20 in Santa Rosa National Park, Guanacaste Province, Costa Rica*

No. of filled seeds:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No. of fruits with this many filled seeds:	8	28	28	29	35	37	32	42	45	58	47	46	64	68	70	46	18	8
Total filled seeds:	8	56	84	116	175	222	224	336	405	580	517	552	832	952	1,050	736	306	144
Dry wt. of all fruit tissue without seeds (g):	25	109	137	161	239	247	232	332	430	612	550	560	801	924	953	630	280	114
Dry fruit tissue per filled seed:	3.1	1.9	1.6	1.4	1.4	1.1	1.0	1.0	1.1	1.1	1.1	1.0	1.0	1.0	0.9	0.8	0.9	0.8

TABLE 2. *Weights of seeds as a function of the number of seeds per fruit in two large fruit samples from the 1980 crop of Enterolobium cyclocarpum, number 20, Santa Rosa National Park. When less than 100 seeds were available in a category, all seeds were weighed; if more than 100 were available, a sample of 100 was blindly removed from a thoroughly tumbled bag of seeds*

No. of seeds per fruit:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Avg. seed wt. (mg):																		
Sample 1			880	840	920	900	890	810	830	820	840	810	830	820	810	790	880	810
N			9	20	54	54	54	82	100	100	100	100	100	100	100	100	95	49
Sample 2	860	900	880	910	880	830	860	790	850	800	840	820	830	800	800	820	790	790
N	7	49	60	72	65	96	100	100	100	100	100	100	100	100	100	100	100	80



Fig. 3. *Enterolobium cyclocarpum* number 20 in Santa Rosa National Park (jeep is 2 m tall).

scorched by seasonal fires and no large branches have been destroyed by disease or insect attack. It is about average in size for a healthy adult guanacaste tree in the second half of its reproductive life. The horizontal projection of the crown is about 300 m² and the tree is about 20 m tall at the highest point. The crown is fully insolated (as is usual for adults of this species of highly emergent tree) and not in competition for light with any other tree. By counting the full-sized ripening fruits in the crown of this tree, I estimated that its fruit crop from 1978 to 1981, respectively, was 2,000, 2,200, 709, and 2,000 fruits. Records from numerous other large guanacaste trees in Santa Rosa suggest that the 1980 crop on *E. c.* 20 was neither very small nor exceptionally large for trees of this size in a year that they bear fruit.

The entire crop was collected by picking up all fruits from the bare ground under this tree from about the time that they started falling (mid-April) until the last fruits fell in late May. A few fruits may have been taken by tourists and an occasional free-ranging horse. However, my familiarity with the area and its use lead me to believe that less than 1% of the fruits were lost in this manner.

The fruits were stored in open large plastic bags until they could be dissected in mid-July. About 70% of the fruits fell before the first rains occurred (8 May) and only these naturally air-dry fruits were used in analyses of fruit water

and nutrient content. Likewise, only non-moldy and insect-free fruit pulp was used in the determination of fruit/seed ratios based on data taken from individual fruits (Table 2).

GENERAL BIOLOGY OF A GUANACASTE FRUIT—A large guanacaste tree normally bears opening flowers in early March in Santa Rosa (mid-dry season), at a time when the tree is leafless or just expanding the first leaves. However, budbreak may occur as late as late March to mid-April, with the consequence that the 1–2 month flower-bearing period overlaps both the leafless and the leafy phase. The petal-free florets are white and borne in loose spheres (Fig. 4); these inflorescences are numerous on the flowering branches and a large tree may bear several million in a given year. The florets open in late afternoon and are open all night. They do not wilt until the mid-morning heat. Each floret lasts less than 24 hrs. Pollen flow between guanacaste trees is believed to be mediated by moths, beetles, and other small nocturnal insects (W. Haber, pers. commun.).

After the flowers are fertilized, 0–3 minute cylindrical green fruits (Fig. 5, 8) appear on the pedicel of the inflorescence. These fruits remain tiny and developmentally dormant throughout the upcoming 6-month rainy season (mid-May to mid-December) and then very rapidly expand to a 4–8 cm diameter, full-sized, bright green fruit in January–February. This developing fruit contains photosynthesizing developing seeds with bright green cotyledons (Janzen, 1982f). While as many as three fruits may develop on one infructescence, the more common case is one fruit per fruit-bearing infructescence (Fig. 7).

The fruits ripen in March, about the time those flowers are opening that will produce the fruits of the following year. A mature fruit is smooth, shiny, deep brown in color, indehiscent, and relatively dry (Fig. 1). It is supple and does not usually break into separate pieces when it falls on the hard ground, though it may crack. The hard mature (dormant) seeds are usually one to a cavity and are quite loose in that cavity (Fig. 2). If the mature fruit is torn open by hand, it usually tears between the cavities rather than across them; the seeds cannot be easily removed by simply tearing the fruit into segments. In short, each seed is contained loosely in a tough but flexible and thin-walled sac which I suspect functions to reduce the chance that the cusps of the molars of large herbivorous mammals will scarify the seed coat.

If no dispersal agent eats them, the fruits lie on the ground in a dry and indehiscent state throughout the remaining 1–2 months of the

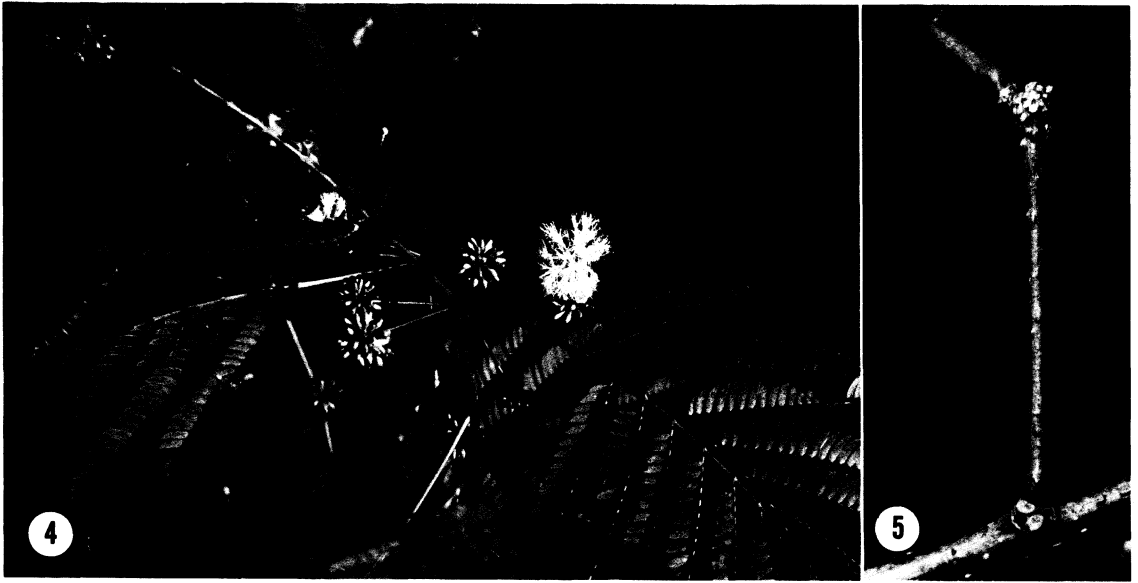


Fig. 4, 5. 4. Inflorescences of *Enterolobium cyclocarpum* late in the flowering season (open inflorescence on right, buds in center and on left). 5. 8-month-old, 7 mm long dormant fruit of *Enterolobium cyclocarpum*.

dry season. Once soaked with rainy season moisture, the fruit walls rot within 1–2 months and the hard dormant seeds are released into the litter. If cattle, horses or tapirs are present, they eat the fruit and swallow some seeds intact (Janzen, 1981a, c). If the seed does not germinate and is therefore not killed by gut fluids, it is then dispersed by defecation at a later date (Janzen, 1981b, 1982a). Likewise, in the absence of large mammals, the seeds are often cut out of the newly fallen fruits (they also collect them from the litter) and taken to a burrow by a small rodent (*Liomys salvini*, Janzen, 1982b; Hallwachs and Janzen, 1982a) that consumes most of them but may also disperse some. The dormant or germinating seeds are also collected from livestock dung by rodents (Janzen, 1982c, d). Hard and dormant seeds that have been dispersed to the litter and are not located by animals germinate over a period of many years, as the seed coat is gradually scarified by the action of degradation processes in the litter.

Rather than drop all its ripe fruits during a period of a few days or weeks as is commonplace among trees of other species in this forest, a large guanacaste tree drops its fruit crop over a period of about 2 months. A ripe fruit may remain on the tree as long as 6 wks. Presumably this attenuated fruit drop is functional in spreading the seeds out among many different individual dispersal agents over a long time, and therefore minimizing the ratio of seeds

to dung as the seeds are defecated. The latter trait is functional in lowering the probability that a rodent will find the seeds in the dung (Janzen, 1982c).

There are two kinds of seed mortality before the fruits drop from the tree. First, the florets are galled by a small cecidomyiid fly (*Asphondylia enterolobii*, Gagné, 1978). The gall remains minute and developmentally inactive while the tiny green fruits on adjacent inflorescences are likewise inactive (Fig. 8), and then abruptly expands to about 1.5 cm diameter at the same time that the fruits expand. The larva then develops in a central cavity in the gall (Fig. 9), apparently feeding on the hyphae of a white fungus that is growing on the inner walls of the cavity in which the larva lives. The adult fly emerges from the gall at the same time that the next year's flowers are opening, and presumably oviposits on them within a few days. One may find opening flowers, nearly ripe fruits, and mature galls from which the flies are exiting on the tree on the same day in mid-March. The fly may reduce the fruit crop by a direct nutrient drain, which in turn causes the tree to abort fruits, or it may reduce the fruit crop by galling florets that would have become fruits. A tree with a very heavy gall load (Fig. 6) usually bears no fruits and trees with heavy fruit loads are usually gall-free or only very mildly infested. A pyralid moth larva (Fig. 9) may mine in full-sized galls, consuming the fly larvae in the process.



Fig. 6, 7. 6. View through nearly leafless crown of heavily galled *Enterolobium cyclocarpum* at the time of flowering. 7. Galls of *Asphondylia enterolobii* containing pupae (left); on right are guanacaste fruits of the same age as the galls and about one month before ripening.

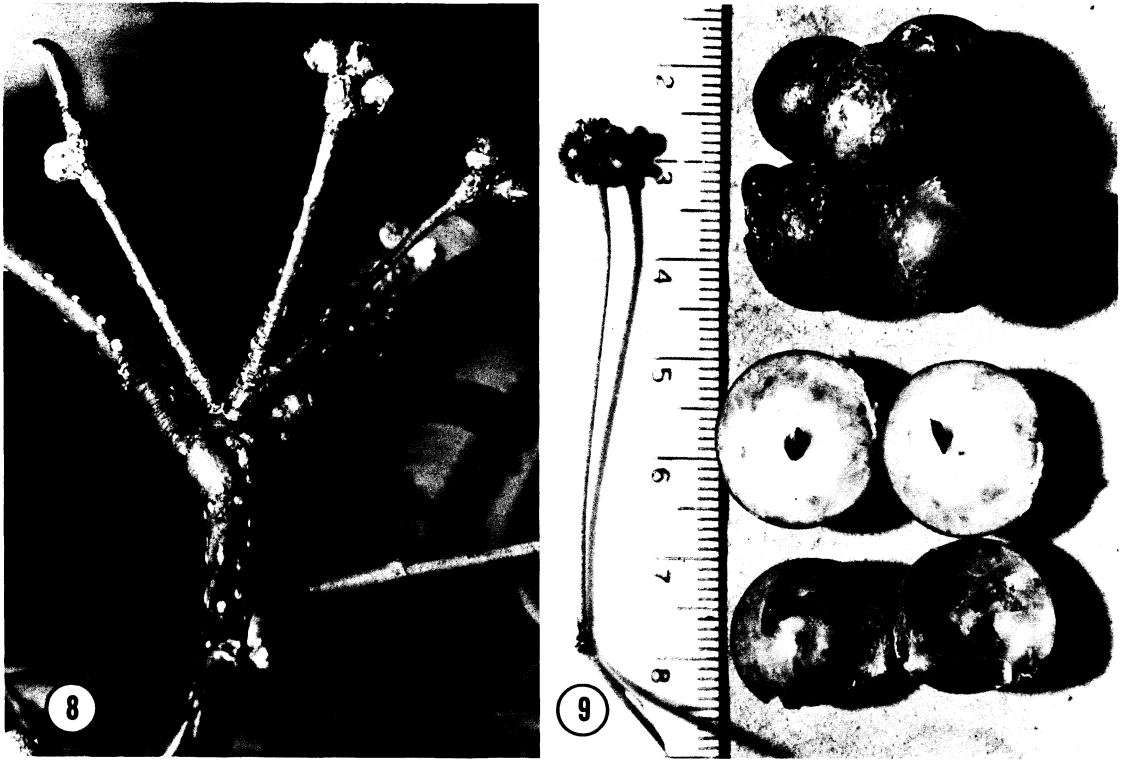


Fig. 8, 9. 8. 8-month-old dormant fruit and galls on *Enterolobium cyclocarpum*. 9. Cluster of full-sized galls from one inflorescence (top); 2 galls sectioned to reveal pupae of *Asphondylia enterobii* and the cavity in which they developed (center); gall that is being eaten by a pyralid moth larva.

Second, if a guanacaste tree is growing in the vicinity of approximately intact lowland deciduous forest with its usual fauna of large *Amazona ochrocephala* parrots, the immature but full-sized seeds are heavily preyed on by these parrots. The birds cut through the fruit wall, through the seed coat, and remove the green embryo with its large cotyledons. If a crop is small (e.g., only several hundred fruits), these birds may destroy the entire crop in 1–2 months. There is no indication that howler monkeys or other arboreal herbivores feed on the green fruits.

THE 1980 CROP OF E.C. 20—This crop contained 709 fruits and these contained 7,295 filled seeds. The distribution of filled seeds among fruits is given in Table 1. All fruits contained at least one filled seed and none contained more than 18. The most common fruit size was 15-seeded (9.6% of the fruit crop). The 18-seeded fruits did not contain any aborted seeds, suggesting that they originally contained only 18 ovules. However, fruits from other guanacaste trees occasionally contain as many as 24 filled seeds.

Pooling all fruits within a size class ('size,' as used here, refers to the number of filled seeds in a fruit), the weight of dry fruit tissue per filled seed in each fruit size class varied from 0.8 to 3.1 g (Table 1). In the progression of 1–5 filled seeds per fruit, the amount of dry fruit tissue per seed fell from 3.1 to 1.4 g. However, for 6–18-seeded fruits, there is only a very slight drop in amount of dry fruit tissue per seed from 1.0–1.1 to 0.8–0.9 g. The cause of the difference between 1–5- and 6–18-seeded fruits is evident on inspecting the fruits (Fig. 1). A 1–5-seeded fruit is usually formed by multiple abortions of seeds between filled seeds, leaving large pieces of fruit tissue that contain no filled seeds. In the case of 6–18-seeded fruits, the fruit usually contains a row of adjacent filled seeds. Aborted seeds are usually at either end of the row and only rarely lie between the filled seeds.

To examine the dry weight of fruit tissue per seed for perfectly constructed fruits I selected 18 unblemished 4–17-seeded fruits (\bar{x} = 12.4 seeds/fruit, S.D. = 4.2), with highly uniform rows of seeds, smoothly and evenly rounded ends to the fruit and no trace of aborted seeds.

They had an average of 1.04 g of dry weight fruit tissue per seed (S.D. = 0.15) and there was no correlation of the amount of dry weight fruit tissue per seed (y) with number of seeds (x) ($r = 0.05$, $y = 0.0018x + 1.014$). By inspection, the value of 1.04 is not significantly different from the mean ($\bar{x} = 0.99$, S.D. = 0.107) of the values for 6–18-seeded fruits for the crop as a whole (Table 1).

While 15-seeded fruits were the most common size (9.6% of the total) and contained the most filled seeds (14.3% of the total) the mean number of filled seeds per fruit for the entire crop was only 10.29 (S.D. = 4.36). The median number of filled seeds per fruit was between 10 and 11, which reflects the leftward skewness of the frequency distribution of n -seeded fruits. Given that the ratio of fruit dry weight to seed number for 6–18-seeded fruits only ranges from 0.8–1.1 g, it is not surprising to find that the largest amount of fruit tissue dry weight for the total crop is in 15-seeded fruits (Table 1).

As the seeds were removed from the fruits, the work was done in batches of 200–300 fruits. The seeds were separated according to the size of fruit from which they were taken in two of these batches, and a sample of 100 randomly chosen seeds were weighed from each of the 16 or 18 subsamples (fewer than 100 seeds were weighed if 100 were not available). There was a significant correlation between the number of seeds in a fruit (x) and the mean weight of the seeds in that fruit (y) (Table 2; sample 1, $r = 0.576$, $N = 16$, $y = -4.71x + 891.92$; sample 2, $r = 0.802$, $N = 18$, $y = -5.83x + 891.50$). However, inspection of the data in Table 2 suggests that much of this correlation is generated by the high seed weight values in the fruits with seven or less seeds in them. These fruits constitute only 28% of the total crop of 709 fruits. However, if the 3–7-seeded fruits for sample 1 and the 1–5-seeded fruits for sample 2 are compared with the seeds in the fruits with higher numbers of seeds, the seeds in the smaller fruits have a higher mean seed weight (Table 2; sample 1, $\bar{x} = 886$ mg, S.D. = 29.7 for 3–7-seeded fruits, $\bar{x} = 823$ mg, S.D. = 23.3 for 8–18-seeded fruits, $t_{14d.f.} = 4.20$, $P < 0.01$; sample 2, $\bar{x} = 886$ mg, S.D. = 20.0 for 1–5-seeded fruits, $\bar{x} = 816$ mg, S.D. = 24.0 for 6–18-seeded fruits, $t_{16d.f.} = 6.28$, $P < 0.01$). It appears that when seed numbers fall to the point where a high proportion of the seeds have an unfilled seed adjacent on each side, the average seed weight of these seeds rises about 8%. Likewise there is no significant correlation between the average seed weight and the number of seeds in the fruit in either sample for 8–18-seeded

fruits (Table 2; sample 1, $r = 0.078$, $n = 11$, $y = 0.546x + 815.66$; sample 2, $r = 0.395$, $n = 11$, $y = -2.55x + 844.91$). Inspection of the average seed weights for the different sizes of fruits with eight or more seeds in them shows clearly that this value stays essentially constant from 8–18-seeded fruits. Since the average amount of fruit tissue per seed also stays essentially constant over this same range, it is clear that for about 70% of the fruit crop, the amount of fruit tissue per gram of seed is about the same.

DISCUSSION—A large herbivore foraging on guanacaste fruits below tree number 20 in April–May 1980 would have encountered fruits with 1–18 seeds in them, but 78% of the fruits would have been 6–16-seeded. I have already shown that with 5–18-seeded guanacaste fruits, horses generally swallow about the same percent of the seeds in each fruit (Janzen, 1981a). This means that a seed's chances of being spit out are not influenced by the size of its fruit if there are more than five seeds in its fruit. This behavior by the horse is consistent with the finding here that over the 6–16-seeded size range the amount of dry fruit tissue per filled seed is about 1 g per seed, and therefore the masticated fruit-seed mix in a horse's mouth when eating a single fruit will be about as seedy for a 6-seeded fruit as a 16-seeded fruit. A horse or cow eats guanacaste fruits one at a time.

The dry fruit tissue per filled seed was about 3–1.5 times as great for 1–5-seeded fruits (Table 1) as for 6–18-seeded fruits, and therefore seed dispersal costs more per seed as fruit size decreases below 6-seeded fruits. In a habitat rich in potential guanacaste fruit consumers, such as perhaps occurred with a normal Pleistocene megafauna or as occurs today in pastures with large herds of horses or cows, such an increased cost probably resulted in no proportionate increase in gain because all fruits were probably consumed. However, if the habitat contains a low density of herbivores, and if some of these herbivores are very sensitive to the seediness of the fruit, it is possible that the tail of the distribution represented by overly fruity fruits would be selected-for by having the very fruity fruits preferentially taken by some animals. These could even be animals that generate a distinctive portion of the seed shadow.

When the fruits of a guanacaste tree fall, the fruit tissue (without seeds) contains 12–20% water. As the fruits lie in the hot sun on dry soil below a largely leafless canopy, they may dry out to where the fruit tissue contains as little as 8% water (measurements based on fruits

from the crop described here). When the rains come, the fruits very rapidly take up moisture and begin to mold (although in livestock-rich habitats, there are normally none left on the ground at this time). None of the data recorded to date suggest that any aspect of the moisture content, loss or uptake by the fruit tissue is related to the number of seeds in a fruit. The seeds are 10–20% water at the time the fruit ripens (Janzen, 1977) and remain that way irrespective of the moisture content of their immediate environment, unless the seed coat has been scarified and the seed imbibes moisture in the early stages of germination. In the 1980 crop of the crop examined here, only 3% of a sample of 1,000 dormant, filled seeds shelled out of the fruits by hand (untouched by metal objects or soil) germinated when placed in water; all of a subsample of 200 of these seeds germinated when the seed coat was notched with a file before placing the seeds in water.

For 8–18-seeded fruits it appears that the maternal parent guanacaste tree is controlling the average seed size quite carefully around a mean of 823 gm (for the averages, S.D. = 23, range 790–880 mg). However, individual filled seeds in this crop ranged from about 300–1,200 mg in weight. There are many potential sources of variation in individual seed size that have no expected reason to be associated with the number of seeds in a fruit. For example, depending on the orientation of an individual fruit to the sun and its detailed location in the finely heterogeneous light regime within the crown, the amount of photosynthate that it produces for its contained seeds will vary. Similarly, the amount of photosynthate the chlorophyllous embryos (Janzen, 1982f) can produce will vary with the light experienced by the fruit. On a finer level of heterogeneity, the individual embryos within a fruit will receive different amounts of light owing to variation in fruit surface curvature, folding, overlap, and thickness. Finally, the embryos in each fruit are not genetically identical and each has not only what the parent plant gives it for reserves but also what it makes with its own photosynthetic machinery (Janzen 1982f). Therefore, there may well be genetic heterogeneity of seed size spread over the fruit crop in a manner quite unrelated to fruit size.

On the other hand, few-seeded fruits had an average seed weight about 8% greater than did the many-seeded fruits (sample 1 and 2, Table 2). This implies that one of the mechanisms that determines seed size is the amount of photosynthetic fruit tissue per seed. There is definitely more dry fruit tissue per seed in the seed-poor fruits than in the seed-rich fruits (Ta-

bles 1 and 2). Such a bias toward large seeds in seed-poor fruits could have a very interesting effect on seedling recruitment in the case whereby a different set of animals eats the seed-poor fruits than the seed-rich fruits and might thereby generate a different portion of the seed shadow. This unique part of the seed shadow might well contain a greater proportion of large seeds than the seed shadow generated by the animals feeding on seed-rich fruits.

While it is tempting to hypothesize that seeds of different sizes (weights) would have different fates during passage through a large herbivore, the only study to date shows that the heaviest seeds have the same passage rates through a cow as the lightest seeds (Janzen, 1982a). However, unpublished studies of guanacaste seeds show that as the seed increases in weight it also increases in volume, with the consequence that the specific gravity of seeds ranging from 300 to 1,200 mg is about the same (≈ 1.3). It is probably the specific gravity more than the seed weight that will influence guanacaste seed passage rates through large herbivores.

The description of the 1980 crop of guanacaste tree number 20 in Santa Rosa National Park shows clearly that the distribution of dry fruit pulp among the seeds in multiple-seeded fruits may be quite constant on average among a certain set of fruit size classes and different from this in another. Furthermore, average seed size may stay quite constant over a wide range of fruit sizes, yet change at one end of the range of sizes. Finally, the distribution of seediness and seed weight over the fruit crop varies in such a manner that it could conceivably influence the dispersal component of population recruitment by guanacaste trees.

LITERATURE CITED

- GAGNÉ, R. J. 1978. A new species of *Asphondylia* (Diptera: Cecidomyiidae) from Costa Rica with taxonomic notes on related species. Proc. Entomol. Soc. Wash. 80: 514–516.
- HALLWACHS, W., AND D. H. JANZEN. 1982a. Guanacaste seeds (*Enterolobium cyclocarpum*) as food for Costa Rican spiny pocket mice (*Liomys salvini*). Ecology (submitted).
- , AND ———. 1982b. Toxicity of germinating guanacaste seeds (Leguminosae: *Enterolobium cyclocarpum*) to hispid cotton rats (Cricetidae: *Sigmodon hispidus*). Brenesia (in press).
- JANZEN, D. H. 1977. How southern cowpea weevil larvae (Bruchidae: *Callosobruchus maculatus*) die on nonhost seeds. Ecology 58: 921–927.
- . 1981a. Guanacaste tree seed-swallowing by Costa Rican range horses. Ecology 62: 587–592.
- . 1981b. *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. Ecology 62: 593–601.

- . 1981c. Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* 13 (Suppl.): 59–63.
- . 1981d. Lectins and plant-herbivore interactions. *Recent Adv. Phytochem.* 15: 241–258.
- . 1982a. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. *Oikos* (in press).
- . 1982b. Seed removal from fallen guanacaste fruits (*Enterolobium cyclocarpum*) by spiny pocket mice (*Liomys salvini*). *Brenesia* (in press).
- . 1982c. Variation in seed removal by rodent seed predators from Costa Rican horse dung. *Ecology* (in press).
- . 1982d. Attraction of *Liomys* mice to horse dung and the extinction of the response. *Anim. Behav.* (in press).
- . 1982e. Seed content of wild tapir dung in a Costa Rican deciduous forest. *Brenesia* (in press).
- . 1982f. Ecological distribution of chlorophyllous developing embryos among perennial plants in a tropical deciduous forest. *Biotropica* (in press).
- , AND M. L. HIGGINS. 1979. How hard are *Enterolobium cyclocarpum* seeds? *Brenesia* 16: 61–67.
- , AND P. S. MARTIN. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215: 19–27.
- PENNINGTON, T. D., AND J. SARUKHAN. 1968. *Arboles tropicales de México*. Instituto Nacional de Investigaciones Forestales, México 21, D.F., México.
- STANDLEY, P. 1922. *Trees and shrubs of Mexico*. *Contrib. U. S. Nat. Herb.*, 23 (part 2): 171–515.