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NATURAL HISTORY OF GUACIMO FRUITS (STERCULIACEAE: GUAZUMA ULMIFOLIA) WITH RESPECT TO CONSUMPTION BY LARGE MAMMALS[1]

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ABSTRACT

Guazuma ulmifolia (Sterculiaceae) is a shrubby tree common in the Central American lowlands in deciduous forest, and in the pastures cut out of it. The tree flowers in April–May (end of dry season) and bears dormant, incompletely expanded fruit until the end of the rainy season (November–December), at which time the fruits rapidly expand and ripen to fall during the first half of the dry season. The fruits are avidly eaten by livestock. A horse may consume 300–2,100 fruits in a meal, does not distinguish between fresh fruits that have been attacked by bruchid beetles and intact fruits, and defecates large numbers of viable seeds 2–5 days later. Moistened seeds germinate readily in horse dung or in soil. There are hard letter-shaped structures in the mesocarp of the fruit wall and a very hard core, both of which are large enough to function in preventing complete occlusion of the molar mill, an act which would crush the soft small seeds. *Guazuma ulmifolia* (guacimo) is probably one of the trees whose fruits would have been eaten and the seeds dispersed by the Pleistocene herbivorous megafauna that once roamed Central America.

GUAZUMA ULMIFOLIA (Sterculiaceae) is a 2–15-m-tall and often multi-trunked common tree in the deciduous forests in the Pacific coastal lowlands of Mexico and Central America (Standley, 1923; Bressani and Navarrete, 1959). Guacimo (or *cualote,* Bressani and Navarrete, 1959) is a member of undisturbed deciduous forest as well as a tree of naturally-occurring forest edges. It persisted as the forest was cleared for cattle pasture and farming because: 1) it sprouts readily from cut stumps; 2) it bears fruit when as young as 6–10 yrs of age; 3) it can germinate and grow to adult status in wind-blown and fully insolated sites (heavily grazed pastures, roadsides, fence rows, etc.); 4) its foliage and fruits are eagerly eaten by livestock so there is no strong incentive to cut it out of pastures; and 5) its seeds survive transit through horses and cows and are therefore dispersed in widespread and intense seed shadows by these animals. Since guacimo is readily browsed and dispersed by the contemporary large herbivores in its habitat, it probably had an intense interaction with the large herbivorous mammals of the Central American Pleistocene (Janzen and Martin, 1982). As part of an ongoing study of the interactions of Costa Rican fruits and seeds with the large mammals that eat them (Janzen, 1981a–f, 1982a–d), I here describe the guacimo fruit, stressing those traits of greatest importance to the interaction: fruit dormancy and ripening, attractants and structural protection of the seeds, fruit attack by insects, fruit consumption by livestock, and seed survival in passing through livestock. My interest is in the function of guacimo fruit traits rather than in their description per se.

STUDY SITE—All observations were made on the indigenous population of *Guazuma ulmifolia* (Janzen and Liesner, 1980) growing in Santa Rosa National Park (SRNP), which lies between the Pan-American Highway (Costa Rica Route 1) and the Pacific Ocean, 25 km south of La Cruz and 35 km north of Liberia, in northwestern Guanacaste Province, Costa Rica. SRNP was a cattle ranch since the early 1800's, but at most, only about 30% of its 10,800 ha of forest were cleared to pasture. Ranching was stopped in the late 1960's and the last cattle removed in 1977–1978. The grassy vegetation is now changing gradually back to deciduous forest (with some evergreen patches). Guacimo is a common tree in this grassland-forest mix, and is found from the centers of open grassy areas to the mature deciduous forest with a closed continuous canopy. However, the phenology, growth form, fruit crop size, and other individual traits of guacimo trees vary substantially in this mosaic of microhabitats.

The climate of SRNP is highly seasonal, with

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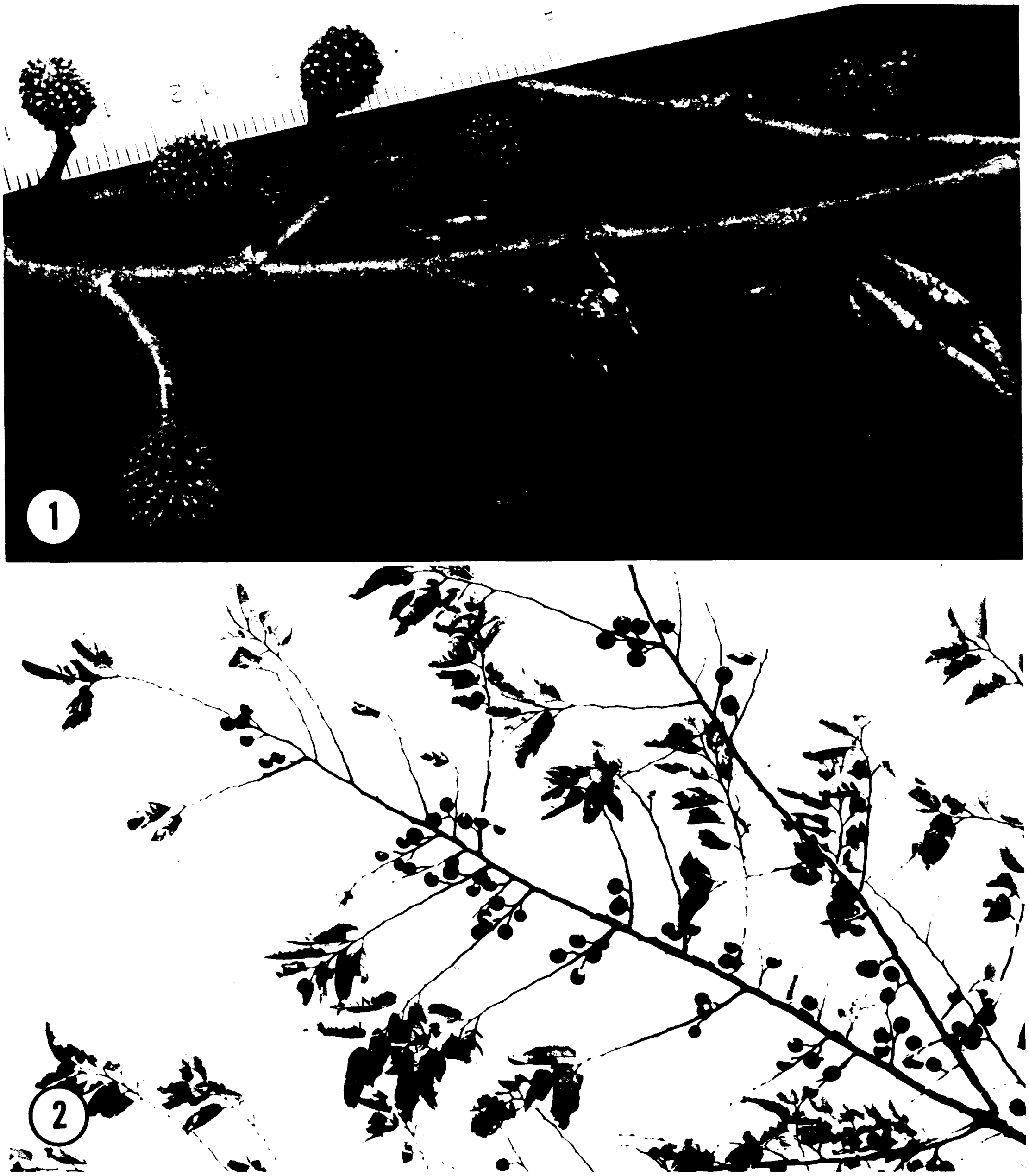

Fig. 1, 2. **1.** Six-month-old dormant fruits of *Guazuma ulmifolia*. **2.** Normal branch of *Guazuma ulmifolia* with full-sized ripening fruits; leaves have been removed from the lower half of each branchlet to expose fruits to view.

approximately 6 mos of rain-free and windy weather (late December through early May) and 1,500–2,000 mm of rain in the rainy season. Such a climate, found throughout the geographic range of guacimo, is associated with many species of trees and shrubs that display very striking habitat-wide synchrony of fruiting and flowering with the dry season (e.g., Janzen, 1967; Frankie, Baker and Opler, 1974; Opler, Frankie and Baker, 1980); guacimo is one of these tree species.

THE DEVELOPING FRUIT—A representative large guacimo tree bears flowers from April (last month of the dry season) through the end of May or even until mid-June. Since the first rains appear about the first week in May, full flower crops are present in both the wet and

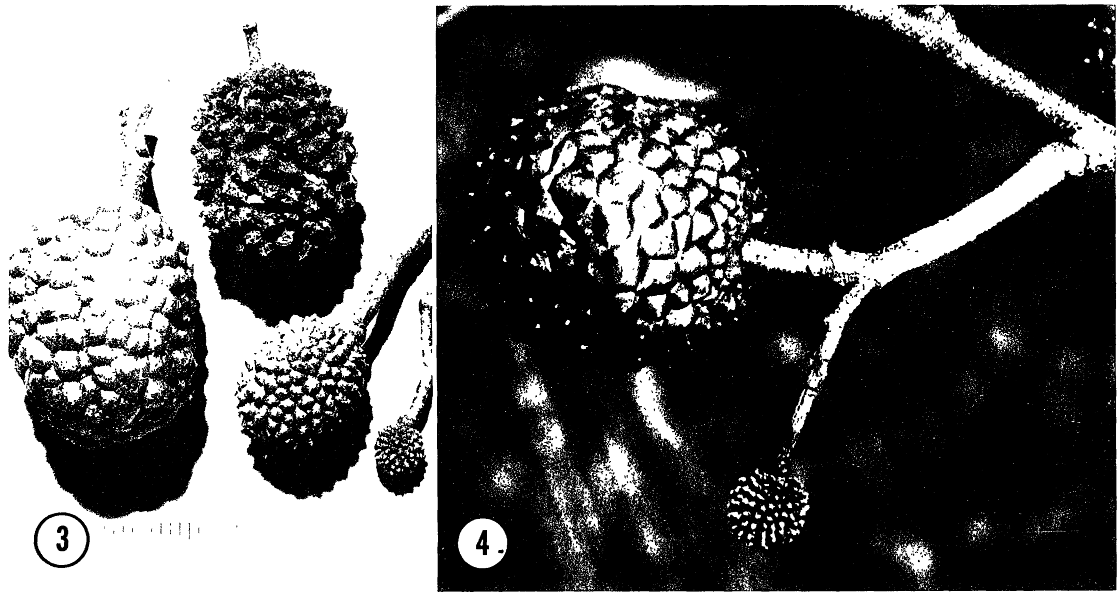

Fig. 3, 4. **3.** Developmental stages of *Guazuma ulmifolia* fruits from dormant (lower right corner) to ripe (top center). **4.** Full-sized nearly ripe fruit (large, left) and dormant-sized fruit about to be aborted.

the dry season. At the beginning of the dry season, large guacimo trees gradually begin to lose their leaves. By the time of heavy flowering the branches often bear only inflorescences. However, with the first rains and in some trees before, a new leaf crop is produced and is borne concurrently with the flowers. During the first half-month of the rainy season, guacimo trees with a full crop of new leaves and flower-rich inflorescences are commonplace.

Each inflorescence bears 10–50 small cream-colored flowers, each of which lasts a single day. The flower buds open progressively, a few each day per inflorescence. While a few small insects are occasionally encountered at the flowers, the pollen vectors are not known. In the 1–2 wks following flowering, about half of the inflorescences produce 1–10 green fruits, each about 2 mm in diameter. These fruits are gray-green in color, finely covered with tiny protuberances, and extremely hard (Fig. 1). Because the new infructescences are borne among the newly produced leaves, these tiny fruits are not fully insolated, but rather in intermittent shade (Fig. 2).

At this stage, the only kinds of herbivory on the tiny immature fruits is that committed by browsing mammals feeding on the foliage. Deer, peccaries, horses, cattle, and tapirs readily eat the foliage when it is low enough to reach, and presumably the Pleistocene large herbivores did as well. The weevil larvae (Curculionidae: *Phelypera distigma*) that feed heavily on new leaves in early to mid-June (Janzen, 1979) ignore the young fruits. I have seen no sign of predation by parrots on the small green fruits, but the parakeet *Aratinga canicularis* occasionally feeds on the flowers.

The tiny fruits do not begin to increase noticeably in volume or weight until the last mo of the rainy season (November–December) (Fig. 3; Table 1). There is no sign of abortion of immature fruits during the rainy season. However, some of them do not expand and are shed at the time of fruit expansion (Fig. 4b). During the 3 mos of fruit expansion, a wide variety of sizes may be found. The variation has two major sources. First, trees that flowered as early as March of the previous year (mid-dry season) begin to expand their fruits earlier in the rainy season; full-sized fruits can be found on these trees, or on certain branches in these trees, as early as the end of October. Second, development within the crown is not very tightly synchronized. Fruits may range from 0.10 to 3.88 g fresh weight on a single branch in mid-January. Likewise, mean fresh fruit weight on adjacent branches may vary from 0.72 to 2.41 g (Table 2). These differences in fruit development rate generate a population-level, ripe fruit fall from late January to early May, with the variation being extensive among and within trees.

After having expanded to full size between late November and February, the fruits ripen

Fig. 5. Green full-sized fruits (upper right), ripe fruit (lower right) and half-ripe fruit (center left) of *Guazuma ulmifolia*.

TABLE 1. *Live weights, dry weights and percent dry matter of fruits of* Guazuma ulmifolia *at different points in their 10-mo development cycle*

			Live wt (g)		Dry wt (g)		% dry matter	
Tree no.	Date	No. fruits	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
1	22–28 Nov (dormant fruits)	36	0.15	0.06	0.04	0.02	25.8	4.6
2	22–28 Nov (dormant fruits)	36	0.35	0.17	0.09	0.04	25.9	4.9
3	22–28 Nov (dormant fruits)	36	0.10	0.04	0.02	0.01	20.6	5.3
4	22–28 Nov (dormant fruits)	36	0.12	0.04	0.03	0.02	25.4	4.6
5	22–28 Nov (dormant fruits)	36	0.61	0.36	0.15	0.08	25.3	4.8
6	22–28 Nov (dormant fruits)	36	0.25	0.10	0.07	0.03	26.6	5.1
		$\bar{x}$	0.26		0.07		24.93	
		S.D.	0.19		0.05		2.17	
1	4–15 Jan (expanding fruits)	36	0.72	0.73	0.18	0.14	24.7	4.4
7	4–15 Jan (expanding fruits)	36	1.87	1.10	0.42	0.13	22.6	5.1
8	4–15 Jan (expanding fruits)	36	2.82	1.91	0.68	0.21	24.1	6.3
9	4–15 Jan (expanding fruits)	36	0.92	0.86	0.19	0.60	20.4	4.6
10	4–15 Jan (expanding fruits)	36	1.35	0.86	0.29	0.71	21.3	4.7
11	4–15 Jan (expanding fruits)	36	1.80	1.13	0.43	0.14	23.8	4.7
		$\bar{x}$	1.58		0.37		22.82	
		S.D.	0.76		0.19		1.69	
1	3–8 Mar (ripe fruits)	36	3.12	0.64	2.49	0.55	80.0	6.1
12	3–8 Mar (ripe fruits)	36	4.62	0.71	3.60	0.56	78.2	7.1
13	3–8 Mar (ripe fruits)	36	3.13	0.68	2.47	0.58	78.9	6.8
14	3–8 Mar (ripe fruits)	36	3.00	0.76	2.40	0.61	80.1	7.0
15	3–8 Mar (ripe fruits)	36	3.81	0.63	3.12	0.41	82.0	5.2
16	3–8 Mar (ripe fruits)	36	3.19	0.71	2.54	0.59	79.6	6.7
		$\bar{x}$	3.48		2.77		79.80	
		S.D.	0.63		0.48		1.29	

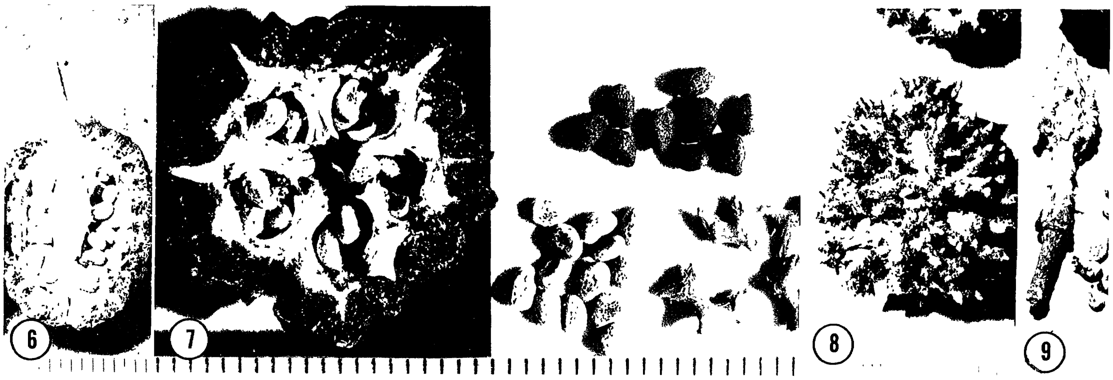

Fig. 6–9. **6.** Intact ripe indehiscent fruit of *Guazuma ulmifolia* split longitudinally to expose two seed-filled locules and central core. **7.** Cross section of intact ripe fruit exposing five locules, letter-shaped structures (LSS) imbedded in fruit wall, and dark layer of sweet outer pulp (core has been removed from this fruit) (left side of photograph); seeds and LSS of *Guazuma ulmifolia* (right side of photograph). **8.** Intact fruit with fruit pulp eaten off by insects, leaving LSS exposed in place. **9.** Core from fruit.

in the increasingly dry air and intense insolation of the dry season. The green fruits turn dark brown and develop deep 1–2-mm-wide cracks in their surfaces (Fig. 5). The surface changes from bumpy-smooth (Fig. 4) and dry to extremely rough and slightly sticky (Fig. 5). When a green fruit is chewed, it is very hard, moist, slimy, and tasteless; once ripe it is hard (but crumbles easily with pressure), dry-sticky, and sweet. No astringent or bitter aftertaste is left from eating many ripe fruits. In the transition from immature green to ripe, the fruit composition changes from 75–80% water to about 20% water (Table 1).

Throughout the period of fruit maturation there is no indication of any kind of herbivory by insects directed at guacimo fruits or the seeds they contain. In the expanded green fruit the developing embryos are achlorophyllous (Janzen, 1981f). When removed from the tree and offered to range horses or a captive tapir, the expanded green fruits were eaten as readily as were the highly desired mature fruits. Horses and cattle actively seek the fruit-laden foliage, and I suspect Pleistocene browsers did as well.

In summary, the immature fruits remain very small and undeveloped through the rainy season, and then expand and begin to ripen during the 2-mo change from wet season to dry season. They have this pattern of development in common with a number of other trees in SRNP (e.g., *Pithecellobium saman* (Janzen, 1982a), *Enterolobium cyclocarpum* (Janzen, 1982b), *Cassia grandis* (Janzen, 1977)).

Ripe fruits—"Mature" or "ripe" is best ecologically defined as the time when the fruit falls to the ground; that is to say, the fruit is ripe when it is "behaviorally" presented to large terrestrial seed dispersers by the act of having a sufficiently weakened stem that it falls or is blown off the tree. However, for 1–10 wks before the fruits fall, they are fully ripe, physiologically disconnected from the parent, dry, and brittle. They contain viable mature dormant seeds no longer physiologically connected to the parent and taste sweet to me. If picked from the tree these brown fruits (Fig. 5) are readily eaten by horses and cattle. It appears that the fruits become fully physiologically ripe

Table 2. *Live weights, dry weights and percent dry matter of fruits of* Guazuma ulmifolia *on five different branches in the crown of tree 1 (Table 1) on 15 January, at the time when the fruits are just beginning extensive expansion (Santa Rosa National Park, Costa Rica)*

Branch no.	No. fruits examined	Live wt (g)		Dry wt (g)		% dry matter	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
1	36	0.72	0.73	0.18	0.14	24.7	4.4
2	36	1.61	1.21	0.34	0.25	21.0	3.6
3	31	1.35	0.87	0.27	0.17	20.1	4.6
4	36	2.41	1.52	0.51	0.35	21.2	5.2
5	32	1.40	0.92	0.32	0.25	23.1	4.6
	$\bar{x}$	1.50		0.32		22.0	
	S.D.	0.61		0.12		1.85	

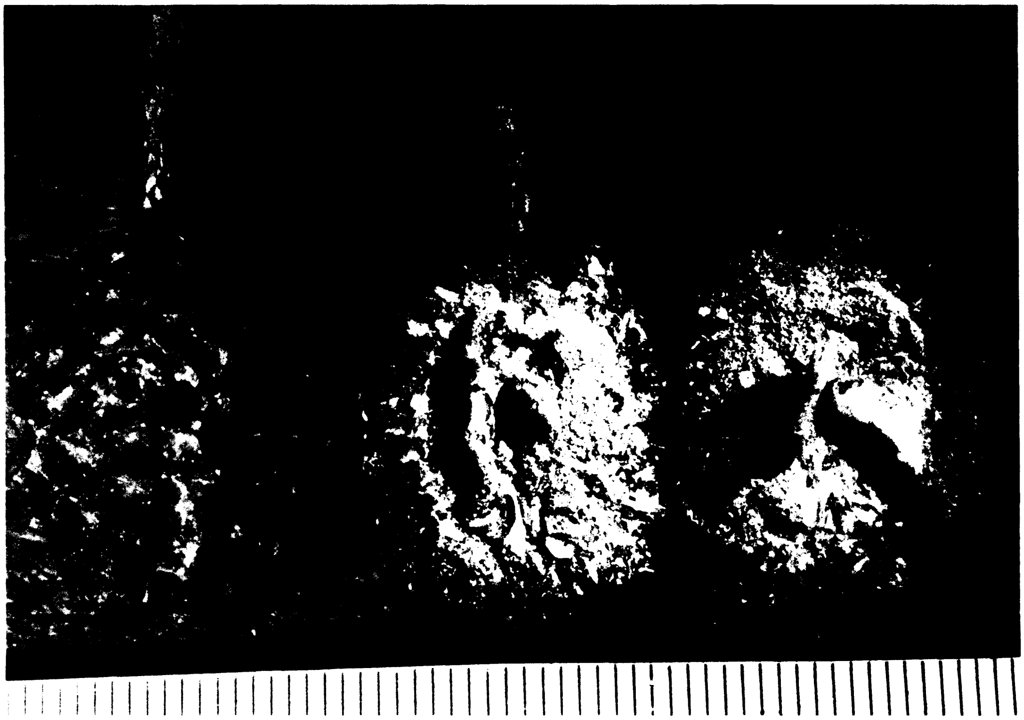

Fig. 10. Fruits of *Guazuma ulmifolia* that have been attacked by larvae of *Amblycerus cistelinus*; an adult beetle lies on the left side of the fruit on right; the hole in the core of the center fruit is the beetle pupation chamber.

on the tree in the early dry season, but are shed over a period of 4–8 wks in the mid to late dry season, a behavior that presumably spread the seeds among a larger set of dispersal agents than would have been the case were all ripe fruits dropped at once. It is also likely that some of the larger members of the Pleistocene megafauna ate the ripe fruits directly from the tree.

Directly beneath the thin sweet layer of sticky tissue on the surface of a ripe fruit is a 3–5-mm-thick layer of very hard "Y"-, "V"-, and "T"-shaped woody multicellular structures (letter-shaped structures, or LSS) (Fig. 6–9). The LSS are connected in such a manner as to form a loose network, the solid portions of which are separated by deep fissures. When the fruit is chewed, the network breaks apart easily and the LSS become scattered through the mash of sweet outer fruit pulp, seeds, core and more friable dry fruit tissue. The letter-shaped structures (LSS) are not only very hard, but are dense enough to sink in water. Along with the core, the LSS are probably functional in preventing complete occlusion of mammal molars (see below).

Moving inward from the network of LSS, one encounters the very thin parchment-like wall of the locules (endocarp) (Fig. 6). There are five locules arrayed symmetrically adjacent to the core, with the long axis of the locule parallel to the long axis of the fruit (Fig. 7). Each locule contains a maximum of 18 seeds, but more commonly there are 8–12 fully developed seeds in each locule. A sample from one tree of 36 mature normal-sized fruits undamaged by insects had 22–83 filled seeds in each fruit, with an average of 59.8 filled seeds per fruit (S.D. = 14.4). The 2,152 filled seeds weighed 13.14 g fresh weight (6.1 mg/seed). Oven-dried to constant weight, this seed sample contained 20% water. This sample of 36 fruits also had 1–5 aborted seeds (empty seed coats) per fruit (1.19 per fruit, S.D. = 1.54). These 36 fruits ranged in fresh weight from 2.04 to 4.26 g (oven-dry weight, 1.50 to 3.88 g) and 11.8% of the weight of the fresh fruit was fresh seed (S.D. = 3.23, range 5.1–18.3 g). Of the oven-dry fruit, 8.6% of the weight was oven-dry seed (S.D. = 2.81, range 2.4–16.1 g). This reduction from 11.8% to 8.6% by drying indicates that the seeds are on average more moist than is the fruit tissue.

The seeds are gray and finely flecked with black (Fig. 6–8). The surface is relatively smooth, but with fine surface reticulations and undulations. The seeds are 2–3 mm in diameter, spheroidal but flattened or strongly curved

TABLE 3. *Weights of newly emerged bruchid beetle adults whose larvae prey on guacimo* (Guazuma ulmifolia) *seeds (beetles weighed within 2 days of emergence)*

Beetle	Live weight (g)		Dry weight (g)		% dry matter	
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
Amblyceras cistelinus						
Females (8)	0.0354	0.0024	0.0178	0.0011	50.25	1.58
Males (9)	0.0257	0.0044	0.0128	0.0024	49.78	3.07
Acanthoscelides guazumae (10)	0.00050		0.00024		48	

along 1–3 sides, and have a gentle point at the end of attachment to the fruit. The seed coat is 0.10–0.13 mm thick and neither exceptionally hard nor tough. The seeds can be easily bitten in half with human incisors or ground finely between human molars. When I chew up mature seeds, they leave no distinctive unpleasant taste in my mouth. Filled viable fresh guacimo seeds sink in water and therefore have a specific gravity greater than 1.0.

In the center of the fruit and between the locules lies an elongate ovoid 5-sided core that is about 8–11 mm long and 3–5 mm thick at the center (Fig. 7, 9). The core is light brown, woody, fibrous, and extremely hard. It cannot be cracked, cut or ground up by my teeth. The core specific gravity is greater than 1, since the cores sink rapidly in water.

SEED PREDATION BY INSECTS—Seed predation by bruchid beetle larvae is the major cause of pre-dispersal seed death in guacimo (Janzen, 1975; Johnson and Kingsolver, 1971). After the fruits turn brown (ripen) on the tree but before they fall, a large buchid beetle (*Amblycerus cistelinus,* Fig. 10) clambers about on the fruits and glues a single large egg to each; the egg is placed well down in the crevices in the fruit wall. The larva mines through the fruit wall (which is very soft between the hard LSS). Once in a locule, it eats the seeds and mines from locule to locule until the contents have been eaten out of all or nearly all of the seeds. It normally consumes or kills all the seeds in a fruit. The locules are then filled with a beige-colored dry powdery frass and seed coat fragments (Fig. 10). This material is tasteless to me and I suspect also to the livestock. The larva then cuts a depression in the side or end of the core and constructs a pupation chamber (Fig. 10). Before pupating, however, the larva also cuts an exit hole nearly through the fruit wall. After 1–2 wks in the pupal stage, the adult ecloses and immediately leaves the fruit, leaving a 2–3-mm-diameter, very round hole in the side of the fruit (Fig. 10).

The newly emerging female *A. cistelinus* are longer and heavier than are the males (Table 3). They contain about 50% water. For an average of 60 seeds per fruit, and 0.00488 g dry tissue per seed, a 0.0150 g dry weight beetle was produced by 0.293 g dry weight seeds (conversion ratio of 0.051). In interpreting such a figure, it must be considered that the beetle larva probably gets no nutrients from the seed coat, and seed coat tissue is at least 20% of the dry weight of the seed.

It is unknown if the newly emerging *A. cistelinus* produce a second generation in fruits that ripen late in the fruiting season or if they immediately move away to other vegetation in order to wait until the following guacimo fruit crop. I have found adult *A. cistelinus* active on flowers of other plants and among foliage in the forest in all other months of the year. The period from oviposition to adult emergence is about 5–6 wks in length. When eggs are laid on the earliest fruits to ripen in the guacimo population as a whole, there appears to be ample time for a second generation in March and April from the first adults that emerge in February.

Once the fruits have fallen to the ground, the seeds in them are also attacked by a much smaller bruchid, *Acanthoscelides guazumae* (Table 3) (in Janzen [1975] this beetle was misnamed *Acanthloscelides guazumicola*). This tiny bruchid enters fruits opened by large mammal trampling, rodents, natural breaks, and *Amblycerus cistelinus* exit holes. It glues a single egg to each intact seed. The larva mines into the seed, develops inside and emerges as an adult (Johnson and Kingsolver, 1971). The newly emerged adults then oviposit on other intact seeds in their fruit and search for intact seeds in other fruits. It appears that *A. guazumae* has repeated generations in the fallen fruit crop until the seeds are exhausted by fruit consumption, predation by *A. guazumae,* and fruit rotting caused by the rainy season rains. The free-ranging adult *A. guazumae* are encountered on foliage and in flowers of other plants throughout the rainy season and early dry season.

Fig. 11, 12. **11.** Coati feces made up entirely of fragments of ripe *Guazuma ulmifolia* fruits; several LSS are visible on the surface of the feces. **12.** On left, seeds, LSS, core and wall fragments of *Guazuma ulmifolia* fruits taken from dung from Baird's tapir.

Neither *Amblycerus cistelinus* nor *Acanthoscelides guazumae* have other seed hosts in SRNP (Janzen, 1980), nor have they been found in other seeds in other parts of the Neotropics (*Guazuma tomentosa,* listed as a host of these two bruchids in Johnson and Kingsolver (1971), is a junior synonym of *Guazuma ulmifolia*).

When ripe fruit samples are collected from the ground below large adult guacimo trees growing in and near those edges of deciduous forest where horses and cattle have been excluded, *Amblycerus cistelinus* is found to have killed 10–40% of the seeds in the crop (Janzen, 1975). *A. guazumae* kills another 0–5% of the seeds, depending on how long the fruits were left on the ground before being sampled.

FRUIT CONSUMPTION BY LIVESTOCK—Horse (Equidae: *Equus caballus*) and cattle (Bovidae: *Bos indicus*) eagerly eat fallen guacimo fruits in large amounts. No detailed data are available on amounts or rates of consumption by cattle, or on seed survival in this animal. However, I have experimented with guacimo fruit consumption by horses and seed survival in these animals.

The range horses observed were geldings, stallions, and mares in the herd of approximately 30 animals used as riding stock by SRNP personnel. These horses range widely in large brushy and partly forested pastures, and consume guacimo fruits as a regular part of their diet in the dry season. Horses daily visit guacimo trees in their pasture and eat the newly fallen fruit. They do not intensively pick the fruits from low branches, though they do so occasionally. In a 10-ha pasture containing 22 adult guacimo trees, for example, a herd of ten horses keeps the ground quite clean of fallen guacimo fruits throughout the several months of fruit fall.

To determine the satiation level of horses that had an excess of guacimo fruits, ripe freshly fallen fruits were collected in March–April 1979 and stored dry in large closed plastic bags. These air- and sun-dried fruits do not rot until rained on or subjected to very humid air (in very humid air, the thin, sweet outer layer of fruit pulp takes up moisture from the air and rotting starts). Tethered horses were handfed these fruits by counting fruits into a large bowl from which the horse ate. Fruits were offered until the horse turned away. These horses were simultaneously tethered in sites with ample growing grass for grazing to satiation (Janzen, 1981a, b). Fruits were offered only once in a morning or afternoon. A meal lasted 20 to 58 mins. The three horses whose guacimo fruit consumption is described in Table 4 were adult-sized geldings, in good health and well fed. They had not eaten guacimo fruits for about 8 mos. Meal sizes ranged from 312 to 2,152 fruits (1.89 to 9.16 ls) with a grand mean for each horse of 1,356, 1,035, and 905 fruits per meal. Large samples of these fruits were 5–6% water. They averaged 2.7 g fresh weight per fruit for the 12–17 November sessions and 1.8 g fresh weight per fruit for the later meals. It is striking that the lowest amount of fruit eaten by each horse was eaten on the first day of feeding, suggesting that it may take the horse a short time to adjust to adding ripe guacimo fruits to a green grass diet.

I was not able to keep exact records of the number of fruits eaten per meal by horses foraging below guacimo trees, but when a horse was turned loose in the vicinity of a guacimo

TABLE 4. *Number and volume of ripe* Guazuma ulmifolia *fruits eaten in a meal by three hand-fed horses*

Date	No. of fruits			Liters of fruits		
	Blanco	Tuerto	Colorado	Blanco	Tuerto	Colorado
12–17 Nov, 1979	559	365	312	3.39	2.21	1.89
	1,266	1,256	653	7.67	7.61	3.96
	1,340	395	411	8.12	2.40	2.49
	765	910	882	4.63	5.52	5.35
	1,515	404	620	9.18	2.45	3.76
	1,435	1,061	636	8.70	6.43	3.85
	1,278	889	661	7.75	5.39	4.01
$\bar{x}$	1,165	754	596	7.06	4.57	3.62
S.D.	360	363	185	2.18	2.20	1.13
13 Dec–4 Jan, 1980	1,225	1,532	1,331	5.21	6.52	5.66
	2,106	2,152	1,468	8.96	9.16	6.25
	1,188	795	705	5.05	3.38	3.00
	1,650	1,100	1,050	7.02	4.68	4.47
	1,978	1,375	1,600	8.42	5.85	6.81
$\bar{x}$	1,629	1,391	1,230	6.93	5.92	5.24
S.D.	421	510	358	1.79	2.17	1.52
8–9 Feb, 1980	1,380	1,120	1,230	5.87	4.77	5.23
	1,450	860	950	6.17	3.66	4.04
	1,210	1,310	1,060	5.14	5.58	4.51
$\bar{x}$	1,347	1,097	1,080	5.73	4.67	4.59
S.D.	123	226	141	0.53	0.96	0.60
Grand $\bar{x}$	1,356	1,035	905	6.75	4.97	4.35
S.D.	391	472	382	1.81	1.97	1.34
n	15	15	15	15	15	15

tree with a large crop below it, it often foraged for 15–60 mins, eating continually. The number of fruits eaten approximates that eaten by the tethered horses.

The guacimo fruits that were handfed to the horses were about 50% attacked by *Amblycerus cistelinus* bruchids, but the beetles had left the fruits months before. There was no indication that the horses discriminated between intact fruits and those in which the seeds had been eaten by the bruchid larvae. However, once the fruits became moldy, they began to taste flat and sour to me, and the horses did not eat them.

If a meal of guacimo fruit is fed to a SRNP horse on the morning of one day, seeds and LSS begin to appear in the dung about the middle of the next day (approximately 30 hrs later). From a single meal of guacimo fruits, seeds continue to appear in large numbers through the evening of the second day (approximately 60 hrs later). During the third and fourth day there are a few seeds and fruit fragments in the dung. The fruit cores begin to appear in the third day after feeding and most appear in the fourth day. A few, however, may be defecated as long as 10 days later. This information was gathered as a side-product of the *Enterolobium cyclocarpum* fruit-feeding studies performed on these same horses (Janzen, 1981a, b).

If the dung from horses that were fed guacimo fruits is left intact on the ground or spread about by dung beetles, it produces a dense stand of guacimo seedlings. There is no indication that guacimo seeds are killed by passage through the horse. There are no partly digested seeds, seed coats or other seed detritus in the dung; the filled seeds have a greater than 90% germination success in the 3 wks following exit from the horse, if they are kept moist on soil or dung. If guacimo seeds are shelled out of the fruits by hand and placed in moist soil or thin dung, there is also better than 90% germination of filled seeds in the following 3 wks. No scarification is necessary. Since the seed passage rate through the horse is rapid, and since the horse's function is dispersal of a seed that produces a fast-growing ruderal plant that does best in insolated habitats, there is no reason to expect a seed form that requires chemical scarification of the seed coat for perception of germination cues.

In SRNP, as elsewhere in similar habitats in Guanacaste Province, Costa Rica, it is clear that horses and cattle are the major dispersal agents of guacimo. Whether they are good dispersal agents cannot be determined without further study of where the relevant animals defecate and the fate of the seeds at such places in the seed shadow.

Horses do not merely swallow guacimo fruits. They chew them to a pulp of particle sizes about 4 mm or less in diameter. They do not spit out any of the parts. How do the soft seeds escape the molar mill? I suggest that the LSS and the central core serve as unbreakable impediments to complete occlusion of the molars. The quite fragile fruit easily crumbles to a mix of relatively uniform consistency. A horse probably learns quickly that this mix cannot be further reduced in average size by even extensive chewing.

Among the wild fruits at SRNP eaten by range horses, guacimo is near the top of the preference list. For example, I spread 50 kg of fresh guacimo fruits in a 10-ha pasture along with the same fresh weight of fruits of jicaro (*Crescentia alata*), cenízero (*Pithecellobium saman*) and guanacaste *Enterolobium cyclocarpum*). Each fruit type was spread evenly over one pie-shaped quarter of a circular area 50 m in diameter. There were 17 adult-size range horses in the pasture. After 4 hrs they had eaten all the guacimo fruits and were just starting in on the jicaro fruits. The guanacaste and cenízero fruits, both species that are eaten extensively by SRNP range horses, were left until all the guacimo and jicaro fruits had been eaten. This experiment was repeated on 2 other days, with the same result.

Only a very small amount of the SRNP guacimo fruit crop is harvested by vertebrates, since cattle are now nearly eliminated from SRNP and the free-ranging horses are restricted to an area of a few km^2. However, other animals do sometimes eat the fruits. I have found viable guacimo seeds and cores in the dung of tapirs (*Tapirus bairdii,* Fig. 11), peccaries (*Tayassu tajacu*), ctenosaurs (*Ctenosaura similis*), and coatis (*Nasua nasua,* Fig. 12). Squirrels (*Sciurus varietatoides*) have been observed to eat the fruits, but it is unknown if they swallow the seeds.

Domestic pigs (*Sus scrofa*) in Guanacaste farmyards eagerly consume fallen guacimo fruits. Bressani and Navarrete (1959) fed ground guacimo fruits (including ground seeds) to chicks and found that substitution of ground guacimo fruit for up to 12% of the corn in the diet had no effect on growth. Up to 48% of the corn diet could be replaced with guacimo fruit flour without toxic effects (no higher concentrations were tried) but growth rate was reduced, as though the chicks were not getting enough food for optimal growth. Considering that well over half of a guacimo fruit is inert core, LSS and other indigestible fruit tissues, this result is not surprising. Bressani and Navarrete (1959) give a variety of chemical and nutrient analyses values for ground guacimo fruits; however, these values have no meaning whatsoever in understanding the value of the fruits to a horse, cow, or any other large herbivore. The large herbivores do not mill the fruit to a flour-like consistency; all the minerals and nutrients in the core, LSS and seeds are unavailable to animals that do not grind them up.

Discussion—In contemporary SRNP habitats lacking horses and cattle, the bulk of a *Guazuma ulmifolia* fruit crop lies below the tree until the rains come and then the fruits rot. The seeds in these fruits may germinate, but the seedlings do not escape from the rotting fruit. Before the rains, a few fruits are eaten by wild animals and viable seeds defecated. Presumably, the usual post-Pleistocene recruitment to the guacimo population was from such seeds. However, where cattle and horses are present no guacimo fruits are left below the parent. These large animals generate a widespread seed shadow within the confines of their pastures, a habitat where guacimo seedlings and saplings are common plants.

However, as postulated as a general case by Janzen and Martin (1982), I suspect that the guacimo-livestock interaction is much more similar to the circumstances under which guacimo evolved than is the case in livestock-free habitats such as much of SRNP at present. There is no fossil record for guacimo fruits or pollen but we have to either accept the highly unlikely hypothesis that the fruit type evolved in the past 10,000 years or else guacimo fruits were contemporary with Pleistocene and earlier large herbivorous mammals. I think it much more likely that those animals responded to guacimo fruits as do contemporary horses and cattle, than that they ignored this large food source. Furthermore, the ability of the guacimo core and LSS to prevent seed crushing by horses is very likely to have evolved specifically to meet this dental challenge. Neither hard cores nor LSS-type structures are found in other Central American sterculiaceous fruits. Costa Rican Pleistocene horses had molars and other morphology extremely similar to those of modern Costa Rican range horses and there is no reason to believe that the Pleistocene horses would not have also fed on guacimo fruits and dispersed the seeds. In a certain sense, then, Santa Rosa National Park with horse herds is a more "natural" habitat than it is without them.

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