

# CENÍZERO TREE (LEGUMINOSAE: PITHECELLOBIUM SAMAN) DELAYED FRUIT DEVELOPMENT IN COSTA RICAN DECIDUOUS FORESTS<sup>1</sup>

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## ABSTRACT

*Pithecellobium saman* (Leguminosae: cenízero) is one of several species of Costa Rican deciduous forest large trees that flower at the end of the dry season and then bear dormant tiny fruits through the following rainy season, to then abruptly enlarge and mature them during the first third of the next year's dry season. I postulate that this pattern of fruit development in *P. saman* minimizes the duration of exposure of immature seeds to parrot and insect seed predators, increases the tree's flexibility in the use of photosynthates accumulated for later fruit maturation, increases resource storage costs, and decreases the photosynthetic contribution that fruit and immature seeds can make to the parent tree's resource budget. These consequences imply that the fruiting phenology of *P. saman*, like that of other trees, is evolutionarily determined by its interactions with the habitat as well as by internal physiological factors.

IN THE LOWLAND DECIDUOUS FORESTS of the Pacific coastal plain of Costa Rica there are numerous species of trees with fruits that mature as long as 8–12 months after the tree flowers. Some of these trees produce nearly full-sized green (immature) fruits within 1–2 months after flowering (e.g., *Hymenaea courbaril*, *Hemiangium excelsum*, *Crescentia alata*, *Sapranthus palanga*). In such species it is very difficult to distinguish between: 1) long fruit development times that are caused by necessarily slow developmental processes; and 2) long development times as physiological behavior that is adaptive in generating a ripe fruit crop at an appropriate point that is long after the best time for flowering in the seasonal cycle. In other words, do these trees 'require' 8–12 months to mature fruit or do they 'use' 8–12 months to mature their fruits? In striking contrast are those species of trees that produce minute fruits after flowering and then keep them tiny and dormant for the 6–10 months (throughout the rainy season), and then quite rapidly develop them into mature fruits in the dry season (e.g., *Pithecellobium saman*, *Guazuma ulmifolia* (Janzen, 1982a), *Enterolobium cyclocarpum* (Janzen, 1982b), *Cassia grandis* (Janzen, 1971, 1977a)). It is clear that in such a delayed fruit maturation pattern the tree is 'using' 8–12 months to mature its fruits rather

than requiring 8–12 months to meet some internal constraint on fruit development. Here I examine, from an ecological viewpoint, the process of delayed fruit development and its consequences in *Pithecellobium saman* (cenízero, rain tree).

THE TREE AND HABITAT—Cenízero is a native riparian and hillside large tree of the deciduous forests of lowland Guanacaste Province (below 400–600 m) on the northwestern Pacific coastal plain of Costa Rica. It occurs as a native tree throughout the dry neotropics from Mexico to Venezuela and Colombia, and throughout the tropics as a planted tree. However, its 'native' contemporary distribution is probably in part generated by seed dispersal by introduced horses and cattle (Janzen and Martin, 1982). In Santa Rosa National Park (extreme northwestern Guanacaste Province), cenízero occurs as a conspicuous tree in pasture and forest, a spreading life form in open sites (Fig. 1–3) and a tall thin life form in intact forest. Santa Rosa is subject to a 5-month rain-free and windy dry season (mid-December to early May), during which nearly all the non-riparian tree species lose their leaves. Cenízero is one of these deciduous species, but is somewhat irregular in the timing of leaf drop and may keep its leaves longer in more moist riparian habitats than in dry ones. I have been studying the tree in this habitat for six years, initially with respect to seed predation by bruchid beetles (Janzen, 1977b) and more recently with respect to seed dispersal by large mammals. Various aspects of cenízero biology have been examined in other parts of the world

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Fig. 1-3. 1. *Pithecellobium saman* in full leaf and flower (May) in Santa Rosa National Park, Guanacaste Province, Costa Rica. 2. Same tree as in Fig. 1, nearly leafless and bearing a crop of ripening fruits (March). 3. On left, same tree as in Fig. 1; on right, another *P. saman* in full leaf and flower and having dropped nearly all of its mature fruits (March).

(Chicco, Garbati and Muller-Haye, 1973; Greshoff, 1890; Hatheway and Baker, 1970; Janzen, 1969; Leonard and Sherratt, 1967; Panditsekera and Elikewela, 1947; Thomas et al., 1976a, b; van Itallie, 1932; Varshney and Khanna, 1978; Varshney and Vyas, 1976; Wiesner et al., 1953), but none of these studies examined fruit developmental biology or ecology.

**CENÍZERO REPRODUCTIVE CYCLE**—In Santa Rosa, a representative cenízero reproductive cycle is as follows. In early March, 2 months before the rains came, most trees stand almost totally leafless and still bearing many mature pods (Fig. 2). The ground below is littered with mature fruit baking in the hot sun, fruit that have fallen within the previous month (assuming there are no cattle or horses to consume the fruits). In late March to early April, the tree produces a dense crop (Fig. 1) of large leaves and at the ends of the leaf-bearing branches produces terminal inflorescences of typical mimosoid multi-floret inflorescences (Fig. 4). The flowers are pollinated by night-flying insects. By the end of May, the last inflorescences have fallen and the old inflorescence-bearing branches are covered with small green fruits 2–3 cm in length, which remain about this size through the rainy season (Fig. 5, 6). In late November a few begin to expand (Fig. 7). By early January, well into dry sunny weather, most of the fruits are expanding or expanded to full size (about 20 cm in length). Leaf drop is gradual, but the tree is leafless by early February (Fig. 2), and the first pods to have expanded are turning brown and beginning to fall. By the end of March, nearly all of the fruit have fallen (Fig. 8) and the cycle begins again. If the tree is fully insolated, it may have an equally heavy flower and fruit crop for several years in succession, rather than display a regular cycle of large crops followed by small crops as occurs in many other large trees in Santa Rosa deciduous forests. However, there are years of heavy fruit production followed by years of low production for some fully insolated trees. I have no records of fruiting periodicity for *P. saman* growing in dense forest where their crowns are partly shaded, but such trees may behave differently than do the fully insolated ones. Within a population, there is inter-tree variation in the timing described above, even when the trees are only a few meters apart. Some trees put out new leaf crops while others are still maturing fruits (Fig. 3), and some trees mature fruits as early as mid-January. Some trees leaf out as late as the end of April and are still in full flower at the beginning of June. However, none have been encountered that begin expansion of young fruits before mid-November. In other words, all the trees bear

very small dormant fruits throughout the rainy season. Within a crown there is variation between fruit as to when they begin to expand (Fig. 7) and when they mature and fall from the tree.

As the basis for a description of a representative fruit development cycle (Table 1), I chose two of the three adult cenízero trees growing over the stone corral walls between the Casona and the tourist Area de Acampar at Santa Rosa (Fig. 1, 2 is a photograph of the third tree). These two trees have a leafing and fruiting cycle almost exactly like that described as representative in the previous paragraph and they are at least 100 years old.

Between the end of flowering in late May and late November, nearly all fruits lengthened by about 0.4-fold and increased in wet and dry weight by about 0.2-fold (Table 1, compare 6 June and 24–30 November values). While these changes over a six month period are significant ( $t$  tests,  $P < 0.05$ ), I suspect that they are not of great biological significance. These changes in length and weight do not represent breaking of fruit developmental dormancy.

In late November, about 5% of the fruits in each of these two trees had obviously broken developmental dormancy since they abruptly began swelling and lengthening. A sample of these fruits showed a 3-fold increase in length, a 28-fold increase in wet weight, and a 20-fold increase in dry weight over those of their still dormant neighbors only a few cm away (Table 1, Fig. 7). By early January, at least 90% of the fruits on these two trees had begun to expand, and most of those not showing any sign of expanding were being aborted by the parent. These aborted small fruits broke off the branch with a light touch, while the expanding fruits were very firmly attached. In early January, I selected from each tree a set of 22 fruits that were fully expanded and undamaged by insects, and free from seed abortions (as indicated by uniform fruit expansion throughout the length of the fruit). They had full-sized seeds inside (Fig. 9) but the embryos were still only partly developed (green cotyledons still expanding). These fruits were 1.5-fold longer, about 5-fold heavier in fresh weight, and 5.3-fold heavier in dry weight than the average newly expanding fruit 1.5 months earlier in late November (Table 1). In early February, the first ripe fruits began to fall (these were the fruits that had been the first to expand in late November). These mature perfect fruits were slightly shorter, had about 60% as much water in them, and had about twice the dry weight than did the full-sized green fruits in early January. In summary, a fruit that begins expansion in late November (with a full complement of

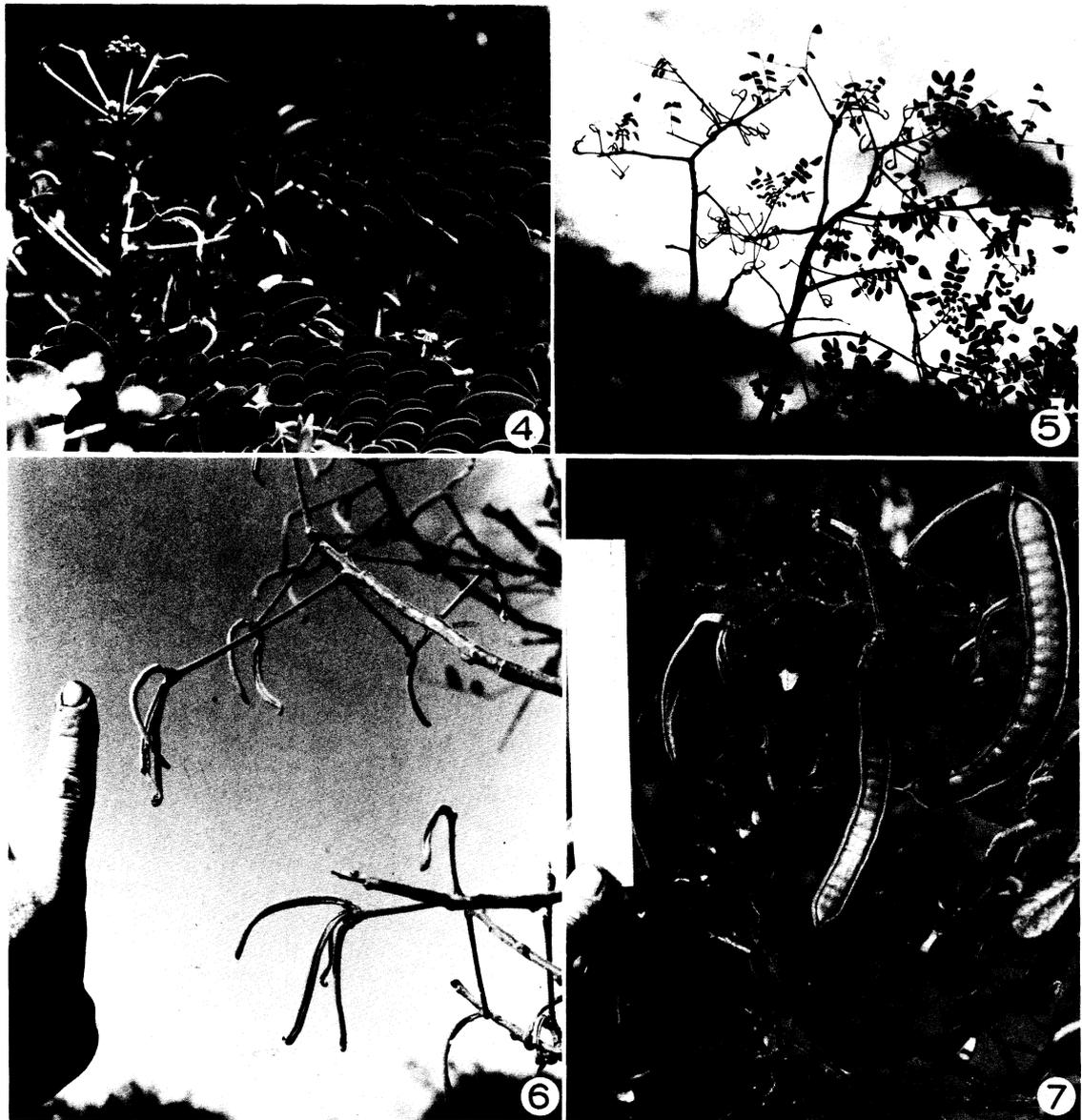


Fig. 4-7. 4. Inflorescence of *P. saman* with flower buds and small green fruits, projecting above large leaflets and leaves in crown of tree in Fig. 1. 5. View through crown of tree in Fig. 1 in November; small dormant fruits are visible as hooked structures at ends of straight peduncles. 6. Small dormant fruits in crown of tree in Fig. 1 in November. 7. Fruits in various stages of development in crown of tree in Fig. 1 in December; fruit on right is approaching full size (rule is 15 cm long).

developing seeds and no insect damage to the fruit) is fully mature and drops from the tree about 2.2 months later. All the members of a fruit crop normally change from dormant to developing over about 1.5 months (late November to early January), and fruit drop from a single crown is normally spread over about two months (February to early April).

INTERACTIONS WITH ANIMALS—As background needed for an ecological interpretation

of the developmental timing described above, I need to briefly describe the interaction of cenízero with animals. The first mortality experienced by the fruits occurs during the month following flowering. A small fly (*Cecidomyiidae*) galls as many as half of the small fruits and the attacked fruits are shed by the parent tree by mid-June. The attack occurs while the fruit is expanding from the size of the flower's ovary to the 2-3 cm long dormant fruit. Where

TABLE 1. *Weights and dimensions of perfect and normally developing Pithecellobium saman fruits (including seeds) on two trees in full sun, Santa Rosa National Park, Guanacaste Province, Costa Rica*

Fruit type (n)	Fruit length (mm)		Fruit width (mm)		Fruit weight living (g)		Fruit weight oven dry (g)		Percent water in fruit
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	
UNEXPANDED GREEN, 6 JUN 1979									
Tree 3 (36)	31.3	6.2	2.9	0.16	0.20	0.071	0.070	0.017	65
Tree 4 (36)	34.1	5.8	2.9	0.17	0.19	0.082	0.068	0.018	64
UNEXPANDED GREEN, 24-30 NOV 1979									
Tree 3 (36)	36.4	8.7	3.1	0.20	0.24	0.065	0.081	0.017	66
Tree 4 (36)	48.8	7.8	3.0	0.18	0.23	0.065	0.088	0.019	62
NEWLY EXPANDING GREEN, 24-30 NOV 1979									
Tree 3 (20)	139.9	22.2	13.8	2.69	6.38	2.71	1.60	0.59	75
Tree 4 (20)	130.2	19.1	13.3	2.76	6.52	3.01	1.69	0.55	74
MAXIMUM EXPANDED GREEN, 7 JAN 1980									
Tree 3 (22)	209.4	17.9	21.4	1.17	33.4	7.01	8.93	2.68	73
Tree 4 (22)	203.3	16.4	20.8	1.12	31.3	6.93	8.45	2.91	73
NEWLY FALLEN MATURE BROWN, 9 FEB 1980									
Tree 3 (22)	202.3	19.3	20.1	1.61	19.1	5.5	16.62	2.48	13
Tree 4 (22)	201.1	18.1	19.2	1.41	19.0	5.6	16.38	2.62	14

this insect waits for the next year's young fruit crop is unknown. From June through November there is no further noticeable loss of fruits to animals, though occasionally a leaf-eating insect also eats a portion of a green fruit.

Once the fruit has expanded to full size, parrots (species unknown) pick the fruits and excise the seeds with the bill, cut open the soft seed, and eat the seed contents (discarding the seed coat). The amount of parrot damage is highly variable from tree to tree and habitat to habitat. In areas of Santa Rosa where the forest (and hence parrot density) is fairly natural, as many as a third of the expanded green fruits may be harvested by parrots. This seed loss, of major importance in interpreting fruit developmental dormancy, has several distinctive components. First, parrots are long-lived seed predators that breed once a year. The maximum numbers that can arrive at a given tree's seed crop will depend only on how many are in the habitat at that time. These birds pass the year subsisting on the seeds of a variety of species of perennial plants, and parrot density is set by the carrying capacity of the habitat (ignoring the possibility of migratory parrots). Second, parrots do not cache seeds. The maximum number of seeds that will be eaten by a flock that knows of a cenizero tree's seed crop will be the number of seeds a bird needs to fill its digestive tract (50 to several hundred, depending on body size) multiplied by the number of birds multiplied by the number of days the crop is available. Third, while the number of birds to arrive will be that number available

(or fewer) in the habitat, if there is a good food source that persists, parrots are sufficiently migratory on a local basis to accumulate at a food source, and thereby gradually raise the pool of seed predators that are feeding on the seed crop.

In short, then, seed predation by parrots is the type such that whatever percent of the seed crop is to be eaten will be importantly determined by how long the full-sized immature fruits are available, and seed loss per day is likely to increase slightly with longer periods of fruit availability.

At the same stage that parrots begin feeding on the fruits, a small pyralid moth (*Anypsispylla univittella*, Phycitinae) lays eggs on the fruits. The larvae mine through the moist fruits, eating immature seeds and some fruit tissues. Massive necrosis follows and these green fruits are usually aborted (dehiscid) without further development. These moths continue to oviposit on the fruits until the fruits have matured and even after they have fallen from the tree. The larvae mining in the fruit consume seeds until the stage at which the fruit is so mature that the seed coats have hardened. Larvae mining in the walls of mature fruits consume fruit pulp, do not kill intact seeds, and do not appear to reduce attractiveness of the newly fallen fruits to livestock. However, if fruits lie on the ground for several months during the last half of the dry season without being consumed, the pyralid moth larvae eventually consume most of the fruit tissue. These severely damaged fruits are rejected by horses and cattle in preference



Fig. 8, 9. 8. Ripe fruit fallen below tree in Fig. 1 (March); *Merobruchus columbinus* bruchid exit holes are visible in the fruit in center of photograph (pen is 13.5 cm long). 9. Dorso-ventral longitudinal section through full-sized maturing fruits of *P. saman*; upper fruit has expanding embryos on left, expanded embryos on right, while lower fruit has larvae of *M. columbinus* mining in the embryo.

to intact fruits. In short, the amount of seed predation and fruit damage by the pyralid moth larvae is determined largely by the amount of time that the full-sized fruits are present.

Once the fruits are full-sized and contain full-sized seeds, a bruchid beetle (*Merobruchus columbinus*) glues small eggs to the fruit surface. One larva develops in each seed (Fig. 9)

and the adults emerge from the brown and drying ripe fruits shortly before or after the fruits fall from the tree. These beetles killed 43% of the filled seeds in a sample of 14,500 seeds from 81 *P. saman* trees in Guanacaste (Janzen, 1977b). The newly emerged adult beetles then wait about 11 months for the next crop. Since they have only one generation per year, the number of beetles to arrive at a tree's crop rather than the duration of the fruit stage susceptible to attack is probably the critical variable. However, were the susceptible stage much longer (e.g., 2–3 months), the behavior of having a second bruchid generation each year might well evolve.

Once the *P. saman* fruits have fallen in livestock-free habitats in Santa Rosa, they either lie there until the rainy season comes and then rot (the usual case), or they are eaten by tapirs and collared peccaries. If eaten by tapirs, some of the seeds survive passage through the molars and intestine to be defecated where they have some chance of survival (Janzen, 1982c). If the fruits are eaten by collared peccaries, the seeds are ground up by the molars. In the fruits left to rot, tiny bruchids (*Stator limbatus*) enter cracks in the fruit wall and the exit holes of the larger bruchids (*Merobruchus columbinus*) and oviposit on the seeds (Janzen, 1977b). Between March and the coming of the rains in May, these beetles on occasion kill all the seeds to which they have access. However, it was probably not always like this, if I may use the interaction of cenízero with horses and cattle as a rough approximation to the situation up until 10,000 years ago, when lowland Central America had a more normal large fauna of large herbivores (Janzen and Martin, 1982). If livestock are present, all ripe fruits below a cenízero tree are eaten within a few days of falling. The longevity of a ripe fruit depends on the details of foraging patterns by livestock. The number of animals in the area also influences the fruit removal rate. The intact hard dormant seeds in the fruits pass through cattle and horses, and are defecated in the dung (some are, however, digested), where they either become incorporated in the litter (to lie dormant or germinate with subsequent rains) or are removed by small rodents that are predators on the seeds (see Janzen, 1981a, 1982f). The probability that rodents will get the seeds is in part determined by how many seeds there are in the dung; seed-rich dung has a greater chance of having its seeds harvested than does seed-poor dung (Janzen, 1982d). Seeds that begin to germinate in the dispersal agent are generally killed by digestive fluids (see Janzen, 1981a, 1982e). The large mammals are removing the seeds from the area of high predation percent-

ages by the small bruchid (*S. limbatus*), dispersing the seeds to germination sites not below the parent, and exposing the seeds to predation by small rodents.

**DISCUSSION**—I hypothesize that the delayed development by *Pithecellobium saman* fruits is primary of value to the plant in shortening the period when the seeds are large enough and well enough developed to attract seed predators. With animals like parrots and pyralid moth larvae, the effect should be continuous; every day less that the green full-sized fruits with filling seeds hang on the tree, the fewer seeds are likely to be killed. However, with pre-dispersal seed predators like the bruchid *Merobruchus columbinus*, considerable variation in the duration of the large fruit or seed stage may have little effect, *until* the longevity of large seeds in fruits becomes great enough that a second generation of the bruchid can occur in a single seed crop or fruiting season. Such a shift in bruchid behavior will presumably require more than the occasional tree or fruit that is available to the emerging adults of the first generation; there will have to be enough seeds available for selection for the behavior of immediate oviposition rather than enter a state of reproductive dormancy and wander about in the vegetation in search of adult food (pollen and nectar).

Delayed fruit and seed development has some costs. The photosynthate made by the leaves during the rainy season must be transported and stored, and later reallocated to the rapidly expanding fruits (during most of the fruit expansion and subsequent seed development the tree is leafless, so the only source of resources for the fruit is stored material plus what it and the seeds make). A second cost is that in being very small for 6 full months, the immature fruit is producing much less photosynthate than it would be able to make were it full-sized.

There are some advantages to delayed fruit development in addition to those associated with increased freedom from seed predation. First, if a natural catastrophe occurs, such as a failure of the rainy season as happened in southern Guanacaste Province, the subsequent abortion of all the fruits in order to have resources for vegetative repair will be a smaller loss than if much resource had already been invested in them. Second, the photosynthate being stored for later fruit development can be used at any moment to meet vegetative demands should they appear unexpectedly. Third, if it becomes necessary at the end of the rainy season to abort a portion of the fruit crop to tailor its size to the resources available for seed and fruit maturation, the aborted fruits rep-

resent a comparatively small loss. Fourth, less intensive chemical and morphological defenses should be necessary to protect dormant undeveloped fruits from herbivores than would be needed for a large and nutrient-rich developing fruit.

This study does not address the question of why the best time of year for *P. saman* fruit maturation is the middle of the dry season, a question that will be answered with studies in progress on the feeding preferences of livestock at different times of year. However, given that the second half of the rainy season is the best time for fruit ripening, and given that the dry season is the best time for flowering, a mutant *P. saman* that flowered and fruited in the same dry season would drop its fruits at the very end of the dry season or perhaps somewhat into the rainy season (assuming about 2 months of fruit development after flowering).

In conclusion, it is clear that a consideration of why a tree such as *P. saman* has its particular flowering and fruit development pattern rather than one of the others displayed by other members of the habitat must take into account more than just the physiological traits of the tree. It appears to me that details of fruit timing are no more immune to the biotic parts of the habitat than are the details of secondary compound chemistry.

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