

WEIGHT OF SEEDS IN 1-3-SEEDED FRUITS OF *LONCHOCARPUS COSTARICENSIS* (LEGUMINOSAE), A COSTA RICAN WIND-DISPERSED TREE

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ABSTRACT

The mature dormant seeds from a single large crop of *Lonchocarpus costaricensis* were found to weigh about 4 percent less when they came from 2-seeded fruits as when they came from 1-seeded fruits in the deciduous forest of Santa Rosa National Park, Guanacaste Province, Costa Rica. *L. costaricensis* has 1-3-seeded, wind-dispersed fruits and the seeds are not subject to post-dispersal seed predation by insects or rodents. Despite the very small differences in seed weight between 1-, 2- and 3-seeded fruits, the normal living seeds within each fruit category varied about 2-fold in weight. Possible causes are discussed.

Lonchocarpus costaricensis (Leguminosae; Papilionoideae) is a medium-sized to large deciduous tree that occurs throughout the lowland deciduous forests of the Pacific side of Costa Rica (Guanacaste Province and northern Puntarenas Province). While occurring in many different habitats, it is normally encountered as scattered individuals rather than in patches. Every 2 years, or sometimes at longer intervals, a *L. costaricensis* tree produces a crop of a few to several thousand flat indehiscent wind-dispersed fruits (Fig. 1). Flowering toward the end of the dry season (April), it matures the fruits in the middle of the following dry season a year later; full-sized green fruits are borne by the tree throughout the rainy season. The population is not synchronized in its supra-annual cycle of flowering or fruiting.

The majority of the tough and fibrous fruits are single-seeded, but a few are 2- or 3-seeded. In the process of shelling many seed crops of *L. costaricensis* for chemical analysis, I have been left with the impression that the seeds from 1-, 2- and 3-seeded fruits average about the same weight, even though there is a wide range of seed weights. To examine this impression, the seeds from a sample from a 2000-fruit seed crop was collected from a representative healthy adult *L. costaricensis* growing on the banks of the río Guapote in Santa Rosa National Park (northwestern Guanacaste Province, 8 March 1977). This was a maximum-size seed crop for a *L. costaricensis* of this size (12 cm DBH). This tree fruited in 1975, 1977, 1979

and 1981. The fruits were dry and dead, the seeds were dry and dormant, and the fruits were just beginning to be broken off by the dry season winds. The sample was collected by pulling down a large branch, breaking the fruit blade at the attachment point, and putting the fruits in a cloth bag. The branches sampled were fully insolated in the upper part of the crown. The fruits were split open by hand and the seeds saved according to the number of seeds in the fruit from which they were obtained.

The seeds were weighed in their living but dormant state. They were categorized as normal or as aborted (shriveled, twisted and shrunken). A sample of 50 "normal" seeds germinated in a few days when placed on moist toweling; none of the aborted seeds germinated when wetted. A sample of 21 haphazardly chosen normal seeds were split in half and oven dried (60°C) to constant weight (living weight average 283 mg, s.d. = 52.1); they had contained an average of 7.5 percent of water (s.d. = 0.87%, range 6–9%).

The seeds from the 1-seeded fruits weighed significantly more than did those from 2-seeded fruits (Table 1) ($t_{308} \text{ d. f.} = 2.70, p. < 0.05$). However, the difference of 10.9 mg between the means is very small (4.1% of the mean weight of seeds from 1-seeded fruits). The seeds from the 1-seeded fruits did not weigh significantly more than did the seeds from the 3-seeded fruits ($t_{179} \text{ d. f.} = 0.750, \text{ N.S}$) but the sample size of seeds from the 3-seeded fruits is so small that this test is probably not meaningful. Likewise, the weights of seeds from 2- and 3-seeded fruits are not significantly different (by inspection). In all three sets of seeds, there was 2-3-fold variation in weight of normal living seeds across the range of weights.

In this crop, 83 percent of the fruits were 1-seeded, 17 percent were 2-seeded, and 1 percent were 3-seeded (Table 1). The single-seeded fruits had 96 percent normal (non-aborted) seeds, the 2-seeded fruits had 92 percent normal seeds, and the 3-seeded fruits had 83 percent normal seeds (Table 1). This suggests, probably incorrectly, that a seed is more likely to be aborted in a 2- or 3- seeded fruit than in a 1-seeded fruit. My results could easily be the consequence of the tree being more likely to shed a 1-seeded fruit with an aborted seed than it is to shed a 2- or 3-seeded fruit with a single aborted seed. In no case were all the seeds aborted in a 2- or 3-seeded fruit.

In this crop, 71 percent of the good seeds were contained in single-seeded fruits, 28 were contained in 2-seeded fruits, and 1 percent were contained in the 3-seeded fruits (Table 1). What these proportions mean to the fruit shadow, seed shadow and subsequent seedling production by the parent tree cannot be determined with the data at hand, but they should influence them (e.g. Janzen 1978). Fruits with more seeds in them will weigh more, and presumably be blown a lesser distance from the parent tree (assuming that fruits are not attached to the tree with increasing tenacity as seed number per fruit rises). A 4.1 percent decrease in average seed weight from 1- to 2-seeded fruits may seem a very small difference but may well be important in seedling competitive events. Since the seeds germinate directly out of the

rotting fruit, and since the seeds germinate or die at the beginning of the rainy season following dispersal, the 2- and 3-seeded fruits will generate pairs and triplets of *L. costaricensis* seedlings only 1–2 cm apart in the same growing season.

Rarely in Santa Rosa, and commonly in more southern Guanacaste Province, the seeds of *L. costaricensis* are killed by the larvae of the bruchid beetles *Ctenocolum crotonae* and *C. tuberculatum* (Janzen 1980). The adult beetle glues eggs to the domed portion of the fruit wall over the seed(s). The larvae mine through the fruit wall and into a seed. Up to 4 larvae may develop to maturity in one seed and the adults emerge about 6 weeks after oviposition. There is no indication that 1-, 2- or 3-seeded *L. costaricensis* fruits are oviposited on any differently from one another, or that there is differential seed mortality in fruits with different members of seeds. There was no bruchid attack of the seeds in the crop described in Table 1.

In an ongoing study of post-dispersal seed predation of wind-dispersed seeds in Santa Rosa, I have found that the common small forest-floor seed predator rodent *Liomys salvini* (Heteromyidae) will starve to death rather than eat seeds of *Lonchocarpus costaricensis*. This is true irrespective of whether the intact fruits or shelled seeds are offered. Furthermore, I never encounter dispersed *L. costaricensis* fruits with their seeds shelled out of them by any vertebrate (occasionally a phytophagous beetle, grasshopper or caterpillar eats the developing seed out of the immature fruit during the rainy seasons). This means that the wind-generated seed shadow of a *L. costaricensis* tree is not thinned by seed predators nor can its properties be viewed as the evolutionary consequence of post-dispersal seed predation.

A wind-dispersed seed is not subject to constraints associated with seed spitting by animate dispersal agents, passage rates through animal intestines, or fruit crop sizes as relate to satiation and attraction of dispersal agents. On the other hand, the fruit or seed shadows of wind-dispersed fruits (or seeds, if the fruit is dehiscent) should be strongly responsive to the variation in the weight of the dispersal unit. For example, since the seeds in 2-seeded *Lonchocarpus costaricensis* fruits weigh the same as those in 1-seeded *L. costaricensis* fruits, the 2-seeded fruits are probably substantially heavier than are the 1-seeded fruits. Whether 1- and 2-seeded fruits end up in the same or different parts of the seed shadow will then be determined by the strength of attachment of the fruit to the parent (i.e., the amount of wind that is required to put the fruit into dispersal). Additionally, the fact that within the commonest fruit size category, 1-seeded fruits, there is a 2-fold variation in seed weight may result in a much broader seed shadow than were the seeds quite uniform in weight. On the other hand, it may be that fruit size also varies strongly in weight, and certainly a widespread seed shadow can be as much generated by variation in fruit weight (and attachment intensity) as in seed weight.

Perhaps a more productive way to view the variation in *L. costaricensis* seed weight is through its cause. If the seed size is not fine-tuned to meet the swallowing, etc. demands of an animate dispersal agent, then variation in seed weight generated by variation in seed developmental history may well not be selected against. For exam-

ple, the developing embryos of *L. costaricensis* are imbedded in a large flat green photosynthesizing structure for at least 8 months. The leaf-like are borne in bunches that shade each other and are also shaded by leaves on occasion. If a seed's size is at least in part determined by the amount of sunlight received by its fruit, then there should be widely varying seed sizes. Additionally, if the embryo of *L. costaricensis* is chlorophyllous during development (e. g., Janzen 1981), the same heterogeneity of insolation of the fruit will also affect the embryo directly. It may well be that up to a certain weight limit, each seed of an *L. costaricensis* seed crop does its best to grow as large as possible with the resources offered by the parent (fruit photosynthesis and direct resource input from other parts of the parent vegetative structure) and what it can make itself. The upper weight limit might be set by the fate of a seed that made so much resource that the fruit that contained it usually fell directly below the parent plant and died in competition with the parent. On the other hand, it may be that the parent provisions each embryo with a fixed small amount of resources and variation in seed weight then comes about through variation in the photosynthate harvesting abilities of the individual fruits and the embryos. However, in closing I should point out that the equal variance of weight of 1-seeded and 2-seeded fruits (Table 1) strongly implies that in addition to the above mentioned processes, if indeed they do occur, there is some kind of monitoring system going on as well whereby the parent plant generates the same distribution of seed weights among seeds in 1-seeded fruits as in 2-seeded fruits.

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Resumen

Se observó que las semillas vivas y latentes de una cosecha de *Lonchocarpus costaricensis* pesaron, aproximadamente, 4 percent en frutos 2 semillas que los de frutos de 1 semilla, en el bosque caducifolio del Parque Nacional Santa Rosa, Provincia de Guanacaste, Costa Rica. *L. costaricensis* tiene frutos con 1-3 semillas que son dispersadas por viento, que no son comidas por insectos o roedores después de su dispersión. Aunque las diferencias entre semillas de los frutos con 1-, 2- ó 3-semillas son muy pequeñas, las semillas normales de cada categoría de fruto varían en peso más o menos dos veces. Las posibles causas se discuten.

Literature Cited

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Table 1. Weights of live seeds and fruit parameters in 1064 fruits of *Lonchocarpus costaricensis* with 1-3 seeds.

Seeds	1-seeded fruits	2-seeded fruits	3-seeded fruits
n	168	142	13
\bar{X} (mg)	267.2	256.3	258.0
s.d.	45.4	47.6	41.9
range (mg)	139-376	105-368	194-348
Fruits			
	879	179	6
% good seeds	96	92	83
total good seeds	844	329	15
% of seed crop in			
n-seeded fruits	71	28	1
% of fruits n-seeded	83	17	1

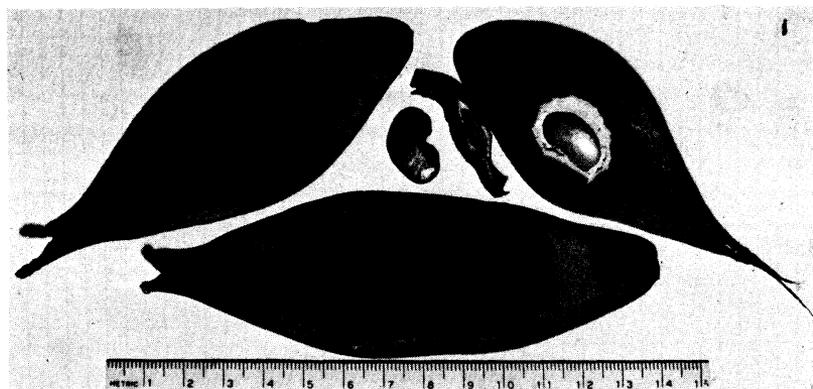


Figure 1. Intact mature 1-seeded fruit of *Lonchocarpus costaricensis* (upper left); intact mature 2-seeded fruit of *L. costaricensis* (lower center); fruit with fruit wall cut away to expose normal seed (upper right); intact mature seed and cross-section of fruit (center). Santa Rosa National Park, Guanacaste Province, Costa Rica (March 1981).