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VARIATION IN SEED SIZE WITHIN A CROP OF A COSTA RICAN MUCUNA ANDREANA (LEGUMINOSAE)[1]

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ABSTRACT

The mature viable seeds within the seed crop of one individual of Costa Rican *Mucuna andreana* varied in fresh weight from 2.6 to 9.4 g (average of 6.81 g, s.d. = 1.09 g, n = 282). The seed coats weighed 14 to 17 percent of the fresh seed weight and variation in their weight was not the cause of the variation in seed weight. There was no significant difference in average seed weight of seeds from pods with 1 to 5 filled seeds. The great range of seed weights within one plant's seed crop is interpreted as possibly of adaptive significance in generating a more homogeneous seed shadow than would be the case with a narrow range of seed weights.

NOTHING is known of the variation in seed size within the seed crop of an individual wild tropical plant, and almost nothing is known of variation of seed size within a population of wild tropical plants (e.g., Harper, Lovell, and Moore, 1970). Here, I describe the variation in seed weight in part of a seed crop of one individual large *Mucuna andreana* (Leguminosae), and outline some of the ecological and evolutionary questions it brings to mind.

M. andreana is a canopy-member woody perennial large vine (liane) that is found throughout moist and wet Costa Rican forests below about 1100 meters elevation. In the drier parts of its range, where this study was conducted, it is restricted to riparian vegetation. The particular plant examined was growing along a stream passing through the remains of deciduous forest near the intersection of the dirt road from Monte Verde and the Pan American highway, Puntarenas Province (about 100 m elevation). The plant has a sprawling canopy covering several tree crowns and is fully insolated. It is as large a size as is generally attained by *M. andreana*. It bore a large seed crop in 1967, 1968, 1970, 1972, 1974, 1975 and 1976 (in the missing years the plant was not examined). *M. andreana* is best known for its penduliflory and bat pollination (Baker, 1970), and for the fact that its seeds are free of seed predators, probably because the seeds are very rich in the toxic non-protein amino acid L-dopa (Bell and Janzen, 1971; Rehr, Janzen and Feeny, 1973).

The extremely hard, large black seeds are produced in a thin, dry, brown pod that dehisces in the last half of the dry season (April–May). The seeds gradually fall to the ground as the fruits are blown by the wind. There is no succulent aril or other potential reward for an animate dispersal agent. The seeds are conspicuous for their variability in size within pods that have no sign of insect or other damage which might have disrupted their growth and caused seed malformation.

OBSERVATIONS—*The pod crop*—Approximately one quarter of the total seed crop was collected from the vine crown. All pods that had not lost seeds were collected from one area haphazardly chosen in the crown; this insured no sample bias toward pods or seeds of a certain size. Less than 5% of the seeds were shriveled and otherwise badly distorted; these were discarded. Past germination trials with *M. andreana* have shown that all filled seeds germinate immediately if a small hole is filed in the seed coat and the seed is placed in moist dirt.

The seeds were pooled according to the number of seeds present in the pod that bore them. The maximum number of filled seeds in the pods was five; it is obvious from inspection of pods that a reduction in this number occurs through failure of ovule development, animal damage to one ovule or the pod fraction containing that ovule, and (in less than 1 percent of the cases) through failure of an approximately full-sized seed coat to contain an enlarged embryo. There were 15 pods with one seed, 31 with two, 36 with three, 17 with four, and 7 with five, for a total of 106 pods.

Seed weight versus number of seeds per pod—Does seed weight vary with the number of seeds in the pod? The mean fresh weight of the seeds from single-seeded pods was 6.48 g (s.d. = 1.39, n = 15), that of two-seeded pods 6.72 g (s.d. = 1.15, n = 62), that of three-seeded pods 6.91 g (s.d. = 1.04, n = 106), that of four-seeded pods

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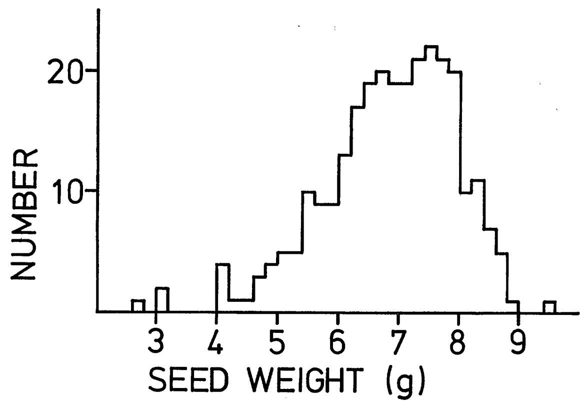

Fig. 1. Distribution of seed weights within the seed crop of one adult *Mucuna andreana*.

6.88 g (s.d. = 0.91, n = 68), and that of five-seeded pods 6.68 g (s.d. = 1.35, n = 31). The smallest mean weight is not significantly different from the largest. However, the coincidence of the peak in mean seed weight with the largest category of pods (3 seeds/pod) suggests that there may be a slight trend for the heaviest seeds to be associated with the most common kind of pod. There is no suggestion that the heaviest seeds are in pods with the fewest seeds.

Distribution of seed weights—The distribution of seed weights in the crop (Figure 1) is extremely broad. The largest filled seed in this sample of the crop is 3.62 times as heavy as the smallest seed (2.6 to 9.4 g range). The range 4.8 to 8.7 g contains 96 percent of the seeds but within that range there is a very broad distribution of seed weights ($\bar{x}$ for all seeds = 6.81 g, s.d. = 1.09, n = 282). This broad distribution is also very evident among the seeds of many other adult *M. andreana* growing in the neighborhood of the study plant, and is replicated in a set of 9,000 seeds collected from an undetermined number of adults in 1967.

Weight of seed contents—Is the variation in seed weight due to variation in seed coat weight or seed contents? To examine this question, a set of 15 seeds was chosen from the "three-seeds/pod" sample in such manner as to uniformly cover the range of seed sizes. The heaviest weighed 9.4 g and the lightest 4.7 g. Each was weighed, smashed, oven-dried to constant weight, reweighed, freed of seed coat, and reweighed. The seed coats contain 4 to 5% water. The mean fresh weight of these 15 seeds was 7.27 g, (s.d. = 1.41) and the fresh weight of the seed coats was 1.01 g (s.d. = 0.28); the lightest seed coat (0.9 g) was on the lightest seed and the heaviest seed coat (1.4 g) was on the heaviest seed, with an even progression between the two. The mean fresh weight of the seed contents was 5.51 g (s.d. = 1.27) and the mean dry weight was 5.09 g (s.d. = 1.18). These weights were taken in the last week of May, 1976, about the time that the seeds would have all fallen to the ground in nature. The extreme dryness of the live seed content (8% water) is also manifested by the fact that they can be drilled with an electric drill, leaving a fine light powder (Janzen, 1976).

Since only 14% of the fresh seed weight is seed coat, variation in seed coat weight cannot account for the extreme of 3.62-fold range in seed weight in Fig. 1. The coefficients of variation are revealing, however. They increase from entire seed (0.19) to fresh seed content (0.23), but stay the same as the seed is dried. The seed coat has the highest of all (0.29). However, 70% of the variance is still present in the dry weights of the seed contents, indicating that the great range of seed sizes in Fig. 1 is biologically meaningful to the ensuing seedling as well as to the parent that produced the seed.

Discussion—It is evident that the amount of reserves received from the parent plant by the developing embryo is not greatly (if at all) influenced by how many siblings occupy the same fruit, once the physiological decision has been made as to how many filled seeds will be produced by that fruit. It is remarkable that this is so, considering that the seeds vary 3.36-fold in weight. In short, it appears to make no difference to the seed which fruit it occupies, once it is among those destined to be fully developed. It makes me wonder why there are any pods with less than 5 seeds, or even more curiously, why natural selection has not resulted in a *M. andreana* with a small number of very many-seeded fruits, as a way of conserving on fruit tissue costs.

There are several possible answers to these questions. First, the fruit may photosynthesize sufficiently to pay its own production and maintenance costs. The flat broad green pods hang in the full sun for at least six months between flowering and fruit maturation (death). Larger fruits with the same number of seeds may therefore cost the parent little or nothing. Second, something less than 30% of the flowers on a *M. andreana* inflorescence ever set fruits. By having a small number of ovules per fruit (flower) and a large number of ovaries (flowers) per inflorescence and per flower crop, the parent plant maximizes its options to abort ovules and young pods without destroying its ability to make a final seed crop as large as its reserves will permit. For example, if it has 30 five-seeded ovaries on an inflorescence, it can abort all but the few ovaries that contain the largest number of seeds fertilized with the very best pollen (cf. Janzen, in press) in order to make the 15 seeds that an inflorescence can bear; if there were only three 50-seeded ovaries on the inflorescence, the 15 "best" seeds would be scattered throughout the 150 ovules. The plant would therefore have to produce and support a great deal of non-functional fruit tissue in the large fruits with an average of only 5 seeds in each.

Third, that there are pods with less than 5 filled seeds implies that there is either physiological failure, uncertainty of pollination, or the plant is discarding (aborting) ovules fertilized by pollen tubes derived from parents that are unacceptable in some sense. It is unknown whether such abortion always accurately adjusts the number of highest possible quality seeds per inflorescence to the seed-producing abilities of that inflorescence, or whether such abortion operates only with respect to a fixed set of criteria. The outcome of these two processes should be indistinguishable in the absence of other data, but the outcome of the latter process should vary strongly with pollinator activity and proximity of unrelated *M. andreana* adults. Of course, both processes may be operating to differing degrees at different levels of parent robustness and pollinator activity.

The very large variation in seed weights within the crop is potentially of great ecological significance to the seedlings. I have shown that the removal of 5–10 % of the food reserves of a *M. andreana* seed can drastically reduce its ability to withstand intense artificial herbivory in the greenhouse; even a 1 % removal has a significant depressant effect on the seedlings' ability to replace shoot tips (Janzen, 1976). In Fig. 1 it is clear that the smaller seeds are frequently only 60 % of the weight of the larger. Since extremely tight control of intra-crop seed weight is certainly physiologically possible in plants (e.g., Harper et al., 1970), and since the variation in seed weight is not the simple outcome of sibling competition for resources within the fruit in *M. andreana*, these data cause me to suspect that the broad range of seed weights is adaptive in the context of the fitness of the parent plant.

There are at least two possibilities. First, such a wide range of seed weights may generate an optimal seed shadow by the parent plant. The seeds are dispersed by falling to the ground and then being carried off by floods, rain runoff, and ordinary stream action. By having a large variety of seed weights, the parent may generate a maximally homogeneous seed shadow, rather than the more heterogenous one that would result were the seeds of very similar weight. This is because seeds of different weights will be dispersed by water to different points in the habitat, resulting in an overall more thorough coverage of the habitat. I should note, however, that a homogeneous seed shadow of a water-dispersed seed could perhaps be more cheaply achieved by producing a seed crop with highly varied floating abilities yet with quite similar nutrient reserves. Second, it may be that the array of challenges and opportunities that confront a *M. andreana* seedling are very extensive, and so the parent has the highest fitness if it produces a wide array of seedling reserve sizes coupled with a maximally homogeneous seed shadow. Both of these possibilities imply a form of parental manipulation of the reserves in the seed, which in turn implies strong control over the developing embryo. This in turn is compatible with the observation that a seed's size is not influenced by the number of developing siblings in its immediate physiological vicinity.

The extreme dryness (and hence, dormancy) of the newly dispersed seed (6.3–8.3 % water in the seed contents), coupled with a seed coat that is very impervious to water, may also be a mechanism for homogenizing the seed shadow. In nature, the seeds of *M. andreana* require many and variable numbers of years of abrasion to germinate. They are probably relocated many times during that period, attaining a seed shadow quite different than would be the case if each crop of seeds germinated in the rainy season immediately following the dry season in which they were produced.

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