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DEVELOPMENTAL DEMOGRAPHY OF *BAUHINIA PAULETIA* PERS. (LEGUMINOSAE) SEEDS AND OVULES

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ABSTRACT

Within 16 seed crops of *Bauhinia pauletia* (Leguminosae) in the deciduous forest lowlands of Guanacaste Province, Costa Rica, it was found that the mean number of ovules per pod (21.3 to 24.1) was less variable than the number of filled seeds per pod (12.0 to 20.1); the standard deviations of these values followed the same pattern (1.16 to 2.73, as opposed to 3.0 to 6.6). The mean number of partly developed but aborted seeds per pod ranged from 0 to 5.84, but the average of the means was only 0.94.

It is commonplace to open a mature dry legume pod (fruit) and find that a number of the ovules or zygotes are undeveloped or aborted. The causes for such undeveloped ovules and zygotes are potentially multiple and difficult to demonstrate. As part of a study of pre-dispersal seed predation on *Bauhinia pauletia* Pers., a caesalpinaceous legume shrub of the Guanacaste Pacific coastal lowlands of Costa Rica, I had the opportunity to obtain data on the developmental demography of 16 seed crops (Janzen, 1977). This data and its interpretation is presented below.

Methods

As described earlier (Janzen, 1977), all or most of the crops of mature pods of 16 *Bauhinia pauletia* shrubs were collected while still hanging unopened in early March 1976. The site ("Forest Patch" of Janzen, 1977) is about 10 km south of Cañas on the property of the Ministerio de Agricultura y Ganadería Experiment Station in the interior of Finca Taboga. The plants were full sized adults (2-4 m tall) in apparently healthy condition and bore normal pod crops for this species.

The pods were opened to assay pre-dispersal seed predation by two species of bruchid beetles. Filled seeds (including those attacked by insects), aborted seeds (0.1- to 0.5-sized seeds with shrunken, wrinkled or badly discolored seed coats) and undeveloped ovules (0.5 to 1 mm in diameter, occupying a space in the pod morphologically engineered for a seed (Fig. 1)] were counted. Filled seeds, if not attacked by a bruchid, display 100 per cent germination in the greenhouse if the seed coat is broken with a file. Aborted seeds never germinate irrespective of treatment. Throughout this paper, I will treat aborted seeds as zygotes. Undeveloped ovules may be either zygotes or purely maternal tissue; the alternatives cannot be determined with the technology at hand. All three units may be counted easily and unambiguously after the dry pod has been split open. Insect attack occurs late enough in the life of the seed such that it is full-sized when it occurs. The paucity of aborted seeds with insect attack suggests that the larvae cannot develop in aborted seeds rather than seed abortion (as here defined) being caused by insect attack.

Reults

The results are presented in Table 1. The mean of the mean number of ovules per pod ($\bar{x}$=22.38, s.d.=1.00, n=16) is highly significantly greater than the mean of the mean number of filled seeds per pod ($\bar{x}$=17.08, s.d.=2.55, n=16) ($t_{16 d.f.}$=7.79, $p<.001$). By inspection, both means are highly significantly greater than the mean of the mean number of aborted seeds per pod ($\bar{x}$=0.94, s.d.=1.70, n=16).

Of more interest is the observation that the standard deviation of the number of ovules (filled, aborted and undeveloped, pooled) per pod ranges from only 1.16 to 2.73 while the standard deviation of the number of filled seeds per pod ranges from 3.0 to 6.6; the mean and the range of these standard deviations is much greater for filled seeds than for total ovules per pod.

There is no correlation between the mean number of ovules per pod and the mean number of filled seeds, aborted seeds, or pod crop size (by inspection). The same statement may be made about the standard deviations of ovules per pod and the other parameters. I could find no significant correlation between any of the columns in Table 1.

In only 31 per cent of the samples was there a pod with a number of filled seeds equal to the largest number of ovules to be found in any pod in that sample. However, in all samples, it was commonplace to encounter a number of pods with better than 80 per cent of the ovules represented as filled seeds.

Discussion

The number of ovules per fruit in general will be a trait coevolved with pollinator behavior; pollinator predictability; supply physiology and anatomy within the plant; abortion of fruit, ovule and zygote options; average reserves available to the plant; supra-annual fruiting and flowering phenology; fruit morphology; responses of pre-dispersal seed predators to absolute and relative numbers of seeds per fruit;

responses of dispersal agents to absolute and relative numbers of seeds per fruit; etc. All of these apply to the specific case of *Bauhinia pauletia* except for the penultimate, because *B. pauletia* has explosive capsules. For a plant with inanimate dispersal, I can see no reason why the mean number of ovules per fruit should vary among trees, and thus I expect the number to be the most constant between trees of any fruit trait. Not only is the mean number of ovules per pod of these 16 *B. pauletia* plants very tightly grouped (range 21.3 to 24.1), but I expect a very small standard deviation; the standard deviation of 1.00 fulfills this expectation. Likewise, within the individual crop, I can see no reason why there should be a selective value to a particular distribution of number of ovules per fruit (unless the tree uses sibling competition within a fruit as a mechanism for generating a particular distribution of seed weights), and thus I expect the mean number of ovules per pod to be the most constant of any fruit parameter within the crown. Again, the extremely tight range of standard deviations (1.16 to 2.73) fulfills this expectation if compared with the standard deviations of the number of filled seeds per pod (3.0 to 6.6).

I assume that the tree is producing some optimal number of ovules for all the different processes listed in the previous paragraph. If it were to produce a number of ovules equal to the average number of filled seeds, the various reductive processes could not occur (abortion of poorly sired seeds, abortion of fruits with too few ovules fertilized, or abortion of ovules fertilized by inappropriate parents). Further, being a perennial plant, *B. pauletia* has the option to store reserves rather than be forced to expend them on high cost fruits (fruits with an exceptionally small number of seeds) or poorly sired seeds [since it is self-compatible (Heithaus *et al.*, 1974), it may often be its own father as bats could easily move pollen from one branch to another within a crown].

The difference between the number of ovules and the number of filled seeds is probably a rough measure of how predictable is the world for *B. pauletia*, since the number of ovules is contemporarily completely under control of the parent. However, it probably should be used only comparatively among conspecific individuals and populations, since entire pod abortion is an adjustment mechanism that is not included in my measurements. In other words, to one species of plant that on average produced filled seeds with 75 per cent of its ovules, the world might be quite differently predictable as compared with another species with the same ovule maturation percentage, since the first might achieve this with a 10 per cent abortion of entire flowers and young fruits while the second might achieve it with a 98 per cent abortion of entire flowers and young fruits.

While there are many potential and quite different causes for the total non-development of an ovule, the causes of the abortion of a developing seed seem a bit less obscure. Once the plant is committed to the development of an entire fruit, the abortion of a partly filled seed is probably due largely to genetic incompetence of the developing embryo (through mutation or expression of lethal genes during development) or rejection by the maternal parent of the zygote owing to parental recognition of an offspring that is deemed to be not worth continued investment of resources. That such seeds are relatively rare in the samples (range 0 to 5.84 per pod, $\bar{x}$=0.94) suggests that the parent plant accurately discards flowers and young fruits with a high percent of potentially abortable seeds very early in the game, or that virtually all pollen is acceptable and only rarely leads to a zygote that fails physiologically during seed growth. I favor the former hypothesis.

Heithaus *et al.*, (1974) noted that a highly variable per cent of *B. pauletia* hermaphroditic flowers were retained by the parent plant per day (to the very small green pod stage, after which there is still further abortion), and that the average was about 30 per cent. Since pods with less than 10 filled seeds made up only 5 - 10 per cent of the pod crops in my samples, much of the early flower abortion may be due to nothing more than the failure to obtain enough pollen on the stigma to guarantee at least 10 developing embryos of kinds generally acceptable to a *B. pauletia*.

Resumen

Es corriente encontrar que las legumbres presentan un número de semillas con desarrollo incipiente o abortado y un número variable de semillas u óvulos fecundados y bien desarrollados. A raíz de un estudio de la dispersión de frutos y actividad predatoria sobre semillas de *Bauhinia pauletia* Pers. (Leguminosae), se obtuvieron datos de dieciséis cosechas y se aplicaron al estudio demográfico de las semillas de esa especie, en Guanacaste, Costa Rica.

El número promedio de óvulos por legumbre es de 21,3 a 24,1, y resultó menos variable que el número de semillas fecundadas por legumbre (12,0 a 20,1). La desviación estándar de esos valores obtenidos sigue el mismo patrón (1,16 a 2,73, vs. 3,0 a 6,6). El promedio de semillas parcialmente desarrolladas pero abortivas es de 0 a 5,84 por legumbre, el promedio de promedios de sólo 0,94.

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Literature Cited

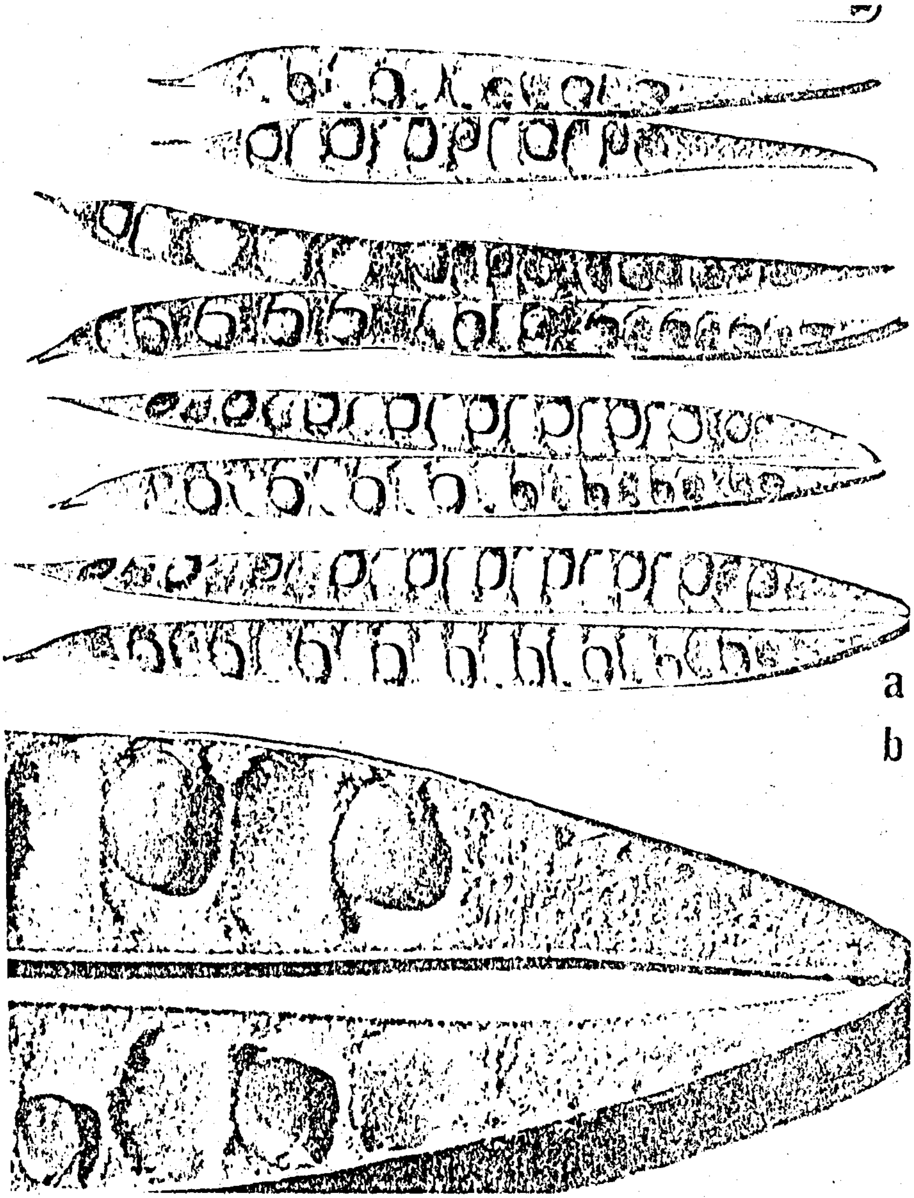
Heithaus, E. R., P. A. Opler and H. G. Baker 1974. Bat activity and pollination of *Bauhinia pauletia:* plant-pollinator coevolution. Ecology 55:412 - 419.

Janzen, D. H. 1977. Reduction of seed predation on *Bauhinia pauletia* (Leguminosae) through habitat destruction in a Costa Rican deciduous forest. ms.

Table 1. Ovule and seed demography of 16 seed crops of *Bauhinia pauletia* (tree numbers correspond to those in Table 1 of Janzen 1977).

Tree	Number of pods on tree	Number of pods examined	$\bar{X}$ ovules per pod	s.d. ovules per pod	Range ovules per pod	$\bar{X}$ filled seed per pod	s.d. filled seeds per pod	Range filled seeds per pod	$\bar{X}$ aborted seeds per pod	s.d. aborted seeds per pod	Range aborted seeds per pod
1	84	25	22.6	1.16	20–24	16.1	4.8	8–23	0.56	1.00	0–4
2	109	50	22.6	1.18	20–25	16.4	5.9	5–24	0.22	0.51	0–2
3	260	50	23.5	1.76	18–27	12.0	6.6	1–22	5.84	4.32	0–23
4	41	41	22.1	2.17	19–26	17.5	4.2	7–24	0.32	0.32	0–4
5	76	33	20.4	1.79	14–23	18.1	4.2	7–23	0.27	0.52	0–2
6	58	58	22.0	1.36	17–25	13.5	4.1	2–20	4.59	2.32	0–11
7	83	29	22.5	1.74	13–25	19.4	4.0	10–25	0.07	0.26	0–1
8	79	50	20.9	2.70	10–24	14.0	5.4	5–22	0.42	0.81	0–4
9	130	25	22.4	1.55	[illegible]	19.6	3.0	14–25	0.60	0.91	0–3
10	48	20	21.3	2.27	19–25	19.3	3.3	12–25	0.05	0.22	0–1
11	6	6	24.0	1.90	22–26	18.0	3.1	13–22	0.33	0.52	0–1
12	32	20	22.2	1.64	19–26	12.7	3.5	2–19	0.55	0.69	0–2
13	110	25	24.1	1.01	22–28	20.1	4.0	7–26	0.04	0.20	0–1
14	142	21	23.0	1.20	21–26	19.5	4.2	9–26	0	0	0
15	600	20	22.1	1.33	21–25	17.0	4.6	6–22	0.95	3.35	0–1
16	23	23	22.3	1.77	19–26	18.8	3.0	7–23	0.22	0.52	0–2

Fig. 1. a) Representative artificially dehisced pods of *Bauhinia pauletia* (scale in mm, 15 cm long). The lower pod contains 16 filled seeds, 3 aborted seeds, and 5 undeveloped ovules; the second pod from the bottom contains 11 filled seeds, 6 aborted seeds and 3 undeveloped ovules; the top pod contains 7 filled seeds, 4 aborted seeds, and 12 undeveloped ovules. b) Tip of lower pod in (a) above, showing 3 filled seeds, 1 aborted seed and 5 undeveloped ovules.



a

b