ESCAPE OF CASSIA GRANDIS L. BEANS FROM PREDATORS IN TIME AND SPACE

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Abstract. In Central American deciduous forests, most of the seeds of the caesalpinaceous legume tree Cassia grandis are killed by the larvae of two bruchid beetles, Pygiopachymerus lineola and Zabrotes interstitialis. Pygiopachymerus lineola oviposits on the large pods, the first-instar larvae bore into the seeds, and the emerging adults cut large exit holes in the pod wall. Moth larvae gain access through these holes and eat clean much of the sticky pulp around the seeds. Simultaneously, the adults of Z. interstitialis enter through the P. lineola exit holes and oviposit directly on all clean seeds. In heavily disturbed communities where vertebrate dispersal agents are absent, these host-specific bruchids achieve almost 100% predation on the C. grandis seed crop; however, the more rapidly the dispersal agents remove the seed pods, the less seed predation there will be by Z. interstitialis. Since C. grandis bears mature fruit every other year, the size of each seed crop is large enough to surpass the predation abilities of the bruchids that survive the distance in time and space between seed crops. The system may be viewed as an example of predator satiation. The potential for further co-evolution of the bruchid-Cassia interaction is high, but numerous opposing forces in the selective process can be identified.

INTRODUCTION

The following theoretical points were emphasized in discussing the coevolved predator-prey relationships between seed-eating bruchid beetles and their legume hosts (Janzен 1969): (1) the degree of pre-dispersal seed mortality should be directly proportional to the rate at which bruchids locate the seeds (pods) and oviposit on them and inversely proportional to the rate at which the seeds are dispersed; (2) pod and seed morphology should strongly influence the rate of seed mortality; and (3) distance between individual seed crops in time and space should strongly influence the pre-dispersal seed mortality from any particular complex of seed predators and dispersal agents. The present paper discusses predation on the seeds of a caesalpinaceous legume tree, Cassia grandis L., by two bruchids, Pygiopachymerus lineola (Chevrolat) and Zabrotes interstitialis (Chevrolat), and by the larvae of several species of moths in lowland Central American deciduous forest. This predator-prey system exemplifies seed escape by predator satiation and is probably representative of the interactions of many host-specific tropical seed eaters with their prey.

Unfortunately, this system is representative of tropical insect-host interactions in another way. The communities in which the bruchid-Cassia interaction coevolved have largely been destroyed, since most of the geographic range of the tree in Central America is under cultivation. Therefore, I will try to infer some of the environmental challenges that produced the behavior, morphology, and physiology displayed by the predators and prey, even though these challenges may no longer exist in communities disturbed by agriculture.

The natural history of C. grandis and its seed predators is detailed here since it is not available in the literature.

GENERAL REPRODUCTIVE BIOLOGY OF Cassia grandis Range

Cassia grandis is native to Central American mid- and low-elevation deciduous and semideciduous forests with a dry season of 4–5 months’ duration and little or no rainfall. Adult trees are 10- to 20-m tall canopy members in natural habitats. The largest easily accessible native population is on the Pacific side of Central America in eastern El Salvador, in the general vicinity of the Pan-American highway from San Salvador to San Miguel in low mountains at 300–600 m elevation. Here, trees of all ages are scattered from riparian to hillside habitats and are found in all ages of woody succession. More isolated groups of C. grandis are found in riparian habitats (with rare scattered individuals on adjacent hills) in deciduous forest throughout the Central American lowlands. Showy pink flowers and the sweet pulp (a flavoring and purgative in milk) around the seeds are responsible for the introduction of C. grandis throughout Central and South America as a garden and fence-row tree (Standley 1922, Allen 1956, Little and Wadsworth 1964, Kingsolver 1970). Isolated adults and very small populations may therefore be introduced or be remnants of larger populations long since destroyed. However, like other Central American fence-row and garden trees that have been moved to new habitats within their gross geographic range (e.g., Erythrina costaricensis, Gliricidia sepium), introduced C. grandis hardly ever forms a breeding population.

Throughout its contemporary range C. grandis has

1 Received July 2, 1970; accepted December 18, 1970.
a variety of common names in English, Spanish, and Indian dialects, “carao” and “caña fistula” being the commonest. *Cassia grandis* is often confused with *Cassia fistula* L., which is also known as “caña fistula,” but has yellow flowers and a thinner pod than *C. grandis*. *Cassia fistula* was introduced to Central America from southeast Asia, but breeding populations in Central America have not been recorded.

**Flower and immature fruit production**

Like many other lowland deciduous trees in Central America (Janzen 1967), *C. grandis* bears its pink bee-pollinated flowers in the early part of the dry season (late January through February for most sites and most trees). Ten to thirty flowers are produced for each fruit that is set, and 200–600 for each fruit that is matured. Flowers are borne on 5- to 20-cm branchlets distributed along a sexual branch up to 50 cm long. The ratio of flowers to fruits seems to stay quite constant over flower crops ranging from five to a hundred thousand flowers; it is likely that the floral excess is primarily to attract pollinators. When in flower the trees are very conspicuous, but would not be if bearing a number of flowers equal to the number of pods set.

Fruits require 11–12 months to mature. The pattern of attrition of immature fruits during the maturation period appears related to the total reproductive strategy of the plant. Detailed data on this attrition are not available for a large sample of trees, but are offered below on one representative fruit crop.

The number of fruit set per flower-bearing branchlet shows no consistent gradient along the sexual branch axis (Table 1). Of the 134 branchlets censused in Table 1, there were 45 with one young fruit, 39 with two, 21 with three, 14 with four, nine with five, three with six, and one each with seven, eight, and 10 fruits. During the first 5 months of development (through the dry season and first 2 months of the rainy season, until July 13, 1969), pods showed very little elongation or increase in thickness. The average length of the pods in Table 1 was 10.9 cm (sd = 2.6 cm, range 5.0–14.5 cm). Then, during the next 2 months, 18% of these pods expanded (average length 23.1 cm on September 11, sd = 6.2 cm, range 13–40 cm), 72% were shed, and 10% remained small (average length 12.9 cm, sd = 1.8 cm, range 9.5–16 cm) and were shed later. The expanded pods were 1.5–3 cm in maximum diameter as contrasted to 0.4–1.1 cm for the undeveloped ones. These figures are based on branches number 1, 2, 3, 4, 7, 9, and 11 in Table 1. Early pod shedding yielded a final distribution of five, three, seven, four, five, three, and eight expanded pods on these same branches on September 11, compared to 51, 10, 16, 19, 32, 38, and 30 of all sizes on July 13.

**Table 1. Numbers of new green fruits (pods) set per branchlet on the sexual branches of a representative *C. grandis* tree in a representative segment of the canopy**

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<th>Sexual branch number</th>
<th>Number of green fruits on each flowering branchlet, from the base of the sexual branch to the tip</th>
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</table>

*The tree shed branchlets lacking fruit, so the zero category is missing. This tree is the one bearing pod numbers CR-11-#1 to 15 (see Table 2), is 4 m tall, and has reproduced for at least 4 years (July 13, 1969). The pod crop is 5 months old.*

Of 400 shed pods picked up under the parent tree, 81.2% had been partly to totally bored through by an unidentified species of moth larva that started at the distal end of the pod while the pod was still hanging on the tree. Of the expanded pods on the tree, only 31.6% of a sample of 85 had been attacked, and of these, the larvae had damaged only the pod tip.

The absence of full-sized green pods on the tree until the sixth or seventh month after flowering is in striking contrast to many adjacent species of trees whose fruits attain full size during the first few weeks after flowering, but then require the next 8–11 months to mature (e.g., *Hymenaea courbaril*, *Guazuma ulmifolia*, *Swietenia macrophylla*, *Crescentia alata*, *Hippocratea malpgihraefolia*, *Randia* spp., etc.). These plants are probably using the pods as the direct recipient of photosynthesize. On the other hand, plants such as *C. grandis* (and *Acacia farne-siana*, *A. collinsii*, *A cornigera*, etc.) appear to store the products needed for fruit maturation, and then abruptly relocate them in the pods. An alternative hypothesis is that *C. grandis* does not have enough reserves to expand its fruits until the dry season has been passed, the rainy season leaf crop has been produced, and energy deficits have been made up. If in fact delayed fruit expansion is adaptive in respect to the fruit crop rather than forced by lack of photosynthesize, it insures that the fruits destroyed by the moth larvae represent a comparatively minor energy loss.

It is noteworthy that the tree shed only about 20% of its undamaged young pods to reduce the pod crop to a size that could be matured with the tree's available reproductive energy. Delayed fruit production may, however, lead to additional translocation and storage costs.

In the context of the crown’s energy budget for
pod production, it is interesting that pods fail to mature on branches from which the leaves have been pruned. An experiment done with branches 5, 8, and 10 (Table 1) suggest that the photosynthate for later pod development comes from the 20–40 full-sized leaves produced at the end of each sexual branch by the end of the first 2 weeks of the rainy season. On three pairs of equal-sized branches in different parts of the crown, the petioles of all leaves were severed from one branch of each pair (July 13, 1969, about 9 weeks after the rains began). By September 11, 10, 18, and 19 new half-sized leaves had appeared on the ends of the experimental branches. No new leaves had appeared on the three control branches, and defoliated sterile branches did not produce new leaves. The control sexual branches had five, seven, and 12 expanding green pods, but the experimental branches had zero, one, and one expanding pods. The tree must translocate photosynthate between branches when the sexual branch is first produced, but this process apparently does not continue for pod maturation. This failure was partially expected, in view of Kozlowski and Keller’s (1966) review indicating that for orchard trees the removal of a few leaves in the vicinity of a fruit results in reduced fruit size.

The failure to translocate photosynthates between branches places a constraint on the options open to C. grandis as evolutionary responses to the predation to be described later. Increase in the cost of the seed or pod crop cannot readily be charged against the tree’s entire energy budget. Either the photosynthetic ability of the leaves on the sexual branch must increase, or there must be a change in re-allocation of total photosynthate within the tree. These observations also suggest that the total seed-crop size is determined by a competitive interaction between the vegetative and sexual demands on the plant’s energy budget.

**Mature fruit and seed**

Almost none of the immature but fully expanded pods are shed. The expanded pod continues to draw materials from the tree for at least 4–5 months. The mature indehiscent pods (Fig. 1A) hang for 2–5 months until blown down or removed by dispersal agents. The hard flat seeds (Fig. 1B) are encased in a sweet, odiferous, molasses-like, water-soluble material that gradually hardens with age. In natural habitats it attracts dispersal agents such as white-tailed deer (*Odocoileus virginianus*), which swallow the seeds and pass them intact, and squirrels (*Sciurus variegatoides*), agoutis (*Dasyprocta punctata*), and pacas (*Cuniculus paca*). These three large rodents easily carry off the 120- to 300-g pods. All four animals chew through the hard pod wall with ease. In areas of very low hunting pressure, these animals, and perhaps some others, usually remove or chew up the entire pod crop in 1–3 months. In many contemporary communities cows eat the pods, but then the seeds germinate in open pastures where they hardly ever survive.

The seeds of *C. grandis* are rather large in comparison with those of most hard-seeded legumes that display predator satiation as an escape from bruchid beetles (cf. Table 1 and 3, Janzen 1969). Samples of viable seeds from three pods of the same tree (M. A. G. Station, Finca Taboga, 6 mi SE, 6 mi W Cañas, Guanacaste Prov., Costa Rica, July 12, 1969) had average seed weights of 0.690 g (n = 54, sd = 0.052), 0.634 g (n = 50, sd = 0.060), and 0.531 g (n = 53, sd = 0.148). The ranges were 0.291–0.735 g, median 0.70; 0.356–0.726 g, median 0.64; and 0.283–0.702 g, median 0.63, respectively.

According to the number and weight of seeds per cubic meter of canopy, *C. grandis* is more representative of the predator-satiation strategy than if only seed weight is examined, though it is still a borderline case. A fully mature tree with a fully insolated crown (e.g., in an open field) bears about 300 pods in one crop (based on numerous counts from Costa...
Table 2. Fate of seeds of *Cassia grandis* in individual pods from five different and widely spaced, but representative trees

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<td>Number of exits in pod wall</td>
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<table>
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<th>Pod number</th>
<th>Pool length (cm)</th>
<th>Total number of seeds</th>
<th>Viable seeds at time of collection</th>
<th>Minimum seeds killed by P. beloniformis (%)</th>
<th>Minimum seeds killed by Z. interstitialis (%)</th>
<th>Seeds killed by P. beloniformis only (%)</th>
<th>Seeds killed by moth larvae + Z. interstitialis (%)</th>
<th>Minimum number P. beloniformis emerged</th>
<th>Minimum number Z. interstitialis emerged</th>
<th>Large <em>P. pronopalis</em> larvae in pod (no.)</th>
<th>Small <em>Meth. + P. pronopalis</em> in pod (no.)</th>
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</table>

*Pods selected purely for availability when climbing the tree and for not being broken. Seed mortality cannot be estimated by external appearance of the pod.*

1. Late-instar bruchid larvae in seeds were counted as “emerged adults,” since once they have reached this stage, mortality is extremely low. Seeds with more than two hatched *Zabrotes interstitialis* eggs (first-instar larvae) on them were counted as attacked or killed by this beetle, since where time was available, two or more eggs nearly always produced at least one adult (and a dead seed). Minimum percentages refer to the fact that had the pod remained on the tree, there would have been further mortality (columns 4-7).

2. Numbers of emerging beetles (columns 8, 9) are recorded as a minimum because of the occasional use of one exit hole in the seed by two adults.

3. Minimum numbers of oothecae (column 12) are recorded because the oothecae sometimes are weathered off the pod wall.


Rica to El Salvador), though exceptional trees may bear as many as 700 pods. Each pod contains 10–90 seeds, with an average of 40–55 per pod, depending on the individual tree (e.g., column 2 in Table 2). If 50 per pod is chosen as a representative number, such a crop represents about 9.45 kg of seed. A tree of this type has a crown volume of about 400 m³ (cf. method of estimation in Janzen 1969) and thus about 37.5 seeds, or 23.6 g of seed, per cubic meter. In forests where tree crowns are contiguous and therefore only the upper surface of the *C. grandis* crown is insolated, the pod crop is generally about 200 pods and the crown volume reduced to about 200 m³. Such a tree, with about 50 seeds/m³ of crown volume, is probably representative of *C. grandis* adults prior to agricultural disturbance.

*Cassia grandis* normally flowers every other year when part of a forest canopy. Throughout Central America any count of 50 or more adult trees during the dry season shows 45–55% in full flower. If only pasture trees are counted, the percentage may be as high as 70. Marked pasture trees, from 1965 to 1970 in the Cañas area of Guanacaste Province, often bore two large consecutive crops and then were sterile for a year. It appears that *C. grandis* in the forest cannot store enough reserves, while maturing one large seed crop, to produce a flower crop the following year. That the tree does not produce half as
many pods annually is probably directly linked to the behavior of predator satiation and will be discussed later.

The few seeds that escape insect predation germinate at the beginning of the wet season if the seed coat has been scarified by passage through a mammal or by other means. Unscarified seeds can live at least 8 years (based on germination of seeds from herbarium sheets). Seedling survival in contemporary habitats is influenced by fire, length of the dry season, cattle grazing, insect defoliation, shading by other early successional species, and occasional natural gaps in the forest canopy (e.g., see Hatheway and Baker 1970). *Cassia grandis* seedlings and saplings grow extremely slowly in heavy shade.

**Insect Predation on Mature Cassia grandis Seeds**

Predation on juvenile *C. grandis* has at least two major components: (1) predation on the seeds while still on the tree and (2) predation on seeds and seedlings following dispersal (Janzen 1970). Pre-dispersal predation will be dealt with here because it is more readily examined, because most of the seed population dies before dispersal in contemporary communities, and because there is apparently almost no post-dispersal seed predation on the large hard seeds.

The general progression of events for a seed pod is the following. A small number of females of the large bruchid *Pygiopachymerus lineola* oviposit on the nearly mature pod, and the larvae eat a moderate to large number of seeds by the time the seeds are mature (column 4, Table 2). The percentage of a tree's seed crop killed by *P. lineola* should be directly proportional to the ratio of the number of beetles finding the crop to the number of seeds in the crop. After *P. lineola* adults chew out through the pod wall, and during the time when dispersal agents are removing pods, the larvae of several species of small moths gain access through the bruchid exit holes (or natural cracks in the pod wall). They eat the molasses-like pulp around the seeds (and sometimes seeds; column 7, Table 2). Females of the small bruchid *Zabrotes interstitialis* then enter the exit holes made by *P. lineola* and the Lepidoptera larvae and oviposit on the cleaned seeds. Given adequate time before the pods are dispersed, these beetles kill all remaining seeds (column 3, Table 2). Here, then, the degree of predator satiation achieved by a large seed crop is directly proportional to the rate of pod dispersal.

The bruchids are called "predators" in this system for two reasons. First, I wish to emphasize that a female bruchid searching for a *C. grandis* pod crop is no different in process from a weasel searching for a nest of baby mice. Secondly, while the female bruchid does not eat the seed, she effectively does so by laying an egg on or near it; the bruchids' capacity to lower the *C. grandis* population should be directly proportional to the number that find a pod crop and the number of eggs they can lay. Again, in process these numbers are analogous to the number of birds that find a 17-year cicada outbreak and the number of cicadas that the birds can eat before their stomach capacities are reached, during the time that the cicadas are available; we may thus speak of "predator satiation" (Lloyd and Dybas 1966) as the process whereby the tree produces more seeds at one time than all the bruchids that find the tree can destroy. To follow Holling's (1961) terminology, bruchids exhibit a functional response to a pod crop, though some species of bruchids (e.g., *Z. interstitialis*) also exhibit a numerical response by having several generations within one crop. If we view the system from the viewpoint of the bruchid larva, the bruchid is a "parasitoid" of seeds, in the terminology used in biological control studies.

**Predation by Pygiopachymerus lineola on Cassia grandis**

*Pygiopachymerus lineola*, described in 1871 by Chevrolat from Brazilian specimens, has been discussed in the bruchid literature as *Pachymerus lineola*, *Bruchus lineola*, *Phelomerus aberrans*, *Phelm-erus lineola*, *Pseudopachymerus lineola*, *Bruchus aberrans*, and *Phelomerus aberrans var. distinctus*. It has been recorded in collections or in the literature from Brazil, Venezuela, Trinidad, Colombia, Panama, Costa Rica, Nicaragua, Honduras, and El Salvador. Except for the questionable records discussed below, it was always reared from *Cassia grandis*.

When the pods of *C. grandis* are full-sized, are just beginning to turn brown, and contain milk seeds (still soft but only slightly larger than when mature), females of *P. lineola* appear on the pods after having passed the rainy season as free-living adults. Depending on the individual tree, this occurs from early January to late February in the Cañas (Guancaste Prov., Costa Rica) area, and pods of the appropriate age for oviposition are on the tree throughout this time since the time of pod maturation varies at least 2 months within any given pod crop. The bruchid chews a slight depression in the pod wall and lays a group of 4–15 eggs in it (Fig. 2A). They are glued together with a clear and tough material (an "oophone," following Bondar's (1931) terminology) that is probably produced by the accessory glands along the oviduct. The 148 oothecae on 12 pods from the tree described in Table 1 had an average of 7.9 eggs per ootheca (SD = 7.97, range 2–22). This figure is rep-

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2 I am deeply indebted to Dr. John Kingsolver of the National Museum of Natural History for working out the taxonomic problems with this beetle and its South American sibling species *P. theresae* (Kingsolver 1970).
gesture, the oothecae tabulated in column 12, Table 2. Occasionally, oothecae fall off after the eggs hatch, so these are minimal values. On rare occasions (2–10 per pod) single eggs are glued to the pod by *P. lineola*.

The mean fecundity of *P. lineola* is unknown, but probably does not exceed 100. This clutch size is inferred from egg production in Howe and Currie's (1964) laboratory studies, in which various bruchid species were not fed the types of food they find in nature (pollen and nectar). To make this estimate, the clutch size that they usually recorded was doubled because of the observation that egg production can be about doubled by feeding sugar-water (Larsen and Fisher 1938, Zaaou 1948). Finally, the figure is divided by 3 and multiplied by 2 because *P. lineola* eggs are about three times the volume of those of the species they studied, but the adults of *P. lineola* are about twice as large as the species studied.

Newly hatched bruchid larvae pass through the pod wall via a single hole chewed under the ootheca by the first larva. As long as it is capped by the ootheca, this hole does not admit fungi or other insects. The larvae immigrate both up and down the pod from the entrance hole. An undetermined number bore into each seed, but a maximum of seven can mature there (one to four is usual). If an attacked seed is in an excessively moist environment, as is the case when a pod falls in a puddle, the hole (0.5 mm diameter) in the seed coat will admit water, leading to germination and death of both seed and bruchid. Cursory examination of the first pods to be attacked in a crop indicates that if a seed is entered before the seed coat is stiff, the seed coat collapses and the seed rots, killing the larva within. Emergence of the adult bruchid is so early in the development of the seed that developmental distortion of the seed coat often occurs around the exit hole (Fig. 2B); it appears that *P. lineola* enters the seeds as early in the life of the pod as is possible.

That the first-instar larvae space themselves among the seeds is suggested by two observations. First, in the rare case of only a single ootheca on a major section of the pod, the seeds directly under the ootheca have no higher numbers of larvae per seed (one to two) than do those attacked seeds far from the point of entry. Second, it is commonplace for each of 5–15 consecutive seeds in the pod to produce one or two *P. lineola* when there is a low density of oothecae (e.g., one ootheca per 3 cm of pod length). When there are many eggs, the larvae are still distributed quite evenly. For example, pod number CR-11-2 in Table 2 had the following representative distribution of emerging adults among the seeds, recording from the base to the tip of the pod: 1, 2, 2, 2, 2, 1, 2, 2, 2, 2, 1, 2, 1, 2, 1, 3, 2, 1, 2, 0, 2, 2, 3, 3, 3, 4, 3, 3, 3, 2, 3, 4, 4, 3, 3, 3, 4, 3, 3, 3, 3, 3, 3, 3, 4, 1, 2. The frequency distribution of adult bruchids per seed for nine representative pods is given in Table 3.
Competition among larvae within the seed may produce some of the evenness of larval distribution at high larval density but not at low density. Once a larva has entered a seed, it does not leave and enter another seed if it encounters other larva. Within the seed the larvae are approximately equidistant, and when three or more are present, no single piece of cotyledon is large enough for the development of another *P. lineola*. How this positioning is achieved is not clear, but the larvae may wander as far as 7-12 mm through the seed before eating out a permanent feeding chamber. The ultimate volume of this chamber is about twice that of the larva, indicating that the seed contents are of high nutritive value, and that the larva expends little energy on movement.

Development time is less than 2 months for *P. lineola*. Most of the emergence takes place during the last half of the dry season (February to April in lowland Costa Rica). More than 90% of the exit holes (Fig. 2C) are chewed through the dorsal or ventral pod ridge, which is the thickest part of the pod wall (Fig. 1B). If column 8 is compared with 10 plus 11 in Table 2, it becomes obvious that most beetles exit through holes made by the first beetles to emerge from the pod.

Members of this first generation of *P. lineola* do not oviposit on the infested pods from which they emerge. Probably because almost all pods in the crop are infested, the beetles enter into a behavioral pattern associated with survival until new pods appear at the end of the rainy season, rather than lay eggs on the old pods where most of the larvae would not find intact seeds. This behavior means that the percentage seed mortality attributed to *P. lineola* in column 4, Table 2, would not change significantly in the short-term absence of dispersal agents and can be regarded as representative of conditions prior to heavy hunting pressure. On rare occasions a pod segment is missed by the initial oviposition of *P. lineola*; new eggs may be laid on this pod segment at any time during the dry or rainy season. This indicates that some females in reproductive condition are always present. Incidentally, their presence makes it unlikely that a mutant strain of *C. grandis* that bore fruit at a different time could avoid predation by *P. lineola*. Eggs laid on these later pods are successful; occasional adults have been taken emerging in June, July, August, and September in Costa Rica, and a few large larvae were found in old pods in the El Salvador and Nicaragua samples (Table 2) in September.

The sequence of pod development and the bruchid's oviposition behavior suggest the potential for the evolution of an escape mechanism by *C. grandis*. Occasional developmental seed abortions lead to a strong constriction in the mature pod (Fig. 2D). The constriction contains hard tissue that the larvae of *P. lineola* and other insects do not penetrate. Moth larvae and *Zabrones* bruchids can only enter uncracked pods through *P. lineola* exit holes. Freedom of a pod segment from *P. lineola* attack, because it is bounded by two short aborted segments, usually means freedom from all attack. Of the 28 pods examined in detail in this study, two had segments of 10-20 viable seeds each that had been missed by ovipositing *P. lineola* (Table 2, El Salv #1 and #2). The other segments of these two pods had been entered and all seeds killed by the combined effects of *P. lineola*, *Zabrones*, and the moth larvae.

The frequency of constricted pods varies widely between trees. The physiological cause of seed abortions is unknown, and it is impossible to know if the intertree variation in frequency could be easily modified by natural selection. Abortions leading to constrictions can be produced artificially by sticking the young green pod with a pin (before pod expansion).

To determine what chance seeds have of escaping by seed abortion, the positions of the 98 oothecae (the eggs of 14 or more females) on 12 pods were recorded in the pod crop preceding the immature one described in Table 1. For a total of 462 cm of mature pods (equals approximately 670 seeds if there are no abortions, but equals 481 seeds because of abortions), 21 sections contained seeds (332 cm of expanded pod) and 22 sections did not (130 cm of aborted pods). The mean length of normal sections was 15.8 cm (sd = 10.3 cm, range 3-45 cm) and of aborted sections was 5.8 cm (sd =3.2 cm, range 1-30 cm). All normal sections had at least one ootheca, but there were none on aborted sections. The distances between adjacent oothecae along the pod on normal sections ranged from 1 to 7 cm with the following frequencies respectively: 36, 26, 15, 18, 8, 7, and 5. Three exceptions were two oothecae 12 cm from the previous ootheca.

The above data make it obvious that only extreme subdivisions of the pod through abortions would significantly increase the number of escaping seeds. A further difficulty with evolution in this direction is that the abortions themselves cost seeds at about the rate of 1.44 per linear centimeter of pod. This effect may be partially countered, however, by the energy that might have gone into aborted seeds being channeled into other or larger seeds. It is impossible to know what the increase in predation by *P. lineola* (column 4, Table 2) would have been had abortions been absent; there would have been a slight increase since the abortions reduce the ability of the first-instar bruchid larvae to distribute themselves evenly among the seeds.

Treating the pods from CR-11 in Table 2 as representative, a single *C. grandis* seed crop of 200 pods may be viewed as a source of about 9,500 adult *P.*
lineola every other year. If we regard each female as being able to lay 100 eggs and assume that all mature, at least 95 females on the average find a C. grandis pod crop (a slight underestimate since all eggs probably do not mature). Alternately, this means that 90% mortality of adults occurs while waiting approximately 9–10 months for the next pod crop and while moving between trees. To attain a population density of 9,500 adults per tree, the beetles killed 69.27% of the seed crop (taking CR-11, column 4, Table 2, as representative). These figures are representative of the population of C. grandis and P. lineola from Costa Rica to El Salvador. The mortality appeared to be somewhat lower on isolated trees in gardens. The overall variation in mortality between pods (column 4, Table 2) is primarily the result of (1) aborted seeds blocking larval movement (e.g., El Salv #1 and #2, CR-11-#7), (2) exceptionally early entry of Lepidoptera larvae through a break in the pod wall, which in turn left few seeds for P. lineola (e.g., Nicar #5), and (3) failure of P. lineola to find the pods (e.g., CR-12-#1, CR-12-#5, CR-12-#17).

Cassia grandis, by producing this large seed crop every other year, rather than one-half as large each year, is clearly successful in satiating the P. lineola population at the present density of adult trees. Were the density of pod crops to increase in time or space, it seems very likely that the percentage seed mortality owing to this bruchid would rise as well. Were the size of the pod crop to be decreased, and for example, the tree to fruit every year as a consequence, the percentage seed mortality would probably increase. This increase has two components. First, more females will probably survive between crops if they do not have to search for a tree other than the one they emerged from. Second, each year there will be a lower absolute excess of seeds over the number that can be killed by the number of females that find a tree irrespective of its fruiting periodicity.

As with many host-specific tropical seed predators presently under study (e.g., Janzen 1971a, and unpublished data), P. lineola appears to be almost entirely free of host-specific insect predators and parasites. Hymenopterous egg parasites occurred on only the two El Salvadorian pods (Table 2); of 36 oothcae, three had parasite exit holes. Cursory examination of several hundred other pods from El Salvador to Costa Rica has yielded no other parasitized oothcae. This parasite was probably not specific to P. lineola since this bruchid’s eggs are only common during a 2-month period of the year. Larvae of P. lineola have almost 100% survival in the seeds once they are large enough to leave an obvious feeding chamber. Two hundred dissected adults from the Cañas area had no obvious internal parasites. Large populations of P. lineola are so widely separated in time and space that they probably constitute a very poor host for a potential host-specific parasite. It definitely appears that the density of P. lineola is set by the combined action of (1) general mortality agents operating while the bruchids are searching for seed crops (and are thus limited by proximity of host plants) and (2) by competition for seeds among first instar larvae (at high bruchid densities).

It should be emphasized that if P. lineola were the only predator on seeds of C. grandis, considerable numbers of seeds would escape. Furthermore, selection for traits that reduce predation by P. lineola could result in substantial increase in seed survival. However, in contemporary communities that lack dispersal agents, such an increase in seed survival would probably only result in more mortality caused by the moth and by Zabrotes, since they need only one P. lineola exit hole to enter the pod. Of course, if P. lineola were completely removed, mortality due to the moth and Zabrotes would be greatly reduced.

**Predation by Pygipoachymerus lineola**

on other hosts

It is obvious that the presence of an alternate host for P. lineola in natural habitats would influence the system described above. Although P. lineola has been

<table>
<thead>
<tr>
<th>Pod number</th>
<th>Number of seeds from which 0-7 beetles emerged</th>
<th>Number of seeds in pod</th>
<th>Number of P. lineola reared</th>
</tr>
</thead>
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<tr>
<td>CR-11-#1</td>
<td>17 18 24 10 1 0 0 0</td>
<td>70</td>
<td>99</td>
</tr>
<tr>
<td>CR-11-#2</td>
<td>1 8 14 18 6 0 0 0</td>
<td>47</td>
<td>43</td>
</tr>
<tr>
<td>CR-11-#4</td>
<td>28 14 9 1 0 0 0 0</td>
<td>52</td>
<td>28</td>
</tr>
<tr>
<td>CR-11-#5</td>
<td>25 1 3 0 1 0 0 0</td>
<td>46</td>
<td>12</td>
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<td>30 0 1 0 0 0 0 0</td>
<td>31</td>
<td>2</td>
</tr>
<tr>
<td>CR-11-#8</td>
<td>0 14 21 0 2 0 0 0</td>
<td>37</td>
<td>58</td>
</tr>
<tr>
<td>CR-11-#9</td>
<td>6 13 5 3 0 0 0 1</td>
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<td>39</td>
</tr>
<tr>
<td>CR-11-#15</td>
<td>1 1 18 10 4 0 0 0</td>
<td>34</td>
<td>83</td>
</tr>
<tr>
<td>CR-12-#4</td>
<td>14 36 15 0 0 0 0 0</td>
<td>66</td>
<td>45</td>
</tr>
</tbody>
</table>
recorded from the seeds of several other hosts (Kingsolver 1970 and included references), it appears to be obligate to *C. grandis* in the natural habitats examined in this study. No other native Central American legumes have pods the size of *C. grandis*. The native legumes with similar morphology (indehiscent, round in cross section, seeds imbedded in molasses-like pulp) are all much smaller and are in the genus *Cassia*. *Pygiopachymerus lineola* is recorded from *Cassia fistula* L. and *Cassia javanica* L. (= nodosa Hamilt.). Both are native to tropical Asia. Neither of these introduced species has escaped from cultivation in Central America except on Caribbean islands (Little and Wadsworth 1964). They have indehiscent pods about two-thirds the diameter of *C. grandis* pods and have a molasses-like laxative pulp around the seeds. The seeds of these two species are, however, only about one-fifth the weight of *C. grandis* seeds and are thus probably an inferior host in terms of beetles produced per seed. A third putative host is *Cassia bicapsularis* L. This native shrub breeds throughout lowland Central American deciduous second-growth and has even smaller pods (10–20 cm long, 1 cm in diameter) and very flat seeds that weigh about the same as a live *P. lineola*. Many seed crops collected in the same habitat with *C. grandis* have never shown evidence of *Pygiopachymerus* bruchid damage; this host record is probably a host misidentification or a labeling error on the beetle. No information is available on the biology of *Cassia moschata* H.B.K., *Cassia ferruginea* Schrad., and *Cassia carnaval* Spec. (= leptophylla Gris.) (all South American "hosts" of *P. lineola*), but I suspect that they will fall into the "introduced plant" or "misidentification" category. The host records of *Hymenaea courbaril* L. and *H. "rugosa"* given by Zacher (1952) in his general compendium of bruchid host plants are likewise probably mislabeled specimens. I have collected over 50 crops of *H. courbaril* pods from areas with large populations of *Pygiopachymerus lineola* and found no damage by any bruchid (Janzen, unpublished data). Furthermore, the pods of *H. courbaril* differ from those of *C. grandis* in so many respects that successful predation by any bruchid would require major changes in the bruchid's behavior throughout its life cycle. Records such as those of *Hymenaea* and the various species of *Cassia* listed above must be viewed also in the light of Bridwell's (1918) comments that some female bruchids are rather indiscriminate in choice of oviposition site.

Host records of *P. lineola* on cultivated *C. javinica* and *C. fistula* are numerous. This illustrates a type of interspecific interaction among plants not generally considered in studies of community structure. *Cassia grandis* will have a distinctly negative impact on any *Cassia* species with similar pods that immigrates into its habitat, even though the plants may never be in close proximity. The usual seed predators that these plants leave behind when emigrating may be replaced in great part by *P. lineola* (and the other seed predators on *C. grandis*). Further, if a second species of *Cassia* should become established, it is clear that a third species would be confronted with an ever larger community of predators. The potential impact of seed predators on tree-species richness and morphological diversity in the community is obvious in this case (Janzen 1970).

Predation by *Pygiopachymerus theresae* on *C. grandis*

*Pygiopachymerus theresae*, which is apparently restricted to *C. grandis*, is a slightly larger Colombian and Panamanian edition of *P. lineola* and was described in 1911 by Pic; *Phelomerus ochropygus* Pic is a junior synonym of *P. theresae*, likewise described from Colombia (Kingsolver 1970). The host record of "*Cassia fistula"* given for *P. theresae* on the first page of Pierce (1930) is clearly *Cassia grandis*. "Cañafistula beans" (host record in Kingsolver 1970) are likewise *Cassia grandis*.

*Pygiopachymerus lineola* has also been recorded from Colombian *C. grandis* (Kingsolver 1970). Since beetle vouchers were not obtained for the Colombian *C. grandis* recorded in Table 2, the seed damage may have been done by both beetles. The two sizes of bruchid exit holes in the pod walls substantiate this conclusion. The smaller ones were the same diameter as those made by Central American *P. lineola*. Nothing about the *Pygiopachymerus* damage to the Colombian pods indicates a difference between *P. lineola* and *P. theresae* acting in concert, and *P. lineola* acting by itself, except that a substantially larger number of the Colombian seeds had only one bruchid in them as contrasted with all Central American samples.

Predation by Lepidoptera larvae on *Cassia grandis*

As is commonplace with large fruits of tropical trees, the larvae of a complex of small moths eat the mature pulp around the mature hard seeds of *C. grandis*. They also eat seeds damaged by bruchids, thereby making it difficult to distinguish between *P. lineola* and moth damage (as in the Nicaraguan sample in column 7, Table 2).

Lepidoptera larvae enter through the exit holes of *Pygiopachymerus*, breaks in the pod wall caused by squirrels or birds, natural cracks, and holes in the pod caused by other moth larvae feeding on the immature pod. Since bruchid exit holes are the usual means of entrance, moth larvae are usually absent until some bruchids have emerged. In Central Amer-
ica seeds are eaten only when larvae enter a green pod, but in the Colombian sample one species of larva was able to eat intact mature seeds, leading to the high mortality recorded in column 7, Table 2. As many as 30 larvae may mature in one pod, and within 2 months after the exit of *Pygiopachymerus*, most of the molasses-like pulp has been converted to frass. Each larva feeds within one to four of the pod compartments (Fig. 1B), moving between compartments by chewing a hole through the thin woody partitions. Pupation occurs within the pod, and the adult moth leaves through a bruchid exit hole or one cut by the moth larva. Development is relatively synchronous within a given pod, and most adult emergence is during the latter half of the rainy season (July through October) from eggs that were laid during the previous dry season.

Since the moths do not appear to oviposit in the pods from which they emerge (almost no pulp remains), they may have a second generation each year in some other species of fruit. If this is not the case, the adult moth has a 4- to 8-month wait until another pod crop is available. If only a small number of moths find a particular pod crop, the first generation of larvae does not consume all the pulp in all the pods on the tree. A second generation then emerges much later from the pod crop, and the moths have only a few months to wait for the next pod crop, though they will still have to migrate to another tree. This shortening of the waiting period between crops may result in a much higher number of adults surviving to the date when new pods are available than when there is only one generation of moths per crop. Thus a mechanism exists for regulation of the moth population density, which is mediated through intraspecific competition for the food supply.

From the tree’s standpoint, two aspects of the moth’s activity are more important than direct seed predation. First, tame white-tailed deer, squirrels, pacas, and agoutis are still mildly interested in the pods after the moth larvae have eaten out the pulp, but quickly lose interest after breaking them open. Rodents do not carry off moth-infested pods. Deer do not eat seeds that have been cleaned of pulp. Second, *Zabrotes interstitialis* bruchids will not oviposit on the seeds unless they have been cleaned by the moth larvae (see below). Thus if only a few moths initially find the pod crop, leading to a slow rate of seed cleaning, the rate of predation by *Zabrotes* is reduced. This decrease should increase the time available to the dispersal agents to remove pods with live seeds.

In old pods the usual community of Nitidulidae and Tenebrionidae beetles feeds on the bits of pulp and seed fragments missed by the moth larvae.

**Predation by Zabrotes interstitialis on Cassia grandis**

The small black *Zabrotes interstitialis* and about 25 other species form a genus distributed from the east-central United States to South America; *Z. interstitialis* has been reared only from *Cassia grandis*. Collection records in the National Museum of Natural History (Mexico, Costa Rica, Panama, Venezuela, and Brazil) indicate that it is probably spread throughout the range of *C. grandis* (*Kingsolver, personal communication*). Its absence from the Colombian collection (column 5, Table 2) indicates, however, that *C. grandis* can be locally free of this predator; more than 50 pods from five crops were examined at the Colombian collection site and none had *Z. interstitialis*. This beetle has been present, however, in each of at least 30 different pod crops examined from Costa Rica to El Salvador.

*Zabrotes interstitialis* normally enters the pod through the exit holes of *P. lineola*, but will also use natural cracks to gain access. Since somewhat less than 10% of the pods in a pod crop are opened by agents other than *P. lineola*, seed predation by *Zabrotes* is heavily dependent on *P. lineola*. *Zabrotes interstitialis* oviposits only on clean seed surfaces (Fig. 3) and thus is dependent on the moth larvae for preparation of oviposition sites. On rare occasions *Zabrotes* will oviposit on the inner wall of the cavity that a *P. lineola* larva leaves in the seed. To oviposit, she moves in either direction from the entrance point. Although she may lay her eggs on seeds that already have eggs on them, one female usually produces the majority of beetles that emerge from one seed. *Zabrotes interstitialis* does not appear to discriminate between intact seeds and those from which *P. lineola* have emerged. The eggs are spaced at a distance of 1–3 mm and are most commonly glued singly to the broad side of the seed. The first-instar larva bores through the seed coat, filling the hatched egg with white frass. Hatched eggs are thus easily distinguished from unhatched, and egg viability is almost 100%. At densities of less than 7–10 eggs per seed, the larvae space themselves rather evenly through the intact seed or those parts left by the *P. lineola* larvae. The maximum number of beetles per seed is about 15, but the average number is three to nine for most seeds that have not been previously attacked by *P. lineola* (Table 4). As with *P. lineola*, the larvae excavate a cavity about twice their own volume. Development takes less than a month (also Utida (1967) records about 23 days for development of *Zabrotes subfasciatus*), and the adults exit through all sides of the seed (Fig. 3). They leave the pods immediately, and their activities until the next pod crop appears are unknown. These newly emerged beetles, or beetles newly locating the
TABLE 4. Emergence of Zabrotes interstitialis as a function of the number of eggs laid on intact Cassia grandis seeds

<table>
<thead>
<tr>
<th>Pod number</th>
<th>Number of seeds censused for eggs&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Max – Min eggs per seed</th>
<th>Eggs per seed</th>
<th>Max – Min adults emerged</th>
<th>Adults emerged per seed&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR–12–#5</td>
<td>23</td>
<td>23 – 1</td>
<td>9.95</td>
<td>16 – 3</td>
<td>8.57</td>
</tr>
<tr>
<td>CR–12–#7</td>
<td>14</td>
<td>23 – 1</td>
<td>11.85</td>
<td>15 – 1</td>
<td>7.71</td>
</tr>
<tr>
<td>CR–11–#1</td>
<td>36</td>
<td>16 – 1</td>
<td>5.92</td>
<td>14 – 0</td>
<td>3.73</td>
</tr>
<tr>
<td>CR–11–#5</td>
<td>24</td>
<td>26 – 1</td>
<td>7.58</td>
<td>15 – 1</td>
<td>5.29</td>
</tr>
<tr>
<td>CR–11–#6</td>
<td>19</td>
<td>37 – 1</td>
<td>9.84</td>
<td>9 – 1</td>
<td>4.26</td>
</tr>
</tbody>
</table>

<sup>a</sup>The only pod segments considered were those where the seeds were fresh and it appeared that hatched eggs had not been shed or worn off; whenever the number of emerging adults exceeded the number of eggs (rarely), the number of eggs was increased to equal the number of emerging adults.

<sup>b</sup>The “number of adults” emerging may be slightly underestimated owing to the multiple use of an exit hole by adults; dissection of seeds indicated that this was very rare. The maximum number of eggs found on a single seed in this study was 37 (nine adults emerged) and the maximum number of adults to emerge from a single seed was 18 (at least 21 eggs).

Fig. 3. Seeds of Cassia grandis with eggs and emergence holes of Zabrotes interstitialis. Eggs are white because of frass pushed back into them by first-instar larvae drilling straight down through seed coat.

pod crop, continue to oviposit on the seeds as long as the pod still contains pieces of solid seed. Occasional bruchids with eggs in their oviducts may be found in the pods from the middle of the dry season through the rainy season.

The fecundity of Z. interstitialis is between 90 and 100 eggs, as inferred from the following observations. Taking a doubling of fecundity into account if the female is fed sugar-water (flower nectar in nature, and perhaps some pollen), a female of Zabrotes subfasciatus should have a maximum egg production of about 80 (Utida 1967) or 100 (Howe and Currie 1964). More direct evidence for fecundity of Z. interstitialis was provided by a hanging pod (CR-12-#5, Table 2) that was split at the base, but had not been located by P. lineola. The moth larvae had cleaned all 44 of the seeds except six of the uppermost eight. The number of Zabrotes eggs laid per seed from pod tip to base was 4, 8, 3, 7, 4, 16, 9, 13, 17, 14, 8, 13, 19, 14, 8, 23, 8, 16, 10, 8, 3, 2, 6, 12, 5, 25, 16, 5, 17, 14, 14, 3, 4, 6, 3, 0, 6, 0, 0, 0, 0, and 3 (= 374 in entire pod). In this census, each seed with unhatched eggs on it has its egg number underlined; those with only unhatched eggs are underlined twice. The eggs of four females may be separated from this in the following manner:

1) A total of 95 eggs on 16 seeds had embryos of the same developmental stage, which were probably placed by the last Z. interstitialis to oviposit in the pod.

2) The 24th through 31st seeds had only first-instar larvae in them. These 54 first-instar larvae were probably from eggs laid by the penultimate bruchid to oviposit in the pod, since the unhatched eggs had only slightly developed embryos in them. Twenty-eight first-instar larvae were also found in the 17th through 23rd seeds. This indicates that at least 28 of the eggs on the 17th through 23rd seeds were laid by the penultimate female; her total clutch was then at least 82 eggs on seven seeds.

3) The first through the 12th seeds had many pupae, teneral adults, and old larvae in them. These seeds had 112 eggs on them. Of these, four were unhatched and thus belonged to the last female to enter the pod, and at least 22 belonged to the first bruchid; since there were 22 very old Zabrotes exit holes in these seeds. These figures indicate that the second female to enter the pod laid at least 86 eggs on 12 seeds.

4) The ninth through the 19th seeds contained many old Zabrotes exit holes. These seeds had a total of 150 eggs in them, all of which had hatched. If we subtract 12 for the penultimate female (12 first-instar larvae in these seeds), and 30 for the second female (30 old larvae, pupae, and teneral adults), it appears that the four females (1) laid 108, 86, 82, and 95 eggs; (2) divided the seeds evenly among themselves; (3) probably laid their entire egg supply; and (4) found the pod over a period of about 6 weeks.

Taking 200 pods as a representative crop, and taking the Z. interstitialis emergence in column 9 of
Table 2 as representative bruchid survival, each adult *C. grandis* is a source of 12,000 *Zabrotes* every other year in communities where few pods are removed by dispersal agents. However, the data in column 9 were collected before the beetles had time to complete development on all available seeds. Based on cursory examination of many pods whose seed reserves were completely exhausted by *Zabrotes*, the average number of beetles produced per seed is probably about two. In this case, the maximum number of generated *Zabrotes* per pod crop would be about 20,000. This population size is based on the assumption that dispersal agents are not operating on the crop. If we assume that, on the average, four females find each pod, we must conclude that the population of female *Zabrotes* fluctuates between 10,000 and 800 within each year in the habitat space occupied by two adult *C. grandis* (there is a 1:1 sex ratio in large samples of *Z. interstitialis*). The fluctuation in, and mean of, population density should decline (1) as the dispersal agent complex becomes more efficient at removing pods at about the time the *P. lineola* are emerging from them; (2) as the ecological distance between *C. grandis* trees increases; and (3) as predation by *P. lineola* and moth larvae increases.

To understand the low survival of *Z. interstitialis* between seed crops, it is important to realize that this bruchid does not have another host species. I have reared at least 25 species of bruchids from samples taken from most of the legume flora in the habitats around the Costa Rican *C. grandis* in Table 2 without finding *Z. interstitialis*. By the middle of the rainy season, *C. grandis* pods are rare and thus the population has to wait at least 6–7 months before new oviposition sites are available. Occasional *Z. interstitialis* may be swept from the foliage of *C. grandis* bearing a green pod crop. This indicates that they may wait on the parent tree itself. Since the length of the wait is proportional to the rate at which *Zabrotes* destroys the seeds, the bruchid-plant interaction has a potential intrinsic population-regulation mechanism for the beetle. Increased predation by *P. lineola* and Lepidoptera larvae should likewise lengthen the time that the *Zabrotes* population goes without food.

Just as the population density of bruchids is influenced by other insects, dispersal agents, and distance between pod crops, so is the large inter-pod variance in seed predation recorded in columns 5 and 6 of Table 2. For example, pod CR-11-#1 in Table 2 had the time for *Zabrotes* to kill all seeds missed by *P. lineola*, whereas pod CR-11-#7 had been found by only one female at the time of sampling and probably would have required at least another month for total seed mortality. The pods removed from *C. grandis* by dispersal agents will be highly variable in the number of viable seeds that they carry. However, the later in the season, the lower will be the probability that any live seeds will be found in the pod. This system is complicated by the fact that pods with intact pulp (and thus with few *Zabrotes*) are preferred over those eaten out by moth larvae. A final complication is that even if many *Zabrotes* find the pod crop, they cannot oviposit any more rapidly than the seeds are cleaned by the moth larvae.

A pod is not freed from attack by *Zabrotes* by falling from the tree. *Zabrotes interstitialis* continues to oviposit in the pod until it becomes waterlogged or termites destroy it. Dry pods, however, may be freer from damage on the ground than in the tree, since ants often nest or forage in the pods on the ground and kill both moth larvae and bruchids. The freedom of the Colombian samples from *Zabrotes* attack may be due to the large moth larva that eats mature seeds as well as the pulp around them. In Central America a large part of the *Z. interstitialis* population matures in seeds first attacked by *P. lineola*; in the Colombian samples, nearly all seeds damaged in this manner were eaten by the moth larvae. Further, these moths ate a large number of intact seeds (column 7, Table 2). Successful moth attacks on intact seeds may depend on small irregularities in the hard seed coat where the larva's mandible can gain first entry. The entrance holes of *Z. interstitialis* first-instar larvae could well provide such an entry point.

There is no evidence that parasites regulate the population density of *Z. interstitialis*, although much of the adult mortality between seed crops is probably caused by vertebrate and invertebrate general predators. Parasites of *Z. interstitialis* were found only in pod Nicar #2 (Table 2) and are the only ones seen among many other pods cursorily examined. These undetermined Hymenoptera were of little direct significance to the plant, since they allowed the beetle to mature and then emerged from its pupal chamber. Indirectly these parasites could be responsible for a small amount of seed survival since their presence should slightly slow the rate at which the bruchid population locates viable seeds.

**Other bruchids as predators of C. grandis**

At least 100 species of bruchids, and probably many more, attack the seeds of Leguminosae in the habitats occupied by *C. grandis* in Central America. With one exception, *P. lineola* and *Z. interstitialis* were the only species of bruchids reared from at least 200 pods from at least 30 different seed crops collected from El Salvador to Costa Rica. The exceptions were five *Acanthoscelides muricatus* (Sharp), an extremely rare Central American bruchid whose host was previously unknown (Kingsolver, personal communication). These beetles emerged on...
February 4, 1970, from a sample of six *C. grandis* pods taken off a backyard tree about 2 miles east of Puntarenas, Puntarenas Prov., Costa Rica. The pods had just matured and the *P. lineola* larvae were still small; either oviposition was well before that of *P. lineola*, or the *A. muricatus* larvae develop much faster than those of *P. lineola*. Since the female *A. muricatus* laid two to three single eggs on each pod surface, *C. grandis* may not be the normal host plant. The newly emerging beetles cut exit holes laterally through the pod wall instead of through the dorsal or ventral ridges in the pod as does *P. lineola*.

As Bridwell (1918) has pointed out, *C. grandis* has been introduced into Hawaii along with a bruchid fauna of at least eight species. In the field one of these, *Caryedon serratus* (Olivier), lays its eggs on *C. grandis* pods, and the larvae find their way into the seeds much as do *Pygiopachymerus*. Bridwell (1918) also found that *Calllosobruchus chinesis* (L.) and *Stator pruinosis* (Horn) oviposit on *C. grandis* seeds in laboratory choice tests, but the larvae die after feeding on the seed contents.

*Cassia grandis* has been introduced throughout the Old World tropics. J. P. M. Brennan reports (personal communication) that of the Old World *C. grandis* pods in the Kew Herbarium, only seeds from a pod collected in Burma (Parkinson, 14042) had what appeared to be bruchid emergence holes.

**Discussion**

Degree of contemporary predation

Owing to lumbering, agricultural, and hunting disturbance in most of Central America, it is no longer possible to document the dynamic interaction between seed predators, dispersal agents, phenology of adult trees, and density of adult *Cassia grandis* as the interaction existed during its evolution. However, the contemporary interaction system, although incomplete, allows several useful inferences.

1) Since *Pygiopachymerus lineola* predation occurs before the pods of *C. grandis* mature enough to attract dispersal agents, the mortality in column 4 of Table 2 may be seen as representative of undisturbed *C. grandis* habitats.

2) In view of the effectiveness of *Zabrote interstitialis* at killing seeds remaining in pods on the tree after the emergence of *P. lineola*, there was probably strong selection favoring *C. grandis* phenotypes with seed pods especially attractive to climbing vertebrates that removed the pods immediately after maturation.

3) The high percentage of seed mortality recorded in column 3 of Table 2 is probably representative of communities where the dispersal agents are not particularly effective at removing pods rapidly.

4) At present, *Z. interstitialis* is probably a commoner species in most *C. grandis* habitats than when the pods were removed rapidly by dispersal agents, but since *C. grandis* does not appear to be reproducing in woody regeneration of most Central American dry lowland farming communities, the beetle may be driving its host plant toward extinction. The failure of reproduction occurs despite the fact that many remaining adult *C. grandis* are fully insulated and thus yield very large pod crops.

5) The trait of flowering and fruiting every other year, rather than producing half as many pods annually, was probably very effective at reducing both *P. lineola* and *Z. interstitialis* populations (and hence predation by these beetles). In the absence of dispersal agents, fruiting every other year still must result in reduced predation by *P. lineola*. A reduction in predation by *Z. interstitialis* is less likely, since the bruchids now have much longer to find the pods than when dispersal agents were present.

6) Since the percentage seed mortality is clearly related to the number of adult bruchids that find the seed crop, it should be positively correlated with (a) decreasing distance between adult *C. grandis* as measured in units of the percentage of one tree's crop of beetles that find their way to the next seed crop, and (b) decreasing severity of the intervening dry and wet seasons from the bruchids' viewpoint (measured in the same units as the distance between trees mentioned above).

Since the distance between adult *C. grandis* can influence the degree of seed predation by bruchids, the bruchids can strongly influence the equilibrium density of adult *C. grandis* in an undisturbed community. For any given climatic regime, the success of a particular adult *C. grandis* at reproducing itself during its lifetime should be inversely proportional to its distance from other adult *C. grandis*. Interestingly, if its conspecific neighbors happen to be synchronized with it in their fruit production, it should have a higher percentage of seed escape than if its neighbors were out of phase and therefore providing food for the seed predators in the "off" years of the tree under observation. Synchronized or not, as the density of *C. grandis* in any local area increases, the rate of increase of adult *C. grandis* population should decline. This is a classical predator-prey system, and the period and amplitude of the fluctuations in *C. grandis* density should be subject to the same rules as those considered for predators and animal prey (cf. Janzen 1970) but with large time lags (Janzen 1971b).

A weather regime favorable to the bruchids may not necessarily be favorable to the establishment and survival of *C. grandis* seedlings. The actual equilibrium densities along microclimatic gradients will thus be the result of complex interactions between the sensitivity of bruchids and seedlings to weather. We can expect, for example, that dry hillside areas would have
a very low population density of *C. grandis* since the beetles probably have high mobility from moister sites (where they may pass the dry season, cf. Janzen and Schoener 1968) to maturing pod crops, and the small number of surviving seeds probably have little chance of surviving their first dry season as seedlings. Wet bottomlands may have about the same seed mortality but much higher seedling survival than on the adjacent dry hills, which may in turn lead to higher density of *C. grandis* for a given seed mortality. On the other hand, in areas with no moist refuges for the beetles during the dry season, seed survival of *C. grandis* may be much higher than in slightly wetter sites; with more trials (seeds) at establishment, the *C. grandis* population may occupy a much greater area than would be possible if the beetle were equally effective at all sites. Likewise, some of the highest *C. grandis* densities should be expected in those areas of high seedling survival coupled with a very effective complex of dispersal agents and (for example) a rainy period excessively inimical to *P. lineola*.

The equilibrium density of adult *C. grandis* should also be sensitive to unpredictable climatic perturbations that influence the beetles more than their hosts. For example, in 1962 the dry season was nearly a month longer than usual throughout the Pacific lowlands of Central America; if this resulted in high bruchid mortality (it is not likely that it killed adult *C. grandis*), it might have been several years before bruchid populations built up to their previous level of seed predation. This may well have resulted in a “wave” of viable seeds into the *C. grandis* habitat, with a subsequent small increase in the density of adult *C. grandis*. As the frequency or intensity of such unpredictable perturbations increases, the *C. grandis* population will be able to escape from the bruchids to a progressively greater degree. To the degree that these perturbations do not destroy as many *C. grandis* seedlings as they save seeds from predation, the equilibrium density of *C. grandis* should increase; the degree of increase should be directly proportional to severity of intra- and interspecific plant competition on the site. Even predictable perturbations function in this manner, provided that they reduce the efficiency of the bruchids in some manner, without comparable inimical effects on *C. grandis*. In communities inimical to all predators (e.g., when the tree migrates to an ecological island and leaves its predators behind) the equilibrium density should be set purely by intra- and interspecific tree competition.

Potential coevolution of the interaction

There is no reason to believe that the bruchid-*Cassia* interaction was coevolutionarily static at the advent of European agriculture, nor is there reason to believe it to be immune to further selection. We may imagine many potential coevolutionary ramifications of the interaction, and a few of those that seem reasonable, since they appear to have occurred with other legumes and bruchids, are mentioned below.

1) A mutant strain of *C. grandis* that produces twice as many seeds, of half the usual size, per pod could have substantially reduced percentage seed predation by *P. lineola*. The predation would probably not be reduced by one-half, however, since the *P. lineola* larvae might distribute themselves more widely among the seeds. Such a change in *C. grandis* would be unlikely to elicit a subsequent change in *P. lineola*, since the number of beetles emerging per pod would be the same.

However, without a concomitant change in the energy-storage ability of the seeds, or in the habitats to which they are dispersed, the fate of the seedlings of such a mutant is not clear. As seed size is reduced, the number of suitable sites for seedling survival is also reduced, but increased seed numbers should result in a higher percentage of the total suitable sites being hit with a seed. However, the number of suitable sites may be reduced faster than the probability of their all being hit is rising. If the mutant strain of *C. grandis* has a superior storage compound in its seed, reduction in seed size may well not reduce the number of suitable sites in the habitat for seedling survival. In the other direction, contemporary habitats, heavily insolated owing to partial clearing of vegetation by cattle and cutting, may have many more sites suitable for survival of *C. grandis* seedlings than do undisturbed habitats. In this case an increase in the number of seeds (each at half size) may be very important in maximizing the number of times that an adult *C. grandis* attempts to escape the vagaries of human cutting, burning, and grazing patterns.

A mutant strain of *C. grandis* with an increased number of seeds per pod would show reduced predation by *Z. interstitialis* only if the bruchid failed to distribute her eggs more widely among the seeds. However, a change in bruchid oviposition behavior is quite likely; the contemporary egg density per seed would result in severe intraspecific competition among the larvae, were the seed volume to be reduced by half.

2) Many legume seeds contain toxic alkaloids and free amino acids which apparently aid in reducing or preventing predation by bruchids (Janzen 1969, 1971b, Bell and Janzen 1970). The seeds of *C. grandis* contain no outstanding amounts of potentially toxic nitrogenous compounds (Bell, personal communication). A mutant strain that sequestered a free amino acid such as canavanine (cf. Janzen 1971b), rather than the present nitrogen-rich storage compounds, might gain total freedom from bruchid at-
tack. If *C. grandis* were the only species of legume in the area, the bruchids would either become extinct or evolve resistance to canavanine. However, the bruchids can pass many generations per generation of *C. grandis* and evolution of resistance is very likely; such a change in the plant would therefore at best result in only very temporary escape, except for the following considerations.

*Cassia grandis* is sympatric with many other species of hard-seeded legumes. Some of these can probably serve as suboptimal hosts for *P. lineola* and *Z. interstitalis*. Then the question becomes one of whether these bruchids will evolutionary shift onto these other hosts (at perhaps much lower population densities) or evolve resistant mutants. If there is a shift of host plant, then many subsequent changes in *C. grandis* are possible, such as doubling seed size and halving seed number.

3) The huge pods of *C. grandis* contain at least twice as much pod material per seed as do other Central American legumes that are attacked by bruchids. Seed size could be increased, without reducing seed-crop size by diverting reproductive energy from the pod to the seeds. In contemporary communities, where dispersal agents are virtually absent (and will probably continue to be absent), such a mutant might be especially favored. However, in natural habitats such a mutant might well be strongly selected against, because dispersal agents would be less likely to remove the pods. The predation by *Z. interstitalis* makes reduction in pod-wall thickness particularly unlikely; thinner walls are more likely to crack when drying, allowing entry by this small beetle before *P. lineola* emerges. Further, if the walls were thinner, the females might oviposit directly on the pod wall and the larvae might be successful in finding the seeds directly.

4) A mutant strain of *C. grandis* that waited 3 or 4 years between seed crops would definitely have reduced seed predation by bruchids if the bruchids that attack a given crop were to come primarily from the previous year's crop on the same tree. Such a reduction in seed predation was probably responsible for the evolution of the present behavior of fruiting every other year. However, it is very unlikely that the bruchid population can survive more than a year without a seed crop. Thus one tree's failure to fruit every other fruiting period would only reduce the predation on its next seed crop by an amount equal to the reduction brought about for the other *C. grandis* in the area. Such a mutant strain would have the disadvantage, however, of putting new seeds into the habitat only every fourth year rather than every second year. Further, its total life-time seed production would be reduced by the cost of accumulating reserves for 4 years before using them. It is impossible to guess to what degree this loss would be compensated for by the larger seed crop that could probably be produced every fourth year. This larger crop should have a lower percentage mortality because *P. lineola* would be satiated with the same absolute number of seeds for any seed crop. However, if dispersal agents are ineffective, the larger seed crop would be unimportant because *Z. interstitalis* cannot be satiated except during the short time before the first generation of beetles emerges from the seeds.

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**Literature Cited**


