INTERACTIONS OF SEEDS AND THEIR INSECT PREDATORS/PARASITOIDS IN A TROPICAL DECIDUOUS FOREST

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In this paper I will touch on some of the patterns and processes that have come to light in an on-going study of how the insects that eat seeds in tropical vegetation influence the structure of that vegetation and the characteristics of its individual members, and how the characteristics of the plants influence the insects. This study began in 1964 in the lowlands of the state of Veracruz, Mexico. While trying to understand the population dynamics and interdependency of obligate acacia-ants and their acacias (Janzen 1967), I was struck by the thoroughness with which the bruchid *Acanthoscelides oblongoguttatus* decimated the seed crops of *Acacia cornigera*. This swollen-thorn acacia was extremely common as a result of farming and grazing practices, and it produced far more fruits than the local community of dispersal agents would eat (a thorough study of dispersal agents was not made, but at least the Plain-tailed Brown Jay, *Psilorhinus mexicanus*, Black-headed Saltator, *Saltator atriceps*, and Grayish Saltator, *Saltator coerulescens*, ate seeds along with the pulp and defecated living seeds). While most of the *A. cornigera* population bore flowers in the later part of the dry season (March, April) and mature fruits about ten months later, individuals in almost any reproductive stage could be found at any time of year in an area as small as a few hectares. The pods remained on the acacia in a stage susceptible to bruchid oviposition for as long as two to three months. Attack was heavy and continuous, both from beetles that could have emerged from other pods on the same acacia, and from beetles coming from other *A. cornigera* out of fruiting synchrony. Only very broad synchrony of flowering and fruiting occurred in the highly mixed and variously disturbed habitats (roadsides, back yards, various age corn fields, pastures, fencerows, creekbanks, marshes).

It was obvious that in the highly disturbed lowlands of Veracruz, the acacia was largely losing the race between the bruchids and the dispersal agents. However, it seemed likely that in a more intact habitat where *A. cornigera* would be much rarer, more synchronized, and further apart, the interaction would not be so one-sided. It was also obvious that such habitats were not available to me, so the subject was shelved while I worked on the interaction between the ants and the acacias.

While working out the ecological distribution of the ants and their acacias throughout Central America during July and August of 1966 and 1967 (Janzen 1974a), I had the opportunity to make general collections of legume seeds in many habitats. Confronted with numerous bags of seed pods, from some of which came large numbers of bruchids while from others came none, it was obvious that there was a pattern. Large-seeded legumes in general lacked bruchids while almost all of the small-seeded ones had bruchids (Janzen 1969). It is perhaps appropriate to add here that the Janzen (1969) paper, which attempts to relate seed size, seed toxicity, and bruchid attack, contains two quite annoying errors. First, after developing the entire paper around the idea that species preyed on by Bruchidae have smaller seeds, more seeds, and more biomass of seeds per unit canopy volume, the first sentence of point one in the "Conclusions" section contains a ludicrous printing error, such that the sentence reads just the opposite (the word "not" belongs between the *first* "are" and "attacked", not the second, page 23, column 1, lines 36-40). Second, the primary biological exception to the tentative rule put forth in the paper was a very small-seeded species of *Indigofera*; further collecting in Mexico and Central America has shown that this legume is heavily attacked by a very small species of bruchid (unpublished field notes, Johnson 1973, and Center and Johnson 1974).

The consideration of large seeds as toxic was nearly as serendipitous as finding that they lacked bruchid attack. I was walking down a hall in the Botany Department at the University of Kansas holding a Costa Rican cycad fruit in my hand, and a person walking the other way commented that he had a whole refrigerator full of them and did I know that they have very toxic seeds? I said no, I did not know that, but that I had a seed upstairs that I was willing to bet would be very toxic and did he wish to analyse it. In a few hours E. Arthur Bell was back with the announcement that my *Mucuna andreana* seed had an extraordinarily high concentration of L-DOPA (L-dihydroxyphenylalanine), an uncommon and non-protein amino acid with well known toxic physiological effects on mammals. This led to a number of examinations of large and bruchid-free seeds for high concentrations of potentially toxic secondary compounds (e.g., Bell and Janzen 1971) and to an increasing frustration with our lack of knowledge of whether these compounds really are toxic to bruchids.

Serendipity struck again. Back in 1966 I had met Paul Feeny while he happened to be passing through the University of Kansas, and he told me about his work with tannins in oak leaves and how he had fed them to armyworms (*Prodenia eridania*) in the laboratory to illustrate tannin toxicity. I had then collaborated with him and Sherry Rehr to test an old hypothesis (Janzen 1966, 1967) that the swollen-thorn acacia leaves would be less toxic to insects than their non-ant-acacia relatives; they are less toxic (Rehr et al. 1973a) and Feeny was an obvious person to test the L-DOPA and other compounds that Bell had found in large legume seeds. L-DOPA and other seed compounds were then found to be toxic to armyworms, depending on concentration (Rehr et al. 1973b,c).

Looking at the bruchids, their interplay with seed dispersal agents, and the toxicity of the seeds to some animals but not all, suddenly caused me to realize that these and other seed predators could be not only influencing the genetic characteristics of individual plant species in the habitat, but also influencing their relative abundance. By asking myself exactly what is it that decides whether an adult of tree species X actually appears at point Y in the forest, I found myself "reinventing" all those things that I should have learned about probability theory when I was an undergraduate. I spent about six months figuring out how to graphically represent the interaction between the size and dispersal pattern of a seed crop, and a seed predator that is differentially effective depending on the number of seeds present. I then asked Richard Levins about it, and he pointed out that the "model" I had invented was the answer to one of the questions on the final examination in mathematical biology that he was teaching that semester. At any rate, the resulting theoretical analysis of the potential impact of seed predators on forest community structure (Janzen 1970) forms the underlying philosophical structure for most of what follows here. Since that time, I have tried primarily to obtain a data base that would allow me to test some of the hypotheses presented in 1970, and have gathered data so as to optimize the discovery of patterns clarifying the questions posed in the first sentence of this paper. I will deal with a series of interrelated but not all-encompassing patterns and apparent hypotheses that have come to light by focusing on one major vegetation type, tropical deciduous forest, in one area, the Pacific coastal lowlands of Costa Rica (primarily Guanacaste Province). This particular study began in 1965 while teaching for the Organization for Tropical Studies and would not have come about without the logistic and intellectual support of that organization, and the students, faculty, and researchers working with it.

DEFINITIONS

There are only two bothersome terminological snarls of concern here: *seed predators* and *secondary compounds*.

Ecologically and behaviorally, the adult bruchid (or weevil, cerambycid, etc.) is acting as a predator (Janzen 1971a). It moves through the habitat searching out and killing individual seeds. It kills them by laying an egg on or near them. It is satiated by running out of eggs in a given time interval. On the other hand, the bruchid larva functions as a different sort of predator, one commonly called a parasitoid in the biological control literature. The larva kills (usually) only one prey individual, does it slowly, does not leave it, etc. From the standpoint of the adult tree, the plant is losing its seed to a seed predator as surely as if it were losing them to a deer or squirrel. From the standpoint of the ecology of the insect, it is traditional to view the insect as a parasitoid. Therefore in discussions of tree ecology, I will think of them as seed predators, but in asking why there are a given number of them found on a host, it will be most profitable to think of them as parasitoids.

Secondary compounds are chemicals found in seeds (and in other plant parts) that are not part of the metabolic processes common to all or most plants. They are usually functional as floral and fruit attractants, antibiotics, repellants, and/or toxicants, and usually occur at much higher concentrations than do other odd compounds operating within the physiology of the plant (hormones, germination inhibitors, etc.). In this paper, my comments about secondary compounds are restricted to those that generally have a negative physiological effect on an animal (e.g. alkaloids, uncommon amino acids, terpenes, phenols, saponins, lectins, etc.).

DENSE VERSUS DIFFUSE POPULATIONS

A core aspect of the potential impact of pre-dispersal seed predators on trees is that as the distance between seed crops in space and/or time increases, the percent seed mortality within an individual tree's crop should decline. This hypothesis is extraordinarily difficult to test in nature, owing to the difficulty of interpreting the data obtained when comparing percent seed mortality among crops of clumped conspecifics with crops of diffusely distributed conspecifics. To illustrate this difficulty, I here present a partial analysis of the predation on seeds of clumped and widely spaced *Acacia farnesiana* ("guisache", Mimosaceae) by two species of host-specific bruchids, *Mimosestes sallaei* and *M. immunis*. Background natural history is given before the actual test.

The study site lies along the northeastern edge of the approximately 25 km^2 forested seasonal swamp behind the hill behind the Organization for Tropical Studies (OTS) Palo Verde Field Station, which is in turn in the southwestern end of the COMELCO ranch, which is in turn to the southwest of Bagaces, Guanacaste Province, Costa Rica (about 10°40' N. Lat., 10 m elevation). *A. farnesiana* is very widely distributed in Central and northern South America, and indigenous to the study site; there is no hint that either species of *Mimosestes* is recently introduced. It is impossible to know how much European man, his cattle, and his lumbering have disturbed the site, but it appears to never have been cleared for field or pasture. However, isolated trees have been cut, firing history is undoubtedly different from the conditions under which the bruchid-acacia interaction evolved, and the site has been foraged in by semi-feral cattle for at least 100 years and perhaps as long as 300 years. It is about as natural a habitat for *A. farnesiana* as can be found in Costa Rica. The swamp and the adjacent forest still contain individuals of what may have been dispersal agents for *A. farnesiana* (white-tailed deer, peccaries, agoutis, pacas, and smaller rodents) but their density and relative proportions undoubtedly do not represent those under which the bruchid-acacia interaction evolved. Cattle now occasionally eat variable amounts of *A. farnesiana* pods and likewise serve as dispersal agents, but there is no way to know to what degree they replace the native animals as dispersal agents.

The study site is at the edge of the swamp, lying to the north of where the swamp edge is cut by the dirt track from the COMELCO main ranch headquarters to the Palo Verde Field Station. In those portions of the swamp not severely damaged by roadwork, fire, and cattle, the vegetation consists of a dense stand of *Parkinsonia aculeata* ("palo verde") in the center, surrounded by concentric variable-width rings of *Pithecellobium dulce*, *Cocoloba caracasana*, *Acacia farnesiana*, and *Acacia collinsii*. Each of these species is found abundantly mixed into the vegetation outside of the ring of its greatest density. As one approaches the edge of the swamp, the species richness of woody plants begins to climb very rapidly and the adjacent hillside may have as many as 150 species of trees, woody shrubs, and woody vines.

The *dense stand* of *A. farnesiana* lies approximately 500 m into the swamp and contains roughly 10 to 30 adults per hectare, with only scattered other species of low trees or shrubs mixed among them. Each *A. farnesiana* is about 1.5 to 3 m tall, with a crown of 5 to 30 m circumference. It is 2 to 30 m between their crowns. The *diffuse stand* of *A. farnesiana* is at the edge of the swamp; the acacias occur at a density of about 1 per hectare, with 50 to 100 m between conspecifics. The intervening spaces are filled with about 30 species of woody shrubs and small trees and it is generally impossible to see one *A. farnesiana* when standing at another.

In an earlier terminology, it would have been customary to speak of the dense stand as being the center of the population and the diffuse stand as the edge of the population. However, since we have not the slightest idea of where the seeds come from to produce any given new acacia, nor what is the longevity of acacias at either site, I am reluctant to apply any terms that carry implications about the spatial dynamics of the population. For all we know, three adults in the diffuse site may contribute all the acacia adults to be recruited to the population during the next hundred years.

The two species of bruchids occur as seed predators on no other species of plants in this habitat. The adults can, however, be taken with a sweep net from the foliage of the habitat at any time of year and both have been caught drinking nectar in the flowers of *Parkinsonia aculeata*. There are at least 80 other species of bruchids that can be reared from seeds growing within a 1 km radius of the site; none of these feed on *Acacia farnesiana* seeds.

A. farnesiana bears scattered flowers from July through March, but the major flowering period is in the dry season at most sites. The flowers are obligatorily outcrossed (if my experimental crosses made in the lowlands of Veracruz in 1964 are representative) and the pods mature by the middle of the following dry season. At the time of pod collection in the present study (14 March 1971), about 50% of the trees had dropped all their pods and on the remainder, most pods were mature. The indehiscent and heavy pods fall straight to the ground, where they are occasionally eaten entirely by deer, peccaries and cattle, chewed up by rodents, or carried off by rodents. Apparently these animals are interested in the slightly sweet pod wall, which may also contain a substantial amount of nutrients if we can reason from the analyses of pods of other mammal-dispersed acacias (Gwynne 1969). Some of the pods fall down the cracks in the drying mud surface and others are probably washed away from the parent plant by the torrential downpours that hit this habitat during the early rainy season. It is doubtful if any of the seeds consumed by mammals are killed by digestive action, but rodents may chew through their hard seed coats.

The bruchids are present in the habitat and will oviposit on a full-sized pod at any time of year, as shown by fresh eggs on pods in miscellaneous collections of full-sized green pods made in and near the swamp in June, July, August, September, December, February, and March. This makes the plant's behavior, of holding the pod size quite small until only a few months before it will mature, very understandable. If full-sized pods were present from flowering to fruit drop, the potential for total seed destruction by multiple bruchid generations within a single acacia crown would be very high. The bruchid larvae bore through the pod wall, into the seeds, and mature one to a seed. Presumably there is intense intra- and interspecific competition among the two species of bruchid, as there can easily be ten times as many eggs laid on a pod as there are seeds inside. Presumably, as in other bruchids (e.g., *Scheelea* palm nut bruchids, Janzen 1971b), the larger larva simply eats the smaller invaders. About a month later, the adult *Mimosestes* emerges through the side of the seed, cuts a hole through the pod wall (or uses some other bruchid's exit hole), and emerges. Apparently, immediately after mating, the female can oviposit within the pod crop. This suggests strong selection against asynchronous pod crops within an individual's crown, and should select strongly for intra-population synchrony if the acacias are close enough to mutually infect each other with bruchids.

The bruchids will also oviposit on pods that have fallen to the ground, which brings out an interesting aspect of their coevolution with the acacia. When the pods are on the acacia, the beetles lay their eggs on all sides of the pod; presumably when a small object like an acacia pod is fully exposed to the breeze, no side is a substantially better microclimate than another. However, once the pod is lying on the fully insolated ground, the situation changes dramatically. There is almost no air movement right at the ground surface, and the soil surface attains temperatures of 50 to 70°C. The female, who oviposits at night, dusk and dawn, responds by laying her eggs almost entirely on the underside of the pod, which is presumably cooler and may be slightly more humid as it is directly against the ground. For example, 25 pods on the ground under an *A. farnesiana* tree in the dense clump had the following number of eggs on the surface of the pods facing upward: 2, 4, 3, 4, 2, 3, 1, 0, 6, 3, 2, 6, 4, 2, 5, 6, 2, 5, 6, 4, 1, 4, 0, 1, and 0 ($\bar{X} = 3.04$); on the surface of the pods facing downward, the same pods had 27, 12, 38, 33, 13, 29, 23, 12, 15, 5, 18, 17, 38, 15, 18, 17, 8, 13, 32, 10, 34, 23, 37, 4, and 9 eggs ($\bar{X} = 20.0$). The eggs on the upper surface were probably laid on the pods before they fell. These numbers of eggs per pod are by no means exceptional for pods on the ground. The number of eggs per pod on the tree averages about 8, with most values falling between 1 and 15. However, though virtually every egg laid on a pod on the tree produces a larva that bores down through the maturing pod wall and into the relatively soft seed, the larvae from eggs on the fallen mature pods have a difficult time penetrating the hard pod wall and the hard seed coat. Dissections of dry hard pods that have been oviposited on *in vitro* showed that once the pod has been off the tree and dried for a month, the larvae do not make it from the egg to the inside of the seed. They can, however, mature from eggs laid directly on mature seeds in the laboratory. It is not known if either species of *Mimosestes* is more responsible for the eggs on the fallen pods or on the pods still on the tree.

If the bruchids were to lay these eggs on the pods while on the tree, at least half of them that were laid near the time of pod fall would run the chance of being killed, since at least half of them would on the average end up on the upperside of the fallen pod. Such a situation should select for a bimodality of oviposition behavior. The female should oviposit indiscriminantly on the pod surface until about the time that the pod is ready to fall, and then stop until the pod is on the ground. It is possible that each species of *Mimosestes* occupies one of these peaks.

With this background in hand we are ready to examine the outcome of asking "do the bruchids kill more *A. farnesiana* seeds in the dense clump than in the diffuse clump"? The first attempt at answering this question, and the only one to be discussed here, was to simply collect up to 200 pods from the ground below each of 36 *A. farnesiana* in the dense clump and 11 in the diffuse clump. The idea was to mimic a dispersal agent removing a set of pods, with the intent of thereby being able to state how many seeds survive bruchid attack (this assumes that these bruchids do not locate dispersed pods or seeds). The method, and interpretation of results, suffer from not knowing how closely the sampling time matches the time at which dispersal agents would normally have removed seeds or pods. The pods were placed in plastic bags and the beetles allowed to emerge. They were shipped to the University of Chicago and a sample of 30 to 100 pods from each bag was x-rayed within six weeks of collection in order to determine how many seeds were intact, aborted, contained bruchid immatures or had exit holes from them (mammography x-ray film is ideal for this purpose). There were no signs of small bruchid larvae in the x-rayed seeds, indicating that in spite of re-oviposition on pods in the bags, none of the larvae had managed to re-infest the seeds.

The results of this sample are presented in Tables 1 and 2. The raw data are presented in full since such data are non-existent in the literature and I suspect may be of use to later workers as our understanding of the interaction between bruchids and seeds increases. There are a number of glaring conclusions to be drawn, but their interpretation is far from simple. In short, in the dense stand of *A. farnesiana*, there were significantly greater numbers of pods per tree and seeds per pod; the dense stand also had an apparent lower percent seed mortality by bruchids and an apparent higher percent of aborted seeds (cf. Tables 1 and 2). However, if these are added, we find that the percent dead seeds is identical in both samples. In the final summation, then, the *A. farnesiana* in the dense clump produced nearly 15 times as many viable seeds per tree as did those in the diffuse stand, but it was done by producing 7 times as many pods per tree as in the diffuse stand rather than through differential seed mortality in the two stands. However, as a member of my audience once said to me long ago, the easy thing is rejecting the null hypothesis. The hard thing is figuring out what alternative to accept. I think that it will be profitable to take each of these parameters and examine it in turn in the ecology of the acacia and the bruchid.

Table 1. Statistics on pod crops of *Acacia farnesiana* in the dense stand (n = 36). For comparison with pod crops in the diffuse stand see Table 2 (see text for details).

Number of pods on tree (est.)	$\bar{X}$ of seeds/pod	% seeds killed by bruchids	% seeds "aborted"	Number of viable seeds produced by tree (est.)
1700	9.6	7.78	88.52	604
340	10.2	10.35	86.10	123
850	8.8	12.03	79.04	668
325	9.7	12.17	85.93	60
669	9.1	13.67	73.83	761
1200	11.8	15.76	77.41	967
1740	10.8	17.34	78.32	816
83	8.1	20.80	72.12	47
5020	9.5	21.94	71.73	3019
350	10.1	28.03	58.92	461
1150	9.8	28.42	62.81	988
57	10.1	28.67	66.33	29
183	14.3	29.52	66.98	91
1175	8.8	29.93	67.15	302
370	9.1	31.18	68.44	13
1622	12.1	35.92	7.08	11186
483	9.9	40.94	55.43	173
1600	6.1	41.77	45.57	1235
1800	4.0	44.90	46.94	587
1800	12.0	51.91	6.08	9073
25	11.1	52.25	27.03	59
240	10.2	52.91	24.45	554
13000	10.5	53.21	12.65	55364
481	10.3	53.35	35.67	544
800	11.1	54.99	10.47	3067
750	9.4	56.35	11.09	2295
6250	9.9	61.38	5.78	20319
1020	10.0	63.93	15.43	2105
750	10.8	64.05	5.48	2468
4600	11.4	64.20	5.34	15974
45	8.7	67.69	5.38	105
575	10.6	69.58	22.73	468
1400	10.2	72.00	5.80	3170
1002	12.9	73.10	3.14	3071
50	7.3	73.59	14.44	43
7500	12.2	74.30	6.82	17276
$\bar{X}$= 1695	10.01	41.30†	38.40†	4391
S.D.=2680	1.90	23.90†	35.41†	10444

†Statistics based on arc sin angular transformation.

Table 2. Statistics on pod crops of *Acacia farnesiana* in the diffuse stand (n = 11). For comparison with pod crops in the dense stand see Table 1 (see text for details). t values for differences between dense and diffuse stands are provided, all of which are significant.

Number of pods on tree (est.)	$\overline{X}$ of seeds/pod	% seeds killed by bruchids	% seeds "aborted"	Number of viable seeds produced by tree (est.)
8	7.1	46.00	50.00	31
29	8.4	46.21	31.15	131
300	9.6	50.47	1.89	1427
20	8.6	53.33	5.00	80
23	7.2	55.41	21.23	74
270	9.0	56.96	42.62	1174
200	7.8	58.10	37.71	654
82	11.2	61.88	18.06	350
26	7.4	65.10	30.73	67
91	7.1	69.76	15.73	195
1600	6.2	76.77	13.03	2304
$\overline{X}$= 240	8.25	58.35†	21.23†	301
S.D.= 463	1.51	11.56†	18.65†	540
t_{45df}= 3.1090**	2.872***	3.4049***	2.1714*	2.3335*

†Statistics based on arc sin angular transformation.

Numbers of Pods per Tree

There are two distinctly different potential causes for the greater numbers of pods on the clumped trees. First, the clumped trees could be growing on a site in which *A. farnesiana* adults can harvest more resources than in the diffuse area. While the crowns of the *A. farnesiana* in the diffuse area were not noticeably more crowded by themselves or other species than in the clumped area, one can say nothing of root competition, soil nutrients, soil drainage regimes, drought impacts, etc. One could even argue that the rarity of adults in the diffuse area is a reflection of this, operating through the difficulty of seed becoming established in that micro-site. However, such a conclusion is confounded by the fact that the adults in the clumped site are producing nearly 15 times as many viable seeds as are the adults in the diffuse site (though it is clear that this need not necessarily lead to a higher density of adults). Such a "resource hypothesis" would be very hard to test unless it happens to be that the nutrients in short supply could be replaced by fertilizers.

Second, the widely spaced trees could be directly pollinator-limited. I am reluctant to accept this as a general reason for small seed crops, as it appears that a tree species would soon adjust its degree of selfing to pollinator ability. However, it can obviously be a cause of small seed crops for small fractions of the population, especially if they carry the genetic material possessed by the majority of the population, a majority that is not normally pollinator-limited. In the case discussed here, it is quite possible that the dense clump, when in flower, produced a very large pollen resource, one in which it was more profitable to forage than the scattered *A. farnesiana* a short distance away.

The third possibility is that dispersal agents are removing the pods much more rapidly from beneath the widely spaced *A. farnesiana*. This possibility was appreciated at the time, and I searched the acacia crowns to see if the numbers of infructescence stalks in the crown was in approximate agreement with the numbers of pods on the ground. It was, so this possibility must be rejected.

With the data at hand, there is no way of choosing between one of the first two hypotheses. This is so even if the inflorescence scars can still be counted. If the scattered trees are genetically programmed for life in the habitat containing the high concentration of *A. farnesiana*, they may well bear flowers in numbers appropriate to the pollinators that normally frequent such dense stands, and may produce flowers in numbers appropriate to the size of seed crop that can be produced by the energy reserves of a plant growing in such a site. However, just as mentioned above for the resource hypothesis, the pollinator hypothesis can be easily tested. One simply has to hand-pollinate the flowers of the scattered plants and then examine the size of the viable seed crop.

There is, however, an even more confusing alternative available. If the widely scattered plants are "programmed for a scattered life", with their flower crops adjusted to both the numbers of pollinators that normally come to the plants, and to the amounts of reserves normally gathered by such plants, then hand-pollination could give a quite false impression of what is going on. The plants might well set more seed and then come to vegetative disaster during the following dry season, or in the next severe crown competition to which they were subjected. I would have concluded that they were pollinator-limited, when in fact they are energy-limited but have not evolved a mechanism to "know" when too many pods have been set and depend on the low pollinator activity to determine this. However, I personally doubt that wild plants become quite so dependent on external factors with such high a potential variance as the number of bees to arrive at a flowering tree from year to year. I should at this time point out that no one has ever recorded this parameter for a tropical plant (and I have never seen such information for a mid-latitude plant). By the same token, it seems highly unlikely that a tree would rely on having the same amount of resources accumulate each year with which to make fruits. Perennial plants must therefore have some internal mechanism to decide how many pods can be set with the reserves of a given year, and they must do it early in the progression of flower primordia to bud to flower to immature pod.

Numbers of Seeds per Pod

This is a most perplexing parameter. Numerous selective forces potentially affect the phenotypic trait "numbers of bits into which the total seed crop is divided".

As the number of seeds per pod declines, the amount of resources (pod walls, pod sugars, pod pulp) expended per seed increases. I hasten to add however, that the amount "spent" per seed *dispersed* need not necessarily increase. This depends entirely on how the dispersal agent community as a whole responds to small packages, large packages, or some size distribution of packages. As the actual animals (how many of what species) to arrive at a given tree depend on that tree's exact location, the tree genotype can be molded only toward some sort of "average" pod crop and dispersal. The variance in seeds per pod that we see among the *A. farnesiana* in each of the sites may be the outcome of direct selection for variance, or the outcome of various selective factors tugging in different directions, or some more horrendous combination of the two. The differences between the two sites can thus be a result of active selection, if each of the two habitats represents a distinct deme. I think this is not likely, though genetic differences between such proximate portions of a plant species are certainly well known. On the other hand, the difference in mean numbers of seeds per pod could also be simply the result of the two factors discussed in the previous section, to wit, either the trees are starving or not enough pollen grains are arriving on the stigmas.

Unfortunately, we have no idea if tropical trees vary the numbers of seeds per pod as the resources available to the tree vary. However, it is quite conceivable that the ability of the tree to attract dispersal agents changes as the pod crop size declines, and with a different array of dispersal agents arriving, the optimal number of seeds per pod should be different. It should be noted that the number of seeds per pod declines in two ways with *A. farnesiana*. On the one hand, there may be fewer seeds in a pod of the same apparent size, and on the other hand, there may be smaller (shorter) pods. Both cases occurred in the samples at hand, but such a distinction was not made in the original census. It was quite obvious, however, that certain trees produced almost entirely very short pods, and other trees produced almost entirely very long pods; this difference in pod length is largely responsible for the differences in mean numbers of seeds per pod from tree to tree, and this in turn means that the widely spaced *A. farnesiana* trees more often had short pods than did the *A. farnesiana* in the dense clump. This conclusion, incidentally, implies that it is reserves that are in short supply rather than pollinators, because if it is only pollinators, there would be no reason for those flowers that *were* pollinated to produce small pods. Furthermore, if it were the number of pollen grains arriving at the stigma that was setting the numbers of seeds at a lower level, then we would expect a high variance in the sizes of pods within a crop, rather than for some trees to have many short pods and other trees to have many long pods.

The bruchids have to be considered as part of the selection for numbers of seeds per pod as well. They figure in two ways. First, if fruit size is important in the *rate* at which seeds are removed from the tree, then a factor in selection for an optimal fruit size will be that the longer the pods stay at the tree, the more seeds will be killed by the bruchids. Second, it is quite possible that there is an optimal distribution of pod sizes (or seeds among the pods) that minimizes the number of seeds actually gotten by the bruchids before dispersal.

Forgetting the dispersal agents and developmental impossibilities for a moment, we may imagine at one extreme the seeds contained in a small number of 1 to 2 meter long pods. At the other extreme, each infructescence could be festooned with 2 cm long pods, each containing only a couple of seeds. If the ends of the pods were done up economically, the many-pod morph might cost little more than the long-pod morph. There is no information that would allow me to determine which of these two extremes might lose the most seeds to *Mimosestes sallaei* and *M. immunis*. These two beetles lay their single eggs at short intervals along the pods and there is no obvious way that one pod structure would result in fewer bruchid-killed seeds than the other. If the pod were long, then the bruchid could simply walk along it laying eggs. When the pods are divided into many small pieces, the bruchid could walk down one, then to the next, and so on.

It is possible that there are external factors operating. A bruchid on the two different pod types could be exposed quite differentially to predators. I cannot, however, see how one of these two contrasting pod types could favor hymenopteran parasitoids (to say nothing of the fact that I cannot recognize how it would be selected for even if it did, provided that the bruchid killed the seed before the parasitoid killed the bruchid).

Finally, we must add that the physiological and developmental costs of the two extreme types of pods should be considered. There are numerous legume pods with many more seeds per pod than that of *A. farnesiana*, and likewise, many with far fewer. This does not free us from the problem that as the selection pressure for a larger number of seeds per pod slides upward, the physiological cost of responding to it also increases, through such things as having to increase the average number of pollen grains (or the size of the polyad) that hit the stigma, which may in turn require changes in the floral attraction to attract a different set of pollinators, etc.

Percent Seeds Dying

This apparently simple parameter has turned out to be the most confusing of the lot. The per cent aborted seeds is significantly lower in the widely scattered acacias but the percent aborted seeds is significantly lower in the widely scattered acacias but the percent unambiguously bruchid-killed seeds is significantly greater to a degree such as to exactly complement the abortion percentage; in the dense acacia site, 21.30% of the seeds were viable and in the diffuse acacia site, 21.35% of the seeds were viable.

The most attractive hypothesis is that the plant aborts a seed when a bruchid larva enters it, if seed development has not progressed past a certain point. If this hypothesis represents the real world, then it suggests that either the pods in the diffuse stand mature earlier or that the bruchids find the pods later in their maturation cycle. Whichever the case, the bruchids kill the same number of seeds in the end in both stands. This simply suggests that from the bruchid's standpoint, the acacias in the diffuse stand are not far enough apart to cause a reduction in seed predation, *at the smaller sizes of seed crops found in the diffuse stand.* If the average seed crop per acacia in the diffuse stand had been the same as that in the dense clump, then it seems reasonable that there might have been a lower percent mortality in the diffuse stand. This assumes that a single tree with a large pod crop is not as conspicuous (in its odor) as is a clump of *A. farnesiana* in fruit.

A second reasonable hypothesis is that the bruchids may search out pods or trees with a low number of aborted seeds. This appears less likely, but should not be discounted. If this should turn out to be the case, then it suggests that the very large number of pods present in the dense clump habitat have satiated the bruchids' ovipositional ability to some degree. It also requires an explanation for why the physiological abortion rate should be lower in the widely spaced plants. A lower physiological abortion rate in the widely spaced acacias would favor the idea that they are pollinator-limited rather than resource-limited.

CARRYING CAPACITY

It is tempting to intuitively consider the number of bruchids generated by the host population's seed crop each season as a primary parameter in determining how many bruchids arrive at the seed crop in the next season. This, however, assumes that the adult mortality between seed crops takes some fairly consistent form each year, and may be practically considered to be independent of host and bruchid density. The latter assumption requires that any one species of adult bruchid makes up such a small portion of any general predator's diet that even if the beetles were to be abnormally common, it is unlikely that a generalist would temporarily specialize on them. Furthermore, there do not appear to be any specialist (arthropod or vertebrate) predators on adult bruchids moving in the habitat at large. However, there are two things wrong with such a simplistic view. First, the adult bruchids (at least some species) do take nectar and pollen from hosts and this may be a resource for which they compete as adults (nectar and pollen fed to laboratory bruchids increases both longevity and fecundity). Second, the adult beetles may congregate in particularly desirable sites in the forest and these high density points may attract predators.

Resource Size of Adult Host Plants

Mimosa pigra (Mimosaceae) is a common low shrub in marshy cattle pastures of Guanacaste (and much of lowland Mexico and Central America), where its seeds are attacked by the larvae of *Acanthoscelides pigrae*, a small bruchid host-specific to *M. pigra*. The natural habitat of this plant is marshy areas along frequently flooding rivers and on river banks. At Palo Verde, mature pods may be found on the plant from late July through March, and the first flowers appear at the beginning of the rainy season (April-May). A new crop of flowers is produced each day. The adult bruchids may be found on the flowers at dawn, appearing to feed on the pollen.

To examine how many adult beetles are associated with a flowering plant, an isolated *M. pigra* bush was selected at the south end of the pasture immediately to the south of the Palo Verde Field Station mentioned previously. The nearest other *M. pigra* bushes were 212 meters away, and these bushes formed a dense patch of about one half hectare in area (i.e., a very large potential source of *A. pigrae*). On the mornings of July 10 to 12, in 1971, I collected all the beetles on all the flowers, for totals of 312, 289, and 314 adults. On the mornings of July 13 to 16, I caught only 26, 19, 24, and 25 beetles. On the mornings of July 17 to 22, I caught the beetles but released them afterward at the center of the bush. The numbers were 24, 41, 72, 69, 136, and 105. It rained on the nights of July 19-20 and 21-22, the two nights preceding mornings in which the beetle numbers did not increase. I interpret these results to mean that the shrub had a carrying capacity of about 300 beetles, and the "island" had an immigration rate of about 20 to 30 adult beetles per night, except when it rained. (This plant would produce a minimum of 60,000 seeds during this fruiting season.)

It seems evident that in this example, conditions were crowded enough somewhere, a good two months after the last seed crop, for the beetles to be migrating among the plants that were to be their oviposition hosts as well as the adult food hosts. In migrating, they expose themselves to a wide variety of mortality factors which can in this sense be viewed as density-dependent. Furthermore, once they arrive at a bush, it appears that the carrying capacity of the inflorescences is very substantially less than that of the bush as a whole, again indicating that conditions may be crowded on the inflorescences.

It should be noted here, however, that *M. pigra* is exceptional among the bruchid larval hosts in the deciduous forest in that the adults are abundant on the flowers. Adults are occasionally taken in sweep samples of general vegetation many hundreds of meters from *M. pigra* plants, but they have not been found on the flowers of any other species of plant.

Concentrations of Adults

As reported in a recent sweep sample study of seasonal changes in insect density (Janzen 1975a), large numbers of small beetles may become concentrated on the shaded understory foliage beneath individual evergreen trees in the deciduous forest during the last half of the dry season. A substantial number of these beetles are bruchids and weevils that probably emerged from seeds earlier in the dry season. It is conceivable that an exceptionally large number of bruchids of one species could contribute to causing small insectivorous birds to concentrate their foraging activity at these sites. However, if this is the case, it is also possible for an outbreak of any other species of insect to do the same, which may be one of the multitude of ways in which the upper limits of insect species richness in such a habitat are set.

AVOID THY NEIGHBOR

A core aspect of the theory advanced earlier (Janzen 1970) is that scattered or dispersed seeds are less likely to be found by seed predators than are seeds in the cluster represented by an undispersed seed crop (either still hanging in the tree or merely fallen to the ground below). That such dispersal is effective has been shown with seedlings of a deciduous forest legume (*Dioclea megacarpa*, Janzen 1971c), nuts of a large palm (*Scheelea rostrata*, Wilson and Janzen 1972) and seeds of a sterculiaceous tree (*Sterculia apetala*, Janzen 1972). However, it should be recognized that, just as with the dense and diffuse clumps of *Acacia farnesiana*, there are lower limits to the distances that seeds can be separated and show a reduction in seed predation. An example is offered by *Spondias mombin* (Anacardiaceae).

S. mombin is a common tree in the deciduous forest around the Palo Verde Field Station. It produces large numbers of ripe fruits from the middle to the end of the dry season, fruits that are eaten entire by monkeys (and probably by birds and other mammals). The large multi-seeded woody nuts are then defecated onto the forest floor somewhat cleaned of their outer pulp. At this time, a large undescribed species of *Amblycerus* bruchid searches them out and glues a single egg on each one found. The larva bores in and eats all the seeds. However, with the present density of dispersal agents in this forest, the majority of the fruits end up rotting on the ground below the parent tree. Once the fruit has rotted off, the *Amblycerus* oviposits on them just as if the fruit had been peeled off by a dispersal agent. This concentration of nuts beneath the parent may be viewed as either a "bruchid sink" that lowers the number of beetles that find the dispersed nuts, or as a "bruchid generator" that probably provides 90% or better of each new generation of bruchids. Incidentally, this is another way that the presence of seed dispersal agents can clearly affect the density of the seed predator, which may in turn influence the density of adult trees.

To examine the intensity of seed predation directly below the crown of the *S. mombin* trees and compare it with that at the outer edge of the seed shadow produced only by fallen nuts, about 100, 1-2 month old nuts were collected from each position from beneath 12 large *S. mombin* growing in the forest about 4 km northwest of the Palo Verde Field Station. The density of nuts can be as high as 200 in a square meter, directly beneath the crown, but the average is about 20 per square meter. The percent of nuts with *Amblycerus* exit holes at the base of the tree and directly under the outer edge of the crown (4 to 8 meters from the base of the tree) were respectively 26, 26, 22, 16, 11, 48, 44, 8, 23, 61, 14, and 38 ($\overline{X} = 28$), and 35, 19, 28, 10, 5, 45, 46, 13, 20, 57, 12, and 40 ($\overline{X} = 28$). There is no hint of a difference between the two means. Furthermore, if the comparison is made pair-wise, the number of exits from nuts at the base of the tree agrees closely with the number of exits from nuts under the outer margin of the crown. A careful dissection of 523 nuts from below three *S. mombin* show that 26% of the nuts lacking exit holes but with bruchid eggs on them have their seeds killed by a bruchid, but the bruchid died before it could emerge. The remaining 74% of the nuts with eggs on them had aborted or rotted seeds inside (cause unknown, but could well be that the bruchid larva attacks the seed and then dies while too small to be seen later on in the decomposing material, as happens with bruchids in *Scheelea* palm seeds). If we add the nuts with eggs on them to the nuts with exit holes, as an absolute measure of how many nuts were at least found by an *Amblycerus* bruchid, the respective percentages are 36, 50, 55, 60, 60, 66, 50, 27, 46, 71, 36, and 45 ($\overline{X} = 50$) for the nuts at the base of the tree, and 41, 49, 49, 58, 19, 69, 46, 43, 30, 61, 26, and 46 ($\overline{X} = 45$) for the nuts under the outer edge of the crown. The differences in the means are not significant. To understand why the remaining 50 percent of the seeds did not generate a large seedling shadow beneath the parent trees, I should point out that of the 523 nuts mentioned above, only 4 contained a viable seed (4% of the 102 seeds that had neither *Amblycerus* exits nor eggs on the outside).

HOST SPECIFICITY

In the Guanacaste deciduous forest, the insects that breed in seeds show amazing specificity. I should add that I have seen nothing in other tropical vegetation to suggest that this is a phenomenon peculiar to Guanacaste deciduous forest. Detailed documentation of this specificity is still in progress, but it seems reasonable to present a preliminary view here as there is no indication that completion of the study will drastically change the picture (the data given here are a refinement on the first approximations mentioned in Janzen 1973a,b; 1974b).

In a flora with about 300 to 400 species of plants (excluding grasses) with seeds large enough for a bruchid or other seed-eating insect to develop in, I can state with certainty that at least 69 species have no pre-dispersal seed predation by insects, 69 species have one or more species of bruchids, 6 have weevils, 2 have cerambycids, and 5 have moth larvae (excluding seed chalcids). In addition, at least 20 other species of bruchids have been collected in and around the forest but their hosts are unknown. This means that a minimum of about 25 to 33% of all the plant species in the deciduous forest suffer considerably from pre-dispersal seed predation by insects that develop in the seeds. If we consider only the large woody plants, this figure moves upward to between 50 and 75%. There is one major source of pre-dispersal seed predation by insects that is not considered here; bugs (Hemiptera) take a very large number of developing embryos of certain species (these are often recorded as aborted seeds) and weevils (Curculionidae) develop in flower buds of many species. We can ask two questions of this information. How are the bruchids distributed among the plants, and how are the plants distributed among the bruchids?

Among the 88 bruchid species whose hosts are known with certainty to date, 73 (83%) have only one host species. All the weevils and cerambycids have only one host species. Thirteen species of bruchids (15%) have 2 hosts (e.g., *Gibbobruchus guanacaste* in *Bauhinia pauletia* and *B. ungulata*, *Amblycerus championi* in *Cordia dentata* and *C. panamensis*, *Acanthoscelides kingsolveri* in two species of *Indigofera*, *Ctenocolum tuberculatum* in *Lonchocarpus costaricensis* and *L. minimiflorus*, and *Megacerus leucospilus* in *Ipomoea pes-caprae* and *I. fistulosa*). One bruchid has three hosts (*Ctenocolum crotonae* in *Lonchocarpus costaricensis*, *Lonchocarpus minimiflorus*, and *Piscidia carthagenensis*) and one has eight and perhaps more (*Stator limbatus* in *Pithecellobium saman*, *Pithecellobium dulce*, two species of *Albizia*, two species of *Lysiloma*, and two species of *Acacia*). All indications are that location of the hosts of the twenty or so un-reared species will swell the "one host only" category.

There are undoubtedly a number of components to the answer to why these seed predators are so host-specific. Certainly it is not the mere outcome of segregation by habitat; with careful collecting, as many as 40 species of bruchids may be reared from the seeds in a five hectare plot, and 22 species were taken in one forest understory sweep sample of 800 sweeps (dry season, Palo Verde, study reported in Janzen 1975a and below). On the other hand, in over half of the cases where a bruchid occurs in two species, the two species of plants are quite definitely habitat-segregated. A conspicuous example is *Megacerus leucospilus* in the seeds of *Ipomoea pes-caprae* growing on ocean dunes and in the seeds of *Ipomoea fistulosa* growing in freshwater marshes along the Rio Tempisque.

Competition among bruchids within a species of plant may contribute to the host specificity. If we regard those species with bruchids as in some sense available, the bruchids appear to be quite evenly distributed among them; of 69 host species, 55% have one bruchid and 35% have two bruchids, while only 7% have 3 bruchids and 3% have 4 bruchids. This concentration of 90% of the plants in the 1 or 2 bruchid range implies that if the numbers rise over two species, inter-bruchid species competition may become very severe. In all cases of 3 or 4 bruchids per host plant species, at least 90% of the bruchids reared from seed samples belong to two species. Such competition may be selecting in favor of specialists by selecting for maximal efficiency on a given host.

The most obvious candidate for a major cause of the specialization is the need to specialize to overcome the chemical, behavioral and morphological peculiarities of the host plant. In short, one is forced to postulate that as the plant becomes better defended (selected for by past generations of bruchids), the beetle has to be progressively more specialized to stay with its host. The more specialized it is on one host, the more difficult it should then be for it to also be adequately specialized to attack a second host. Such incompatibility may take two forms. (1) The critical traits of the attacker of two host species may be chemically difficult to possess simultaneously. For example, the enzyme system that breaks down the toxic secondary compounds in one species' seeds may be biochemically incompatible with the enzyme system necessary to break down the secondary compounds in the seeds of the second host species. Again, to locate the pods of one species, the female bruchid might have to search in moist and dark micro-habitats (e.g., *Spondias mombin* nuts being sought by *Amblycerus* on the forest floor) and in sunny and dry habitats for the other (e.g., *Combretum farinosum* fruits being sought by *Amblycerus* high in a deciduous forest canopy). (2) The critical traits of the attacker of two host species may be energetically (or nutritionally) difficult to maintain simultaneously. For example, it may be energetically very difficult for *Caryedes brasiliensis* to have the enzyme system to both deal with seeds with 5 to 10% canavanine in them (which it does when feeding on *Dioclea megacarpa*, Janzen 1971c) and seeds with a 5 to 10% concentration of L-DOPA as found in *Mucuna andreana* (Bell and Janzen 1971), which grows in nearby habitats and has pods and seeds similar to those of *D. megacarpa*.

In the previous paragraph I was careful not to imply that any combination of attacking abilities is impossible in any absolute sense, as it is clearly not. *Stator limbatus* is the most amazing in this respect. It is clearly a specialist at laying its eggs directly on the exposed but undispersed seeds of four genera of mimosaceous legumes. Associated with this, however, it must be able to deal with the alkaloid pithecolobine in *Pithecellobium saman* seeds (Magnus and Seaforth 1965), the uncommon amino acid albizziine in *Albizia* seeds, and probably other secondary compounds in *Lysiloma* and *Acacia* seeds. In all the other cases of 2 or 3 hosts being attacked by one bruchid, the females oviposit on the intact fruit (and the larvae bore through the fruit wall to the seeds inside), and in all cases the fruits of the two or three hosts are very similar in shape, texture, thickness, size, and odor. The pair of hosts are also congeneric in all cases but one (*Lonchocarpus* and *Piscidia*). Center and Johnson (1974) have recently stressed the fruit wall as a major barrier to bruchid entry, and these results support that emphasis.

There are five ways to get at the role of seed chemistry in this extreme host specificity.

(1) We can ask how readily the bruchids transfer onto introduced species of plants. I have only one example to contribute, that of the shrub *Cassia alata* (which may be native to Central America, but is certainly not wild in the Guanacaste deciduous forest). *C. alata* in gardens very rarely have an *Amblycerus* and a *Sennius* in their seeds, bruchid species that normally live in one or two species of herbaceous weedy *Cassia* that have pods very different from those of *Cassia alata* in superficial aspect. Since

the native and introduced *Cassia* probably have very similar seed chemistry, this example is of very little use. In general, however, it can be stated that none of the numerous introduced legumes (e.g., *Delonix regia*, *Caesalpinia* sp., *Erythrina* spp., *Phaseolus vulgaris*, *Lathyrus* sp.) in Guanacaste have had indigenous bruchids move onto them.

(2) We can ask what happens when a wild female beetle accidentally oviposits on the "wrong" host. The technology of this situation is almost impossible since the only time that a record will be obtained is if the bruchid larva survives. (For the most part, bruchid eggs on the fruit or seed cannot be identified with ease.) However, in all the tens of thousands of bruchids that have been reared to date in this study, I have only one unambiguous case of a bruchid being reared from seeds of a wild plant other than its usual host. At Finca Taboga in southern Guanacaste, R. Carroll found a pile of howler monkey feces containing nuts of *Spondias mombin* (Anacardiaceae) and the similar-sized seeds of *Eugenia salamensis* (*Psidium rensonianum*; Myrtaceae). The site smelled strongly of *S. mombin* fruits. There were 78 *S. mombin* nuts with *Amblycerus* eggs on them and 6 *E. salamensis* seeds with one *Amblycerus* egg on each (out of a total of 354 *E. salamensis* seeds and 197 *S. mombin* nuts). During the following months, the *Amblycerus* emerged from 71 of the *S. mombin* nuts and a single adult emerged from each of 5 of the *E. salamensis* seeds. A bruchid has never been reared from any other of thousands of *E. salamensis* seeds, though an undescribed weevil kills about 5% of large seed crops.

(3) A small amount of data has been gathered about the outcome of offering a female bruchid a series of seeds of wild hosts from her habitat on which to oviposit, but this method has not been exploited fully owing to the difficulty of maintaining most wild bruchids as laboratory colonies. *Mimosestes sallaei* females have been found to oviposit on almost any large smooth round seed if there are *Acacia farnesiana* seeds present in the same container. One experiment has shown that the larvae from eggs laid in this manner can survive in *Acacia cornigera* and *Acacia collinsii* seeds (both occur in the same general habitat with *A. farnesiana*, both are attacked by Bruchids, but neither is attacked by *M. sallaei* in nature). *M. sallaei* do not survive in seeds of *Enterolobium cyclocarpum* (containing albizziine), *Mucuna andreana* (containing L-DOPA), *Caesalpinia crista* (=*Guilandina crista*, containing gamma-methylglutamic acid), *Canavalia maritima* (containing canavanine), *Schizolobium parahybum* (containing schizolobine), *Dioclea megacarpa* (containing canavanine). Only the last mentioned species of plant has a bruchid in its seeds, but all occur within the flight range of *M. sallaei* and none have pod walls thicker or noticeably tougher than those of *Acacia farnesiana*.

(4) A descriptive analysis of seed secondary compound content

over an entire habitat would probably be helpful, but not definitive. If all the seeds in a habitat were found to have similar or the same secondary compounds in them, it would be unlikely that the bruchids would be specific on account of seed chemistry. This analysis is still underway, but it is clear that the diversity of secondary compounds is at the level of about 5 different major constituents for each 10 species of seeds. In addition to the major compounds occurring at 3 to 10% concentration, there are often others that occur at lower concentrations, to say nothing of the concentration of lectins, heteropolysaccharides, endopeptidases, and saponins, all of which occur in bruchid host (and non-host) seeds, are toxic to certain bruchids, and have not yet been extensively sought in seeds of Guanacaste legumes.

(5) Secondary compounds from seeds can be incorporated in bruchid artificial diets, and such a study is currently underway in collaboration with E. A. Bell (nitrogenous secondary compounds) and I. E. Liener (lectins or phytohaemagglutinins). I chose *Callosobruchus maculatus* (stock obtained from the USDA Stored Products Insect Research and Development Laboratory, Dr. E. Jay) since this bruchid is easily reared in the laboratory and feeds readily on black-eye pea seeds (*Vigna unguiculata*) which have no alkaloids or uncommon amino acids. This bruchid may be viewed as biochemically/physiologically naive, and therefore a test of putative seed toxins on its larvae may represent what happens when a wild bruchid lays its eggs on the seeds of a non-host.

The logistics of testing are very straightforward. A Wiley mill in the University of Michigan College of Pharmacy is used to reduce dry black-eyed peas to fine flour. For control seeds, this flour is used to hand make cylindrical tablets 13 mm in diameter and 7 mm deep with a mechanical pill press (also from the College of Pharmacy). The females oviposit readily on these pills when placed in jars containing stock *C. maculatus* cultures (they also oviposit on just about any other smooth surface). All eggs but ten are removed from the pill, so as to adjust the number of developing larvae to where there will be very little intra-specific competition. An average of five to six adults emerge from the ten eggs on such a pill. For the experimental pills, shortly before the pill is made, the secondary compound is mixed in a dry powder form with the flour. To date, experiments have been with 0.1, 1, and 5% concentration of secondary compounds, as this is the range of concentrations at which secondary compounds normally occur in seeds in nature. The pills plus eggs are cultured at 80% RH at room temperature; such care is not necessary for intact seeds but the pills dry out much more rapidly than do intact seeds.

The results to date are incomplete in coverage of the secondary compounds found in Guanacaste bruchid hosts and non-hosts, but provide some interesting previews. For example, lectins or phytohaemagglutinins, compounds well known to be toxic to mammals when taken orally (as well as intravenously) (Liener 1974) have been shown to be toxic to an insect seed predator for the first time. When black bean lectin (*Phaseolus vulgaris* from Guatemala) is incorporated in the pills at 5% concentration it is lethal, and only two beetles emerged from five pills with 1% concentration (at 0.1%, emergence is indistinguishable from the controls).

Alkaloids incorporated in the pills may be even more lethal. Colchicine kills all larvae at 0.1% concentration, and caffeine at the same concentration produced only four adult beetles out of five pills. Caffeine is lethal at 1% concentration. It is appropriate to add here that the beetles that are produced on these marginally toxic diets have not been checked for reproductive abilities, but may well have reduced reproductive fitness.

Uncommon amino acids have been most extensively tested to date, and have produced the most confusing (and interesting) results. The following uncommon amino acids from seeds are lethal at 1% concentrations: L-DOPA, β-aminopropionitrile fumarate, L-djenkolic acid, N-methyl tyrosine, β-cyano-L-alanine, and L-mimosine. All of these also show very severe reduction in emergence at 0.1% concentrations. A moderate reduction in bruchid emergence was obtained with 1% concentrations of canavanine, albizziine, D,L-2, 4-diaminobutyric acid, γ-methylglutamic acid, and m-carboxyphenylalanine. These and others are being tested at the 5% concentration, and canavanine, γ-methylglutamic acid, and m-carboxyphenylalanine are lethal at these concentrations. However, it should be added that D,L-pipecolic acid, L-homoarginine, and S-carboxyethylcysteine at 1% concentrations had no visible effect on the bruchids. In short, the effects are highly variable, concentration dependent, but largely toxic at some level representative of that found in seeds.

A second form of control, especially appropriate to the question of whether uncommon amino acids in seeds are merely nitrogen storage compounds, or defense mechanisms, or both (see Rosenthal 1972 for an example of both in *Canavalia* seeds with canavanine in them), is to see what effect protein amino acids have on *Callosobruchus maculatus*. At the 5% concentration, we have found the L-isomers of tyrosine, tryptophan hydroxyproline, aspartic acid, cystine, and methionine to be lethal, the L-isomers of cysteine, leucine, isoleucine and histidine to be mildly depressant, and the L-isomers of arginine, alanine, glutamine, threonine, proline, glutamic acid, phenylalanine, asparagine, and valine to have no obvious ill effect. It was expected that a 5% concentration would have no effect on *C. maculatus*, and so now the toxic protein amino acids are being tried at 1% concentration. These results emphasize that simple nutrient imbalances among species of seeds could be enough for toxicity. It is of particular interest here that tryptophan, cystine and methionine occur in exceptionally low concentrations in black-eyed peas (e.g., Johnson and Raymond 1964, Evans and Bandemer 1967, Sevilla-Eusebio et al. 1968).

HYPERPARASITOIDS

Any discussion of the coevolution of parasitoids and their hosts, or predators and their prey must take into account their hyperparasitoids or parasites. If we view the bruchids in the seeds as parasitoids, then the parasitoids that they have may be viewed as hyperparasitoids. In the Guanacaste dry forest, all bruchid hyperparasitoids reared to date have been Hymenoptera. However, just as one does not expect all arthropod parasitoids to have hyperparasitoids, not all bruchids have hyperparasitoids. In fact, none have emerged from the seed collections for at least 35% of the 73 bruchid species mentioned earlier. From another 38%, only one or two individual hymenopterans have been reared from collections that produced hundreds to thousands of bruchids. Even in the remainder, there is little suggestion that the hyperparasitoids are taking more than 10 to 20% of the bruchids (I hasten to add, of course, that such a low percent mortality may be of great significance in the population dynamics of the host, but it need not necessarily be the case). It should be added here that I have not made a conscious effort to locate egg parasites, and some undoubtedly exist. However, in collecting pod samples in the field, egg parasites would normally be picked up along with the rest. As will be discussed at the end of this section, low or zero levels of parasitization of tropical insects may be commonplace; the following paragraphs are directed at why they are so low among Guanacaste Bruchidae (there is no hint of such a phenomenon among North American Bruchidae).

The absence of hyperparasitoids is associated in one case with the presence of an effective disease. The two bruchids in *Scheelea rostrata* (Palmae) seeds have no hyperparasitoids (11,000 nuts examined, Janzen 1971b) but as high as 65% of the larvae and pupae may die in a sample of nuts. These dead immatures have their insides reduced to a milky fluid that resembles the insides of a Japanese beetle killed by milky spore disease. Presumably the disease is transmitted through contamination of the female bruchid or nut surface by bacterial spores from the litter containing rotted palm nuts. This is the only disease of a bruchid to be found in the Guanacaste deciduous forest (though the apparently hyperparasitoid-free larvae of the weevils in *Andira enermis* seeds have an effective fungus disease) and this bruchid's habitat is the wettest of all bruchid microhabitats. I assume that the easily accessible *Scheelea* nut bruchids (they are in the nuts for 2 to 10 months) are not attacked by a hymenopteran hyperparasitoid because they would be either "eaten" by the disease or indirectly outcompeted by it. It would seem virtually impossible for the hymenopteran to outcompete the bacterium yet allow the bruchid larva to live long enough to cut its exit hole out of the hard palm nut.

I turn to properties of the bruchid-seed interaction to explain the other cases of low or zero hyperparasitization of bruchids. Some thoroughly examined cases are the following. *Cassia grandis* has three species of bruchids in its seeds, none of which have hyperparasites in Guanacaste (though the egg clusters of *Pygiopachymerus lineola* are very rarely attacked by an unknown hymenopteran, Janzen 1971d). *Pithecellobium saman* has one bruchid (*Merobruchus columbinus*) that kills 40 to 80% of its immense seed crops (a large tree may produce 150,000 seeds annually) and no parasites have been reared from 85 samples of 100-plus pods taken over a three year period. The bruchids have been reared out of 23,285 fruits of *Guazuma ulmifolia* (samples from 206 trees in six major habitats) and the two species of bruchids infesting as high as 99% of these seed crops had no hyperparasites (Janzen 1975b). Of thousands of *Amblycerus* bruchids reared from *Cassia emarginata* pods, there have been only two large Chalcidae, of a species customarily reared from a wide variety of Lepidoptera pupae. A sample of better than 20,000 *Mimosestes* reared from *Caesalpinia coriaria* pods had no hyperparasitoids.

Examples such as these are probably explained by the interaction of several factors. To be a bruchid hyperparasitoid, the hymenopteran must not only be able to survive in the bruchid larva (which may be complicated by the presence of secondary compounds in the larva) but it must be able to get to the larva. However, the more species of bruchids there are in the habitat, the more species of bruchids the hymenopteran will have to be able to attack in order to be able to accumulate enough hosts to stay in the game. The need for this increased generality is predicted because the more species of bruchids there are in the habitat, the fewer individuals there are on the average in each one of them. However, versatility is difficult in the best of times. As the bruchids are distributed among a very wide variety of seed chemistries, pod morphologies, fruiting phenologies, microhabitats, seed morphologies, developmental times, etc., it should be difficult for any one hyperparasite species to accumulate enough attackable bruchids. The more this is true, the more likely the community is to contain some totally hyperparasite-free bruchids. In short, at the upper numbers of plant and bruchid species in a habitat, the number of hyperparasite species operating on them should decrease.

The previous paragraph can be transliterated into an even more general case. Assume a gradient from one very common host species to a moderate number of moderately common host species to a very large number of quite scarce host species. Likewise assume that the total biomass of hosts does not change over this gradient. The number of parasitoids that can be supported along this gradient is expected to rise first toward the middle, and then at the limit fall off to a point considerably lower even than it started out. I view the moderate numbers of bruchid species to be found in southwestern North America, each with several species of hyperparasites, as representing the peak in this curve. The more distinctive is the average host species along this gradient, the more rapidly and severely I expect the numbers of parasitoids to decline at the upper levels of host species richness. Likewise, the more fluctuating (predictably and unpredictably) the physical environment along this gradient, the more rapidly and severely I expect the numbers of parasitoids to decline at the upper levels of host species richness. Thus, for example, I expect the deciduous tropical forest with *n* (large numbers) species of hosts to have as few species of parasitoids as an adjacent evergreen tropical forest with *2n* species of hosts, even if the total annual production of host biomass was the same in both sites.

Following this type of reasoning, I expect a number of Guanacaste bruchids to be very common (in most years) yet have no hyperparasitoids, simply because on some years the prey density falls to very close to zero. In short, I am saying that the more the availability of a lower member of the food chain fluctuates the density, the fewer specialists can survive at higher levels in that food chain. As a case in point, there was a general drought over much of Guanacaste at the beginning of the rainy season in 1971. In many areas it was sufficiently severe to cause the abortion of almost all pod crops of *Pithecellobium saman*. How *Merobruchus columbinus*, the host-specific seed predator of *P. saman*, managed to survive is not clear (it probably re-immigrated from neighboring areas of less severe drought), but I can easily envisage that a host-specific hyperparasitoid would have had an even more difficult time surviving.

The Guanacaste deciduous forest contains some other spectacular examples of freedom from parasitoids. The very large tree *Enterolobium cyclocarpum* frequently has its entire leaf crop eaten off by an unidentified moth larva in early June. One tree may easily contain 20 bushels of caterpillars at a time, and tens of thousands of them pupate under the loose bark and adjacent shelters. Neither the larvae nor the pupae show any sign of emerging parasitoids, though at some trees large numbers die of a disease. I have seen at least five similar cases of other major defoliators without parasitoids. A noteworthy characteristic of these species is that the newly emerged adults do not return to oviposit on the new crop of foliage produced by the defoliated or damaged tree. A tentative hypothesis is suggested by these observations. It may be that the herbivore is genetically programmed for a time when its hosts were much harder to find (rather than being exposed trees poking out of pastures as is currently the case), and total defoliation a much rarer event. When the tree is under heavy competition in the forest, it produces one large new leaf crop (the one that the larvae feed on), and then turns off new leaf production even when a few have been removed by herbivores. In the forest, the herbivore gets one shot at the tree, builds up a moderate population of adults, and stays in the game by being an active adult in reproductive diapause for eleven months until the next new set of leaves appears. Such behavior appears to be adaptive in the context of the individual female, in that she may get more eventual offspring by waiting to oviposit rather than by exposing herself to predators while searching for a few new leaves, and by not producing caterpillars that would be members of a relatively small overall body of arthropod prey items which would be confronted with an array of predators developed on the burst of prey produced by the big flush of leaves at the beginning of the rainy season.

The hyperparasitoids that *do* survive on Guanacaste deciduous forest bruchids are worthy of much more scrutiny, but this portion of the study is still in an embryonic stage. Inspection of the material reared to date along with the bruchids reveals one conspicuous fact. In strong contrast to the highly host-specific bruchids, a given species of bruchid hyperparasitoid is found in many species of bruchids (and I suspect, in many species of other insects inside of seed pods and similar structures). It is of interest to note here that it is the rare bruchids that should be most seriously affected by such Hymenoptera. For example, the hymenopteran might be presented with an array of 1110 pods per hectare, which might for example contain 1000, 100, and 10 pods of three similar legume species each of which is attacked by a specific bruchid. If it finds 30% of the pods, a 30% reduction in absolute numbers of the rare bruchid is much more likely to be lethal to the population than a similar percent reduction in the common bruchid.

As mentioned at the beginning of this section, the finding that a number of bruchids have no hyperparasitoids and that only a few sustain several species of hymenopterans is in agreement with my general findings with sweep samples of the Costa Rican arthropod community. For example, in an English meadow in July, 800 sweeps produced 225 species of hymenopteran parasitoids, which is better than twice as many species as have been found in any Costa Rican "old field" vegetation with 800 sweeps, and most Costa Rican samples are about one quarter of this. The same English meadow had 2401 individuals in 800 sweeps, which is about 15 times as many as have ever been found in a Costa Rican "old field" site. The only Costa Rican sample that has a similar hymenopteran parasitoid species richness to the English meadow was rainforest understory with twice as many species of prey insects (Janzen and Pond 1975). Similar results were obtained with an elevational transect in the Venezuelan Andes; with increasing elevation, the hymenopteran parasitoid species richness was proportionately the least reduced of all groups, presumably associated with the fact that the numbers of prey individuals per species was highest at the highest elevation (Janzen et al. 1975).

SURVIVING THE INIMICAL SEASON

In the light of our mid-latitude biases, bruchids (and other seed parasitoids) in the Guanacaste deciduous forest do a very peculiar thing. Upon completing larval development, they pupate and emerge within a few weeks. In most species of hosts, there are not adequate numbers of seeds of the appropriate developmental stage for them to produce a second generation. The adults are then active, but reproductively inactive, for 9 to 11 months until the next seed crop appears. Some feed on the nectar and pollen of their host plant's flowers (e.g., *Acanthoscelides pigrae* on *Mimosa pigra* described earlier; *Acanthoscelides oblongoguttatus* takes nectar from the extra-floral nectaries of *Acacia cornigera*, its host in Veracruz, Mexico, Janzen 1967), or on nectar and pollen of other species of flowers. However, most species may be taken by general collecting with a sweep net in vegetation that is neither rich in flowers nor contains the beetle's host plants. Presumably the adults have a lower mortality rate if they actively seek out appropriately moist, cool, or shady microsites, and if they can actively avoid predators, than if they attempt to survive as a dormant individual in the damaged seed or a pupal cell in the ground or litter. In this context, it is of interest that the only Guanacaste bruchids with a conspicuous mortality from a disease are those that wait for long times in palm nuts on moist litter before emerging. Furthermore, the only seed parasitoid with a conspicuous fungal mortality are the two *Cleogonus* weevils that attack *Andira enermis* seeds; the larvae pupate in the moist soil below the seeds and may lose better than 30% of the population to an undescribed species of fungus. In short, I am saying that the seed parasitoids are not exceptions to the general hypothesis (Janzen 1973c) that a large number of tropical insects pass the inimical season as active adults, rather than as dormant individuals.

A few examples of exactly where adult bruchids are during the inimical season in the deciduous forest at Palo Verde are instructive. Adults of the *Acanthoscelides pertinax* group, *A. puellus*, *A. megacornis*, and *Stator pruininus*, and two species of *Apion* and one of *Paragoges* (Curculionidae) have been found hiding in the partially opened dried fruits of *Bixa orellana* (Bixaceae); the seeds have a thin covering of a fatty material and have *Stator championi* as their host-specific seed predator. The large clusters of dry and wind-dispersed *Alvaradoa amorphoides* (Simaroubaceae) fruits have been found to contain adults of *Zabrotes* sp., *Sennius morosus*, *Sennius* sp., two species of *Acanthoscelides*, *Paragoges* and *Phillides* (Curculionidae); *A. amorphoides* has no pre-dispersal seed predators that live in the seeds. Similar arrays of adult bruchids have been found in the dry infructescences of *Triplaris americana* (Polygonaceae), another tree with no pre-dispersal seed predators in its seeds. All three of these records are from the last half of the dry season. A sweep sample of a stand of pure *Baltimora recta* (Compositae) in flower in the middle of the rainy season yielded ten males and eight females of *Caryedes quadridens*, a bruchid that breeds in the dry season pods of *Centrosema plumieri*, a legume vine. Sweeping in nearby more mixed "old field" vegetation yielded *Caryedes quadridens*, *Amblycerus championi*, *Sennius instabilis*, and two species of *Acanthoscelides*; the seed hosts of none of these bruchids were available at that time (mid-July). In the adjacent deciduous forest understory, simultaneous sweeps produced adults of *Caryedes quadridens*, *C. cavatus*, *C. x-liturus*, *Ctenocolum tuberculatum*, two species of *Acanthoscelides*, and a species each of *Amblycerus*, *Zabrotes* and *Dahlibruchus*. With the exception of the last species, whose host is unknown, the seed hosts of none of these bruchids are available for oviposition at that time, and only the *Amblycerus* will eventually find its host (*Spondias mombin* seeds) within a few meters of the vegetation swept. In the middle of the dry season (March) a sweep sample primarily underneath scattered evergreen trees in the same forest site yielded the following adult bruchids: *Caryedes quadridens*, *Merobruchus columbinus*, *M. solitarius*, *Gibbobruchus guanacaste*, *Ctenocolum tuberculatum*, *Megacerus impiger* group, two species of *Zabrotes*, three species of *Stator*, two species of *Amblycerus*, *Acanthoscelides quadridentatus*, *A. megacornis*, *A. pertinax* group, *A.* nr. *brevipes*, *A.* sp., *Sennius instabilis*, *Sennius morosus*, *Mimosestes sallaei* and *M.* sp.; the seed hosts of all of these species are well into their infestation cycle by this time, and oviposition has occurred long ago for most species. These adults were undoubtedly newly emerged adults beginning their long wait until next year's seed crop. It is noteworthy that one of the most common large bruchids in this forest rich in trees of *Guazuma ulmifolia* is its host-specific *Amblycerus cistelinus*. While large numbers of these beetles were emerging from *G. ulmifolia* fruits near the site of the dry season understory sweep samples, not one of these beetles was taken there.

DISTURBANCE

It is fitting to close this paper with a brief discussion of the extreme frustration of trying to understand the coevolution of seeds and their parasitoids in habitats that have been perturbed in various ways by exploitative western agriculture and technology over the last 100 to 300 years (and see Janzen 1973d, 1974c). The problem is rather straightforward. When a set of species evolve with respect to each other for thousands of generations, and part are then removed and the remainder have their densities and other properties (e.g., timing of new leaf production) altered, it becomes extremely difficult to interpret the adaptive significance of many of the characteristics genetically programmed into the individuals. Of course the species that are there are still interacting with each other, and therefore it is quite possible to examine their contemporary ecology, especially from a management viewpoint. However, the generation of ecological principles, to say nothing of evolutionary ones, is almost impossible when working with systems that are not only not at equilibrium, but have been recently pushed off equilibrium to an unknown degree by unknown perturbations. For example, the pastures of Guanacaste are full of swollen-thorn acacias containing three species of obligate acacia-ants (*Pseudomyrmex belti*, *P. ferruginea* and *P. nigrocincta*), all fighting actively over and coexisting on a single very narrowly defined resource; how can one understand species-packing in such a situation when all the physical environmental barriers that probably were once quite important in separating these three species have been obliterated to provide the United States with hamburger?

The bruchid-host interaction is particularly susceptible to the thorough types of habitat and species destruction practiced by modern man. In trying to understand how the sizes and timing of seed crops may have been influenced by the interaction with the bruchid, I need to know how long the seeds of a given crop are available to the bruchid. Except with wind-dispersed species this is no longer possible owing to the effective elimination of all the large dispersal agents. Even where dispersal agents are present, the numbers of seeds they remove is closely related to what other food sources are available, and contemporary deciduous forests with their numerous edges, and old and new fields, are a vastly different food resource base than a relatively undisturbed deciduous forest with scattered indigenous farming efforts. Furthermore, as certain dispersal agents are removed, the less desirable plants will suffer disproportionately to the ones with the more highly desired fruits or seeds. *Rhinochenus transversalis* and *R. stigma* (Curculionidae) used to kill as much as 50% of the seed crop of *Hymenaea courbaril* (Caesalpinaceae) in lowland Guanacaste; now only *R. transversalis* occurs in most *H. courbaril* populations. *R. stigma* is going extinct because it depends on dispersal agents to open the indehiscent pod so it can emerge (cf. Janzen 1974c, an article in which the specific names were accidentally reversed when giving this account). It should be stressed that habitat alteration by man is not a new thing (e.g., Long and Martin 1974), but it is now occurring in the tropics at a rate and intensity far surpassing previous events.

I also need to know how many bruchid females can be expected to arrive at the host plant seed crop. By altering vegetation types and changing the relative abundance of alternate adult food sources, contemporary agriculture undoubtedly increases the numbers arriving at some plants and species, and decreases those arriving at others. A *Scheelea rostrata* palm growing in an open pasture will have its seed crop almost entirely free from bruchid attack, while one growing

20 m away in forest may lose 80% of its seeds (Janzen 1971b). However, *Scheelea rostrata* adults left growing in pastures when the forest is cut are effectively seed-sterile, since the dense seedling shadow is eliminated by the fierce dry season sun. Introduced species from other parts of Central America may be expected to make this part of the story even more confusing. H. Dingle has even suggested that the *Dysdercus* that kills so many seeds of *Sterculia apetala* in Guanacaste (Janzen 1972) may be an introduced species.

The effect of all of this is, of course, to cause one to seek out somewhat less disturbed areas for study, such as Santa Rosa National Park in northern Guanacaste and the forest near the OTS Palo Verde Field Station (COMELCO Ranch) between Bagaces and the Gulf of Nicoya. However, even these sites are ephemeral in the face of irrigation schemes, inflation, population pressures, and private interests of surrounding ranchers. The story is a familiar one, but ecologists have a tendency to think of themselves as racing against time. From what I see around me in the tropics, the race is already lost.

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LITERATURE CITED

Bell, E. A., and D. H. Janzen. 1971. Medical and ecological considerations of L-DOPA and 5-HTP in seeds. Nature 229:136-137.

Center, T. D., and C. D. Johnson. 1974. Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts. Ecology 55:1096-1103.

Evans, R. J., and S. L. Bandemer. 1967. Nutritive value of legume seed proteins. J. Agric. Food Chem. 15:439-443.

Gwynne, M. D. 1969. The nutritive values of *Acacia* pods in relation to *Acacia* seed distribution by ungulates. East Afr. Wildl. J.

7:176-178.

Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249-275.

Janzen, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. U. Kans. Sci. Bull. 47:315-558.

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23:1-27.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104:501-528.

Janzen, D. H. 1971a. Seed predation by animals. Annu. Rev. Ecol. Syst. 2:465-492.

Janzen, D. H. 1971b. The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. Principes 15:89-101.

Janzen, D. H. 1971c. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. Amer. Natur. 105:97-112.

Janzen, D. H. 1971d. Escape of *Cassia grandis* L. beans from predators in time and space. Ecology 52:964-979.

Janzen, D. H. 1972. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. Ecology 53:350-361.

Janzen, D. H. 1973a. Community structure of secondary compounds in plants. Pure Appl. Chem. 34:529-538.

Janzen, D. H. 1973b. Comments on host-specificity of tropical herbivores and its relevance to species richness. p. 201-211. *In* V. H. Heywood, ed. Taxonomy and ecology. Syst. Assoc. Special Vol. No. 5. Academic Press, London.

Janzen, D. H. 1973c. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687-708.

Janzen, D. H. 1973d. Tropical agroecosystems. These habitats are misunderstood by the temperate zones, mismanaged by the tropics. Science 182:1212-1219.

Janzen, D. H. 1974a. Swollen-thorn acacias of Central America. Smithson. Contrib. Bot. No. 13. 131 p.

Janzen, D. H. 1974b. The role of the seed predator guild in a tropical deciduous forest, with some reflections on tropical biological control. p. 3-14. *In* D. Price Jones and M. E. Solomon, eds. Biology in Pest and Disease Control. Blackwell Sci. Pub., Oxford.

Janzen, D. H. 1974c. The deflowering of Central America. Natur. Hist. 83:48-53.

Janzen, D. H. 1975a. Sweep samples of tropical deciduous forest foliage-inhabiting insects: seasonal changes and inter-field differences in adult bugs and beetles. Ecology. In press.

Janzen, D. H. 1975b. Intra- and inter-habitat variation in *Guazuma ulmifolia* (Sterculiaceae) seed predation by *Amblycerus cistelinus* (Bruchidae) in Costa Rica. Ecology. In press.

Janzen, D. H., M. Atarroff, M. Fariñas, S. Reyes, N. Rincon, A. Soler, P. Soriano, and M. Vera. 1975. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. In press.

Janzen, D. H., and C. M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. Trans. R. Entomol. Soc. Lond. In press.

Johnson, C. D. 1973. A new *Acanthoscelides* from *Indigofera* (Coleoptera: Bruchidae). Col. Bull. 27:169-174.

Johnson, R. M., and W. D. Raymond. 1964. The chemical composition of some tropical food plants: II. Pigeon peas and cow peas. Trop. Sci. 6:68-73.

Liener, I. E. 1974. Phytohaemagglutinins: their nutritional significance. J. Agr. Food Chem. 22:17-22.

Long, A., and P. S. Martin. 1974. Death of American ground sloths. Science 186:638-640.

Magnus, K. E., and C. E. Seaforth. 1965. *Samanea saman* Merrill: the rain tree. A review. Trop. Sci. 7:6-11.

Rehr, S. S., P. P. Feeny, and D. H. Janzen. 1973a. Chemical defence in Central American non-ant-acacias. J. Anim. Ecol. 42:405-416.

Rehr, S. S., D. H. Janzen, and P. P. Feeny. 1973b. L-Dopa in legume seeds: a chemical barrier to insect attack. Science 181:81-82.

Rehr, S. S., E. A. Bell, D. H. Janzen, and P. P. Feeny. 1973c. Insecticidal amino acids in legume seeds. Biochem. Syst. 1:63-67.

Rosenthal, G. A. 1972. Investigations of canavanine biochemistry in the jack bean plant, *Canavalia ensiformis* (L.) DC. II. Canavanine biosynthesis in the developing plant. Plant Physiol. 50:328-331.

Sevilla-Eusebio, J., J. C. Mamaril, J. A. Eusebio, and R. R. Gonzales. 1968. Studies on Philippine leguminous seeds as protein foods. 1. Evaluation of protein quality in some local beans based on their amino acid patterns. Philipp. Agric. 52:211-217.

Wilson, D., and D. H. Janzen. 1972. Predation on *Scheelea* palm seeds by bruchid beetles: seed density and distance from the parent palm. Ecology 53:954-959.