

127

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CHAPTER 7

**The Ecology and Evolutionary Biology of Seed Chemistry
as Relates to Seed Predation**

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I. Introduction	163
II. What is a Seed?	164
III. What are Secondary Compounds?	165
IV. Maternal Tissues in Direct Seed Protection	166
A. Green Fruits as Protectors of Ovules	166
B. Ripe Fruits as Protectors of Seeds	171
C. Seed Coats as Protectors of Seeds	174
V. Endosperm and Embryo in Direct Seed Protection	178
A. The Ecology of Host Specificity by Seed Predators	178
B. Constraints on Seed Secondary Compounds	190
VI. Who Are the Seed Predators?	194
VII. Community Structure Consequences of Host Specificity by Seed Predators	199
VIII. Conclusions	202
References	204

I. INTRODUCTION

My goal is to understand the ecological significance of seed chemistry to the seed and to its potential consumers and to identify some of the selection pressures by seed predators that may lead to and maintain chemical traits of seeds. This will be a blurred inquiry for two reasons. First, our knowledge of seed chemistry is unusually incomplete; seeds generally have not been studied as organisms but as sources of drugs, chemotaxonomic traits, or food for man and domestic animals. It is the nature of such inquiries to study one aspect of many species of seeds, rather than study many aspects of one species of seed. Second, those who have studied seeds as organisms have treated them largely as inert pills to be dispersed or as black boxes which generate seedlings.

In this review, I will use seeds as a model system for a discussion of the ecology of secondary constituents in plants. Such fractionation of the plant is legitimate not only for convenience of discussion but because much of the discussion will centre on interactions of plants with herbivores. Herbivores almost never eat Latin Binomials; they almost always eat specific plant parts, thus it is the traits of these plant parts that matter.

II. WHAT IS A SEED ?

A seed is a package of resources for the germinating seedling (and to a certain unknown degree, for the dormant seed). It has a seed coat made of maternal tissue; the primarily protective role of the seed coat is variously supplemented by the fruit (also of maternal tissue). The embryo is inside the seed coat and variously surrounded by endosperm. The endosperm has two unique and significant traits, neither of which will I explore here in depth; all resources that the embryo receives are channelled through the endosperm, and the endosperm is a variously polyploid structure more related to the maternal parent than to the embryo. The potential role of the endosperm in mediating sibling-sibling competition among seeds and parent-offspring conflicts is enormous but unexplored.

From the viewpoint of the ecologist/evolutionary biologist, the important traits of seeds are the following.

1. The materials in the seed coat appear not to be used by the newly germinated seedling (except perhaps *via* the external decomposition of the seed coat with subsequent uptake of its nutrients through the roots).

2. Any given chemical in a seed is likely to have several different functions in the seed and seedling.

3. Once a seed begins to germinate, it cannot return to a level of dormancy similar to that of the resting seed.

4. Seed "size" is a very difficult parameter to interpret despite its ease of measurement; what biological trait is measured in determining a seed's "size" is very dependent on the question being asked.

5. The amount of resources in a seed is a deceptively unambiguous result of an enormous number of agreeing and conflicting selective pressures that stem from, among other things: the resources of the parent, sibling competition in fruits and seed crops, the lifetime resource allocation pattern of the parent, the characteristics of the habitat where the seed is likely to germinate, the nature of the dispersal agents, the duration and weather of seed dormancy, and the nature of the seed predators.

6. There is no optimal seed for any parent tree; there is only a seed which is a member of some optimal distribution of seed types produced by one parent.

7. Seeds do vary within a parent's seed crop and this variation is likely to

be a combination of variation that directly raises the fitness of the parent through seed or seedling survival plus variation that is an outcome of other processes that raise the fitness of the parent through its own survival.

8. The chemical and size traits of a seed of one species are not independent of those of others in the same habitat; the interdependency is largely mediated through the organisms that prey on seeds and disperse them.

9. The most direct measure of fitness of a *parent* plant is the number of new adults produced that have maximum probability of dominating later gene pools; the most direct measure of fitness of a *seed* or *seedling* is survival to be a parent (assuming it cannot move about). Since parent plants have finite resource budgets, these two measures cannot be maximized to the same value with a single type of seed, and thus every individual seed is a compromise of adult and seed or seedling fitness. The study of the degree of deviation of this compromise from the potential maxima for the parent and for the seed will be an interesting exercise in the balance between kin and individual selection.

10. Plants reproduce sexually not only by making seed but by siring seeds and thus any really complete discussion of this subject should take into account the fact that the fitness of a hermaphroditic plant as a whole cannot even be approximated by seed survivorship alone. I am thus discussing in this paper almost entirely the fitness of the female portion of the plant genome when dealing with seeds (and see Janzen, 1977a).

III. WHAT ARE SECONDARY COMPOUNDS?

There is a growing dissatisfaction with the term "secondary compound", a dissatisfaction perhaps most broadly expounded with Whittaker and Feeny's (1971) exposition on "allelochemicals", "allomones" and "kairomones", as substitute words. As most commonly used in everyday speech, a "secondary compound" is a chemical, produced by plants or animals, for interactions with organisms of species other than the producer. Thus snake venoms, pheromones, alkaloids in leaves, tetrahydrocannabinol, chemicals in urticating hairs and many others, are secondary compounds. The definition is clearly one of function and not of chemical property. This leads to two major problems.

First, one molecule can be both a secondary and a primary compound. If the selective pressure that led to cellulose being the primary structural molecule in plants was herbivore grazing (most, if not all, higher organisms lack cellulases), is cellulose a secondary or a primary compound? Its chemical traits certainly protect plants. I suspect that the lectins in black beans are probably a major reason why many insects or vertebrates cannot or will not eat raw mature black beans (*Phaseolus vulgaris*) (e.g. Janzen *et al.*, 1976a); if these proteins are then treated as storage proteins by the new bean seedling, are the lectins secondary compounds or primary compounds? The way such

ambiguity is resolved in other areas of ecology is through sentence structure. An individual agouti (*Dasyprocta punctata*, a large neotropical rodent) is both a seed predator and a seed disperser of *Hymenaea courbaril* (Leguminosae) at different times. The answer to the question "What is an agouti?", has to be "Both disperser and predator of seeds". Likewise, the answer to the question "What is abrin?", may have to be "Both secondary and primary compound".

The second problem is that most putative secondary compounds have not been tested on any organism. We tend to define secondary compounds by comparing them to compounds of known physiological activity; if strychnine is toxic to rats and to bruchid beetles, we infer that other alkaloids are also. Such reasonable behaviour is bound to lead to doubts from sceptics. One would not expect any one chemical to be toxic to all organisms and further, there is ample evidence to support the axiom that no plant, no matter what its secondary chemistry, is free of herbivores. It follows then that there must be at least one organism to which any given secondary compound is not lethal at the doses found in its natural food.

I find neither of the above problems to be sufficiently damning to cause me to delete from my vocabulary a word for chemicals that have part or all of their function in interactions with organisms other than the one that made them. In the limit, the chemicals are thus identified by their action but their identity can often be inferred from their chemistry. The question then becomes what to call them? I am inclined towards "secondary compounds" because of the widespread usage of this term, recognizing that taken literally it may be false in some cases. However, I have yet to see a paper whose value was lessened by referring to secondary compounds as "allelochemics" (e.g. Reese and Beck, 1976a,b). However, the scope and meaning of the terms must be obvious from the context of the discussion. Furthermore, I suggest that wherever possible, more refined words be used, for example digestion inhibitors, pheromones, toxins, germination inhibitors, etc., though no compound need belong exclusively to one of these classes. A chemical, therefore, cannot, by its chemical structure alone, be assigned to any of these classes, though some strong inferences may be made. The kinds of secondary compounds found in seeds and their effects on animals are discussed in the preceding chapter by Bell (Chapter 6).

IV. MATERNAL TISSUES IN DIRECT SEED PROTECTION

A. GREEN FRUITS AS PROTECTORS OF OVULES

There are two ways that a green fruit protects the ovules contained within. First, it (and thus the parent tree) controls the rate of resource accumulation and transformation by the fruit and the seeds. Through this control it has

TABLE I

Lengths and dry weights of *Pithecellobium saman* fruits from one tree during fruit maturation (from flowering in late March, 1976, at Santa Rosa National Park, Guanacaste Province, Costa Rica)

	May 15, 1976 (n = 20)	Dec. 1, 1976 (n = 35)	Feb. 26, 1977 (n = 30)
\bar{X} length (mm)	24	34	121
S.D.	3	7	48
\bar{X} dry weight (gm)	0.08	0.10	3.89

the opportunity to minimize the amount of time that nutrient-rich fruit and its ovules are available to predators. For example, in the deciduous forests of lowland Costa Rica, the large tree *Pithecellobium saman* (Leguminosae) flowers in March–April (last half of the dry season) and then keeps the resulting fruits in a minute state through the following six month rainy season and does not begin to expand them until January of the following year (Table I). They then ripen and fall by the end of March, shortly before the parent tree flowers again. I assume that such a cycle is generated by the early dry season being the best time for ripe fruit fall, dispersal and for competitive reasons (Janzen, 1977b), with the very early dry season or the end of the rainy season being inopportune for flowering. I hypothesize that the fruits stay minute throughout the rainy season because seed predators would take a heavy toll of the developing seeds during this long time were the photosynthate from the foliage going directly into them. Parrots (*Aratinga* spp.) take a heavy toll of seeds from green pods when they do expand; therefore minimization of the duration of this stage should minimize the seed predation by these birds. The bruchid beetle *Merobruchus columbinus* has one generation in the seeds during the two months that the seeds are expanding from minute to ripe; if the full-sized seeds were present for four or more months, the beetles would probably be able to pass two or more generations in the seeds, or in mining among the seeds, as do bruchid larvae of some other species in other hosts.

Second, green fruits have their own chemical and mechanical defences. These differ conspicuously from those of ripe fruits and mature seeds, in that the green fruit is physiologically active and thus can have dynamic responses such as phytoalexin production, galling, callous tissue, wound sealing with gums, resins and latex. In general I expect a green fruit to contain about the same kinds of chemical defences as foliage. However, there are some major differences between fruit and foliage. (1) Different species of animals (with different detoxification abilities) may feed on green fruits than eat leaves. (2) The animals that attack green fruits may be seeking only the seeds and

thus be largely immune to secondary compounds that have to be ingested to be toxic. (3) The nutrient quality of a gram of green fruit is likely to be much higher than that of a gram of leaves (owing to the presence of immature seeds and precursors of edible ripe fruit pulp). (4) The loss in fitness to the parent through the consumption of a gram of green fruit will be greater than through the consumption of a gram of foliage (owing to the larger material and strategic investment in a gram of green fruit tissue).

1. *Different Herbivores on Leaves as on Green Fruits.*

It is very difficult to know about the similarity of the guilds of herbivores that feed on leaves as opposed to green fruits. We desperately need studies of the whole array of animals that feed on a plant species, categorized not only by the amount of damage they cause but by what part of the plant they feed on. We do know that howler monkeys (*Alouatta palliata*) eat the green fruits of some plants whose leaves they do not eat (e.g. Glander, 1975), that a large number of species of insects that feed on the foliage of tropical trees do not feed on the green fruits of those trees (D. H. Janzen, unpublished) and that most of the few species of insects that appear to specialize in feeding on green fruit tissues do not also feed on foliage.

These natural history observations do not, however, suggest any similarity of secondary compound chemistry of leaves and green fruits. This is because green fruits are likely to have very different nutrient contents from leaves and are generally available in the habitat for much shorter periods than are leaves. These two factors alone could lead to the observations cited in the previous paragraph, though I doubt that they do. We need direct chemical comparisons.

There may be substantial measurement problems in secondary compound comparisons of green fruits and leaves. A fruit normally has depth and other forms of three-dimensional structure of such magnitude as to be of importance to herbivores. For example, there is a layer of the green fruit wall in *Hymenaea courbaril* pods from which liquid resin quickly oozes when the pod is chewed or cut into. No such layer of copious resin flow exists in *H. courbaril* leaves, though there is resin present. I suspect that when the whole green *H. courbaril* fruit is analyzed for resin content, the amount per gram dry weight will be found to be not much different from that of mature foliage. However, from the viewpoint of the herbivore, it may be much more or much less, depending on where in the fruit the animal is taking its bites.

2. *Animals may Seek Seeds and Discard Fruits*

It is usual for vertebrate seed predators to shuck the green fruit and consume the seed inside. Sucking bugs penetrate the fruit wall with their proboscis

to remove seed contents. They may be able to avoid intracellular secondary compound defences in the fruit as do aphids wending their stylets among cells in leaves. Bruchid, weevil and moth larvae mine through the fruit wall to develop inside the seed or mine from seed to seed. Such miners may, however, also consume some of the tissues that will become edible fruit pulp in the ripe fruit. These tissues may, however, be less well protected than are other fruit parts owing to incompatibilities of cheap defences with later attractiveness of the ripe fruit pulp to vertebrates.

Because the animal seeks the seeds rather than the fruits, many secondary compound defences in the green fruit will be ineffective against vertebrates. As a squirrel carves its way through the resin-rich walls of a fruit of *Hymenaea courbaril*, it simply puts the fruit fragments to one side and receives a minimum amount of the sticky resin on its face. The resin is abundant enough to insure that squirrel damage is only rarely recorded but it is not an absolute defence when other seed crops fail and the squirrels are starving. The same comment applies to the latex-rich fruit walls of *Stemmadenia donnell-smithii* (Apocynaceae). I expect selection favouring especially copious resin, gum and latex flow from the fruits of plants using these defences. For plants with less liquid defensive systems, alkaloids, tannins and other such compounds sequestered inside cells must be extremely toxic to be effective against animals with bills, teeth or claws; here, the seed coat and contents are the only real defence against large animals.

The situation described above for vertebrates need not hold for insects. Even though a mining insect need not ingest much if any of the material that it is passing through, it does have to rupture cells; contact poisons, if any, have a chance to work on it. We know nothing of this subject with fruits (but see below with respect to seed coats).

Opening of an immature fruit by a vertebrate, and thus the destruction of the seeds in that fruit, means something different to the plant than when a leaf is damaged. A leaf is a capital investment and the investment is repaid during the photosynthetic season; the later in the life the leaf is eaten, the less the loss to the plant. A fruit is also an investment, but there is no return on the investment until the fruit matures and the seeds are dispersed; the loss is greater the longer the fruit has hung on the plant, if it is eaten before it matures. The only way this effect may be ameliorated is if the photosynthesis of the fruit pays for much of its own maintenance. While standard horticultural/physiological information suggests that the fruit does not pay its own way, the story may be different with large tropical fruits, especially the ones that are flat and leaf-like (e.g. *Lonchocarpus*, *Hemiangium*, *Myrospermum*, *Machaerium*, *Pentaclethra*, *Albizia*, *Lysiloma*, *Gyrocarpus*, *Pithecellobium*, *Enterolobium*, *Dalbergia*, *Sweetia*).

The rules for abortion also may be quite different for fruits as compared to leaves. If part of the seeds within a fruit are killed, by a sucking or mining

insect, for example, the ripe fruit may still function highly effectively in dispersing the remaining seeds. If such damage occurs late enough in the life of the fruit so that most of the investment has been made, there is little to be gained by fruit abortion and the fruit will add to the total attractant display of the tree (unless the dispersal agents are in danger of being satiated by too much fruit). On the other hand, if the fruit has been opened by a vertebrate, the inner tissues are likely to have been thoroughly exposed to other organisms and thus the plant is likely to abort the fruit.

3. Seeds and Fruits have Higher Food Value than Leaves

Working with black colobus monkeys in Cameroun, McKey (1977) has recently developed the hypothesis that when animals live in a habitat where all the food is poisonous, they might as well eat the poisonous plants with the highest nutrient content. In other words, a bite of leaves containing 0.1 mg of caffeine should be more depressant to fitness than a bite of seed or fruit containing the same amount of caffeine. Therefore, fruits and seeds should be on average more toxic per gram dry weight than foliage even if their value to the plant were the same (which it is not). However, the degree of availability of the food needs to be taken into account here. Fruits and their contained seeds can escape in time more readily than can foliage, thus the disparity in toxicity between fruits and foliage need not be as great as it would have to be if fruits were generally available as long as is foliage for a given species of plant.

There are again measurement problems in the consideration of the nutrient content of immature fruits with their contained seeds along with their secondary compound content. For example, a fruit rich in tannins may be less detrimental than expected if the seeds have a high protein content. Since animals eat plant parts for more than just the calories in them, there may also be some qualitative benefits. The presence of a certain important dietary mineral in a green fruit may greatly offset the costs of consuming that fruit as measured by tissue damage from secondary compounds in the fruit.

4. Green Fruit and Leaves are Differentially Valuable to the Parent

There are three reasons why green fruits should be more valuable to the parent per unit resource present and thus more effectively protected per unit of resource, than leaves. First, a green fruit represents a greater investment than a leaf of equal units. The cost of the fruit crop has to include the flower crop, none of which is visible at the time the green fruit is present. The cost of the chromosomes contributed by the pollen grain cannot be measured by

their caloric or any other content in the green fruit. Second, the loss of a unit of leaf resource is likely to lower the fitness of the plant less than a loss of the same unit of green fruit, because of the nature of replacement of fruits. When a leaf is eaten off, it can simply be regrown and the cost measured in resources invested; if a green fruit is eaten it cannot be replaced without the production of a whole new crop of flowers. Third, a leaf is an investment that amortizes the loan and pays interest. Eaten after a certain stage, its loss is no net drain on the system. A green fruit eaten at any age is a net drain and can only result in a lowering of the parent's fitness.

B. RIPE FRUITS AS PROTECTORS OF SEEDS

In a certain sense, everything in a ripe fruit (exclusive of seed contents) is a secondary compound (except perhaps the packaging material) since its adaptive value is in influencing the behaviour of another organism. Ripe fruits raise the fitness of their contained seeds in at least three conspicuous ways. They disperse, or cause the dispersal, of seeds away from the parent tree and thus away from the seed predators attracted to the concentration of seeds at the parent (Janzen, 1970). They deter the wrong seed dispersers from eating seeds. Finally, they continue to protect the mature seed from seed predators (and from the physical environment in some cases). In all three of these processes, secondary compounds may play a large role. As consumers of ripe fruits we are often aware of these traits, but the study of the interaction of wild animals with secondary compounds in ripe fruits is almost totally unexplored.

1. Dispersal

Why do animals eat entire fruits (and thereby waste gut space on indigestible seeds)? The simple answer is that they consume fruits for the chemicals contained within. One therefore expects the chemical content of a fruit to be an evolutionary outcome of the conflict between what the animal can use and what the plant will relinquish, packaged in a manner such as to optimize some fitness function for each (and see especially McKey, 1975; Smith, 1975). If it were a simple matter of attracting those animals that discard the seeds in the appropriate place and if some unique combination and quantity of chemicals could be found that would attract only the correct set of animals, our job might be much easier. It is likely that many of the more conventional secondary compounds (essential oils, tannins, ketones), in addition to compounds commonly called nutrients (water, sugars, vitamins), in a fruit function

as odour cues, taste attractants and directly useful molecules to the animals that eat ripe fruits. Such an assertion is so obvious and so intuitive that it needs no further comment. However, (a) dispersal is almost without doubt one of those processes where more is not necessarily better, (b) animals do not range evenly over the habitat, but rather certain ones range in certain places and behave in certain ways, and (c) animals' dietary needs are sufficiently alike that a fruit that is highly attractive to one animal is likely to be highly attractive to many others. Consequently ripe fruits are under strong selective pressure to contain compounds that will make them unattractive to most of the animals in the habitat, yet not deter the appropriate animals. Again, such a result is going to be an optimization process, somewhat modified by coevolutionary changes by the animals as well.

2. Deter Wrong Dispersers

When an oil-bird eats a large palm or lauraceous fruit and later it, or its offspring, regurgitates the large seed in a cave (Snow, 1962), it is as much a seed predator as if it had chewed up the seed. If a coati climbs a strangler fig, eats its fruits and later defecates them on a dry hillside far from trees to climb, it may likewise be killing seeds. If a tapir eats an *Enterolobium* fruit but spits out the seeds below the parent as it chews the fruit, all the investment in the fruit by the tree is to no avail. Three hundred palm seeds spread among 50 hornbills may generate a seed shadow of quite different value than if all are eaten by one elephant.

Bearing these comments in mind may help understand why many ripe fruits seem to have such peculiar constituents. Ripe *Andira inermis* fruits appear to have a potent antibiotic in the juicy pulp; they are avidly eaten by Costa Rican fruit bats and rejected by cattle and pigs. I have postulated that this trait is adaptive in deterring animals which depend heavily on a bacterial gut flora for food digestion (e.g. squirrels, monkeys, possums, rats) and in turn reduces the number of seeds that are dropped in areas other than those where the bats would drop them (Janzen *et al.*, 1976b). Fleshy fruits of *Caesalpinia coriaria* (divi-divi) and *Terminalia* spp. are well known to contain 20–40% dry weight hydrolysable tannins when ripe (Howes 1953). I suspect that these tannins are functional in deterring the wrong animals from eating these fleshy fruits (Janzen 1977c). It is interesting that by far the most common source of hydrolysable tannins is ripe fruits and it is these tannins that animals have the greatest chance of being able to degrade. Further, I know of no records of active condensed (non-hydrolysable) tannins in ripe fruits (at least in quantity high enough to have attracted the tannin industry, Howes, 1953). The pulp of *Myrciaria paraensis* fruits contains as much as 2–3% vitamin C (ascorbic acid) (Bradfield and Amalia, 1964); such a con-

centration could be caused either by a bird or other vertebrate with an exceptionally high need for vitamin C or with an exceptionally high tolerance for it. In either case, it could effectively exclude other animals from the fruits and thus from the disperser coterie for this plant. I suspect that the primary reason why howler monkeys do not eat much ripe fruit (e.g. Glander, 1975) but frequently eat green fruits, is that the water, antibiotic or other traits of ripe fruits would disrupt their bacterial flora which is of utmost importance in digestion of foliage rich in secondary compounds.

3. Direct Protection of the Ripe Seed

Seed predators do not stop preying on seeds once the seed is mature. Perhaps the most direct examples of protection by the whole ripe fruit are where dispersal by a vertebrate gut is not involved and the indehiscent dry fruit remains around the seed (bony and stoney endocarps will be treated here as functional seed coats). Most thought has been given to the role of dried husks around seeds in slowing the rate of processing by birds and rodents (e.g. Rosenzweig and Sterner, 1970; Pulliam and Brand, 1975; Willson 1972). In this case the seed predator is confronted with little else than a multilayered seed coat. However, these husks (dried fruit walls) may well contain tannins and other defensive compounds, just as may seed coats (see below). The tannins in the wings and other investing structures of wind-dispersed fruits have been interpreted as "germination inhibitors" (which really means that once they have been leached out of the fruit the seed is able to germinate). However, their prime role may be the deterrence of seed predators, ranging from vertebrates to microbes and fungi. The thick husk of a coconut is probably no more than a physical barrier to entry by crabs and rodents (as well as a float) but its dark brown colour suggests that it may contain chemical barriers as well.

Somewhat more indirectly, the secondary compounds and other traits of ripe fruits may not only keep out the wrong potential seed dispersal agents, but also potential direct seed predators. I only know three examples but suspect that there are many more. When the large bruchid *Pygiopachymerus lineola* cuts its exit hole out through the wall of a mature and indehiscent *Cassia grandis* pod, it then allows entry of moth larvae that eat the fruit pulp. It also allows entry of the adults of a smaller bruchid *Zabrotes interstitialis*. This smaller bruchid then lays its eggs directly on the cleaned seeds and will kill all seeds in the pods if a dispersal agent does not remove the fruits (Janzen, 1971a). The same relationship occurs, but with less thoroughness on the part of the second beetle, with *Merobruchus columbinus* and *Stator limbatus* in *Pithecellobium saman* fruits and *Amblycerus cistellinus* and *Acanthoscelides guazumae* in *Guazuma ulmifolia* fruits in the lowlands of Guanacaste

Province, Costa Rica (Janzen, 1975a, 1977b). Of course, the fruit itself is also a direct mechanical barrier to entry by the three smaller bruchids and secondary compounds in the fruit wall may themselves be relatively unimportant in restricting invasion by the beetles.

C. SEED COATS AS PROTECTORS OF SEEDS

For purposes of ecological convenience, I will here combine hard nuts (usually the fruit endocarp) with seed coats. They are both of maternal origin and thus this merger probably does not invalidate later evolutionary discussions. Nothing is known of the ecological biology of seed coats on immature seeds and thus they will not be discussed. The shape and texture of seed coats, as well as the degree of attachment of the fruit to the seed coat, strongly influences the fate of animal-dispersed seeds but will likewise not be further discussed here.

It is very difficult to separate the effects of seed coat hardness from seed coat toxicity, since we know almost nothing of the secondary compound chemistry of seed coats and the animal simultaneously encounters the toxicity and the hardness of a seed coat. It has also not helped that for the past ten years I have stupidly regarded seed coats as largely inert containers, as far as chemical defences are concerned. This neglect of seed coat chemistry was largely caused by the observation that many animals need not actually consume the seed coat, but merely pass through it. I reasoned that with seeds, as with eggs (Orians and Janzen, 1974), it would not be difficult for any animal with a good physical means for entering seeds to pass this barrier. This was wrong.

In early 1976 I set out to test the relative hardness of a variety of legume seeds as measured by the ability of the first instar larvae of *Callosobruchus maculatus* to drill through them. This was done by placing bisected seeds in a laboratory culture of *C. maculatus*. The females laid their eggs on both the seed coat and the exposed seed contents. The larvae drill into the seed directly under the eggs. There were conspicuous differences in the ability of the larvae to penetrate the seed coats; of 63 species of non-hosts, the larvae were unable to penetrate the seed coats of 17%, made a shallow pit in 30%, made a deep pit in 13% and passed through the seed coats of the remaining 41% (Janzen, 1977d). When a larva makes a pit in the seed coat but does not pass through it, there are currently no means of ascertaining whether it died because the seed coat was too hard, too toxic, or some combination of the two. However, the more shallow the pit, the more likely that the seed coat is directly toxic. When the larva passes through and later dies in the seed contents, we know it probably was not too toxic (though the possibility of delayed action cannot be excluded). However, when the larva never even scratches the surface of

the seed coat, it seems highly probable that the seed coats are themselves toxic.

The larvae died on the surface of the following seeds without making the slightest mark on their surface: *Acacia angustissima*, *Albizia lebbek*, *Canavalia brasiliensis*, *Canna indica*, *Cassia emarginata*, *Mucuna mutisiana*, *Ormosia venezolana* and *Peltophorum inerme*. Under a dentist's drill, these seed coats seemed no harder than those that were partly penetrated or passed through on the other species of seeds. Nothing is known of the seed coat chemistry of the above species of plants, though I am starting such a study with the help of my phytochemical colleagues.

What do we know of potentially toxic secondary compounds in seed coats of seeds (or in nut walls)? Tookey *et al.* (1963) stated that the endosperm galactomannan gum of *Crotalaria intermedia* is free of the alkaloids that seem to be "localized in the germ and seed coat", but did not tell us how they knew of this localization.

It would be enormously helpful to know if a bruchid larva eats the materials it is drilling through to get to the seed, or if it can cut a hole and merely discard the material chewed into. Consumption of chewed material is in no sense mandatory for insects and is evidenced by many chewing insects that do not eat what they break up with their mandibles (e.g. carpenter bees, ants, wasps, termites). It seems reasonable that the sucking bugs should be able to digest or otherwise force their way through a seed coat without ingesting its contents. Birds and mammals that crack or chip up seed coats with their bill or teeth need not swallow the seed coat fragments, though this undoubtedly requires more work (parrots which open seeds and discard the hulls, and agoutis which chip the hard seed coat off legume seeds are two examples). These observations cause me to maintain my earlier reasoning that a seed coat has to be exceptionally toxic to absolutely stop a potential seed predator, though the list of species whose seed coats apparently kill *Callosobruchus maculatus* larvae emphasizes that when an organism is very small, even a very thin toxic layer can be a severe barrier.

However, a toxic seed coat may slow a seed predator. The best example that I can offer comes from the cedar swamps of northern Michigan. Here, pure stands of *Thuja occidentalis* (white cedar) produce large crops of small cones in some years. The cone-laden branchlets are cut off the trees by red squirrels (*Tamiasciurus hudsonicus*) and then harvested from the ground. The squirrel perches on a hummock or log and shells the undehisced cones for their tiny wind-dispersed seeds. Each seed has a winged and membranous seed coat. Instead of simply chewing up the soft seed with its flimsy seed coat, the squirrel takes the time to slit the seed coat with an incisor and then lift out the seed contents to eat. The seed coat is then discarded. If the seedless seed coat is chewed by a human, it becomes obvious why the squirrels take the time and effort to discard the seed coats. One seed coat is enough to fill my mouth

with a very annoying and pungent flavour of turpentine. The source is four to eight oval blisters about 1 mm long and 0.5 mm in diameter in the seed coat over and adjacent to the seed cavity. When broken, they release a small drop of clear fluid. This fluid is approximately 31% γ -terpinene and 26% α -thujone, along with about seven other terpenes (Jones, Meinwald and Eisner, unpublished). Cedar leaf oil contains about 60% α -thujone (von Rudloff, 1961). Thujone is a major component of the flavouring of the liqueur absinthe and in doses of about 30 mg kg⁻¹ body weight, thujone produces convulsions associated with lesions of the cerebral cortex (Hall, 1973).

It is noteworthy that a sucking bug would have no difficulty bypassing the large blisters and thus it seems quite likely that they were evolved in response to a large chewing animal like a rodent. The advantage to the plant of slowing the seed predator is that the more time required to process each seed, the fewer seeds will be eaten by each squirrel during the short period when the seeds are available yet undispersed.

In the tropics there are several examples where the seed coats or nuts contain cavities filled with potentially toxic material. The best known is the cashew fruit (*Anacardium occidentale*) in the poison ivy family (Anacardiaceae). Here, it is the pedicel of the fruit which is the fleshy part that attracts the dispersal agent. The fruit proper is a pair of thin but hard and leathery layers and between them is a liquid with extremely vesicant properties. Presumably this functions in not only deterring the pedicel-eating animal from eating the soft and oil-rich seed but deters rodents on the ground from doing the same after dispersal has occurred. I suspect also that such an envelope of a powerful secondary compound is also an effective deterrent against sucking bugs. Potential candidates for a similar story are the other species of *Anacardium* and the fibrous nuts of *Spondias mombin* (I get a "poison ivy" reaction from picking up nuts long since cleaned of their fruit pulp), and the resin-filled cavities in the nut walls of *Sacoglottis* spp. (e.g. Gentry, 1975).

There is a special circumstance where I expect seed coats to be either toxic or at least contain easily perceived warning chemicals. Many large tropical birds (toucans - Ramphastidae, hornbills - Bucerotidae, fruit pigeons - *Ducula*, *Ptilinopus*, cotingas and bellbirds - Cotingidae, oil birds - Steatornithidae, trogons - Trogonidae) consume large soft seeds with a thin aril or pulp around them (primarily from Lauraceae, Burseraceae, Myristicaceae, Palmae and Leguminosae) and then after the gizzard has stripped off the pulp, regurgitate the seed rather than grind it up and pass it on through. There has never been an experiment showing that *all* the seeds eaten are regurgitated and never digested but I will assume it in the absence of contrary evidence.

We are then confronted with the question of why a large nutrient-rich

food item should be discarded (seeds are not like the bones discarded by carnivores). The standard answer is to avoid filling the digestive tract with indigestible bulk. Therefore, why is it indigestible? I think that there are two reasons. First, the bird's digestive tract is specialized at dealing with the comparatively soft fruit and processing large amounts of it (though comparatively low in nutrients per unit bulk as compared with the seed). To adopt the morphology, gizzard stones and time needed to digest a few seeds would probably yield an overall return lower than can be obtained by fast processing of soft fruit pulp from many fruits. Therefore, even if the net yield is lower with eating fruit rather than seeds, these birds would appear to be on a tall adaptive peak.

Second, I expect natural selection to have raised the secondary compound chemistry of the large seeds to the point where their digestion by these large birds would cost more than the bird can pay for the nutrients obtained in return. Given this premise the seed coats of these seeds can be expected to contain doses of chemicals of sufficient intensity to be perceived easily by the bird's gut. These chemicals should tell the bird's grinding action when to stop and reject the seed. There are two alternative hypotheses. The bird's digestion system may simply stop when it has released the secondary compounds from the first layer of seed tissue, the seed may be set up such that this removal does not lower its fitness; however, these birds spit up intact seeds which suggests that this is not the mechanism involved. The other hypothesis is that the bird's digestion system works solely in response to large spheroidal objects; they are rejected as encountered in the fruit-removal process. However, the story cannot be that simple because many hard and intact spheroidal *fruits* are eaten whole and then processed, yet are the size of some of the seeds spat out from other fruits. Second, some of the fruit pulp processed is as hard and dry as some of the seeds spat out.

Whatever actual experiments eventually show, it seems reasonable to hypothesize that even a very thin and weak layer of secondary compounds in a seed coat of one of these seeds would be highly adaptive in telling the bird to desist from its digestive efforts. Simultaneously, as the system becomes progressively more finely tuned, the seed should need to be progressively less toxic for the bird to reject it. In fact, there may be many large soft seeds that could be digested with impunity by large frugivorous birds if they had the appropriate digestive machinery; by virtue of their large size they may be free from seed predation by those birds with effective grinding gizzards. We cannot even exclude the possibility of Batesian mimicry among large soft seeds.

In closing this section, I should add that bird regurgitation of large soft seeds is just one example of the general question, why do vertebrates spit out seeds? Both cluttering of the gut with unusable bulk (e.g. Snow, 1975) and minimizing the risk of poisoning may be answers.

V. ENDOSPERM AND EMBRYO IN DIRECT SEED PROTECTION

For the purposes of this discussion, I will treat the endosperm and the embryo (cotyledons plus associated offspring tissue) as though they are the same genetic organism, though future explorations of their biology may find this to be unacceptable. It should be evident by now that there is a potentially enormous experimental error in almost all that follows. It is a simple fact that the vast majority of chemical analyses of seed chemistry are based on grinding up seed coat along with the seed. This introduces two errors. First, the secondary compounds may be in the seed coat, rather than in the seed contents and thus never (or rarely) encountered by the animal that eats seed contents. Second, by including the weight (and bulk) of seed coat in the calculations of the percentage of secondary compound(s) in the seed, the concentration of secondary compounds assumed to be in the seed contents may be greatly in error. For example, only 37% of the dry weight of an *Enterolobium cyclocarpum* seed is edible contents (Janzen, 1977d); if one grinds up the seed and states that it contains, for example, 4% albizzine, in fact the edible parts are 11% albizzine (assuming that the seed coat contains none). The difference between 4% and 11% albizzine may be huge, especially since uncommon amino acids exhibit strong dosage effects over this range (e.g. Janzen *et al.*, 1977).

Rather than attempt a complete review of what we know of secondary compound chemistry of seed contents, I will focus on some of the conspicuous ecological and evolutionary biology questions about seeds and their seed chemistry.

A. THE ECOLOGY OF HOST SPECIFICITY BY SEED PREDATORS

1. *Why are Seed Predators Host-Specific?*

From the viewpoint of the seed predator and its prey specificity, there are a number of important traits of seeds: (a) On a dry weight basis, seeds are the most nutrient-rich of all readily isolated plant parts; (b) Seed availability, at the individual, species and habitat level, generally fluctuates greatly and/or erratically in space and time; (c) Seed secondary compound chemistry varies greatly among species within a habitat but *seems* to be quite constant within a species within a habitat; and (d) The secondary compounds found in seeds are in fact disruptive to the digestive processes or physiology of seed predators. Confronted with these four facts about seeds, an ecologist-evolutionary biologist is inclined to predict that seed predators especially the smaller ones, should be very prey-specific. This is generally true but there are numerous instructive exceptions.

Before a discussion of the details of this assertion, the terminology should

be considered. The words "generalist" and "specialist" have always been common categorizations in ecology (along with their trichotomized synonyms monophagous, oligophagous and polyphagous) and are at the moment playing a prominent role in discussions of certain herbivore guilds (e.g. Rhoades and Cates, 1976; Feeny, 1976). As should be evident from the present paper, the words are becoming progressively less useful and I find it more profitable to speak directly of what is meant (just as I never use the word "niche" for the same reason). For example, if a beetle feeds on seven species of legume seeds and all seven are found to contain the same secondary compounds, is that beetle a specialist or a generalist as compared to a beetle that feeds on three species of legume seeds, each containing different uncommon amino acids in large amounts? *Caryedes brasiliensis* larvae (Bruchidae) feed on only one (*Dioclea megacarpa*) of the approximately 2000 species of woody plant seeds in Guanacaste Province, Costa Rica. *Amblycerus robiniae* (Bruchidae) feeds on the seeds of only one (*Gleditsia triacanthos*) of the 50 or so species of woody plants found in eastern Kansas. Is *C. brasiliensis* more specialized than *A. robiniae*? Is it recognized that an extra-tropical sparrow that feeds on 50 species of grass seed during the year is performing a very different biochemical feat to a parrot that consumes the immature seeds of 50 species of tropical trees in a year? A Costa Rican agouti feeds on several hundred species of large seeds in a yearly cycle; a Minnesota squirrel feeds on several tens of species of large seeds and several tens of other kinds of food (ranging from maple tree sap to mushrooms to bird eggs to insects). Which of the two is the specialist and which is the generalist? It is evident that for the words specialist and generalist to have meaning, they must be clearly defined in context. I believe that wherever possible we should be using the direct nouns that are being discussed, rather than an obfuscation in the name of hypothetical erudition.

.. (a) *Seeds are nutrient-rich.* This fact seems indisputable. The volume and weight of a seed are under a variety of dispersal constraints and within these constraints, the more reserves the seedling has available, the greater are its chances of survival. The seed is generally dormant and therefore can minimize water content. It is not gathering resources and can therefore minimize inert internal construction materials. I therefore expect a seed to have little weight and bulk that is not of direct resource value to a seedling (and therefore little that is not direct resource value to a seed predator). Bomb calorimetric analyses of seeds confirm this concept and it is no accident that seeds have the highest nutrient value to humans of any bulk plant food.

However, animals are not bomb calorimeters and man does not wander about in the woods (especially in tropical woods) just eating seeds at random. Therefore, it is only in a somewhat ecologically sterile sense that we know how nutrient-rich are seeds. We do not know how much of what an agouti

eats is really of value to it. If *Hymenaea courbaril* seeds are found to contain 10% dry weight of protein, that protein may be largely lectins and protease inhibitors which are destructive and indigestible in the agoutis' gut, the price that it has to pay to attain the fat or carbohydrate content of the seed. However, for the purposes of the following discussion, I will consider seeds as very rich in nutrients. What should this then mean to the ecology of host-specificity?

The higher the general nutrient (resource) content of a food item, the greater the chance that the animal can obtain all of its food from it (bearing in mind that a seed is likely to be a more balanced diet than any other plant part, except perhaps shoot tips). This minimizes the necessity to feed on several species of plants merely to obtain different nutrients. Simultaneously, the high nutrient content maximizes the return to the animal for successfully locating a single food item (greatly augmented by the tendency for seeds to occur in clumps). The epitomy of this process appears to be the fact that many seed predators mature within a single seed.

The higher the general nutrient (resource) content of a food item, the greater the chance that the animal can tolerate the damage done by secondary compounds ingested while feeding on the seed. This fact may push the system in opposite directions, depending on other variables. On the one hand it allows the animal to specialize on one or a few species of seed, because the animal is nullifying the effects of secondary compounds through paying for them rather than by diluting them through the consumption of many different kinds of foods (and thus through the consumption of small amounts of many kinds of secondary compounds, cf. Freeland and Janzen, 1974). On the other hand each species of seed eaten by some large vertebrate could contain enough nutrients to recompense for its damage, and thus allow the animal to feed freely among all the seed species with this trait in the habitat. The black colobus monkeys (*Colobus satanus*) in Cameroun rainforest on white sand soils may represent this side of the story (McKey, 1977). This author's basic argument is that these monkeys specialize on apparently poisonous seeds for the reason that if all the plant parts are toxic, at least those with simultaneous high nutrient content are overall least detrimental.

The higher the general nutrient (resource) content of a food item, the greater the chance that the animal can survive as a specialist at locating just that kind of food item. There are two reasons for this. First, once the item is found, it has a higher chance of containing something worth the search. Second, the more a particular item (e.g. a species of seed) is the sole item searched for, the more the animal can afford to specialize at dealing with its defences (chemical as well as others) and the more net profit is likely to accrue from the location of the one food item. In summary then, I would conclude that there are at least three reasons why the higher the nutrient content of food per unit weight, the more likely an animal is to specialize on it, given

the other three food traits mentioned at the beginning of this section (V A1). As seed toxicity and interspecific variability decrease, and seed availability increases, I would expect the forces toward specialization to be weakened (provided of course that competitors are held constant in their effects).

However, it is at this point that an important reservation must be added. I noted earlier that all of the "nutrients" or resources in a seed may not be available to the animal that consumes it. Many legume seeds have a high protein content but if most of that is lectins and protease inhibitors, then an animal may suffer an actual nitrogen depletion by eating the seed. There are animals that can feed on many species of seeds (birds with grinding gizzards being one of the most spectacular examples) but perhaps to them a seed is of little more value than other plant parts *if it is a seed that is well protected chemically*. A very large number of the seeds fed on by vertebrates with long lists of seed prey are produced by grasses, bamboos, conifers and various extratropical trees that appear to escape from seed predators largely through mast seeding rather than by seed chemistry (Janzen, 1971c, 1974, 1976a). However, seeds that are very poisonous to many animals may be quite innocuous to others. *Caryedes brasiliensis* pays whatever it costs to make an arginyl-tRNA synthetase that can distinguish between arginine and canavanine in order to be able to feed on the seed contents of *Dioclea megacarpa* seeds; further, it then pays for the arginase and urease to degrade the canavanine to ammonia which is likely used as a source of nitrogen for amino acid synthesis (Rosenthal *et al.*, 1976, 1977). Thus to *C. brasiliensis*, the seed is nutrient-rich. I am tempted to speculate that this applies to many insects that are specialized to one species of seed.

(b) *Seed availability is not constant*. There is a widely held opinion among ecologists that fluctuations in food availability lead to more species of organisms which are fed on by a species of predator and to more generalized prey capture methods. This opinion is largely derived from studies of carnivorous animals; the differences between a rabbit and a mouse are not so much the chemistry of its muscles in the predator's stomach, as its running speed, its biomass subdivision and its rate of replacement when removed. Animals that feed on chemically well protected items can be expected to have two kinds of responses as food begins to become more erratic in abundance. They may develop a secondary compound processing system that can handle more kinds of secondary compounds (e.g. the rumen of a ruminant) or they can evolve various mechanisms for waiting between food items and maximizing their return when the food is present. Except with respect to mast-fruited species of plants, I think that seed predators have very often taken the second route (and thus they decrease rather than increase their prey list as food gets scarcer).

For example, it appears that the bruchids and weevils that feed on tropical

deciduous forest trees deal with the extreme within- and between-year variation in seed abundance for a given species by being highly patient and mobile rather than by being able to move between different host species (Table II). When the adults of *Amblycerus cistellinus* (Bruchidae) emerge from the fruits of *Guazuma ulmifolia* (Sterculiaceae) (Janzen, 1975b) in the middle of the dry season in Guanacaste Province, Costa Rica, for example, they then range freely in the environment for the remainder of the dry season and six months of rainy season (a total of at least ten months) rather than attempt another generation in the other plants in the habitat that are fed on by other species of *Amblycerus* of similar size (e.g. *Spondias mombin*, *Hippomane mancinella*, *Pterocarpus rohri*, *Cassia* spp., *Prosopis juliflora*) or in the numerous other plants in the habitat that produce seeds quite large enough for an *Amblycerus* larva (e.g. *Eugenia salamensis*, *Swietenia macrophylla*, *Swartzia myrtifolia*, *Casearia* spp., *Machaerium* spp., *Andira inermis*, *Sterculia apetala*, *Hura crepitans*). Undoubtedly the driving force for the specificity of *Amblycerus cistellinus* is more than just the secondary compound chemistry of *G. ulmifolia* and all the other species of seeds in the area, but on the other hand, were the seeds of all the other species chemically available to *A. cistellinus* larvae, I see no reason why it would not have a much longer host list and have multiple generations throughout the year. The three species of *Cleogonus* weevils that feed on *Andira inermis* seeds are an even more extreme example. All three weevils treat the seeds in about the same manner (one larva per seed) and have to wait two full years between seed crops, as more than 99% of the population of *A. inermis* trees is synchronized to fruit every other year (Janzen *et al.*, 1976b; Janzen, 1977e); I have reared the weevils and other insects (if any) from most of the other plants in the *Cleogonus* habitat that have seeds large enough to support a *Cleogonus* larva and can state with certainty that they do not have alternate hosts.

For animals with long prey lists, I still expect fluctuations in availability of toxic seeds to lead to concentration in feeding on one species of seed. If, for example, agoutis have inducible enzymes that can counteract certain classes of secondary compounds to be found in seeds and if there is the production of a large crop of *Hymenaea courbaril* seeds in one area in one year, I would not be surprised to find the animal becoming a facultative physiological specialist on that seed for as long as they last. When I tried to force such an event in pilot studies, three animals simply lost weight on a pure diet of *Hymenaea courbaril* seeds and had to be taken off this diet before they died. On the other hand, such animals may also be expected to react to the periodic appearance of a rare seed in the habitat by simply eating whatever small number per day as can be handled by their detoxification system. For example, both squirrels (*Sciurus variegatoides*) and agoutis eat an occasional *Dioeclea megacarpa* seed in Guanacaste but never more than one or two a day (Janzen, 1971b and unpublished).

TABLE II

Seed prey of insect seed predators in lowland Guanacaste Province, Costa Rica

Insects	Plants
Bruchidae	
<i>Pachymerus</i> sp. 1	<i>Scheelea rostrata</i> Burret
<i>Caryobruchus buski</i> Bridwell	<i>Ipomoea pes-caprae</i> (L.) Roth
<i>Megacerus leucospilus</i> (Sharp)	<i>Ipomoea carnea</i> Jacq.
	<i>Ipomoea</i> 1 (Palo Verde)
<i>Megacerus flabelliger</i> (Fahraeus)	<i>Merremia umbellata</i> (L.) Hall. f.
<i>Megacerus porosus</i> (Sharp)	<i>Merremia aegyptia</i> (L.) Urban
<i>Megacerus maculiventris</i> (Pic)	<i>Ipomoea hederacea</i> Jacq.
<i>Megacerus cubiculus</i> (Motsch.)	<i>Ipomoea hederacea</i> Jacq.
	<i>Ipomoea meyeri</i> (Spreng.) G. Don
<i>Megacerus cubicus</i> (Motsch.)	Convolvulaceae VI-20-1972-XXVII
<i>Megacerus bifloccosus</i> (Motsch.)	<i>Merremia umbellata</i> (L.) Hall. f.
<i>Pygiopachymerus lineola</i> (Chevrolat)	<i>Cassia grandis</i> L.
<i>Ctenocolum acapulcensis</i> Kingsolver	<i>Lonchocarpus eriocarinalis</i> Micheli
<i>Ctenocolum biolleyi</i> K. and W.	<i>Piscidia carthagenensis</i> Jacq.
<i>Ctenocolum janzeni</i> K. and W.	<i>Lonchocarpus minimiflorus</i> D. Smith
<i>Ctenocolum tuberculatum</i> (Motsch.)	<i>Lonchocarpus costaricensis</i> D. Smith
	<i>Lonchocarpus rugosus</i> Benth.
<i>Ctenocolum crotonae</i> (Fähr.)	<i>Lonchocarpus minimiflorus</i> D. Smith
	<i>Lonchocarpus costaricensis</i> D. Smith
<i>Gibbobruchus guanacaste</i> W. and K.	<i>Lonchocarpus rugosus</i> Benth.
	<i>Piscidia carthagenensis</i> Jacq.
<i>Gibbobruchus cristicollis</i> (Sharp)	<i>Bauhinia pauletia</i> Pers.
<i>Caryedes brasiliensis</i> (Thunberg)	<i>Bauhinia unguolata</i> L.
<i>Caryedes helvinus</i> (Motsch.)	<i>Bauhinia glabra</i> Jacq. (one record)
<i>Caryedes incensus</i> (Sharp)	<i>Bauhinia pauletia</i> Pers.
<i>Caryedes quadridens</i> (Jeckel)	<i>Dioclea megacarpa</i> Rolfe
<i>Caryedes paradisensis</i> K. and W.	<i>Centrosema pubescens</i> Benth.
	<i>Centrosema plumieri</i> (Turp.) Benth.
<i>Caryedes juno</i> (Sharp)	<i>Calopogonium caeruleum</i> (Benth.)
<i>Caryedes cavatus</i> K. and W.	Hemsl.
<i>Caryedes x-liturus</i> (Sharp)	<i>Galactia striata</i> (Jacq.) Urban
<i>Megasennius muricatus</i> (Sharp)	<i>Bauhinia glabra</i> Jacq.
<i>Sennius breveapicalis</i> (Pic)	<i>Cassia grandis</i> L.
<i>Sennius instabilis</i> (Sharp)	<i>Cassia bacillaris</i> L.
	<i>Cassia obtusifolia</i> L.
<i>Sennius morosus</i> (Sharp)	<i>Cassia alata</i> L. (introduced)
<i>Sennius celatus</i> (Sharp)	<i>Cassia obtusifolia</i> L.
	<i>Cassia leptocarpa</i> Benth.

(continued)

TABLE II (continued)

Insects	Plants
<i>Bruchidae (continued)</i>	
<i>Sennius auricomus</i> J. and K.	<i>Cassia biflora</i> L. <i>Cassia leptocarpa</i> Benth.
<i>Sennius biflorae</i> W. and K.	<i>Cassia biflora</i> L.
<i>Zabrotes interstitialis</i> (Chevrolat)	<i>Cassia grandis</i> L.
<i>Zabrotes subfasciatus</i> (Boh.)	<i>Phaseolus lunatus</i> L.
<i>Zabrotes</i> sp. 1	<i>Cassia leptocarpa</i> Benth.
<i>Merobruchus columbinus</i> (Sharp)	<i>Pithecellobium saman</i> (Jacq.) Benth.
<i>Merobruchus</i> sp. 1	<i>Pithecellobium mangense</i> (Jacq.) Standl.
<i>Merobruchus cordifer</i> (Sharp)	<i>Mimosa guanacastensis</i> Standl. <i>Mimosa albid</i> a Humb. and Bonpl. ex Willd.
<i>Stator pruininus</i> (Horn)	<i>Sesbania emerus</i> (Aubl.) Urban <i>Mimosa quadrivalis</i> L. <i>Mimosa guanacastensis</i> Standl.
<i>Stator championi</i> (Sharp)	<i>Bixa orellana</i> L.
<i>Stator vittatithorax</i> (Pic)	<i>Acacia tenuifolia</i> (L.) Willd. <i>Acacia retusa</i> (Jacq.) R. A. Howard <i>Acacia tenuifolia</i> (L.) Willd.
<i>Stator limbatus</i> (Horn)	<i>Pithecellobium saman</i> (Jacq.) Benth. <i>Pithecellobium oblongum</i> Benth. <i>Pithecellobium</i> vine 10365 <i>Albizia caribaea</i> (Urb.) Britt. and Rose <i>Albizia adinocephala</i> (Donn. Smith) Britt. and Rose
<i>Amblycerus perfectus</i> (Sharp)	<i>Combretum farinosum</i> HBK
<i>Amblycerus</i> sp. 1	Malpighiaceae vine (SRNP)
<i>Amblycerus geminatus</i> (Sharp)	Malpighiaceae vine (FLP)
<i>Amblycerus cistelinus</i> (Gyll.)	<i>Guazuma ulmifolia</i> Lam.
<i>Amblycerus biolleyi</i> Pic	<i>Cordia alliodora</i> (Ruiz and Pavan) Cham.
<i>Amblycerus</i> sp. 2	<i>Cassia leptocarpa</i> Benth. <i>Cassia obtusifolia</i> L. <i>Cassia uniflora</i> Mill. <i>Cassia alata</i> L. (introduced) <i>Combretum farinosum</i> HBK
<i>Amblycerus</i> sp. 3	<i>Cassia emarginata</i> L.
<i>Amblycerus</i> sp. 4	<i>Prosopis juliflora</i> (Sw) DC.
<i>Amblycerus</i> sp. 5	<i>Cissus</i> aff. <i>rhombifolia</i> Vahl.
<i>Amblycerus</i> sp. 6	<i>Spondias mombin</i> L.
<i>Amblycerus</i> sp. 7	<i>Hippomane mancinella</i> L.
<i>Amblycerus</i> sp. 8	<i>Cordia alliodora</i> (Ruiz and Pavan) Cham.

TABLE II (continued)

Insects	Plants
Bruchidae (continued)	
<i>Amblycerus</i> sp. 9	<i>Cordia gerascanthus</i> L.
<i>Amblycerus championi</i> Sharp	<i>Cordia panamensis</i> Riley
<i>Algarobius</i> sp. 1	<i>Prosopis juliflora</i> (Sw) DC.
<i>Mimosestes nubigens</i> (Motsch.)	<i>Acacia farnesiana</i> (L.) Willd.
	<i>Acacia</i> 1
<i>Mimosestes dominicanus</i> (Jeckel)	<i>Acacia farnesiana</i> (L.) Willd.
	<i>Acacia</i> 1
	<i>Parkinsonia aculeata</i>
	<i>Caesalpinia coriari</i> (Jacq.) Willd.
<i>Mimosestes amicus</i> (Horn)	<i>Parkinsonia aculeata</i>
	<i>Prosopis juliflora</i> (Sw) DC.
<i>Mimosestes viduatus</i> (Sharp)	<i>Acacia collinsii</i> Safford
	<i>Acacia cornigera</i> (L.) Willd.
<i>Acanthoscelides quadridentatus</i> (Schaeffer) }	<i>Mimosa pigra</i> L.
<i>Acanthoscelides</i> sp. 1	
<i>Acanthoscelides</i> sp. 2	<i>Triumfetta lappula</i> L.
<i>Acanthoscelides kingsolveri</i> Johnson	<i>Indigofera suffruticosa</i> Mill.
	<i>Indigofera costaricensis</i> Benth.
<i>Acanthoscelides guazumae</i> J. and K.	<i>Guazuma ulmifolia</i> Lam.
<i>Acanthoscelides obrienorum</i> Johnson	<i>Cassia skinneri</i> Benth.
	<i>Cassia biflora</i> L.
<i>Acanthoscelides griseolus</i> Fall	<i>Sesbania emerus</i> (Aubl.) Urban
<i>Acanthoscelides puellus</i> (Sharp)	<i>Calopogonium mucunoides</i> Desv.
<i>Acanthoscelides argillaceus</i> (Sharp)	<i>Phaseolus lunatus</i> L.
<i>Acanthoscelides</i> sp. 3	<i>Calopogonium caeruleum</i> (Benth.)
	Hemsl.
<i>Acanthoscelides flavescens</i> (Fähr.)	<i>Rhynchosia minima</i> (L.) DC.
<i>Acanthoscelides apicalis</i> (Sharp)	Malvaceae (herb, Bagaces)
<i>Acanthoscelides brevipes</i> (Sharp)	<i>Sida</i> 1
	<i>Sida</i> 2
<i>Acanthoscelides difficilis</i> (Sharp)	<i>Mimosa pudica</i> L.
	<i>Mimosa albida</i> Humb. and Bonpl.
	ex Willd.
<i>Acanthoscelides</i> sp. 4	<i>Mimosa guanacastensis</i> Standl.
<i>Acanthoscelides pertinax</i> (Sharp)	<i>Aeschynomene americana</i> L.
<i>Acanthoscelides</i> sp. 5	<i>Aeschynomene americana</i> L.
	<i>Mimosa dormiens</i> Humb. and
	Bonpl.
Curculionidae	
<i>Cleogonus armatus</i> Champ. }	
<i>Cleogonus rubetra</i> (Fabr.) }	
<i>Cleogonus</i> nr. <i>fratellus</i> Fiedler }	<i>Andira inermis</i> (W. Wright) DC.
<i>Apion samson</i> Sharp }	

(continued)

TABLE II (continued)

Insects	Plants
Curculionidae (continued)	
<i>Rhinochenus transversalis</i> Chevrolat } <i>Rhinochenus stigma</i> (L.) }	<i>Hymenaea courbaril</i> L.
<i>Conotrachelus</i> sp. 1	<i>Casearia corymbosa</i> HBK
<i>Apion</i> sp. 1	<i>Pterocarpus rohrii</i> Vahl
<i>Phymatophosus</i> sp. 1	<i>Cayaponia racemosa</i> (Sw.) Cogn.
	<i>Cayaponia attenuata</i> (Hook. and Arn.) Cogn.
<i>Chrysapion chrysocomum</i> (Gerstaeker) } <i>Apion</i> sp. 2 }	<i>Aeschynomene americana</i> L.
<i>Apion</i> sp. 3	<i>Ateleia herbert-smithii</i> Pittier
<i>Apion sublaterale</i> Kissinger	<i>Lonchocarpus</i> 1 (Boucher 544)
Cerambycidae	
<i>Leptostylus spermovoratis</i> Chemsak	<i>Diospyros nicaraguensis</i> Standl.
<i>Leptostylus gibbulosus</i> Bates	<i>Sapindus saponaria</i> L.
<i>Leptostylus spermophagus</i> Fisher	<i>Manilkara zapota</i> (L.) v. Royen

The most spectacular examples of great fluctuations of seed availability are the supra-annual community-wide synchrony of seeding in bamboos and *Strobilanthes* (Janzen, 1976a), Dipterocarpaceae (Janzen, 1974), extra-tropical conifers and hardwoods (Janzen, 1971c). That such synchrony is habitat-wide is a function of both the commonness of the species involved and their synchrony with each other as well as with conspecifics. In these communities the seeds are characterized by having low toxicity (if any at all) and by the animals that prey on the seeds being able to feed on those of many species. The most interesting recent case is that just as the *Curculio* weevils that feed on acorns in North America tend to have long prey lists (Gibson, 1964, 1969), the *Nanophyes* and *Alcidodes* weevils that feed on dipterocarp seeds in Malaya likewise feed on many species of dipterocarps; the extreme recorded to date is nine species of dipterocarp hosts for *Alcidodes dipterocarpi* (Singh, 1974) but I suspect that more thorough collecting will greatly lengthen this list rather than reveal new species of weevils.

The grasses of open savannas represent a case somewhat intermediate between the large mast-seeding perennials and the toxic seeds to be found generally on species that seed at annual or nearly annual intervals. When growing in large stands, grasses can produce enormous numbers of seeds every year in the same site and it is well known that birds, rodents and insects can eat many species of these seeds in great numbers. While some preferences

among the seed species may be exhibited by the animals, there is little evidence that the preferences are controlled by extreme differences in seed chemistry. I suspect that the grasses are simply generating a mast seed crop every year. When the grass seeds are absent, there is a much reduced amount of food (and cover during the winter or dry season) for the animals that live in these communities; thus the animals are unlikely to build up in large numbers and be maintained by a sudden pulse of grass seeds each year. Furthermore, there are occasional years when the grass seed fails to be produced. It is notable that the major avian grass seed predators are either migrants from the north (e.g. in Arizona, R. Pulliam, personal communication), or migrants that characteristically follow grass seed production (e.g. *Quelea* in Africa; Ward, 1971).

Apart from grasses and mast-seeding species, the other major sets of highly edible seeds are among plants with very hard outer nuts. In general I suspect that the work involved in cutting through the hard nut to reach the seed may be equivalent to the loss that would be incurred to an animal eating a seed of the same size with more usual amounts of toxins or digestion inhibitors in them (and see Smith, 1975). The examples with which I am most familiar are coconuts (*Cocos nucifera*), palma real in Central America (*Scheelea rostrata*), *Coula edulis* in Cameroun and *Panda oleosa* in Gabon (Emmons, 1975). There are probably many more examples. However very hard nuts need not be correlated with seeds that are very poorly protected chemically. Very poisonous seeds may have very hard seed coats (e.g. *Caesalpinia bonduc* and many other legumes from dry areas).

(c) *Great interspecific variation in secondary seed chemistry.* The more dissimilar are the secondary compounds in seeds of different species, the more host-specific the animals that feed on seeds are likely to be. At the extreme, were each seed species to have a set of highly unique defensive compounds, there would be only two kinds of seed predators. There would be those small enough to have a generation on a single seed crop and feed only on that species of seed and those that could feed on a number of seed species by eating such a small amount of each that a lethal dose was not accumulated from any seed. The more unique the defences of the seeds in the habitat, the fewer species of the latter category would exist.

No survey has yet been completed for the secondary compound chemistry of all the seeds in any one habitat. However, all the circumstantial evidence suggests that there is substantial uniqueness among seeds (except in areas which contain large proportions of individuals that synchronously mast seed at supra-annual intervals). First, it appears that most seeds have three or more classes of defensive compounds (e.g. one or more protease inhibitors and/or lectins, alkaloids or uncommon amino acids, some other glycosides, a polyphenol or others). As each group of compounds is known to be very

diverse, it seems unlikely that there would be many seeds with the same defences by chance alone. Second, there are strong selective pressures for divergence in seed chemistry among sympatric species. Seeds are of such a morphology and location in the habitat that a seed predator should have little difficulty locating many species of seeds. Any pair of species with the same defence would jointly present a larger and more reliable food source to the seed predator, thereby creating strong selection favouring any mutant that caused them to diverge in secondary seed chemistry (cf. Janzen, 1973; Cates and Rhoades, 1977). Third, surveys of seeds for single classes of secondary compounds among a taxonomic group show very great diversity in their nature and concentration. For example, it appears that almost every lectin isolated from a seed has different binding specificities from those from other species of seed; some seeds may have as many as three varieties in them (cf. Liener, 1976). Cates and Rhoades (1977) have summarized data to show that the largely sympatric sets of *Argyrea* species (Convolvulaceae), *Lupinus* (Leguminosae) and *Erythrina* (Leguminosae) have unique combinations and concentrations of alkaloids in their seeds.

These examples are not meant to suggest that every seed species in a habitat will have totally unique secondary compounds. For example, in Guanacaste Province, Costa Rica, the deciduous forest contains four species of plants with canavanine in their seeds and all are within range of the same seed predators: *Sesbania emerus*, *Canavalia maritima*, *Canavalia brasiliensis* and *Dioclea megacarpa*. Apparently all Australian acacias contain the same uncommon amino acid in their seeds (E. A. Bell, personal communication). However, I predict that each will be found to have its own unique set of lectins, protease inhibitors and other secondary compounds.

(d) *Seed secondary compounds are detrimental to seed predators.* If seed secondary compounds were not significant to seed predators, seed specificity would be much reduced. There would probably be the same kinds of specificity as exhibited by insectivorous birds. Apart from noxious insects, these birds often take a much restricted number of the total species of insects present in the habitat because they forage in only one part of the habitat. Rosenzweig (1973) suggests that desert rodents may also gain some organization along these lines; they feed on many species of seeds from annual plants but they only feed in certain microhabitats. If the seeds are dispersed in a non-random manner among the microhabitats, these rodents may regularly feed on only a fraction of the species of seeds present simply because they do not encounter any more than that.

However, I suspect that the toxicity of secondary compounds to seed predators will select for host-specificity for two reasons. First there is the obvious reason that the more toxic the food, the more physiologically and biochemically specialized the animal may have to be to use it (though I am

not here discussing the intriguing question of why small animals often do not seem to have specific detoxification systems for more than one or two sets of different secondary compounds). Second, the more a population is restricted to a particular seed species over evolutionary time, the more likely it is to evolve to a state where it is actually dependent on the secondary compounds in the seed. Such appears to be the case with *Caryedes brasiliensis* in *Dioclea megacarpa* seeds; not only does the larva avoid the canavanine but it metabolizes it and apparently uses the resulting ammonia in amino acid synthesis (Rosenthal *et al.*, 1977). Such systems are probably commonplace among insects that feed on seeds, but have not really been looked for.

2. How Host-Specific are Seed Predators?

We do not yet really know what fraction of the available species of seeds are taken by large seed predators, or in what numbers, in any habitat and for any species. The primary problem is in knowing what is available to the animal and what it actually ate (finely comminuted seeds are difficult to recognize in gut contents). There is ample evidence that no animal, large or small, eats seeds in proportion to their biomass or numerical abundance. Furthermore, many species of seeds are clearly avoided by foraging vertebrates. However, many things besides seed secondary chemistry will influence this choice (e.g. size, hardness, ease of location, hunger, learning, availability of alternates) and this is not the place to discuss them. Additionally, there are no theoretical reasons to expect vertebrates to take seeds in proportion to their abundance, since the monomorphism implied in the single word "seed" is a developmental bias masking enormous interspecific variability of traits that should be important to any foraging animal.

Insects are even more conspicuously careful about what seeds they feed on or in. All those with many hosts have some peculiar aspect to their natural history. *Curculio* weevils in extratropical oaks, microlepidopteran larvae in conifer cones and *Alcidodes* and *Nanophyes* weevils in dipterocarp seeds are all involved with mast-seeding species of plants. Harvester ants (*Pogonomyrmex*, *Veromessor*) feed on seeds of annuals and grasses that satiate the seed predator community following heavy rains in the desert. Puncturing bugs may be obtaining only a small fraction of the tissue from a growing seed and may not have to contend with many of the defences of the fruit or seed. The scolytid beetles with very many hosts (e.g. Schedl, 1961) feed largely in palm seeds (noted for their lack of secondary compounds), or if in other kinds of seeds, may be enlisting the aid of fungi or microbes to deal with the seed content.

However, the vast majority of insects whose larvae live in seeds have very few hosts. Table II contains a provisional list of bruchids, weevils and

cerambycids whose larvae live in the seeds of plants in the deciduous forest (and associated riparian sites) of the Guanacaste lowlands on the Pacific coastal plain of Costa Rica. While the list is not yet complete, I have done enough sampling to be convinced that the overall picture will not change when the study is finished. In short, most of these insects have only one or two host plants out of 2000 or more available. Again, as with the vertebrates, I am certain that more than just seed secondary chemistry determines this host-specificity, but consider only secondary chemistry here.

How are the prey lists of seed predators distributed among the total array of seeds in the habitat? For animals with long prey lists, there is no information on this subject. However, for the array of beetles that have been reared from seeds in Guanacaste Province, a few comments are possible. It is evident from Table II that the maximum number of species of beetles feeding on the seeds of any one species of plant that has beetle seed predators is 3 and the mean is only slightly greater than 1. Therefore, one of the consequences of extreme host-specificity is that in no one species of plant are the seeds under the selective influence of many species of very host-specific seed predators at one point in its evolutionary history. Since there are many fewer species of animals with long host lists in the habitat, the total number of species of seed predator operating on one species of plant at any instant is probably less than 10 in most cases.

B. CONSTRAINTS ON SEED SECONDARY COMPOUNDS

A number of constraints can be identified that should guide the evolution of seed secondary compounds: The direct usefulness of the compounds to the germinating seed should be maximized; the probability of autotoxicity (or the cost of avoiding it) should be minimized; the cost of the compounds to the parent plant and seedling (in direct costs and in displaced nutrients of more value) should be minimized; and the effectiveness of the compounds against the relevant seed predators should be maximized.

It is evident that there are many contradictions among these four constraints and thus the actual seed secondary compounds for any particular species will be a compromise, an optimization of at least these four processes. It is also evident that in different habitats and with different phyletic backgrounds (starting points), different members of the four will receive more emphasis. Furthermore, because seeds are dormant and often eaten quickly in entirety, there seems to be little chance for effective inducible secondary compound systems. No seed species has ever been simultaneously analysed with respect to these constraints and the information does not exist in the literature to do it for any one species. Below, each will be discussed as a relatively separate subject.

1. Usefulness to the Germinating Seedling

Very little is known of what happens to the secondary compounds in a seed when it germinates. In a study in progress, Eric Conn has found that at least during the first week after germination, the total cyanogenic glycoside (linamarin) content of a *Phaseolus lunatus* seedling remains the same as that in the seed before germination. This implies that it is neither being synthesized nor degraded at germination, but merely redistributed (presumably for seedling defence). Incidentally, there is nothing about being a seedling that prevents the synthesis of cyanogenic glycoside; sorghum seedlings (*Sorghum vulgare*) are 25% dry weight cyanogenic glycoside (dhurrin) three days after germination (E. Conn, personal communication) yet the seed contains none. There is at least one case where the lectin content of the newly germinated seedling decreases at a rate which parallels the loss of reserve proteins (Rougé 1974a, 1974b) which suggests that the lectin is serving double duty – it protects the seed and it is a peptide or amino acid source for the seedling.

It is important to note that a secondary compound may be just as valuable to a seedling as are standard peptides. If the seedling does not obtain its protective compounds from the seed, it must manufacture them and thereby have fewer building blocks for growth and other functions. However, here is one of the areas for compromise. Many of the animals that feed on seeds, especially insects such as bruchids, do not also feed on seedlings. The secondary compounds that might be very effective against a bruchid might be very ineffective against a grazer of seedlings (e.g. a paca, *Cuniculus paca*).

I suspect that kinds of secondary compounds that are common in other parts of plants but only rarely encountered in seeds may be absent because they cannot do double or more duty for the seed and seedling. The most conspicuous examples are polyphenols that are normally sequestered in vacuoles in the cell. It is my (crude) understanding that once in the vacuole, they cannot be removed by the plant and thus must remain in the cotyledons (could this be why ripening of fruits involves the condensation of their tannins rather than their mobilization out of the fruit?). I therefore expect tannins or other immobilizable polyphenols to be quite rare in the seed contents of small seeds and restricted to the largest seeds (such as those of the avocado, *Persea americana*, cola nut, *Cola* spp., and cacao, *Theobroma cacao*) if they occur at all.

I would also predict that compounds easily obtained by the seedling would be rare as defences in the seed. Silica crystals may be an example. However, this particular example contains the difficulty that nutrient content of a seed is high and an animal would not consume enough silica to damage its molars while eating enough food to stay alive (the opposite of a horse, which has to process a very large amount of silica-rich grass).

Eric Conn has pointed out to me that cyanolipids liberate lipids upon hydrolysis, rather than the sugars released when cyanogenic glycosides are degraded. This suggests that cyanogenic glycosides are found in a wide variety of plant parts but cyanolipids are exclusively found in seeds (especially of the Sapindaceae, Seigler, 1977). Where there is a constraint on seed size or weight, it seems reasonable that there would be strong selection to replace ordinary inactivator sugar molecules with ones that would be of much more calorific value to the seedling. Are there lipid alkaloids that replace glycosidic alkaloids in seeds, etc? Ordinary sugars may also be replaced with sugars that themselves are potentially toxic; here the ideal molecule would be inactive when undisturbed but have its constituent parts act as anti-herbivore compounds when attacked by the herbivore's enzyme system or that of the masticated plant part.

2. *Avoid Autotoxicity*

Avoidance of autotoxicity in seeds is probably a problem intermediate between that of dead tissue such as bark and heartwood and that of very active tissues. The most conspicuous and probably universal method of avoiding self-poisoning by plants is the production of glycosides with a variety of sugars (and with lipids as mentioned in the previous section). Seeds contain cyanogenic glycosides, cardiac glycosides, alkaloid glycosides, uncommon amino acid glycosides, lectin glycosides and probably every other kind imaginable. Basically the sugar masks the active site (e.g. Liener, 1976) and is later removed by gut enzymes or plant enzymes in the masticated plant tissue. Why a sugar should be the universal masking agent is not clear; however, it may be the cheapest complex organic molecule that is large enough for the role. The only part of a plant where toxic compounds are often not glycosides is in heartwood (autotoxicity is obviously not a problem here) and I would predict that the same may apply to material in seed coats (and maybe even vacuoles). Glycosides appear to be transported with impunity through the vascular and other parts of a plant, though there must be an organization that keeps them out of contact with the cell's own enzymes.

Probably the next most common kind of avoidance of self-poisoning is sequestering the secondary compound in cellular vacuoles. We have one well documented example; 11-13% of the cells in the cotyledons of *Theobroma cacao* (Sterculiaceae) seeds contain very large vacuoles containing caffeine, theobromine and polyphenols; the remaining cells appear to be totally free of defensive compounds (though if there are lectins or protease inhibitors, I would expect them to be in the other cells, Forsyth and Quesnel, 1963).

Arthur Bell (personal communication) is finding that L-dopa is located in specific cells within the cotyledons of *Mucuna andreana*.

I also expect that different tissues within the seed contents will have different secondary compounds and that these differences will reflect ease of avoiding autotoxicity as well as other considerations. Certainly in those plants with a massive carbohydrate-rich endosperm, there are quite different opportunities for defensive sugars in the endosperm and embryo. There is some evidence that bruchids may be differentially affected by different parts of the seed contents. The larvae of *Callosobruchus maculatus* mine through the endosperm of *Schizolobium parahybum*, *Parkinsonia aculeata* and *Delonix regia* and then develop in the embryo without eating the endosperm (Janzen, 1977d). It may be simply that the endosperm does not offer usable nutrients, but its sugars may be the types reported by Applebaum and Guez (1972) to be toxic to bruchid larvae.

3. *Minimal Cost to the Parent.*

While it is easy to hypothesize that a plant should put the cheapest compounds into the seed that will do the job, it is very difficult to know how to look for this; we know so little of what different secondary compounds are worth to the parent plant. A cheap compound for one plant may be very expensive to another. A common question is: do legumes use many alkaloids and uncommon amino acids as defence compounds (in seeds as well as other plant parts) because they have a relatively large supply of nitrogen from their nitrogen-fixing bacteria? We will have to know much more about the internal budgets of plants before tackling that question. A generally unappreciated and complicating part of the story is that if the adult legume has a relatively large supply of nitrogen, the seedling will be at the opposite end of the scale until its bacterial symbionts are well established, making nitrogenous compounds of particular value to the legume seed if it is to establish physiological patterns that will later depend on a strong supply of nitrogen. In other words, the adult may not supply the seed with nitrogenous compounds because it has an excess but because it must in order to produce another machine like itself.

The cheapest compound that a parent plant can put in a seed is water but I do not yet see how it can be viewed as a secondary compound. However, that seeds sometimes do have a high water content suggests that they should be of a volume or weight greater than that produced by the amount of resources that the parent plant has allocated to each seed. It is of interest in this context that moist seeds tend to be large and dispersed in a manner such that weight and volume probably do not have as strong a ceiling on them as is the case with seeds dispersed, for example, by vertebrate guts.

4. *Maximal Effectiveness Against Seed Predators*

There is another possible reason why phenolics seldom appear to be present in seeds. The richer the content of classical nutrients, the less effective will be a given amount of phenolic or other kind of digestion inhibitor. The same does not apply to the more toxic compounds that act against the central nervous system or other intracellular physiologies. Among the more toxic compounds, again one expects differences among classes of compounds. However, since we know nothing of what it costs to make these compounds or what other constraints are put on their use by the three factors discussed above, it is difficult to guess the patterns. For example, since alkaloids are very toxic in very low concentrations, should we expect them to be the dominant protective compounds in seeds? Perhaps, once the frequency distributions for secondary compounds in seeds have been calculated, the patterns will suggest more processes but at present we only know that for the same seed predator, different groups of secondary compounds are strikingly different in toxicity for a given dose (e.g. Janzen *et al.*, 1977). This means that the nature of the seed predator guild will be very important in determining what array of secondary compounds will be very effective against seed predators.

There may be a substantial optimization problem with respect to particular seed predators. For example, even small amounts of certain compounds may deter the majority of potential seed predators yet an impossibly massive escalation of other compounds may be required to eliminate a specific seed predator that coevolves with the increased dosage. This may be one of the reasons why seeds often contain a variety of secondary compounds in very small amounts, amounts that would appear to have no effect on any insect specializing on that seed species (the alternative hypothesis is that plants are simply inefficient in their biosyntheses). Examination of this hypothesis will require much more detailed characterization of seeds and the effects of secondary compounds on seed predators than has been done to date. Even synergisms among the compounds present in a seed are likely to be a selective pressure favouring mixtures of secondary compounds in seeds. In other words, a seed predator does not confront particular defences; it confronts a defence system. Simultaneously, there may be combinations of secondary compounds that are not very effective. For example, I would not expect the lectins in seeds to be designed such that they do not bind readily with the other seed chemicals released when a seed is chewed up, but rather to retain their activity until they arrive in the animal gut.

VI. WHO ARE THE SEED PREDATORS?

Man, dogs, cats and rats are not the seed predators that have caused most of the selection for secondary compound chemistry of wild plants, though it

can be argued that small rodents have been very important. Furthermore, the relevant route to the seed predator is oral, not intravenous, intramuscular or subcutaneous. It should be apparent what is drastically wrong with most of the pharmacology of secondary compounds from seeds, from the viewpoint of the ecologist-evolutionary biologist. The major seed predators of the world are outlined below with the hopes that this may guide pharmacologists, biochemists and experimental evolutionary biologists to test groups whose responses are relevant to the biology of the animal-seed interaction.

A. MICROBES

While various microbial diseases of seedlings, green seeds and a variety of plant parts are commonplace, I do not know enough about them to characterize their membership in the seed predator guild. However, it seems quite likely that a number of seed traits, both green and mature, will have been the outcome of selection by these seed predators.

B. FUNGI

My comment is identical to that for microbes. In addition the fungi that prey on grain have complicated the system by themselves manufacturing very potent secondary compounds (e.g. aflatoxins) which probably serve simultaneously to protect both the fungi and the grain from predation by higher animals (Janzen, 1977f), and thus may on occasion result in survival of seeds.

C. NEMATODES

My comment is identical to that for microbes.

D. INVERTEBRATES

Unless worms digest small seeds in the litter they consume, invertebrate seed predators are restricted to insects. Among insects, virtually all seed predators are contained in the Hymenoptera (bees, wasps and ants), Lepidoptera (moths and butterflies), Coleoptera (beetles) and Hemiptera (true bugs). There are a few cases where tettigoniid grasshoppers may be predators on the seeds of grasses and herbaceous plants, and cecidomyid midge larvae may gall seeds and fruits.

Hymenopteran seed predators are confined to two groups. The ant seed predators are primarily the genera *Messor*, *Veromessor* and *Pogonomyrmex*

with occasional predation by other genera (cf. Cole, 1968; Bequaert, 1922; Tevis, 1958). Most seed predation by ants occurs in xeric habitats and is directed against small seeds of annual dicotyledons and grasses. Seed size and sculpturing, hardness and degree of investment is probably very important in their success at capturing and killing seeds. The seeds are taken back to the nest by workers and often stored in underground granaries; a few may be dispersed in the process but there seems to be no real evidence that these ants are selected as seed dispersers. There has never been a study of the tolerance of seed predator ants for secondary compounds found in seeds; they certainly have preferences among the species of seeds available in a desert habitat (Tevis, 1958).

The other seed predator Hymenoptera are the so-called seed chalcids. The most famous ones are the fig wasps (Agaonidae), where the seed predator is also the pollinator (e.g. Ramirez, 1970); it is likewise interesting that the developing endosperm feeds the fig wasp larva. The other seed chalcids (in the Eurytomidae and Torymidae) are also tiny wasps that lay their eggs directly on or in the seed. The larva eats the seed contents and the adult emerges. Without detailed natural history studies, they are often difficult to distinguish from the parasites of the larvae of other seed predators and probably evolved from them. They are a trivial part of the seed predator guild in most habitats but can occasionally be very common (as in the attack of herbaceous legume seeds in some extratropical areas). I expect the Agaonidae to be highly and mutualistically coevolved with the chemistry of fig seeds. The other seed chalcids have never been tested against the secondary compounds found in seeds, nor discussed with respect to other seed traits.

With the exception of an occasional butterfly larva that eats green seeds in fruits (usually while it is also feeding on foliage), lepidopteran seed predators are moth larvae. The most famous one is probably the larva that lives inside of the Mexican jumping bean, or the yucca moth (*Tegiticula* spp., Powell and Mackie, 1966), though the most well studied is the cotton boll worm (*Heliothis zea*), a predator on immature cotton fruits (and the contained immature seeds). Seed predation by moth larvae usually occurs by the larva mining from seed to seed in a nearly mature fruit, or by the larva eating the mature fruit and occasionally consuming a mature seed along with it. Many moth larvae appear to have difficulty penetrating hard seed coats. They most commonly eat seed fragments that are left behind by previous seed predators. While there are some moth larvae that feed on exceedingly toxic mature seeds (there is a moth larva that consumes seeds of the alkaloid-rich Costa Rican *Erythrina berteroaana*, for example), they generally consume immature seeds (much like eating green leaves?) or ripe fruit with minimal seed interaction. Those species that live in ripe fruit tend to have quite long host lists and are probably not particularly adept at dealing with secondary compounds in

mature seeds. Fruit-inhabiting moth larvae have never been tested against the secondary compounds found in seeds (though army-worm moth larvae (*Prodenia eridania*) were used in bioassays of various uncommon amino acids from seeds; Rehr *et al.*, 1973a, b).

Seed predation on immature seeds is widespread among bugs in the families Coreidae, Pyrrhocoridae, Cydnidae and Lygaeidae and occasionally among Pentatomidae, Scutelleridae and Myridae (e.g. Vanderplank, 1960; Janzen, 1972a; Sweet, 1964; Slater, 1972). The bugs penetrate everything from flower bases to full-sized fruits and tap directly into the soft seed. They may remove only certain parts of the seed, since many have long host lists. The length of the host list suggests that they are either largely immune to secondary compounds (which is unlikely) or else are able to tap into the parts of the growing seed that are low in secondary compound defences. The standard reaction by the plant is to abort such ovules or young seeds but often to save the fruit in multiple-seeded fruits that have suffered only partial seed mortality. Such aborted seeds are impossible to distinguish from physiologically aborted seeds, at least at the level of gross inspection; it was recently discovered that a major part of the seed abortion recorded in west coast conifers may be due to seed predation by a coreid bug that lives high in the tree crowns and punctures young cones (Koeber, 1963). I know of no tests of seed secondary compounds against bugs that prey on seeds.

Once the seed has matured, it is taken by a different guild of sucking bugs, primarily in the families Pyrrhocoridae and Lygaeidae. Pyrrhocorids are renowned as the cotton-stainers and are probably major predators of dispersed seeds in the Malvaceae-Sterculiaceae (e.g. Janzen, 1972a). Lygaeidae have been named "seed bugs" and many have raptorial forelegs for picking up seeds and holding them while puncturing them with the proboscis (e.g. Slater, 1972). The impact of Lygaeidae on seed populations must be enormous, as inferred from their great abundance in many habitats, but is essentially unknown. Again, I know of no tests of seed secondary compounds against the bugs that feed on mature seeds, though they display very strong preferences among seeds and different numbers survive on different species of seeds.

Beetle larvae are the most conspicuous of the insect seed predators. The whole family Bruchidae, with about 1000 described species in the world and probably half as many again undescribed in South America, specializes on seeds (they are, in fact, little more than chrysomelid beetles whose larvae live in seeds). The eggs are laid on the seed or fruit, the larvae drill through into the seed where development usually takes place (a few species mine from seed to seed through the fruit) and the adults exit through a very round hole in the seed and often the fruit wall as well. They are major economic pests of stored legume seeds, but feed on many other families of seeds in the wild. Bruchids have been the subject of a number of direct tests of

seed secondary compounds (e.g. Janzen *et al.*, 1976a; Applebaum and Guez, 1972).

The weevils (Curculionidae) are the largest family of beetles and have a moderate number that attack immature and mature seeds (though there are probably many more living in flowers). Their biology is essentially the same as that of bruchids, except that the larvae tend to mine more extensively in the fruit and one larva often kills several seeds in a multiple-seeded fruit. The cotton boll weevil (*Anthonomus grandis*) is the best known species. I know of no tests of seed secondary compounds against seed predator weevil larvae, with the exception of numerous synthetic pesticide tests on boll weevils. Both bruchids and weevils tend to be extremely host-specific in nature (less so in commercial bean stores).

The Cerambycidae (long-horned wood borers), Scolytidae (bark beetles), and Anobiidae (shot-hole borers) each contribute a few species that are seed predators. The cerambycids have biologies very similar to those of bruchids and weevils. Scolytids are quite different; the adult female burrows into a seed and treats it as other species treat a tree trunk. There may be several generations in a seed and it may well be a race between the germination rate of the seed and the growing colony of scolytids (e.g. Janzen, 1972b). Anobiids often enter after other seed predators take their toll and eat seed fragments and attack intact seeds. I know of no tests of seed secondary compounds against any of these beetles.

E. BIRDS

Seed predator birds may be divided into those that open green fruits for the seeds inside (e.g. parrots – Psittacidae, finches and weaver finches – Fringillidae) and those that often pick up mature seeds off the ground or from the mature fruit (e.g. pheasants – Phasianidae, guans – Cracidae, tinamous – Tinamidae, nutcrackers – Corvidae, doves and pigeons – Columbidae, sparrows and weaver finches, ducks and geese – Anatidae and ostrichoids). Both a shelling action by the bill (especially parrots and finches) and grinding in the gizzard is important to seed predator birds and I suspect that sensitivity to secondary compounds occurs primarily in these two regions (though the softer areas in between are obvious suspects for sensitivity). Birds are major seed predators (and thus potential selective agents for seed traits) in mast-seeding systems (with perhaps the exception of dipterocarp forests), grasslands, early succession, forest understory and the crowns of many species of large perennial plants. Any bird that preys on seeds is likely to also be a seed disperser and thus its impact on different species of plants will be complex and variable. I know of no studies testing seed secondary compounds on avian seed predators, though cardiac glycosides administered

in mild doses are becoming a standard tool for inducing vomiting in seed-eating bird dietary studies (R. Pulliam, personal communication).

F. MAMMALS

There is more diversity in the ways of seed predation among mammals than in any other group previously listed. Like birds, they eat seeds in every stage from the flower to newly germinated. The gnawing abilities of rodents surpass the gizzard for penetrating hard seed coats or nut walls and the massive cracking and grinding abilities of molars open seeds that a bird gizzard would take weeks to grind through. Large mammals also eat many immature seeds as part of the foliage they consume. While members of every omnivorous or herbivorous group of mammals occasionally eat seeds, the primary mammalian seed predators are rodents (Rodentia), pigs (Suidae), peccaries (Tayasuidae), primates (Primates) and scattered members of the ruminant artiodactyls (e.g. forest antelopes such as duikers). The biggest difficulty in understanding seed predation by many of these animals is that they are often seed dispersers as well (often simultaneously) and that the more classical mammalian dispersal agents (e.g. rodents, elephants, coatis, tapirs) frequently grind up seeds in passing. Squirrels and other hoarding rodents are the biggest problem, in that here it is reasonable to view the plant as paying seeds rather than fruit for dispersal (the ultimate in parental manipulation). With the exception of laboratory rats and humans, the impact of seed secondary compounds on mammals is almost unknown (a few particularly toxic compounds such as strychnine, abrin and ricin have been tested on other mammals but not in a manner that would help one understand how a wild African squirrel can eat *Strychnos* seeds).

G. OTHER VERTEBRATES

Fish, lizards and turtles occasionally consume green or ripe fruits but the degree of digestion is unknown. Presumably *Uromastix* (from African xeric habitats) is a seed predator with the same problems as a bird on arid-land seeds.

VII. COMMUNITY STRUCTURE CONSEQUENCES OF HOST SPECIFICITY BY SEED PREDATORS

The simplest example is that of a bruchid whose larvae eat the seeds of only one species of tree in a habitat with many species of trees. Assume that

the larvae consume about half of the seeds produced by any tree's crop in the habitat. In contemporary time, the specificity of the beetle means that any failure of the seed crop (e.g. due to weather or other seed predators) will result in a depression of beetle density in future years. Conversely, consecutive runs of good seed years will result in the maximum possible beetle density (and presumably seed predation) for that combination of host-plant, inter-plant density and intercrop timing (though subsequent increases in parasite density may alter the story). Therefore, the extreme host-specificity of the beetle will result in fluctuations of production of surviving seeds, greater than would be the case were the beetle to have other hosts in the habitat. This should in turn result in years when other species of trees, though perhaps inferior competitors, have enough resource base to continue in the same habitat. The final outcome should be a greater richness of tree species in the habitat than if all the beetles had several species of hosts (and see Janzen, 1970 for elaboration of this idea).

The specific seed predator should have an elevating effect on plant species richness in a second manner. If it is dependent on a particular species of seed, when these seeds become scarce, it will persist in searching for them rather than adapting to some other, more available, food source. Depending on the pattern of seed production by the host tree, this may decrease the average number of seeds surviving, consequently decreasing the average recruitment by that plant species. This argument can be transliterated into the following natural history. When a new plant species arrives in a habitat, its chances of raising the species richness of the habitat are small if other plants in the habitat will share seed predators with it. This is because if it shares seed predators with several species of plants, there is a chance that the predator will build up on one and then eliminate the other (note that this is not the same as a seed predator with many hosts moving from host to host as it begins to depress the one currently of interest).

Since plants cannot move around, it is evident that there should be a spatial component to the system. Again, the more dependent a particular animal is on a single species of mature seed, the more likely it is to produce an area near the parent plant that is free of seeds. This in turn lowers the chance that any one species will be able to competitively dominate the habitat and thus the species richness should increase. It is noteworthy that in cases of severe mast fruiting, the animals cannot (do not) clear an area around the parent and thus competition among the seedlings should be the primary determinant of community structure. The outcome of mast fruiting should be progressively purer stands of species of plants finely adapted to particular edaphic circumstances (through the consequences of selection for seedling and adult competitive ability), accompanied by little selection for dispersal (owing to the danger of ending up on the wrong edaphic type).

On an evolutionary time scale, the consequences of extreme host-specificity

should be that a few animals completely pass the chemical (and other) barriers of the seed (though their fitness may be reduced somewhat by the costs of detoxification and the inability to use other hosts in time of short food supply). Their impact on the plant should be great until they have pushed the density of the plant to a point where they can no longer find the seeds at a rate (or pattern) which would push it any lower. In some cases this lower level will be extinction. When a mutant plant appears there are several possible outcomes. The seed predator may evolve to prey on other plants, it may produce counter-mutants, or the populations may be reduced.

The seed predators with long host lists are never expected to pass completely, the secondary compound chemical (and other) barriers of a seed species and thus to select for the maintenance of those various barriers that have been passed by the very host-specific species. Therefore, one can identify at least three levels at which there is selection on secondary seed chemistry. (a) There are those compounds which may be part of a coevolved escalation with the seed predator that eats only that seed species (e.g. the concentration of canavanine in a seed may slow the developmental rate of the bruchid that regularly eats a canavanine-rich seed; see Beck, 1974 relative to the question of how much even a host-specific insect is damaged by the secondary compounds it can overcome). (b) There are those compounds that exclude the seed predators which feed on other similar species of seeds and have crossed the barriers common to that group of seeds (e.g. canavanine probably excludes many species of bruchids and the protease inhibitors in seeds are probably ineffective against most species of bruchids). (c) There are those compounds that exclude in part or totally the seed predators that eat small quantities of many species of seeds, or are facultatively very host-specific during the seasonal progression (e.g. protease inhibitors in legume seeds probably exclude many species of rodents and greatly reduce seed consumption by others).

What does it mean to the animal that most of the seeds in the habitat are toxic? Seed availability to any animal cannot be measured or even approximated by the overall amount of seed present (e.g. in a seed trap). Second, if the animal has a long host-list (and presumably, cannot eat large amounts of any one of these unless there is facultative gut response), it probably needs to eat small amounts of many species of seeds to avoid extinction (and thus is unlikely to be severely territorial in a species-rich forest). Third, it should have large amounts of behavioural caution (conservatism) in consuming seeds new to its memory span; this caution should be coupled to easy regurgitation or intestinal voiding in the case of mistakes. As the cost paid for eating a toxic seed is unknown at present, the amount of resources available to a seed predator cannot be estimated from the biomass or numbers of seeds present in its habitat. This generalization applies less to comparisons within a species of seed over time or space but even here the availability of alternative foods

to be mixed with the seeds may determine how much can be harvested, rather than the absolute amount of seed to be eaten.

VIII. CONCLUSIONS

What can phytochemists do for secondary compound seed chemistry and its ecology? They can provide chemical determinations and pure compounds (for testing) for those experimenters working in the rainforest. I suspect that there will be little difficulty in convincing natural-products chemists that their determinations need to be more specific; the statement that *Abrus precatorius* contains abrin means nothing to a biologist – it only has meaning to the chemist and drug companies. We need to know how much, where and when in the plant, growing under what circumstances. Furthermore, the concept of variance and variation will have to be introduced into natural-products chemistry. A seed is not a seed is not a seed, even if some Botanical garden gives all three samples the name *Phaseolus lunatus*. Just how much variation in secondary compound seed chemistry is there among the seeds of an individual fruit, crop, population, habitat and species? It is tedious to have to determine the concentration of L-dopa in 30 seeds from one seed crop, but the results may have vital consequences to ecologists. If there is Batesian mimicry among seeds within or between individual seed crops, for example, the effects would be far-reaching.

There is a conspicuous absence of seed parasites in nature (as opposed to bruchids, weevils, etc. which act like parasitoids, to use the terminology of workers in biological control – e.g. Janzen, 1975b). Why does a seed select against the animal that takes a small bit of the resource with minimal damage to the plant (thereby minimizing the chance that a specific defence against it will be selected)? I suspect that part of the explanation is that damaged dormant seeds are quickly killed by other organisms, especially fungi and bacteria that enter through the exit hole of the incipient parasite. Thus the effect of the parasite is the same as if it had killed the seed. Second, only small amounts of damage to a seed can result in severe reduction of its seedling's survival in the face of competitive and herbivore challenges that are commonplace in nature (e.g. Janzen, 1976b).

The superficial similarity to various subsets of a plant's seed output to the clutches of birds suggests to me that there may be a deluge of papers analogizing plant clutch size to bird clutch size and repeating all the ecological and evolutionary thought that has accompanied the determinants of bird clutch size. I suspect that the analogy is unlikely to be as fruitful as direct study of the determinants of seed crop size. The analogy is strained largely because either the fruit or the individual seed crop may be viewed as a clutch, because the egg and the seed are deposited in the outside world in very different

points in the progression from maximum to zero parental care and because the technology of resource harvest by seedlings and fledgling birds is so different. I do not wish to discourage exploration of the analogy, but rather to point out that we do not know enough about plant natural history to make the analogy productive.

A different kind of analogy might be extremely interesting. Tubers (and their other ecological analogues) are essentially seeds composed of maternal tissue. They are often not involved with dispersal agents but represent large stores of high quality food that probably requires defence as much, if not more, than seeds (though their frequent underground location may alleviate this requirement in part). Tubers are known to contain all the classes of secondary compounds found in seeds and are fed on by many of the same groups of animals that feed on seeds. It is of interest that apart from orchid pseudo-bulbs (which must, incidentally, contain some very potent anti-herbivore chemicals), the only place where I have seen above-ground tubers to be prominent is at high elevations, on tropical islands and in forest on white sand soils; all three habitats are well known to have reduced herbivore biomass.

Recently the search for patterns in secondary compounds of plants has turned to emphasizing the dichotomy between the compounds that inhibit digestion and those that have very direct physiological effects and noting that the former type appear to be associated mostly with plant parts that are readily located by herbivores while the latter type are associated with plant parts of more ephemeral nature (e.g. Rhoades and Cates, 1976; Feeny, 1976; Futuyama, 1976). Such an exploration must be very careful not to use the putative cause to explain the effect, and then turn about and use the effect to prove the cause. There are two major reasons for not attempting to analyse seed secondary compounds in terms of this dichotomy. First, many seeds contain both digestion inhibitors and more potent poisons in large amounts. Second, I really do not yet know enough of the natural history of seed predators and seed production to make independent guesses about the ease of location or "apparency" of seeds to seed predators. Seeds will be particularly complex in such an analysis because one seed may be available to a certain type of seed predator (e.g. the host-specific species that is very competent at locating it) and difficult to locate by the seed predator dependent on more gross methods of seed location in time or space. Therefore it is necessary to determine which of these animals is selecting for which classes of chemicals.

We know very little about the genetic programming for seed secondary compound chemistry. Not only is this knowledge of great potential value in breeding resistant crop plants and breeding seed crops that require less processing but it is very relevant background to understanding the coevolution between seed predators and their prey. Can a plant change the alkaloid content of its seeds merely by a single allele at a particular locus? Can a

biosynthetic pathway be changed to generate a cyanolipid rather than a cyanogenic glycoside by a single mutant allele? What are the quantitative genetics of polyphenol content in *Theobroma cacao* seeds? I have found no answers to these questions but they are clearly very important for a relatively complete picture.

As is the fashion these days, I should close with a few words about the relevance of all of this to human resource exploitation. It has been evident to many (e.g. Leopold and Ardrey, 1972) that the evolution of cooking by humans probably was primarily driven by the need to denature toxic proteins in vegetable matter (and especially seeds of legumes and grain) and to leach out water-soluble toxins from the same foodstuff (alkaloids, uncommon amino acids, cyanogenic glycosides). It is also obvious that man has probably done a considerable amount of selection for less toxic seeds. He did it consciously by selecting seeds that gave him less of a stomach-ache or took less time to prepare and unconsciously by selecting for higher yields (thereby selecting for less resources being put into defences). He is probably paying rather dearly for this selection at the present, though I would be the last to argue that man's pesticide problems can be solved solely by breeding plants as toxic as wild ones. A far bigger problem is probably that recently underlined by Feeny (1976) in stating that agriculture consists largely of making unapparent plants apparent.

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