

The Defenses of Legumes against Herbivores

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I. Introduction

The planners of this conference have asked me for a discussion of the interactions between legumes and herbivores. This is a request for an examination of traits of legumes as pertains to herbivores. On the one hand, I am happy to do this because it is a useful sort of focus. On the other hand, I feel it is a bad move. Such an approach fosters the tendency to search for and accept single selective pressures as the evolutionary causes of what appear to be single traits. A single trait, such as the concentration of canavanine in a *Dioclea megacarpa* cotyledon or the force to crush an *Enterolobium cyclocarpum* seed is no more the result of a single selective pressure than is the number of times you can open and close your hand in 30 seconds. A single trait, as we describe it in biology, is simultaneously i) under contemporary design constraints, ii) a temporal and spatial anachronism, iii) under contemporary budgetary constraints, iv) multi-functional, and v) optimal (not maximal) in performance rate and pattern. The huge fruit of *Cassia grandis* is photosynthetic, protective against herbivores with a multitude of defenses, heavy, derived from a minute tissue, expensive per flower, cheap per seed, indehiscent, toxic when unripe, edible when ripe, and probably was eaten by mastodons. We are only just now, again, learning to take a single trait of an organism and simultaneously explore the significance of that trait to that organism's physiology, anatomy, ecology, behaviour, and so forth. And I worry that this review may be taken as a digression from such a holistic approach to understanding form and function. However, while our contemporary research may be becoming holistic, it is clear that most of what we have to work with is not, and that much of the day to day data collection is likewise not. I proceed accordingly.

Perhaps the most gross insult to a holistic approach to understanding legume traits is the traditional separation of animal herbivores from microbial and fungal herbivores, as though they were two different kinds of challenge to the plant, to be met by two different kinds of defenses. Yes, it is evident that different physiological processes work most effectively against the fast-chewing elephant in contrast to slow growing fungal hyphae; but, elephants and aphids likewise require very different defenses. It is almost laughable that induced chemical defenses, called phytoalexins, have been stock in trade in phytopathology studies for decades, yet induced protease

inhibitors as a response to larger herbivores (e.g. Ryan, 1978) are just being discovered.

Equally offensive to a holistic approach is the desire to ascribe a single function to a single *class* of traits, with the possession of lectins (phytohaem-agglutinins) being the largest contemporary offender. It is obvious that in different concentrations, sites and organisms, lectins play grossly different roles. This is not hypothesis. This is fact. It is however quite fashionable to regard the presence of a number of different research reports, each showing a different function for something like lectins, as evidence that their function is not understood. There need be no conflict in these statements. Biology keeps forgetting that natural selection favours parsimonious function; one trait is likely to function in many roles, and one class of traits even more so.

In discussing the adaptive significance of legume traits, there is a particularly annoying historical phenomenon. It was natural and commonplace for natural products chemists, physiologists, anatomists, and other dissectors to puzzle over the adaptive significance of the traits they were describing. They were astute and respected researchers in their respective areas.

By and large they knew nothing of an enormous fraction of the selective forces that shaped the traits they were examining. They often therefore suggested function with no more rationale than an Australian aborigine first confronted with a defunct automobile. However, it is a property of science that the very act of making the suggestion, and publishing it, along with other "facts" of much more considered nature, gives it both weight and momentum. Thus we have "hypotheses" floating about in the contemporary literature that were they to be suggested in the light of contemporary knowledge would never get past the author's pen, to say nothing of the reviewer's. There are still physiologists who think it reasonable to suggest that mimosoid extra-floral nectaries have their adaptive significance in getting rid of excess sugar, and ecologists that think it reasonable to suggest that there is selection for bruchid attack of hard legume seeds because their penetrance of the seed coat "aids" in germination.

In discussing the interactions of herbivores with legumes it is tempting, and at this stage of knowledge rather necessary, to divide the plant into traditional parts and examine each as a battleground. However, I must stress a poorly understood and even less appreciated fact. *Herbivores interact with each other, and hence with the plant, through the medium of the resource budget of the plant in both contemporary and evolutionary time* (Janzen, 1973a), as well as through direct consumption of each other's resources. This means that the ultimate discussion of the cyanogenic glucoside content of *Lotus* leaves will have to include a discussion of *Lotus* root protection against nematodes through phytoalexin production, and how each defense is bought at the expense of the other, and how each kind of herbivory lowers the fitness of the plant rather than how much it lowers the yield of leaves or roots.

If asked what an herbivore does to a legume plant, most biologists would answer that it consumes foliage (or some other part), and have a vague mental image that this consumption somehow may damage the plant. This answer is sufficiently inadequate as to be misleading and is a major stumbling block in the development of understanding how animals (and other organisms) and

legumes interact. Further, it provides a totally inadequate basis for dealing with paradoxical questions such as 'why does mild defoliation increase soybean yield?' (e.g. Chester, 1950) and 'what will be the consequences of a lectin-free soybean?' (e.g. Pull et al., 1978). Organisms that consume legume parts have had and will continue to have an all-pervasive influence on what a legume is, and how it uses the resources at its disposal. The impact of herbivores on legumes can be roughly divided into six categories: defense costs, direct damage, damage repair, death, outcrossing and seed dispersal. Each category contains at least one major dichotomy, the division of losses into actual resources lost and into constraints on allocation. In addition, every act of herbivory, whether by a cow, pollinator or frugivorous bird, has a cost. The question is then to what degree is this cost balanced by a return to the individual plant.

II. Defense Costs

One of the two most unappreciated costs that a legume bears because of the existence of herbivores is the cost of the plant's standing and facultative defenses. The standing costs and the programming component of facultative costs have the salient features that if the herbivore does not materialise in a given season or life cycle, there was no gain to the plant. Such costs are thus weakly analagous to insurance and most of the well known rules for determining the amount of insurance needed will apply to defenses against herbivores as well. An observation such as 'Normal insect grazing (from 5 to 30 percent of annual foliage crops) usually does not impair annual plant (primary) production ... it may accelerate growth ... after an outbreak has subsided, there is evidence that the residual vegetation is more productive than the vegetation that was growing immediately before the outbreak' (Mattson & Addy, 1975) is rendered unrealistic by an understanding of defense costs to a plant.

What fraction of a plant's available resources are expended on defenses? An approximate answer to this superficially simple question requires consideration of: a) what traits are defenses? b) what do they cost?, and c) what does the plant have to expend?

A. *What traits are defenses?*

Certain kinds of defenses are obvious and unambiguous. It cannot be argued seriously that the hard nut wall of a *Dipteryx (Coumarouna)* fruit, the complex, very toxic alkaloids in *Erythrina* seeds, and the high tannin content of *Mora* foliage are anything other than defenses against herbivores. However, I expect natural selection to result in one trait of an organism having several functions, and defensive traits are no exception. Lectins and protease inhibitors in legume seeds may be storage proteins for the seedling as well as defenses for the seed, ants in obligate ant-acacias protect against competing plants as well as herbivores, and tannins in immature *Caesalpinia coriaria* fruits may determine which dispersal agents take the ripe fruits as well as deter herbivory of immature fruits. At the extreme end of this progression lies

cellulose. Obviously the plant needs a strong structural compound, but the fact that of the many possibilities, the plant uses one that is indigestible to higher animals is probably no coincidence. I may also note that at least one cost paid for this insurance is that the cellulose carbohydrates cannot be recovered when leaves are discarded.

However, the construction of molecules that impede herbivore attack is not the only defense of a legume. The genetic programming and other standing cellular machinery used in the construction of facultative chemical defenses (protease inhibitors, polyphenols and flavonoid phytoalexins) must also be charged to the defense budget. Likewise, the programming and machinery for the storage and abrupt release of seeds, flowers, fruits, and new leaves at certain times and even in synchrony with conspecifics and even unrelated plants must likewise be charged to defense to the degree that such behaviour is not associated with avoidance of weather events and attempting to win in competitive interactions.

So to return to the question, defenses are those traits which are found, through careful natural history observations and field experiments, to function in this manner. Always be wary of the person who says, in effect, 'I cannot imagine what this trait does and therefore it must not have a function for the plant', since the sources of such comments are notorious for their unfamiliarity with the biology of plants in nature. Of course, as mentioned earlier, legumes are collections of anachronisms, and it is quite possible that a given trait no longer functions as it once did. Such an answer should always be viewed with extreme scepticism.

B. What do defense traits cost?

While defense traits clearly cost as much as their actual content in calories, minerals and other building blocks, they also cost the enzymes and programming to produce them. You cannot measure the cost to a society of producing a car by measuring any trait of that car. You cannot even approximate it. Probably the most unappreciated costs are strategic. Carbon and calories tied up in a polyphenol in a leaf cell vacuole cannot be re-allocated elsewhere as the need arises. Flavonoids deposited in dead heartwood are likewise unavailable for use elsewhere. Another unappreciated area of cost derives from the way complex molecules are constructed by plants. Apparently it is commonplace for a chain of enzyme driven and spontaneous reactions to construct a molecule in such a manner that the various intermediate products along the way are not available to other synthesis systems. Therefore when enzymes and substrates are tied up in synthesis of defensive molecules they are not available for use elsewhere. This means that defensive molecule budgeting may have to include the cost of the entire synthesis rather than being partly budgeted to other synthetic processes in the cell.

In fact, it seems that without great advances in the understanding of the micro-physiology/biochemistry of cell activity, the cost of defense traits to a plant probably cannot be approached through the study of the defenses themselves. Rather, cost will have to be measured in some unit of reduced reproductive output (which it may be possible to relate to fitness with the

appropriate understanding of natural history). This type of cost measurement can be approached only through explicit careful experimental mimicry of the herbivore and direct use of herbivores on the plants growing in natural circumstances. I emphasise 'careful mimicry' because it is evident that the exact way, timing and place of herbivory can strongly influence the impact of the herbivore on the reproductive output of the plant. If 100% of a leaf crop is eaten off one week after the leaves are produced the effect is much less than if 100% of a leaf crop is eaten off half-way through the life of the leaves (e.g. Chester, 1950). Eating 30% of a leaf blade by cutting small holes out of it is quite a different thing from eating 30% of the blade with a single hole. I emphasise 'natural circumstances' because herbivore damage may be greatly amplified through second order complications with competitive or edaphic circumstances. Ant-acacias without their ants, and therefore heavily damaged by herbivores, survive much longer in open pastures than in fast-growing second growth vegetation where the stunted plants are quickly overtopped and shaded (Janzen, 1967a). Seedlings of rain-forest trees that have a mycorrhizal association may survive defoliation better than non-mycorrhizal plants (Janos, 1975). Herbivore damage to shoot tips with subsequent release from apical dominance may increase yields in crop plants through the production of a bushier plant. Such an event could be lethal in the more normal circumstance of tightly packed intercrown competition.

C. What is available for expenditure?

The cost of a defense is clearly circumstance dependent. Plants would seem to have large resource budgets compared to the cost of, for example, an alkaloid that makes up only 1% of the dry weight of leaf tissue. However, easily more than half of what a plant makes it has to expend on maintenance metabolism of the standing organism and a substantial portion of what is left after this has to be expended on competitive interactions and in dealing with edaphic conditions. These are fixed costs. The remainder can then be divided among defenses on the one hand and sexual reproduction on the other. Viewed in this way, even 1% of the total resource budget spent on defenses may be reflected in a considerably greater reduction in potential sexual reproduction than 1%. In short then, a plant has relatively little that it can spend on defenses against herbivores in the first place. Likewise, even small amounts of damage owing to a lack of defense can lead to large decreases in sexual reproductive output.

In addition to the internal budgetary circumstances, external factors enter in as well. It may well be that Leguminosae with nitrogen-fixing symbionts will find nitrogen-based defensive compounds (alkaloids, uncommon amino acids, protease inhibitors, lectins, cyanogenic glycosides) comparatively cheap, which may in turn explain why these compounds are so frequently encountered in legumes. Carbohydrate-rich extra-floral nectaries may be comparatively much more expensive to maintain in heavily shaded forest understorey habitats than in fully insolated crowns of early successional species of plants. As the impact of herbivory rises owing to poor soils and thus higher costs of replacement of plant parts, the relative return from

expenditures on defenses should rise, rendering defenses comparatively cheaper (Janzen, 1974a). Using a polyphenol for defense in a seed costs more than using a protease inhibitor, even if they cost the same per gram, and each gram gives the same amount of protection. The developing seed probably cannot use the polyphenol and therefore leaves it behind in the cotyledons whereas the protease inhibitor can be degraded and the parts used by the seedling.

Given all these precautions, I am forced to the conclusion that there is probably only one way to measure defense costs (and the gain from them). First we need to know the reproductive output of genetically well adjusted phenotype mutants that lack this or that defense mechanism as compared with wild types. Does a plant that produces lectin-free soybeans also make more of them? This one is a bit difficult because a lectin-free soybean may simply have the lectin replaced with a non-toxic storage protein with the same production costs as the lectin. Or, it may make seeds with a lower protein content and use the extra resource for additional seed production, more competitive activity, better soil use, or other similar purposes. Second, we need to know how the reproductive output of plants in nature is influenced by herbivory generated by herbivores, herbivore mimics or removal of defenses. The latter is very difficult except in the case of spines (dead tissue that can be cut away) or plant-ants. What should be of interest to biologists in ant plants is not the spectacular nature of the defense, but rather that the defenses of the plant can be removed without altering the plant in any other way.

At this point it is evident that I am worrying more about what we need to find out than what we already know. I am afraid that the entire area of interactions between herbivores and legumes is in a state that justifies such an attitude. Given this, there is a set of precautionary statements about herbivore-plant interactions that anybody working in this area should carry as intuitive and basic working assumptions.

1. *Herbivores do not eat Latin binomials.* Virtually no herbivore consumes all parts of a plant (except in the cases of small seed predators) and therefore lists of herbivores eating this or that species of plant are next to worthless.

2. *The world is not coloured green.* Chlorophyll is green but the rest of the plant is coloured nicotine, tannin, lectin, strychnine, cannabinal, sterculic acid, canavanine, lignin, etc., and every bite contains a horrible mix of these.

3. *Not all animal-plant interactions are co-evolved.* In many cases the specialist herbivore has evolved resistance to the defenses that keep off the rest of the herbivores in the habitat, and the plant shows no evidence of having evolved in response to this specialist. Likewise, many plant defenses that evolve may simply cause the partial or total removal of the herbivore, with no subsequent evolutionary changes by the herbivore.

4. *All plants and their herbivores are anachronisms.* The set of animals feeding on any given plant is clearly not that set that the plant has always dealt with. Depending on the rate of change in this set's biology and the counter changes in the plant, the plant's traits will be to various degrees anachronistic. The same model applies to the set of plants fed on by an

herbivore.

5. *Distances are not in meters but in arrivals.* Proximity of similar plants, and therefore the likelihood of reciprocal interchange of seed predators, pollinators, dispersal agents, and other animals that play a similar role has to be measured in the number that arrive. One hundred meters across a forest understorey may be a greater barrier to insect movement than 1000 meters across open grassland or vice versa.

6. *Herbivores compete through the budget of the plant.* Every bite taken by an herbivore today potentially lowers the resource available to some other herbivore in the future, irrespective of what part of the plant it feeds on. Likewise, if an herbivore's impact is great enough to select for a plant defense, the defense selected for may just as well lower the impact of some other herbivore as the one that initially increased the herbivore load.

7. *Herbivory may be cheaper than the defense against it.* Not all levels of herbivory will select for defenses. It may well be cheaper to lose, for example, an occasional set of easily replaced leaves early in their life than to load them up with a standing defense that is superfluous during most of the leaves' lives (e.g. grasses).

8. *One herbivore's poison is another herbivore's food.* 'Toxic' is not an intrinsic trait of any chemical or defense structure. No one chemical defense has the same effect of each herbivore that encounters it and within each herbivore species there will be heterogeneity of response as well. A pregnant doe is a very different herbivore from an ageing buck; canavanine is lethal to *Callosobruchus maculatus* but a dietary necessity to *Caryedes brasiliensis*.

9. *Each defense is breached by some herbivore(s); no herbivore can breach all.* There is enormous variation in the size of herbivore loads among plant species, but they all have them. Likewise, some herbivores can eat a very large number of plant species and parts (though they cheat a bit in that it is really several hundred species of microbes that are doing the eating), but none can feed on all, and many specialists feed on only one.

10. *Herbivore damage is not measured by bite size alone.* The site of removal of an herbivore's meal has an enormous effect on the fitness-depression resulting from the meal. Five mg bitten out of a seedling's shoot tip may have the same effect as 1000 kg of leaves eaten off the adult plant's crown.

11. *Not all plant defenses are standing defenses.* In addition to the usual defenses found in plants, a number of chemical and structural defenses are facultative and appear only following damage by herbivores (e.g. phytoalexins, protease inhibitors, increased thorniness, wood lignification).

12. *No plant part acceptance by an herbivore is absolute.* All herbivores, even monophagous specialists, pause between 'meals'. More generalist species usually stop feeding on any one plant part or species well before their stomach capacity is reached, with a resulting strong mixing of dietary input. This is functional both in nutrient balance and avoiding overload of defense neutralisation systems in the animal.

13. *Degree of host-specificity is circumstance dependent.* Is a bug that sucks the toxin-free phloem fluid from the shoot tips of 30 species of plants less specialist than the moth larva that chews up the toxin-rich leaves of

three widely unrelated species of plants? If a beetle feeds on two species of plant seeds in a 10 species habitat is it more host-specific than if it feeds on two species of plant seeds in a habitat containing 800 species of plants?

14. *All wild plants have defenses against herbivores.* An enormous range of defense intensity is displayed by plants, but there are no known or suspected cases of defenseless plants (though given plant parts may be free of defenses).

15. *Seeds are different organisms from the plant that bears them.* The defense systems of seeds should not only be different from those of the parents, because of their widely divergent life forms, but because of the different way the fitness of each is measured. The parent plant measures its fitness by the number of new adults produced, and a number of seed deaths may maximise this, while the seed measures its fitness by whether it stays alive to become at least an adult plant.

16. *Ripe fruits repel as well as attract animals.* The function of a ripe, animal-eaten fruit is not only to get the seeds into the animal coterie that will generate the best seed shadow, but to keep the seeds out of the remainder of the animals in the habitat.

17. *Longest is not best in seed dispersal.* The optimal seed shadow will be generated by those animals that put seeds where they have the best chance in aggregate of generating new adults. There is no a priori reason to suspect that this seed shadow will be generated by those animals that carry seeds the farthest distance, and there are many reasons to suspect this is not the case.

18. *Parasites are omnipresent in mutualistic systems.* The pollinator coterie and the disperser coterie (and the protective coterie in the case of ants) are each part of a larger group of flower visitors and fruit eaters, many of which are truly parasitic on the system. They neither pollinate nor disperse seeds appropriately, but selection probably cannot tune the system finely enough to the point where these animals are excluded.

19. *Biochemical pathways of defense production should converge.* Owing to economies and constraints of chemical energetics and the similarities of basic resources available to different species of plants, different pathways leading to the same defensive compound in different plant species should, over evolutionary time, often become identical, although this may take a long time after the compound is in use.

20. *Defenses should diverge within plant part life forms but converge among plant parts of the same kind.* Since herbivores tend to feed on the same plant part when they feed on many species of plants, interspecific convergence of defenses among plant parts will be selected against. Conversely, the presence of the same defense in a shoot tip as in a root is unlikely to increase the susceptibility of either.

21. *The number of resources in the habitat depends on the herbivores and vice versa.* Being a resource kind is not an intrinsic property of any plant part; it requires an herbivore that treats it that way. A branch may be one resource to an elephant but 5 resources to 8 insect species. Shoot tips replaced at the rate of 1 per shoot per month may not be a large enough resource to support a moth population but if the rate is tripled, these shoot tips may suddenly become a single kind of resource.

22. *Man and his domestic herbivores are not representative herbivores.* Man has not only bred many of the defenses out of the crops eaten, but

breaches these defenses through heat, fermentation, chemical extraction and extra-habitat mixing. The same applies to the food fed to domestic herbivores. In addition, reproduction is no longer the appropriate fitness measure for most domestic animals.

23. *Application of these axioms is very circumstance dependent.* Does a large seed crop satiate seed predators? It depends on the proximity of other seed crops, weather that year, relationship of crop conspicuousness to size, method of search of seed predators, etc. Does a dry season irrigation ditch increase pest problems in deciduous forest? It depends on whether the herbivores on the crop act like average insects (since the crop is not an average plant, there is no reason for its herbivores to act average). Is there an optimal seed shape, size, weight? No, there is only an optimal distribution of seed shapes, sizes, weights, etc. within the parent's seed crop. We have been taught to think in terms of yes/no answers to biological questions. To understand the interactions of tropical animals and plants, we have to learn to think in terms of distributions as well as mean values.

It is now apparent to me that the call in the biology of animal-plant interactions is for the researcher to take one organism (or population of organisms) and dissect in detail its interactions with the multitude of selective forces impinging on it. We do not need another alkaloid survey of the legumes of the world nearly as badly as we need a natural products chemist to take apart an entire legume and lay before us its chemical profile in health and sickness, in wealth and poverty, in youth and senescence, in marriage and solitude. Such profiles are beginning to emerge piecemeal as a collational spin-off from survey studies organized around classes of traits, but they have all the properties inherent to chairperson-free committee reports, and bad ones at that.

So what approach should be taken? I will tell a series of short stories chosen to either illustrate a broader point, indicate the tip of an iceberg, or cause you to think more broadly about facts to which you are privy. This conference wanted me to relate such observations to the systematics of legumes. I do not seem to be able to do that.

III. Ant-Plants

Like a small number of other plant families (Moraceae, Euphorbiaceae, Passifloraceae, Boraginaceae, Polygonaceae, Verbenaceae), Leguminosae have a small number of spectacular ant-plants (Bequaert, 1922) with obligatory mutualisms with ants: Central American *Acacia* (Janzen, 1966, 1967a, 1967b, 1969, 1973b, 1974b, 1975; Janzen & Beulig, 1969; Rehr et al., 1973), East African *Acacia* (Brown, 1960; Hocking, 1970, 1975), South American *Tachigalia* (Bequaert, 1922, and see Foster, 1977), and West African *Leonardoxa africana* (McKey, 1980). What is of interest is not that they are protected by ants, nor even that they have a mutualism, but rather that they wear their defenses on the outside, so to speak, and therefore the defenses can be removed physically or with pesticides. In short, the ant-plants allow us to ask what would happen to any plant were we able to magically deprive it of its secondary compounds. This general situation has several messages to offer those interested in the defenses of legumes (or any other plant).

1. When a Central American ant-acacia is deprived of its normal defenses, from whence come the herbivores that feed on it? In a large de-anting experiment in the coastal lowlands of Gulf coast Mexico (Janzen, 1967a) and in Santa Rosa National Park, Pacific coastal lowlands of Costa Rica (Janzen, 1974b) all the insects that came to feed on ant-free *Acacia cornigera* and *A. collinsii* were of three sorts. First, there was a greatly increased abundance among species that normally feed on the occupied ant-acacia but are kept at a low density by aggressive action of the ants (e.g. *Coxina hadenoides*, Noctuidae; *Syssphinx mexicana*, Syssphingidae; *Pelidnota punctulata*, Scarabaeidae). Second, there were increased numbers of the species that normally feed only on naturally unoccupied ant-acacias (e.g. *Mozena tomentosa*, Coreidae; *Aristotelia corallina*, Gelichiidae). Third, there was a large number of species of insects normally found feeding on other mimosoid legumes in the same habitat (e.g. *Onicideres poecila*, Cerambycidae; *Coscinoptera mucida*, *Pachybrachis* sp., *Cryptocephalus* sp., *Anomoea* sp., *Griburis* sp., Chrysomelidae; *Chrysobothris* sp., Burprestidae; *Diplotaxis denigrata*, *Phyllophaga* spp., *Pelidnota strigosa*, *Euphoria leucographa*, Scarabaeidae; *Homalodisca coagulata*, *Oncometopia clarion*, *Umbonia orozimbo*, Homoptera; numerous lepidoptera larvae). It is this last group that is of the greatest interest. While I did not assess their presence on non-legumes, or even on non-mimosoid legumes, a year of general collecting in the habitat left me with the distinct impression that the majority of them had mimosoid legumes (other than ant-acacias) as their usual hosts.

Given that this is a reasonable statement, then we find ourself with the conclusion that the fate of a mutant that lacks one of its defenses, ant, chemical or otherwise, depends on the proximity of closely related plants that will contribute their moderately host-specific herbivores. So for example, ant-acacias that have lost their ants in Costa Rican deciduous forest rich in mimosoid legumes may be expected to do more poorly than will ant-free ant-acacias in the understory of Costa Rican rain-forest (e.g. *Acacia allenii* in Corcovado National Park on the Pacific coastal lowlands). This conclusion is a tricky one, however, If generalists are prominent in either habitat, they will greatly confound the result. Second, if the ant-acacia has lost so much of its chemical defenses that it is for all purposes a lettuce plant, then it may be food to a variety of herbivores that would not normally feed on legumes. The take-home message is that the outcome of herbivore experiments with mutants that are lacking a major item of secondary compound defense may vary strongly with the habitat, even if that habitat is a natural one.

2. It is a reasonable hypothesis that ant-acacias will be less rich in secondary compound defenses (of their above-ground vegetative parts) than non-ant-acacias. It is also pragmatically observable to the extent that new and mature foliage of ant-acacias certainly tastes less foul to me than does non-ant-acacia foliage. The first test of this hypothesis was the attempted rearing of *Prodenia eridania* larvae on 5% freeze-dried leaf diets of *Acacia cornigera* (an ant-acacia conspicuously dependent on an ant colony for survival in nature; Janzen, 1967a), and of *Acacia farnesiana* (a common widespread non-ant-acacia) and *Acacia chiapensis* (an *Acacia* with a very local distribution in southern Mexico and that has a weakly mutualistic interaction with acacia-ants); the larvae did very well on *A. cornigera* and died on the other two species of *Acacia* (Rehr

et al., 1973). The second test was a survey of cyanide production by non-ant-acacias (*A. farnesiana*, *A. chiapensis*, *A. macracantha*, *A. cochliacantha x hindsii*) and ant-acacias (*A. cornigera*, *A. gentlei*, *A. hindsii*, *A. sphaerocephala*, and *A. collinsii*); all the former produced HCN in large amounts, none of the latter did (Rehr et al., 1973). The message appears to be that at least for one secondary compound, the hypothesis is confirmed. However, as usual, there are complications, and these complications are instructive for anyone examining the chemical defenses of legumes against herbivores.

In 1976, D. Seigler and his associates initiated a major survey of cyanide production by Central American *Acacia*. In herbarium specimens of *A. collinsii* at Berkeley, they found cyanide production; this ant-acacia would appear after all to be a cyanide producer. However, their subsequent field tests in Mexico and mine in Costa Rica (E. Conn, pers. comm.) found that the *A. collinsii* population in general is free from cyanide production, so that plant should remain on the list as an acyanogenic species. In the field in western Mexico, Seigler et al. found *A. hindsii* to be a rich cyanide producer, and on re-examination of the material used by Rehr et al. (1973) found traces of cyanide production. However, the seed that Rehr et al. used to grow their plants came from the area of Esquintla, Guatemala, and may well be acyanogenic in this area (which is a more mesic habitat than is western lowland Mexico). In other words, whether *A. hindsii* is to be regarded as a cyanogenic ant-plant depends on the source of the test material. Finally, they found 5 of 12 species (42%) of non-ant-acacias in the field to be cyanogenic (Seigler et al., 1978).

First, no plant has only one set of chemical defenses. It is therefore not surprising to find that at least one of the ant-acacias (*Acacia hindsii*) has lost something other than its cyanogenic properties in exchange for the ants. The real question is whether the overall chemical defenses have been reduced. Second, all members of a genus certainly should not be expected to have the same set of primary chemical defenses, and therefore it should not be surprising to find that some of the non-ant-acacias are acyanogenic; the question of interest is whether 42% is different from 100% (or 80% if we include the cyanogenic population of *A. hindsii* in the sample of ant-acacias). Third, all portions of a widely distributed species should not be expected to have the same chemical defenses; *A. hindsii* in western Mexico differs from *A. hindsii* in Guatemala in thorn structure, wetness of habitat, life form, vegetation type (Janzen, 1974b) and it is therefore not terribly surprising to find it to differ in details of chemical defense. Fourth, as will be discussed below, *Acacia* hybridise and the herbarium record of a cyanogenic *A. collinsii* (Berkeley) may well represent a bit of introgression between *A. collinsii* and some nearby non-ant-acacia. It is of interest in this context that the three Costa Rican ant-acacias (*A. cornigera*, *A. collinsii*, *A. allenii*) are all acyanogenic but in the same habitats 60% of *A. farnesiana*, *A. sp. nov.*, *A. retusa*, *A. villosa* and *A. tenuifolia* are also acyanogenic (E. Conn pers. comm.).

In short, the question of the loss of chemical defenses by ant-acacias has only been scratched and the real answer to the question will come only with a complete characterisation of the chemical defenses in quantity and quality of a series of both types of acacia, and their hybrids.

3. When they flower synchronously, acacias appear to hybridise quite readily, and I often encountered what appeared to be interspecific hybrids in the field when working out the geographical and ecological distributions described in Janzen (1974b). These hybrids are of very particular interest with respect to the question of the genetic programming and exchange of information for the production of defenses against herbivores. Most educational of all was a large adult acacia growing outside of Mazatlán, in western Mexico. Morphologically it appeared to be intermediate between *Acacia hindsii* (an ant-acacia) and *A. cochliacantha*, a common non-ant-acacia with spoon-shaped thorns. I collected a large number of seeds and planted them in greenhouses at the University of Kansas and University of Chicago. The offspring (which must have resulted from a backcross against *A. hindsii*, *A. cochliacantha* or both) fell quite neatly into two categories; either they had moderately well-developed Beltian bodies, petiolar nectaries and enlarged somewhat cylindrical thorns, or they had tiny petiolar nectaries, no Beltian bodies, and flattened to needle-like thorns. Later chemical tests showed that the latter type contained substantial amounts of cyanide as well. The former type matches *A. hindsii* quite well, while the latter type matches *A. cochliacantha* quite well (I do not know how to reconcile the cyanide results with Seigler's finding of high concentration of cyanide in *A. hindsii* from western Mexico). In short, it appears that the trait called 'being an ant-acacia', that is to say having the morphological traits that guarantee a protective ant colony, may be transmitted as though it were a single multi-faceted gene or tightly linked group of genes. This means that an ant-acacia species growing alongside a non-ant-acacia could 'donate' this trait to the non-ant-acacia population. This means that the number of ant-acacias in a region could increase with no change in the number of species of acacias in the region. I might add, however, that when an acacia becomes an ant-acacia it apparently also obtains the ability to live in moister habitats than acacias in general frequent (primarily owing to the ability of the ant colony to protect the faster growing plant from insect herbivores and to keep it free of vines). Thus the generation of an ant-acacia from a non-ant acacia may increase eventually the total number of species of acacia over a large array of tropical habitats.

It is quite puzzling that there are at least three and perhaps more, very different lineages within the Central American ant-acacias (i. *Acacia cornigera*, *A. sphaerocephala*, *A. mayana*; ii. *A. collinsii*, *A. hindsii* and others; iii. *A. allenii*, *A. melanoceras* and others). Are we to suppose that the ant-acacia trait evolved independently three or more times? I think a much more reasonable explanation is that the trait of being an ant-acacia has been donated from antacacia to non-ant-acacia on a number of different occasions, with occasional speciation within an ant-acacia lineage as well. If such can occur with as complex a trait as the traits required to be an ant acacia, then it certainly can occur with the biochemical and physiological programming for more conventional secondary compound defenses. The obvious take-home message is that plant defense systems, like weapons in contemporary societies, can be borrowed or stolen from adjacent populations without accepting hardly any of the traits possessed by that population. Defense systems may have a value far disproportionate to the amount of knowledge, biochemical or

otherwise, that it requires to produce them. They may therefore spread rapidly and be totally absorbed into an otherwise integrated genome. And therefore, they are hardly the sort of thing that can be used to delineate lineages and cultural relationships, or genetic ones in plants. Be careful.

IV. Escape in Time

Having just reviewed this subject for tropical plants (Janzen, 1978a), and recognising that this conference is more directed at chemical ecology than at behavioural ecology of legumes, I will simply point out that supra-annual fruiting (and even fruiting periodicity within the year) is a very widespread and powerful way of escaping from seed (and perhaps seedling) predators. The escape comes about in two conspicuous ways. First, the seed predators to attack a supra-annually fruiting tree's seeds must be immigrants rather than a local population associated with that individual tree; escape therefore occurs through the imperfections of prey location common to all colonisation events. Likewise, the efficacy of this kind of escape depends on the ability and proclivity of the seed predators to move about in search of plants bearing seeds. Second, the longer a tree waits between seed crops, the more reserves it may have to produce its seed crop; the larger the seed crop, the more chance that crop has to satiate the seed predators. Upper bounds may be set for this process by satiation of dispersal agents, by seed predators that specialize on very large seed crops, and by the missed colonisation opportunities during seed-sterile seasons.

Often inextricably mixed with the above escape behaviour is the behaviour of seeding synchrony at annual and supra-annual intervals. Within the year, there are many selective pressures that may favour intra- (and even inter-) specific seeding synchrony, and therefore it is difficult to determine the relative importance of seed predator satiation in evolving the phenomenon. However, synchrony at supra-annual intervals can much more clearly be attributed to predator satiation (e.g. Janzen, 1976a; Bulmer, 1977). In short, a plant with even a very small seed crop may escape through predator satiation if it is accurately synchronous with other plants. The neighbourhood effectively becomes one very large seed crop. Two examples may be instructive.

Robin Foster has recently drawn our attention to a set of *Tachigalia versicolor* (Caesalpinieae) trees in the rain-forest on Barro Colorado Island, Canal Zone (Foster, 1977). It appears that the 'population' of these large trees is made up of a number of cohorts that flower and die after a fixed number of years (in a flowering year, *T. versicolor* trees of many sizes flower and I suspect that these are of the same age but have suffered different vegetative fates). Foster has chosen to interpret the semelparous behaviour as adaptive in generating holes (tree fall of the dead parent) for the plant's own offspring. He also noted that 'these trees do not seem to store nutrients and energy for the one reproductive event, for the quantities of flowers and fruits seem no greater than in comparably sized tree species with repeated reproduction'. Semelparity to create a hole for offspring seems reasonable, but why die just to replace yourself? And if the tree reproduces to hit other tree falls (light gaps), then why not do so and remain alive yourself? I do not agree that

'these trees do not seem to store nutrients...' The entire tree is a nutrient store unto itself. One can easily argue that it takes all the nutrients a *T. versicolor* can make over the years to get itself into a position in the canopy where it can have enough reserves to just make one seed crop, given its physiology, etc. The *organism called a tree* is the nutrient and energy for the one reproductive event. I suspect that *T. versicolor* is satiating a seed predator at the level of the individual tree and the level of the cohort of trees. It is perhaps relevant that its seeds are attacked by a bruchid beetle, *Amblycerus*; if we may reason from the biology of other *Amblycerus*, this beetle has at best one or two other hosts in the same forest (and most likely, no other hosts).

Ateleia herbert-smithii (Sophoreae) appears to provide a solid example of predator satiation through supra-annual intra-specific seeding synchrony. In deciduous forest in Santa Rosa National Park (north-western lowland Costa Rica), *A. herbert-smithii* is a common large dioecious tree. In the dry seasons of 1972, 1975, and 1977 the population bore fruit while there were no fruit bearing trees in the intervening years. Predation and crop size records were kept in 1975 and 1977. In 1975, none of the census trees bore less than 10,000 seeds ($n = 20$) and 65% had more than 50,000 seeds. In 1977, 50% of the census trees bore less than 10,000 seeds ($n = 34$, including the 20 trees examined in 1975) and 21% had more than 50,000 seeds. In short, the seed density per fruiting tree was 5 to 10 times greater in the 1975 than the 1977 crop. In 1975, on average a tree lost 36.6% of its seeds to an undescribed *Apion* weevil larva. In 1977, on average a tree lost 83.2% of its seed crop to the same insect. In the 1977 crop, there were even 9 out of 34 trees (26%) that lost 99% of their seed crops to the insect. While the sample size of only two seeding seasons is very small, it is certainly suggestive that after waiting only two years between fruit crops, the population of *A. herbert-smithii* does not have enough reserves to satiate the insect population nearly as well as it does after three years of waiting.

V. Monospecific Stands of Trees

Legume trees are often prominent members of tropical forests on extremely poor soils, or otherwise particularly harsh sites. It is conspicuous that it is caesalpinoid legumes that are almost always responsible for monospecific, or nearly so, stands, in these sites: *Mora excelsa* in Trinidad and northern South America (Rankin, 1978); *Mora megistosperma* in lowland Pacific Costa Rica mangrove edges (Janzen, unpublished); *Prioria copaifera* in lowland Caribbean Costa Rican and Panamanian swamps behind the mangroves; *Dimorphandra* on white sand soils in northern South America (Stark, 1970; Lindeman & Moolenaar, 1959; Heyligers, 1963); *Eperua falcata* on white sand in Guyana (Davis & Richards 1933, 1934; Richards 1941, 1952), and *Gilbertiodendron deweyrei* on white sand in western Africa (Gérard, 1960). The conspicuous exceptions in the other subfamilies are *Pterocarpus officinalis* forests in the coastal lowlands of Costa Rica (Janzen, 1978c), *Erythrina* forests on Trinidad (Rankin, 1978), and dense stands of *Prosopis juliflora* (but mixed with *Caesalpinia coriaria*) in Santa Rosa National Park, Costa Rica (Janzen, unpublished).

In general it is to be expected that trees growing on exceptionally poor soils will be very well protected chemically (Janzen, 1974a). Likewise, if they grow in dense stands where there is little or no escape in space, one can predict that they will be very well protected (just as in our extra-tropical evergreen conifers). It appears that these caesalpinoid legumes meet that expectation. *Prioria copaifera* has resin ducts in the wood and exudes the most copious resin flow upon wounding of any tree I have ever seen. *Mora megistosperma* has a very high tannin content in all foliage from the very youngest to the senesced leaves (P.G. Waterman, pers. comm.), and its dark red heart wood is exceptionally resistant to termites and fungi (Allen, 1956; Gonggryp & Burger, 1948). *Dimorphandra* leaves are very resistant to decay (Stark, 1970), implying that they are very rich in tannins or other protective substances. *Eperua falcata* has very decay-resistant resin-rich wood, fallen leaves that are nearly black (?with tannins), and resin produced in quantity sufficient for commercial harvest (Janzen, 1974a).

Let us assume that the generality holds: caesalpinoid legumes are the most likely among the legumes to form high density stands in tropical forests. This probably suggests that they, among the large tree legumes, have the best standing chemical defenses. However, it also suggests that they are the best at surviving on really bad soil conditions, and perhaps developed their anti-herbivore traits after moving into high density sites. It is also evident that mimosoid legumes commonly form high density stands of low species richness in arid tropical and subtropical habitats. The same class of comment and qualifier applies to them. I may also add that the low harvestable productivity of the habitats rich in caesalpinoid legumes probably aids them in surviving at high density with conspecifics, and the depressant effects of severe dry seasons probably aids mimosoid legumes in like manner. To complicate things more, I might note that caesalpinoid legumes produce water-insoluble resins for the most part, and live in wet habitats; mimosoid legumes produce water-soluble gums for the most part and live in habitats that are moderately dry. Given that one of these defense systems is cheaper than the other, then the subfamily that uses the more expensive is probably being driven to it by the physical environmental conditions of its traditional habitats.

VI. Immature Fruit Defenses

While no survey has ever been done, the secondary compound defenses of immature fruits are probably as varied and intense as those of leaves, and for the same reasons. In fact, they are probably more intense, owing to the greater reduction in parent fitness that occurs through immature fruit herbivory as compared to leaf herbivory. There is no reason to believe that this generalization holds any less for legumes than for other families. However, almost nothing is known of the chemical defenses of immature legume fruits and I suspect there may be some surprises. For example, legume tree leaves and immature fruits are often very rich in tannins, if their astringency to my taste is any measure. However, the full-sized immature fruits of *Enterolobium cyclocarpum* show no browning reaction when cut open, and

instead, produce very large quantities of soapy foam when washed in water. Saponins are suggested.

One generalisation seems possible. Almost no Papilionoideae have fleshy fruits consumed by vertebrates when ripe (exceptions — *Andira* and a few Swartzieae), and relatively few Mimosoideae or Caesalpinoideae do. Many of those that do (e.g. *Acacia*, *Pithecellobium*, *Inga*) have an aril that is really quite distinct from the immature protective fruit wall. *Thus it is that in the vast majority of legume species, the protective secondary compounds in the fruit wall need not be removed or otherwise neutralised during ripening of the fruit* except for internal budgetary considerations. Obvious exceptions do occur — the hardening of the resin in *Hymenaea* pod walls, chemical changes in the walls of *Prosopis* and *Andira* fruits, neutralisation of the saponins in *Enterolobium cyclocarpum* fruits. In some, such as *Caesalpinia coriaria*, not even these changes appear to occur, as the ripe fruit contains very high concentrations of active, though hydrolysable, tannins. It is ironic that many of the seeds that mimic red or blue berries are papilionoid legumes (*Erythrina*, *Ormosia*, *Abrus*, *Rhynchosia*).

On the other hand, internal budgetary considerations may be quite large in legumes, especially with respect to easily mobilised compounds such as alkaloids, non-protein amino acids, cyanogenic glycosides, lectins and protease inhibitors. For example, the immature fruit walls of *Dioclea megacarpa* are rich in canavanine, but the mature dry fruit wall contains only a trace (Rosenthal, pers. comm.); presumably the canavanine is moved to the seed or back into the maternal parent with final ripening of the fruit.

VII. Developmental Fate of Seed Defenses

A seed is more than a bag lunch for the developing seedling. It contains weapons as well. Among the traits of an optimal secondary compound in a seed should be the trait that it can be used either in the metabolism of the seedling or as a defense of the seedling. However, no secondary compound can be all things, and I have to immediately add that selective pressure for defense of the seed may be of a type such as to result in seed defenses that cannot be degraded by the seedling or even moved into it; polyphenolics may be such compounds. To get at these generalised questions, we first need pragmatic details of the fate of secondary compounds in germinating seeds. Legume seeds, rich in non-protein amino acids, alkaloids, lectins and protease inhibitors, all of which are nitrogen-rich and apparently potentially degradable by the seedling, are probably ideal to examine the part of the hypothesis where mobilisation and degradation are expected. Two legumes have been examined in this context: *Canavalia ensiformis* and *Phaseolus lunatus*.

Canavalia ensiformis seeds contain up to 5% dry weight canavanine. During the first five days of germination, about 40% of the canavanine disappears from the cotyledons while the total canavanine in the entire plant only declines 23%. The implication is that by the fifth day 17% of the initial canavanine has been moved intact from the cotyledons to the growing tissues of the plant and not been degraded. The degraded 23% was probably processed in the growing tissues since the cotyledons show almost no canavanine-degrading activity for the first five days of seedling growth. By the end

of the 13th day of germination, there is no canavanine in the remaining shrivelled cotyledons, and the seedling contains 0.59 as much canavanine as did the seed (Rosenthal, 1970). What happened to 41% of the canavanine in the seed is the simplest question. However, without using labelled canavanine we cannot distinguish between the case where all the canavanine exported from the cotyledons to the seedling was degraded and new canavanine manufactured, and the case where 41% was degraded for metabolic use and 59% retained for defense of the seedling. The second case is the most economically parsimonious and, I suspect, the most realistic. It seems likely that the canavanine-synthesis machinery of the growing seedling will not turn on until more canavanine is needed for defense than the seed reserve can provide. In fact, it could be argued that 41% of the canavanine in a wild *C. ensiformis* seed is there solely to protect the seed and could be stored as arginine were the seed predation threat less intense, while 59% is there as a reserve of defensive weapons for the seedling-to-be, as well as seed defense.

Wild Costa Rican lima beans (*Phaseolus lunatus*) offer a somewhat different example. Dry dormant seeds contain 3.45% fresh weight linamarin, a cyanogenic glucoside that will enzymatically decompose to produce 0.37% fresh weight HCN. When these seeds are germinated, the total linamarin content drops immediately from about 8.6 μ moles to 7.5 μ moles (a 13% decline, a decline which may even be little more than sample error) and then remains nearly constant in the developing seedling for at least 25 days. The increase in linamarin in the growing portions of the seedling matched the decrease in linamarin in the cotyledons as their content was exhausted. All aspects of the system suggested that the linamarin is transferred intact directly from the seed to the seedling, and presumably, serves there solely as a defense compound (Clegg et al., 1979). Again, as *C. ensiformis*, the linamarin-synthesising process must switch on shortly after if the linamarin content of the enlarging seedling is to remain high. Here in contrast to the case with *C. ensiformis*, an indeterminable fraction of the linamarin in the seed is there solely as seed defense and essentially all appears to be directly useful to the seedling defense system. In other words, in the unlikely event of the removal of all seed predation challenge in the habitat of *P. lunatus*, the linamarin content of the seed would not be expected to decline over evolutionary time (unless it were replaced with a secondary compound superior in seedling defense once the double duty requirement were relaxed).

The developmental transfer of secondary compounds from seeds to the newly growing seedling is only a small subset of the general question of what should be placed in a seed to make the optimal package for the developing seedling. There should even be cases where a compound is present solely in the seed, presumably as a defensive compound, and upon germination is immediately degraded to other compounds more useful to the seedling. For example, the newly germinated seedling of *Agrostemma githago* (Caryophyllaceae) degrades all the orcyalanine (non-protein amino acid) in its seed and does not synthesise this compound again until it is making its own seeds months later (Hadwiger et al., 1965). Sorghum seedlings, on the other hand, begin synthesis of a cyanogenic glucoside immediately after germination (Stafford, 1969); very shortly they have accumulated enough in their tissues

such that an inclusion of this amount in the seed could have seriously lowered the seed volume for other reserves. All the nitrogen for this cyanogenic glucoside synthesis is derived from nitrogen contained within the seed, but the bulky part, the carbon structures, are at least in substantial part derived from photosynthesis by the seedling.

In summary, it seems safe to conclude that the chemical content of a seed is related over evolutionary time to its volume and specific gravity (vis a vis dispersal processes), synthetic ability of its genotype, seed predator kind and intensity, competitive and resource harvest abilities and opportunities of the seedling, economies of chemical synthesis, seedling defenses, and probably numerous others.

VIII. How to Eat a Poisonous Seed: *Dioclea megacarpa* and *Caryedes brasiliensis*

More is known about the biochemistry of the interaction between this large woody vine and its sole specialist seed predator than is the case with any other legume. *Dioclea megacarpa* is a relatively rare member of deciduous forest lowlands of the Pacific coast of Costa Rica (it has, however, a broad range from southern Mexico to Brazil in the same kind of habitat). Apparently, throughout this range its seeds are attacked only by the larvae of a large bruchid; *Caryedes brasiliensis* attacks only *Dioclea*, and a given habitat contains only one species of *Dioclea* (e.g. seeds of *Dioclea wilsonii* and *D. reflexa* are both attacked by *C. brasiliensis* in Costa Rica, but in high elevation moist forest, and lowland rain-forest, respectively; cf. Kingsolver & Whitehead, 1974). The life history of *C. brasiliensis* in Costa Rican deciduous forest is straightforward. The beetles fly to the plant during the last several months of the rainy season (November-December), and lay clusters of eggs on the full-sized large green pods. The larvae bore through the pod walls and thence into the few large seeds. After consuming the seed contents, they pupate in the seeds and emerge about the time that the pods fall from the vine (late dry season, April-May). Since they do not drill holes through the pod wall, emergence from the semi-dehiscent pod is probably facilitated by rodents that occasionally chew open the pods in search of seeds. The newly emerged adults range free in the habitat for about 5–6 months and do not produce a second generation in any other plant or *D. megacarpa* during this period (Janzen, 1971).

The mature seed of *D. megacarpa* contains up to 13% dry weight canavanine, a non-protein amino acid with decidedly toxic effects on a wide variety of organisms (Rosenthal, 1977; Dahlman, 1977). Since *C. brasiliensis* feeds only on this seed, it is reasonable to assume that it is resistant to canavanine and reasonable to call it a specialist on this food. How does it do it? First, *C. brasiliensis* larvae possess an arginyl-tRNA synthetase that can discriminate between arginine and canavanine, and therefore canavanyl (and presumably non-functional) proteins are not synthesised (Rosenthal et al., 1976). This ability is unique among animals studied to date, but of course it would not be surprising to find that the other insect herbivores feeding on *Canavalia*, *Dioclea*, *Sesbania* and other canavanine-containing plants have the same ability. The plants themselves have this ability, which is of interest in showing how

the same biochemical process can evolve quite independently.

Second, *Caryedes brasiliensis* converts the canavanine to potential food. With an extraordinarily high content of urease (38,500 units as compared to a maximum of 1,400 units in 15 other species of insects examined), *C. brasiliensis* larvae degrade the canavanine to urea and canaline, and then degrade the urea to ammonia which can be used in amino acid synthesis (Rosenthal et al., 1977). This degradation may be particularly important to bruchid larva, since it appears that bruchid larvae lack gut proteases with which to obtain amino acids from the proteins in the seeds they consume (Applebaum, 1964). It remains to be shown, however, how much of the amino acid used by *C. brasiliensis* is obtained from canavanine degradation and how much from the free amino acid in *D. megacarpa* seed contents.

Third, *C. brasiliensis* larvae degrade the canaline (a potent neurotoxic and insecticidal non-protein amino acid) to homoserine and ammonia with a set of enzymes unique to this insect (Rosenthal et al., 1978). In short, with this set of steps, the entire canavanine molecule has been degraded and then used by the larval bruchid.

Now we are in a better position to ask why *Caryedes brasiliensis* is restricted to *Dioclea megacarpa* seeds. The vast majority of seeds of the plants in the habitat occupied by *C. brasiliensis* do not contain canavanine and thus this source of dietary amino acids or amino acid building blocks would be missing for the mutant that oviposited on their fruits. However, in the deciduous forest lowlands of Costa Rica, the seeds of at least five plants do contain canavanine in large amounts: *Canavalia maritima*, *C. brasiliensis*, *Sesbania emerus*, and *Indigofera* spp. However, the seeds of *Sesbania emerus* and *Indigofera* spp. are substantially smaller than the bruchid itself; the shift to one of these host plants would thus require a gross change in larval morphology and behaviour. The two species of *Canavalia* are more enigmatic, especially since in other areas *Canavalia* are attacked by other species of *Caryedes*. Both *Canavalia maritima* and *C. brasiliensis* seeds are quite large enough to mature several *Caryedes brasiliensis* larvae, so the answer must lie in the other defensive secondary compounds found in these seeds (e.g. lectins, protease inhibitors), about which we know nothing. This observation brings me to the conventional answer associated with insect host-specificity questions; *C. brasiliensis* is probably excluded in great part from most other large seeds in the habitat, and thereby restricted to *D. megacarpa*, because of the wide variety of secondary defensive compounds that they contain. However accurate this observation with respect to a new and adventuresome mutant to appear on the scene, over evolutionary time it still leaves hanging the question of why cannot there be a *C. brasiliensis* with multiple abilities to deal with a variety of chemical defenses, and therefore be more generalised at least with respect to legume seeds? In short, the generalised answer to the question posed at the beginning of this paragraph has to be a combination of good defenses in the other seeds in the habitat and dietary specialisation to the unique chemistry of the seeds of *Dioclea megacarpa*.

Caryedes brasiliensis females, however, do not arrive at an oviposition tray on the 1st of November and simply lay their eggs where their larvae will do best. Host plants escape from seed predators in many more ways than through

the traits of the individual seeds (and fruits). In particular, *C. brasiliensis* has to be specialised with respect to the dynamics of host location and pod crop production, and presumably would have to change or broaden this specialisation to change to another host or incorporate more host plants in its biology. I cannot enumerate here all the things that the *C. brasiliensis* female would have to deal with in a host change, but I can point out that she is currently specialised to deal with a conspicuous behavioural trait of *D. megacarpa*. Large vines of *D. megacarpa* produce large pod crops at two or greater year intervals, and the year between appears to be a year of very scarce resources for *C. brasiliensis*. For example, a large *D. megacarpa* vine near Bagaces, Guanacaste Province, Costa Rica produced 118, 37 and 365 fruits in 1976, 1977 and 1978; *C. brasiliensis* killed 54, 78 and 13 per cent of these seeds, which results in 64, 29 and 48 fruits producing new beetles each year. In short, with a ten-fold variation in fruit production there is a two-fold variation in production of beetles. *Caryedes brasiliensis* has probably quite accurately adjusted its options of clutch size versus offspring size with respect to *D. megacarpa* and its reproductive pattern, and a change to a new host plant would probably require extensive changes in this pattern if the beetle's absolute fitness is to remain as high as it is on *D. megacarpa*. One wonders that host changes ever occur, as surely they must. The answer probably lies in the observation that were *D. megacarpa* to produce a single mutant trait that suddenly rendered it unavailable to *C. brasiliensis*, *C. brasiliensis* might find its very low absolute fitness on some other (new or occasional) host to still be much higher than on the new mutant *D. megacarpa*.

Caryedes brasiliensis and *Dioclea megacarpa* are a specific example of what I suspect will be a general pattern of interaction between legume seeds and the bruchids, weevils and moth larvae that prey on them. The majority of bruchids and weevils reared to date from Costa Rican legume seeds, and those of other plants, have only one species of host (Janzen 1976b, 1977b, 1980a). When they have 2 or 3 hosts, they are closely related plants that probably have very similar seed chemistry. There is only one that could be called a generalist; the bruchid *Stator limbatus* has at least 6 hosts in three mimosoid genera (*Albizia*, *Pithecellobium*, *Acacia*; see also Johnson (this volume)). While this extreme restriction to a food type is undoubtedly driven by other plant traits as well as seed chemistry. The biology of different species of beetles on different hosts is sufficiently similar that I suspect the great differences in seed chemistry to be a major driving force in the evolution and maintenance of the beetle's monophagy.

IX. Durable Legume Seed Coats

There are three conspicuous and major selective pressures that favour tough, durable, hard, etc. seed coats on legume seeds: repulsion of strict seed predators, avoidance of desiccation and germination cues, and preventing of dispersal agents from turning into seed predators (seed digestors). In the case of all three selective pressures, maximum hardness, toughness, etc. will not generate maximum fitness for either parent or offspring. What we see in the mature legume seed is therefore a compromise among the demands of these three selective pressures, and a compromise with respect to the variation that

must occur within each of these selective pressures. To a given population of legumes, there is no single seed predator, no single intensity of desiccation, no single potentially lethal dispersal agent. Finally, for all three selective pressures there are directly opposing selective pressures: cost, perception of germination cues, and payment of offspring to dispersal agents. So now, why are *Enterolobium cyclocarpum* (Mimosoideae; guanacaste tree) seeds so hard? The tip of the answer focuses on dispersal and seed predation by large mammals, but the physical properties of the deciduous forest habitat of this lowland Central American tree undoubtedly deserves much attention as well.

The contemporary Central American habitat of *E. cyclocarpum* contains six species of large frugivorous mammals: white-tailed deer, tapirs, collared peccaries, white-lipped peccaries, horses and cattle. While cattle are presently the major consumers of guanacaste tree fruits, I will ignore cattle and horses for the moment since they are introduced. Based on studies with captive native animals, white-tailed deer only rarely eat the fallen fruits and when they do, the seeds are so large that they are spat out when they chew their cud. If dispersal occurs, it is because the seed is too hard to be chewed up (see below) and only if the deer moves away from the parent tree to chew its cud (unknown but suspected). Tapirs and peccaries are more complex, however.

When an adult tapir is offered a mature guanacaste fruit, it chews it up and swallows many of the seeds intact along with the pulp. Reasoning from the presence of intact guanacaste seeds in cattle dung following fruit consumption, I assumed quite incorrectly that the hard seeds would safely make the transit through the tapir but have the seed coat sufficiently scarified during the trip to be then susceptible to germination cues. In fact, in a carefully controlled feeding experiment, only 22% of 125 guanacaste seeds survived the trip through the digestive tract of an adult male tapir (Janzen, 1980b). The seeds that survived required 5 to 23 days to make the trip (ordinary food goes through the tapir in 2 to 4 days). A guanacaste seed fresh from a mature fruit may sit in water for at least 6 months without germinating; guanacaste seeds fed to me begin to germinate within two days – that is to say, while they are still inside of me. If I then reconsume the seed, it is digested during the second trip through. In short, the only guanacaste seeds that will survive the trip through the tapir gut are those that are immune to scarification and are not even likely to germinate immediately once they have been defaecated. I suspect that the caecum of the tapir is the site of delayed seed passage, and hence germination and digestion, but other eddy currents in the intestinal loops may also be responsible.

It is customary to state that ‘germination of hard legume seeds (e.g. *Acacia*, *Pithecellobium*, *Enterolobium*, *Cassia*, *Hymenaea*, *Dialium*, *Tamarindus*) is enhanced by passage through the gut of a vertebrate’. It is probably more appropriate to state that germination is delayed if the usual dispersal agent does not disperse the seed. This phenomenon is essentially one of the seed coat being hard enough to protect the seed during gut transit but destructible enough such that it is defaecated by the animal with a seed coat newly permeable to germination cues. What is consistently left out of this analysis is the possibility that the vertebrate simply holds the seed long

enough that it starts to germinate, and is therefore quite susceptible to the digestive action of the gut no matter how hard the dormant seed. In short, behavioural delay is a digestive mechanism that can get around the hardness defenses of any seed that uses moisture as a germination cue. The tapir is therefore suspect as a seed predator as well as a potential dispersal agent. Likewise, all analyses of dispersal agents based only on counts of seeds in faeces are suspect.

When a captive peccary (either species) is offered a guanacaste fruit, it chews it in such a manner as to remove the seeds. Each seed is then placed between the rear molars and loudly smashed, and the fragments chewed and swallowed. No entire seeds are swallowed and some are spat out unbroken. Is there variation in susceptibility of guanacaste seeds to these seed predators? Do seed coats exist that are immune to peccaries, yet by their existence demonstrate that they are not too expensive or too difficult to construct? By placing guanacaste seeds in an Instron weight-loading machine, we have determined that the average pounds to break a seed laying on its flat side can range from 320 pounds (673 mg seeds) to 402 pounds (862 mg seeds) within one tree's seed crop; another tree only a few hundred meters away ranged from 339 pounds (564 mg seeds) to 459 pounds (842 mg seeds) within its seed crop (Figure 1 in Janzen & Higgins, 1979). Turned on edge, average mid-weight seeds of these two trees broke at about 165 and 175 pounds. In short, a smart peccary would seek out certain guanacaste trees over others, concentrate on the smaller seeds in a seed crop, and turn the seeds on edge to break them; that is, if it wanted to avoid breaking its molars.

If the deer is not moving the seeds, if the tapir is killing most of those it eats, and the peccaries are killing all of those they eat, what animal then selected for a large indehiscent (?) nutrient-rich guanacaste fruit? I suspect that the guanacaste fruit, and a number of other large fleshy indehiscent Central American deciduous forest fruits (e.g. *Scheelea rostrata*, Palmae; *Cassia grandis*, Caesalpinioideae; *Crescentia alata*, Bignoniaceae; *Sapranthus palanga*, Annonaceae) evolved in response to recently extinct large mammals, such as mastodons and ground sloths (Janzen & Martin, 1980) and their presence in contemporary habitats is in great part an anachronism (see following section).

However, large vertebrates are not the only animal to challenge the hard seed coat of a dormant guanacaste seed. The habitat containing guanacaste trees contains at least 100 species of bruchid and weevil beetles whose larvae drill through the seed coats of dormant seeds and eat the seed contents. Many enter the seed while full-sized but encased still in a soft seed coat, but in a number of species the eggs are laid directly on the mature seed coat and the first instar larva drills through the hard seed coat. There is a definite interspecific range of abilities of bruchid larvae to penetrate seed coats. For example, the larvae of *Callosobruchus maculatus* cannot penetrate the seed coats of *E. cyclocarpum* (Janzen, 1977a) but the larvae of *Mimosestes sallaei* can do so. *M. sallaei* occurs in the habitat with *E. cyclocarpum* and glues its eggs directly on the very hard seeds of *Acacia farnesiana*. When induced to oviposit on *E. cyclocarpum* seeds in the laboratory, the *M. sallaei* larvae die after feeding on the seed contents; while the seed coat is an inadequate barrier to the bruchid, the seed content chemistry is apparently adequate. In short, guanacaste seed coats are a barrier to some insect seed predators but

not to others.

In summary then, the seed coat hardness, toughness, and the impermeability of *Enterolobium cyclocarpum* mature dormant seeds is certainly a compromise between a diversity of contemporary and past selective pressures. While there are no studies of seed or seed coat hardness for other legume seeds, it is obvious that it varies greatly within and between species, and within and between habitats. In fact, a whole Ph.D. thesis could probably be done with nothing but Krukoff's seed bank, a flush toilet, patience and a daily supply of newspapers.

X. Coevolution?

How are we to deal with the following scenario? A large lowland deciduous tropical forest palm produces about a bushel of 6 cm long yellow fruits, each containing a large hard nut. A forest mastodon arrives at this tree on a daily basis and chews and swallows entire all the fruits that have fallen in the previous 24 hours. The nuts are passed intact in the animal's faeces a day or two later hundreds of meters from the parent tree; these widely scattered nuts generally escape from the two bruchid beetles that oviposit on any nuts left beneath the parent palm tree. In addition to the mastodon, the palm's dropped fruit crop is visited by agoutis. They eat the pulp coating off any nuts they can find and bury the cleaned nuts. Later, many, but not all of these nuts are exhumed and chewed open to get the seed inside. Again, the buried nuts escape from the bruchid beetles. For the average palm fruit crop, the mastodons disperse about 85% of the nuts, the agoutis about 10%, and the remainder are left beneath the tree or carried off by miscellaneous animals.

In our omniscience, we know that this situation has existed for at least the last million years. Over this time, we also know that the palm nut has evolved from a fragile, relatively thin-shelled nut to a thick-walled structure that takes 500 to 1000 kg of pressure to break when the pressure is applied to its flat side. We also know that early in this interaction the mastodon frequently broke the palm nuts when chewing the pulp off of them, but currently never does. Throughout this evolutionary history, however, the agouti has always buried those nuts it could get for later consumption; its eagerness to bury the nut has not changed as the nuts have hardened (though the work required to enter one has increased). Likewise, over the history of this interaction, we find that the chemical composition of the palm fruit pulp has changed from that which was mildly attractive to the mastodon, to that which is highly attractive to this animal, resulting in a distinct increase in the thoroughness with which the mastodon harvests the newly fallen fruits (and a decrease in the number of seeds dispersed/preyed on by the agoutis). The agouti eats palm nut pulp equally avidly over all this progression.

Enter humans. Humans eliminate mastodons (see e.g. Bryan et al., 1978). The system continues for 10,000 years. Enter a new set of humans. These humans study the palm and the rodent interacting (e.g. Bradford & Smith, 1977). They conclude that *Scheelea rostrata* and rodents coevolved; the fruit pulp traits, nut hardness, and the dependency on dispersal for escape have all coevolved in the interaction with the rodents. For its part, the rodents either

had or evolved the appropriate physiological and behavioural traits (nut burying, eating palm fruit pulp, teeth strong enough to chip through the nut, etc.).

It is possible that the contemporary investigator is quite wrong in this conclusion about the coevolution of the system. However, there is *no* way that the investigator can know if the conclusion is correct. We are in fact forced to the conclusion that just as we can never *know* what were the actual selective pressures that led to the evolution of a particular trait, we can never know with which animal a plant trait coevolved, if it did at all. In short, when an animal suddenly appears in the habitat it will seek out those species of plants that its behaviour, morphology, etc. already match most closely. It may well match very closely without having had *any* coevolution occur; species are not thrown together at random in the historical regime of a habitat. In fact, the very fact of survival in a habitat, following immigration, is likely to be dependent on the presence of a species with which it can interact so closely that it appears to have been coevolved with it. This statement should apply to plants as well as to animals.

The moral of this story is that most members of most habitats are anachronisms. Further, their abundances and distributions are in no necessary sense those that would occur were this or that long or recently extinct species still present in the habitat. It is evident that given a species deletion or addition to a habitat will result in one or more evolutionary 'out of tune' species or interactions in that habitat, and that certain classes of species may generally have bigger effects than others. The removal of one large herbivorous mammal species is likely, on average to leave more major anachronisms than will the removal of one tiny chrysomelid beetle species. There are two reasons. First, the large herbivorous mammal is likely to be exerting effective selective pressure on more species of plants than the beetle. Second, the beetle is accompanied by many species of other insects that in a relatively short contemporary or evolutionary time will harvest the resources it was capturing. However, there should be many species or systems that are exceptions to these two generalisations.

So, what is the dispersal system of *Cassia grandis*? Given the above comments, am I to search among the contemporary vertebrate frugivores in its habitat for the dispersal agent(s) that selected for a 70 cm long 500 g indehiscent fruit that does not fall off the tree? Do I have to twist squirrel or white-face monkey biology around to where *perhaps* they did the dispersing of the seeds in this enormous fruit? I think not. In fact, if this tree grew in Africa, you would be quite happy to hear me say its large fruits were eaten by elephants, so why shouldn't you be happy to hear me hypothesise that it was dispersed by mastodons, mammoths or giant ground sloths (Janzen & Martin, 1980)? Again, the fruits of *Acacia farnesiana* look just like those of many species of ruminant-dispersed African *Acacia*. They currently fall to the ground to rot, or occasionally are carried off by a rodent. Why not realise that they were probably a staple dietary item for Pleistocene neotropical ruminants just as *Acacia* pods are today for East African bovids? *Enterolobium cyclocarpum*, *Samanea saman*, *Cassia grandis* and *Hymenaea courbaril* legumes are not the only fruits susceptible to such an interpretation. *Crescentia alata*, *Mastichodendron capriri*, *Sapranthus palanga*, *Annona* spp.,

Scheelea rostrata and *Acrocomia vinifera* are only a few such examples of those in Costa Rican lowland deciduous forest (Janzen & Martin, 1980).

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