Chapter 8

New Horizons in the Biology of Plant Defenses

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I. INTRODUCTION

The answer to Why do "all the good things which an animal likes have the wrong sort of swallow or too many spikes"? (Milne, 1928) is that the herbivores selected the plants to be that way. Given the acceptance of this answer, there appears to be no more intellectual content to be discovered in the study of the biology of secondary compounds. There appears to be only the working out of the detailed mechanics of how secondary compounds are made, what they cost, how they affect an herbivore, how they are avoided, how they are genetically programmed, etc. However, once Darwinian selection became linked with genetics, the same could be said for all areas of evolutionary biology. So do we pack up and go home? No, I vote for absorption in the challenge of figuring out the details of how systems work, systems that are by and large invisible to us because we are too large, because we cannot go back in time, or because our presence stops the system. I cannot watch a cell construct a morphine molecule, I cannot see how a mastodon responded to a *Simaba cedron* fruit 15,000 years ago, and I cannot watch an

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agouti eating wild seeds since it refuses to eat when I approach it in the rain forest. There are new horizons in the biology of secondary compounds that are of great importance in understanding human feeding and medical biology and involve multiple intricate puzzles about how animals and plants interact. After all, herbivores are responsible for the caffeine in your morning coffee, the tannin to make leather shoes, and synthetic pesticides in the environment.

It is my intent in this chapter to underline some areas of research in plant defense biology where major questions are seemingly being ignored or the major questions do not seem to correspond to observations in the field.

II. FACULTATIVE DEFENSES

The defense systems of all organisms contain facultative as well as standing components. The slower, the more heterogeneous, flexible, and unpredictable the challenges, the more important become the facultative components. It is conspicuous that understanding the defenses of plants against fungi, nematodes, and microbial attack has always involved the study of facultative defenses (e.g., Stoessl, 1970). Secondary deposition of tannin around an area of wood or leaf invaded by fungi has been known since the turn of the century (and probably much earlier), and many phytopathologists have gone so far as to describe an ecological group of secondary compounds as "phytoalexins" (Cruickshank, 1963). Phytoalexins are narrowly defined as those defensive compounds produced in direct response to microbial or fungal invasion of cells (e.g., Stoessl, 1970; Strong, 1977; Harborne, 1978). It is equally conspicuous that researchers working with herbivores larger than fungi were extremely slow to become aware of either the fact of facultative defenses against small beasts or the generalization that there ought to be facultative defenses against all sorts of herbivores. Until Ryan and associates studied the induction of protease inhibitors in foliage following herbivory (for a review, see Ryan, 1978), about the only example was that of African acacias, which make longer spines on shorter internodes following browsing of shoot tips by big mammals. Incidentally, this phenomenon is readily observable in other species of African arid-land shrubs and presumably reflects the facts that spininess is expensive, a substantial number of the members of the plant population are inaccessible to the animals in any given generation, and a plant grows through a susceptible low stage to an unsusceptible tall stage.

Given that we recognize environmental challenges of a type that should produce facultative defenses in plants, where are the new horizons? Ryan (1978) sees the new horizons through ever finer dissections of the system to determine how the plant hormonally controls biosynthesis and storage of defense compounds on the spot at the time of damage-a biochemist's approach. An ecologist, however, tends to go in the other direction. When a leaf-cutter ant colony (*Atta* spp.), a population of moth larvae, or a howler monkey (*Alouatta* spp.) eats the new leaf crop off a tropical deciduous forest tree at the beginning of the rainy season but does not do the same to a replacement leaf crop produced a few weeks later, is it because these animals are prudent harvesters of their resources, is it because they have to mix their diets through time (Freeland and Janzen, 1974), or is it because the replacement leaf crop is different from the original? Development of the last idea is at best embryonic (Janzen, 1978a). When Ryan (1978) tells us that proteinase inhibitors accumulate within a few hours to the highest levels in a leaf that has just had bites taken out of it, the field ecologist's mind turns immediately to the view up through the crown of a tree, the leaves of which have recently been severely damaged by a generation of caterpillars or beetles. Ryan certainly has given us a testable hypothesis as to why these insect larvae often seem to choose an undamaged leaf blade to eat when starting a feeding bout, with the result that the feeding holes are quite evenly distributed over the leaf surface of the tree crown.

This observation, and the postulated cause, bring to mind a totally unexplored area of leaf defense biology. In agricultural entomology it should be a standing principle that the crop pest is reduced in density only to the point where its effects are just slightly greater than the cost of getting rid of it. One doesn't pay $21 an acre to get rid of a pest that damages $3 worth of crops an acre, but one might pay $2.95 an acre to remove the pest. The same applies to the budget of a wild plant. At the time of the evolution of facultative proteinase inhibitor defenses, natural selection should have driven up the speed and quantity of production until the return to the plant in lowered damage about equaled or slightly surpassed the cost of production. But note that "lowered damage" potentially comes in more ways than just lowering the amount of leaf tissue eaten. There are at least two other ways that facultative defenses could be selected for other than in lowering the amount of leaf tissue eaten. One could be in forcing the caterpillars of highly host-specific insects to run their development cycles at maximal rates, thereby minimizing both the duration of the period before the tree can put out a replacement leaf crop and the number of leaves sufficiently damaged to make retention of the remains uneconomical. The aborted partly damaged leaves are replaced, but all that was aborted is a loss caused by the herbivore yet not consumed by the herbivore. The other is that there is undoubtedly some pattern by which, say, 40% loss of leaf surface area can be distributed over the surface of a tree for minimal reduction of the fitness of the tree. It would be most interesting if it turned out that the dispersed pattern of feeding generated by facultative chemical defenses was just this pattern. Here, then, I am postulating that facultative chemical defenses may have been strongly selected for without actually reducing the amount of leaf tissue removed by chewing but rather by influencing the pattern of chewing. This may even be one of those magical cases in which a large return is gained by the plant at a small loss to the herbivore. In fact, if the facultative response by the plant were to raise the levels of proteinaceous protease inhibitor, for example, in all leaves as high as in the leaf recently chewed on (surely this is a physiological possibility, even if an expensive one), the specialist herbivores might simply respond evolutionarily by becoming good at harvesting all that protein.

Although beyond even the wildest of a Darwinist's dreams, it is just possible that some plants can evaluate the kind of leaf-clipping herbivore to which they have been subject and generate an appropriate facultative response. It has been shown that when grass blades are clipped off by a grasshopper or cow, a prairie grass plant responds differently than when the blades are cut with clippers; apparently the saliva makes the difference (Mel Dyer, personal communication). This is an area of plant defense biology that must be approached with extreme caution. Adding various primary metabolites to bacterial systems that are synthesizing secondary compounds can strongly perturb the production status quo (e.g., Drew and Demain, 1977). Damage to living plants can easily mimic this process, and the products may be nothing more than the nonsensical results of a complex machine running out of control. Furthermore, a change in secondary-compound chemistry following foliage damage may be the result of a rearrangement of internal priorities rather than an explicit attempt to produce facultative defenses. For example, it is unlikely that the lowering of alkaloid production by clipping of larkspur (Delphinium *occidentale*) (Laycock, 1975) is a facultative defense against the herbivores that clipping mimics.

Agriculturalists growing plants for commercial extraction of secondary compounds are well aware that the absolute quantity per unit plant tissue harvested changes with the physical environmental conditions and the health of the plant. Of a slightly more esoteric nature, several studies have shown that the concentrations of phenolics in tobacco and *Helianthus annuus* plants vary with "stress" and nutrient conditions for the plant (Wender, 1970; del Moral, 1972). It is obvious that many of these changes in secondary-compound chemistry may occur simply because the "stress" mimics the changes in plant physiology generated by herbivory or microbial attack in nature. On the other hand, it may well be that plants are so finely tuned to the challenges of herbivory and to the degree of fitness-lowering generated by a given act of herbivory in the context of the plant at the moment that they alter their standing defenses according to their individual circumstances. This is roughly like different householders buying different amounts of fire insurance depending on the neighborhood they live in, the details of their house, and the value of the items they have in the house at different times of the year. In nature it is obvious that different individual plants of similar age and stage are subject to different degrees of seed predation and herbivory (also see Moore, 1978a,b; Janzen 1975a, 1977a, 1978b). It is not obvious to what degree this is due to the capricious settling behavior of the herbivores, herbivore response to invisible inter-individual differences in nutrient levels, and herbivore response to interindividual differences in secondary-compound defenses. Clearly all three are operative, but the last is habitually ignored by field biologists because of their frustration at being unable to instantaneously assay concentrations of the multitude of secondary-compound defenses possessed by a given plant. Only when the entire suite of defenses of a few species is worked out can those species be studied in nature with respect to the questions raised at the beginning of this paragraph. On the other hand, it is easy to predict that, once these defenses are determined we may find plants to be amazingly finely tuned in their combination of standing and facultative defenses. It might even be that the only reason why herbivores get through at all is that the time of their appearance at a given plant is extremely unpredictable, whether a given plant is to be attacked at all is very unpredictable, and the impact of that attack on the plant's fitness is very unpredictable.

III. ONE BEAST'S DRINK IS ANOTHER BEAST'S POISON

Toxicity is not an intrinsic property of any naturally occurring molecule, and secondary compounds are no exception. The ally1 glucosinolate in cruciferous plants is very toxic to black swallowtail larvae (*Papilio polyxenes*) moderately toxic to southern armyworm larvae (*Spodoptera eridania*) and harmless to cabbage butterfly larvae (*Pieris rapae)* even when the concentrations in food are considerably higher than those occurring in the plants in nature (Blau et *al.*, 1978). The canavanine in seeds of *Dioclea megacarpa* is used as a nitrogen source by the larvae of the bruchid beetle *Caryedes brasiliensis* (Rosenthal et al., 1978; Rosenthal, 1977). It is, however, extremely lethal at the same concentrations to the larvae of the bruchid beetle *Callosobruchus maculatus* (Janzen et al., 1977) and toxic to a wide variety of other organisms (Rosenthal, 1977). Even three protein amino acids (tryptophan, cystine, and methionine) were lethal when added to the diets of C. *maculatus* larvae (Janzen *et al.*, 1977). These three compounds occur in exceptionally low concentrations in southern cowpea seeds (*Vigna unguiculata*), the normal food of C. *maculatus*. In short, it has become obvious that with respect to a particular organism a toxin or other disrupter of development is to be defined by its effect rather than by some intrinsic characteristic of the molecule. Of course, certain molecular structures have a higher probability of being metabolically disruptive than others [e.g., generally alkaloids kill C. *maculatus* larvae at concentrations of 0.1 to 1% in the diet, whereas uncommon amino acids generally require 1–5% concentrations for lethal effects (Janzen *et al.*, 1977)], but it still holds that a particular compound has not been shown to lack a protective function if it is harmless to one or even many herbivores, or vice versa.

A major frontier in the biology of secondary compounds involves relaxing the phytochemist's mind to the point where a given study derives its value not from traits of the molecules at hand but from how they influence the interactions of animals and plants (and, as well, other kinds of interactions). It is clear, for example, that lectins (phytohemagglutinins) have many potential and likely biological roles both inside and outside the organism (e.g., Liener, 1976). That many different functions of lectins have recently been reported does not mean that the state of the art is very primitive or that no "real function" has appeared. There is nothing biologically improbable about lectins functioning, for'example, as site-specific binding agents at low concentrations within the organism or on its surface (Liener, 1976), as effective antiherbivore compounds when in high concentrations in dormant seeds (Janzen et al., 1976), and as nutrient storage proteins for the developing seedling. Biochemical biology has grown up with a tradition of "one molecule, one function"; ecology operates on a tradition of "one unit, many functions," or at least "one unit, many responses." .

IV. HERBIVORES DO NOT EAT LATIN BINOMIALS

Animals generally do not feed on all parts of a plant; they usually consume quite specific parts. Red colobus monkeys (Struhsaker, 1975), black colobus monkeys (McKey, 1978), and howler monkeys (Glander, 1975, 1979) are all conspicuous in their choice of, for example, leaf petioles over leaf blades for some species, and vice versa for others. Leaf-cutter ants (Attini) feed on many Latin binomials but in fact eat only new foliage from one, only old from another, only flowers from a third species, and only new green fruit from a fourth (G. Stevens and S. Hubbell, personal communication). These preferences may even change within the year. Bruchid beetles eat only the contents of seeds, not the seed coats as well (Janzen, 1977c). Costa Rican tapirs consume ripe fruits and grind up the seeds of the Costa Rican tree *Mastichodendron capiri* but emphatically reject the foliage. The adults of *Tetraopes* beetles eat flowers and green pods but only the tips of the leaves of common milkweed (*Asclepias syriaca*) in Michigan.

Likewise, Latin binomials do not eat plants. Juvenile black rats (*Rattus rattus*) in the Galapagos peel the small fruits of *Miconia* before eating them, whereas adults eat the peel and all (Clark, 1979). Young *Ctenosaura similis* lizards are insectivorous; the adults feed almost entirely on leaves and fruits in lowland deciduous forests of Costa Rica. Adult bruchid beetles eat pollen and nectar from flowers; larvae eat the contents of ripening seeds (usually of quite different species of plants). Most adult lepidopterans take nectar from flowers or rotting fruits of species of plants totally different from the plants whose leaves are consumed by their caterpillars. A thirsty howler monkey may be unable to deal with toxins that can be flushed out of the system by a monkey satiated with water (Glander, 1978).

In short, a list of Latin binomials feeding on other Latin binomials carries almost no information when it is remembered that the secondary-compound chemistry of two different plant parts on the same plant is much more likely to be different than the same. For example, the caffeine content (percent of dry weight) of *Cola nitida* fruit is a trace, that of the seed coat is 0.44%, and that of the seed contents is 1.58% (Ogutuga, 1975); 0.1% is lethal to the seed-eating bruchid *Callosobruchus maculatus* (Janzen *et al.,* 1976). The moral becomes even clearer when it is remembered that two different life forms of the same species of animal are very likely to have different abilities to deal with secondary compounds and different physiologies to be affected by them.

By now it should also be apparent that Latin binomials do not contain secondary compounds, but rather plant parts do. There are two huge offenders in the contemporary literature. First, it is common to report results for a plant and not specify leaves, stems, or other kinds of vegetative foliage. Since concentrations are usually not given for wet or dry weights, one cannot even use such information to understand an herbivore large enough to eat entire tops off of plants. Second, this ecological grievance applies even to apparently carefully divided samples. A phytochemist might be quite proud to report that the fruit pulp and seeds were separated in the analysis (after all, the secondary compounds in a fruit are usually evolutionarily designed to get a fruit eaten and digested by some animal; the secondary compounds in a seed are usually evolutionarily designed to keep the seed from being digested by many animals). However, it is generally forgotten that many seeds are consumed by animals that eat only the contents and discard or avoid the seed coat. The seed coat may constitute as much as 70% of the seed and contains vastly different secondary compounds than do the seed contents (Janzen, 1977c). Therefore, reports of concentrations of secondary compounds in seeds are very commonly off by a factor of 20 to 100% from the viewpoint of the animal who might try to digest one. To make analysis even more difficult, there are additional facts that must be taken into consideration. For example the lectins in bean seeds are not there until just before the seed is mature (J. Hamblin, personal communication); this means that insects and vertebrates that eat the immature seeds, as they commonly do, may be avoiding this major form of defense.

The new horizon is in understanding a plant as an enormous suite of secondary-compound defenses and working with ecologists to figure out how herbivores get past a defense or complex of defenses. We do not need another random screen of qualitative alkaloid content of 5000 species of central African plants. We need a team, or a person who thinks like a team, to try to develop defense profiles through the year and development stages for a given population of plants. At present, if one shows that three of the seven species of *Acacia* in lowland Costa Rica contain cyanogenic glycosides in their foliage (E. E. Conn and D. S. Seigler, personal communication), one has not shown that the four acyanogenic species are any less well protected chemically. Likewise, the demonstration that there is a 20-fold interindividual variation in cyanogenic glycoside content in the foliage within a Costa Rican population of *Acacia farnesiana* occupying a few hectares, whereas the flavonoid content of these same leaves stays constant in kind and quantity (D. S. Seigler and E. E. Conn, personal communication), should cause one to be very wary of correlating herbivore preferences with secondary-compound foliage analyses until all of the defensive repertoire has been reported.

In short, there seem to be two productive directions to take in working out the preferences displayed by animals. One is to develop realistic artificial diets and then tip in solitary and combined secondary compounds and nutrients to define the limits of tolerances and pick out those compounds that invoke exceptionally strong reactions. The other is to focus on a few key species of plants, work out their defense repertoires in detail, and then focus on the specialist herbivores that get around these defenses and the generalists that are deterred by them. The recent work on Cruciferae and Umbelliferae by Feeny, Root, and associates (e.g., Blau et al., 1978; Berenbaum, 1978), Passifloraceae by Gilbert (e.g., Smiley, 1978), canavanine-containing plants by Rosenthal, and legume seeds by Janzen has evolved in these two directions, but it is a miniscule fraction of what should be, considering the importance of secondary compounds in pharmacology, agriculture, and more esoteric ecological studies.

V. PLANTS ARE ANACHRONISMS

Evolutionary biologists are very fond either of pretending that the plant traits we see are selected for and maintained by current interactions or, at the least, of choosing to work on those systems that seem to match this assumption. However, we all know perfectly well that a plant (and its herbivores) is a collection of anachronistic traits that at any given time have caught up with contemporary selective pressures to a highly variable degree. One reason why evolutionary biologists like to sweep this fact under the rug is that for a long time it was a standard loophole for dealing with some conspicuous trait, the natural history of which was not known (the selective pressures for secondary-compound defenses have often been ignored on these grounds). To invoke currently extinct selective pressures to explain the presence of a trait, however, was to mask an incomplete study of natural history. Another reason for avoiding the anachronistic aspects of evolutionary biology is that one is quickly caught in a morass of untestable hypotheses. How does one field-test the assertion, "The single most important aspect of browsing pressure is height [of dinosaurs]" (Bakker, 1978)?

However, there is a huge body of information on the natural history of plant defenses that deserves examination in the light of a strong historical perspective. Lignin, clearly a secondary-compound defense when attached to cellulose, has been identified from Triassic age fossil wood (Sigleo, 1978). Most coal beds are fossilized, polyphenol-rich, peatlike deposits from the beds of swamps that were probably very similar in natural history to contemporary sites of peat deposition. As such they were probably populated by very few herbivores and the plants in them were very well defended with chemical traits (especially polyphenolics) selected for by the herbivores (Janzen, 1974). Regal (1977) stressed that bird-dispersed fruit biology may have been very important in the evolution of angiosperms, which brings to mind an enormous number of questions about the interactions of fruit secondary-compound chemistry and vertebrates. Do fruit flavors come from millennia of adaptation by animals to those secondary compounds placed in fruits by plants to attract the right dispersal agents and repel the wrong ones? Alternatively, do fruit flavors result from millennia of adaptation by plants to the age-old sensory receptors possessed by animals long before they ate fruits? Some combination of the two is, of course, what we are dealing with. T. Swain's examination of the taste perceptiveness of tortoises (they have trouble detecting bitter compounds) is a step in the right direction. Pollination biology studies have long assumed a large historical element to floral morphology (e.g., Sussman and Raven, 1978), but for some reason herbivore relationships do not carry this tradition. It is obvious that contemporary browsing pressures did not produce and maintain the extreme spininess still present in southwestern United States desert plants, but I know of no study that has taken up this subject in detail and related it to the large herbivore faunas that roamed this terrain until a few tens of thousands of years ago. The question of how long defense traits will persist once the herbivore is removed has simply been ignored in the ecological literature. It can be stated with certainty that the rate of appearance of a trait will be in large part a function of the intensity of selection for it, whereas its disappearance rate may depend in great part on its cost of maintenance. For example, spines (dead tissue of low initial cost and no maintenance cost) may appear very rapidly and extensively when a flora is subjected to heavy browsing but disappear very slowly because of their small drain on the resource budget.

There is one largely undeveloped approach to the extinct interactions between large vertebrate herbivores and plant defenses. Field ecologists have long recognized that when herbivorous vertebrates were (are) introduced onto oceanic islands, these herbivores grossly altered the plant species composition and interrelationships (e.g., Pickard, 1976). This is presumed to have occurred because the plant defenses were only weakly developed owing to millennia of evolution without this herbivory. However, island plants give every evidence of having come from mainland floras originally, floras presumably subject to the kinds of herbivory experienced on mainlands today. This means that the island floras have presumably lost many of their defensive traits and not that they never had them in the first place. Oddly, 1 cannot locate a single study of the defense repertoires of island plants as contrasted with mainland congeners, except for a study of the loss of ants as a defense in the island populations of the ant-plant *Cecropia* (Janzen, 1973; McKey and Janzen, 1977). On the other hand, a major pragmatic barrier to a study of this sort is the widespread tragedy of goat, pig, and rat introduction to even the smallest islands that were naturally free of large herbivores.

A second way of studying the interactions between extinct large vertebrates, at least in the New World, is through careful examination of the interactions between introduced large herbivores and the New World flora. Range horses, cows, burros, sheep, and goats have gone a long way toward replacing the fauna of large browsing and grazing vertebrates that become extinct between ten and twenty thousand years ago. For example, many of the chemical and physical traits of uneaten ripe large fruits in the Costa Rican lowland forests can be understood if we assume that they were coevolved for seed dispersal with this very recently extinguished fauna (Janzen and Martin, 1980). For example, in Guanacaste province, the large, round, hard, ripe fruits of the native tree *Crescentia alata* are essentially ignored by all native potential dispersal agents but very eagerly eaten by range horses. Range cattle likewise ignore the fruits of C. *alata* but avidly eat the fruits of *Pithecellobium saman*, which are in turn studiously ignored by range horses. Both animals are very effective dispersers of the seeds of the fruits they eat of these two species. The differences in secondary-compound and nutrient fruit chemistry of these two fruits could hardly be expected to be explicable in terms of contemporary native faunas but in the context of horses and cows may be very clear. It is ironic that I cannot locate a single study on browsing or wild fruit eating of free ranging populations of these two commonest large neotropical herbivores today. In the same context, the 3-in.-long, ovoid, juicy fruits of *Simubu cedron* (Simaroubaceae) fall to the rain forest floor in Corcovado National Park, southwestern Costa Rica. There the fruit pulp rots off, leaving a large, fibrous nut to germinate on the ground surface. There appears to be no dispersal agent at present. Although the fruit pulp has a fragrant smell and a sweet taste, it is conspicuously ignored by local animals and has the reputation of being lethal if eaten in large quantities by human beings. The ground under a *Simaba cedron* reminds me exactly of that under a *Balanites wilsoniunu* (Balanitaceae) tree in the Ugandan forests where all the elephants have been shot. African elephants are extremely fond of the large fruits of *B. wilsoniana* and defecate the nuts unharmed, but they are eaten by none of the other large forest understory mammals. The fruit pulp of four species of African *Balanites* is 4–8% dry weight diosgenin, the precursor molecule for the manufacture of cortisone, sex hormones, and antibiotics (Hardmann, 1969, Janzen, 1978a). It is very difficult to avoid the conclusion that S. *cedron* was dispersed by mastodons and predict that the secondary compounds in the ripe fruit pulp will be atoxic to contemporary elephants.

VI. HOW DOES ONE MEASURE THE IMPACT OF HERBIVORY?

What happens to a plant when its defenses are broached or removed? Such a simple-sounding question involves the most difficult question in evolutionary biology, population biology, and ecology. The only real answer to this question depends on what happens to a plant's fitness when an herbivore takes a bite or is potentially present to take a bite. I gave one example of the complexity of the problem when discussing the possibility that selection for facultatively produced protease inhibitors was generated not through a reduction in herbivory by these compounds but rather through causing the herbivore to distribute its damage in such a manner as to minimize its impact. We can already see that the impact of herbivory cannot be blithely measured by the caloric content of what is eaten, by the grams dry or wet weight of what is removed, by the area of leaf eaten, etc. The removal of 10 cal or grams of leaf tissue means quite a different thing than the removal of the same quantity of shoot tips, since in the former case, the lost tissue can be replaced with a new leaf; but in the latter case there may well be irreparable loss in competitive status through a lowered rate of shoot elongation (e.g., Janzen, 1966). The loss of 10 cm^2 of leaf area early in the life of a leaf means an entirely different thing to the plant than the same loss well after the leaf has been amortized (e.g., Chester, 1950). Likewise, if a 40% leaf blade loss results in a leaf that still functions well enough to pay for itself, a 50% leaf blade loss may not and turn into a 100% loss through leaf abortion. In short, herbivory through the eyes of the plant cannot be measured in units of harvestable productivity. It must be measured in units of reduced fitness of the plant, and this is very difficult, to put it mildly.

How do herbivores affect the fitness of a plant? As in automobile ownership, there are two big costs related to hostiles. There is the cost of insurance and the cost of repairing the actual damage. The cost of insurance for a plant is conspicuously the standing chemical defenses, the resources and programming for facultative defenses, and the tactical losses in competition and other activities that come about through having resources tied up in defenses that cannot be mobilized to deal with other contingencies. Needless to say, herbivores can have a very large effect on a plant's ability to compete and deal with the physical environment through draining its resources for insurance and repair of damage.

There is only one way to know how this drain affects the fitness of plants, at least given our current state of knowledge: Lower the amount spend on insurance by favoring mutants or broach the defenses through artificial herbivory, and observe what happens to standard measures of fitness (seed production on maternal plants or plant parts, pollen donation by paternal plants or plant parts). Effects of herbivory on wild seed plant production have been investigated to some extent (e.g., Rockwood, 1973; Janzen, 1976; Cavers, 1973), but increased seed yields by less well-protected mutants have been examined only very indirectly in the sense that crop plants are generally more poorly protected than are their wild relatives and generally have greater seed yield. However, they have also had other portions of their resource budget diverted into seed production.

This area is wide open for study and guaranteed'to yield results of interest to both agriculturalists and more esoteric biologists. Will the new lectin-free strains of soybeans (Pull et *al.*, 1978) have increased yield per plant with respect to some other trait besides seed yield? The resource that was being used in lectin production is now presumably available to the soybean plant for other functions. The increased protein content in high-protein strains of potatoes is in great part made up of the very protease inhibitors that are part of the defense of the potato (Ryan and Pearce, 1978). How does the morphine-free strain of opium poppy differ from the normal poppy in competitive ability and seed production per plant lifetime? These kinds of questions must be asked of wild plants, where the ultimate equalizer is the contribution to future generations through seeds or pollen. Would a phytolith-free strain of grass be fed on selectively by grazers (see Walker et *al.*, 1978) but have higher leaf production than normal grass? A toxin-free mutant may use the newly available resource in competitive growth and turn out to have a much higher fitness than the wild type, or it may have to use this resource to repair the increased damage incurred by the less well protected plant and thereby end up with the same fitness as the wild type. This kind of field biology is so poorly understood that I can cite no examples.

However, measuring the impact of herbivory has led us into one very confusing area of the biology of the interactions of animals and plants. One class of herbivory, involving ripe fruit, pollen grain, and nectar consumption, clearly raises the fitness of the plant. I caution immediately, however, that not all fruit consumers raise the fitness of the plant (Janzen, 1975b, 1977d, 1979; Howe, 1977; Howe and Estabrook, 1977), and certainly many pollen and nectar consumers can be regarded as nothing but thieves. A second class of herbivory appears to raise the fitness of the plant, but much more field work is needed to solve the puzzle. These are the cases in which the plant's physiological response to certain kinds of herbivory actually appears to produce a plant that has a higher fitness than its uneaten conspecifics. This effect is to be expected in a small number of cases when any complex system is perturbed many times (e.g., the natural history of mutation). The question is, under what circumstances will the situation persist whereby the plant depends on an external agent to perform a physiological task that is usually handled by the plant itself and therefore lacks control over its own actions? This differs from the systems involved in outcrossing pollination and seed dispersal since most plants cannot do that themselves.

Some examples will probably make this clearer. In at least two complex and well-developed ant-plant mutualisms, African *Barteria* trees (Janzen, 1972) and neotropical *Cecropia* trees (Janzen, 1973), the ants maintain a standing crop of scale insects or other homopterans inside the hollow stems. These animals feed on the plant and provide a major food source for the ants with their bodies or their honeydew exudates. The ants are obligate occupiers of the trees and protect the trees from herbivores and vines. The homopterans are zoological devices used by the plants to maintain an ant colony, the ants being directly analogous to the chemical defenses maintained (and paid for) by more ordinary plants. I would not expect there to be selection for traits that reduce the "damage" done by the Homoptera to the level that would debilitate the ant colony and its protection of the tree. The ant-plant has lost some, but not all, control over its use by an herbivore.

Simberloff et al. (1978) presented a reasonable case that the normal multiple root-branching pattern of the mangrove *Rhizophora mangle* is the outcome of repeated and frequent invertebrate attacks of the aerial root tips. They argued that this damage may actually raise the fitness of the plant, since a large number of aerial roots aid the plant in support, nutrient gathering, and oxygen uptake. Is it possible that the mangrove would produce its own root bifurcations to generate the number needed if the invertebrates were excluded (and therefore if the damage associated with invertebrate-induced bifurcations were a drain with no return on the resource budget of this plant)? Also, even if the presence of the invertebrates can be viewed as a "bifurcation-inducing mutation," it would be very exceptional if such damage generated the exact growth response needed to raise the fitness as would a physiological mutation producing the same effect without relinquishing control to an external agent. However, the point of Simberloff *et* al., that a plant's postdamage responses must be considered in the equation when one is tallying the effect of an herbivore on a plant, is well taken.

The sentiments expressed in the following quotation (from Mattson and Addy, 1975) occur periodically in the ecological literature and can almost always be attributed to those who focus on ecosystems rather than their parts (e.g., Harris, 1973; Owen and Wiegert, 1976; Hendry et *al.,* 1976): "Normal insect grazing (from 5 to 30 percent of annual foliage crops) usually does not impair plant (primary) production. In fact, 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." In evaluating such comments with respect to understanding whether herbivores select for chemical defense mechanisms in plants, there are two considerations. Fitness is not measured in units of "production"; only a very small portion of a plant's total resource budget goes into what is commonly measured in "production" (leaf weight, wood increment, etc.), and a plant is quite likely to maintain certain activities at normal levels very much at the expense of others in responding to damage by herbivores [e.g., see reviews of responses to defoliation by Chester (1950), Kulman (1971), and Rockwood (1973)]. For example, a plant that has a medium-aged static crown stripped of its leaves by caterpillars may well turn on a growth phase to replace them and be therefore much more "productive" than the undamaged crown, but consideration of the entire resource budget of the plant makes the error in this reasoning obvious. Such a statement also ignores the insurance expenditures made by plants on defenses, expenditures that otherwise could have gone into growth or reproduction.

Crop plants are particularly deceptive when one is assessing responses to herbivory. For example, light trimming, browsing, or chemical defoliating can increase seed yield in cotton, soybeans, and beans. This damage probably breaks apical dominance of the main shoot, leading to a more bushlike plant. Such a plant catches sunlight better only in nicely spaced crop systems. In wild vegetation with tight intercrown competition, such a loss of height could lead to an irreparable loss of competitive status.

We badly need field experiments with wild plants designed to show how the fitness of these plants is affected by herbivory of different types applied in a variety of competitive and edaphic circumstances. Since plants are well enough defended so that much of this herbivory is very unlikely to occur in a replicated and controlled manner, the arena is very open for the artificial herbivore, especially one that acts in a manner that mimics an herbivore immune to a particular portion of the plant's defenses.

VII. PITFALLS

The biology of plant defenses is beset with more than the usual number of methodological and conceptual pitfalls for an area in science. Much of the confusion could be derived from the melding of two areas in which the practitioners know little of each other's assumptions and weak points. The confusion is not helped by the persistence of researchers lacking strong familiarity with plant or herbivore natural history or with the natural history of secondary compounds (e.g., Jermy, 1976).

Natural history fine points are not trivial. They can be the turning points in many systems. A leaf-cutter ant colony may strip a tree crown of its leaves in 24 hours, whereas a cohort of caterpillars may require 10 days to do the same thing. A facultative defense may be strongly selected for by the latter and strongly selected against by the former. Which kinds of chemical defenses one finds interesting or important, then, may depend on which of these two herbivores one happens to be working with for quite capricious reasons. A person noting that very new foliage of woody plants is commonly red or otherwise strongly pigmented might decide to do feeding tests with new versus old foliage on generalized herbivores as a way of arguing that these pigments are defensive against herbivores. Such a study would undoubtedly show that the very new foliage is avoided by many generalist herbivores. However, the conclusion that the pigments are responsible is preposterous. It ignores the considerable body of information suggesting that new foliage can be very different from mature foliage in chemistry through the possession of a wide variety of known compounds well known to be toxic to animals (e.g., McKey, 1974) and the fact that there is no hint in the literature that the anthocyanins, commonly responsible for the coloring of new leaves, have any effect on herbivores when ingested. When Fowden (1972) isolated several new uncommon amino acids at extremely low concentrations from extremely large quantities of sugar beet waste, he appeared to have made a case for the existence of very small quantities of some secondary compounds in many plants. This indicates that perhaps these compounds had a physiological role in the plant and then later in evolutionary time were produced at higher concentrations through natural selection by herbivores. It is striking how tenaciously natural products chemists cling to the traditional belief that the compounds found in a plant must be of importance within that plant, a belief that no person entering the field of biology today would ever dream of holding if he or she had access to what we now know about plant biology. The uncommon amino acids found at extremely low concentrations in sugar beets could just as easily have been from living or dead environmental contaminants of the initial refuse, from degradation or accidental synthesis in the incredible soup of enzymes and substrates represented by the 10^9 kg of mashed sugar beets, from ordinary biochemical mistakes being made in the cells at the instant of mashing, or from protein amino acids modified after polypeptide synthesis as part of the final tailoring process for the molecule (e.g., Uy and Wold, 1977). Certainly the presence of these compounds is very weak evidence for the existence of genetic programming in the sugar beet genome for the production of very small amounts of these uncommon amino acids.

VIII. ONE LINERS

No plant is an island. It is quite clear that the arrival and departure of herbivores from a given plant depends not only on the defenses intrinsic to that plant, but also on the alternate foods available to the herbivore and the obfuscating nature of the chemical environment generated by the neighboring plants (e.g., McNaughton, 1977; Atstatt and O'Dowd, 1976).

Parasitic plants are herbivores; virtually everything discussed here—host specificity, consumer secondary-compound detoxification, problems in estimating damage, and facultative defenses-applies directly to the attack of plants by parasitic plants (e.g., Atstatt, 1977).

An herbivore is a walking compost heap; virtually all herbivores [with the exception of a wood-boring isopod (Boyle and Mitchell, 1978)] are very dependent on their gut flora for aid in the degradation of secondary compounds in plant parts (Freeland and Janzen, 1974; Langham and Smith, 1970; Oh et al., 1967; Westermarck, 1959). The rumen of wild herbivores should probably be seen more in this light than as a device for gathering calories and proteins (even cellulose can be viewed as a secondary defensive compound, since its extreme indigestibility to both higher plants and animals is probably not a piece of seredipitous natural history).

An herbivore species may consist of many populations, each adapted to broach the defenses of a particular host population. Scale insects (extremely sedentary as adults, aerial plankton as imrnatures) may even have populations adapted to the defenses of an individual tree (Edmunds and Alstad, 1978), whereas one widespread "species" of bruchid beetle or sphinx moth may have as many as 20 allopatric populations, each with larvae that are locally adapted to the defenses of one or two different species of plant.

Why do rain forest understory shrubs contain a large amount and diversity of so-called trace elements such as boron and cobalt (Golley *et al.,* 1978)? I hypothesized that the heavily shaded rain forest understory is a resource-poor habitat where chemical defenses are of utmost importance (Janzen, 1974). Large quantities and many kinds of secondary compounds may require large quantities and many kinds of coenzymes for proper synthesis, and coenzymes normally contain a molecule of a so-called trace element (Janzen, 1977b). Different habitats are likely to have different overall levels of chemical defenses in their floras. On the worst soils or otherwise stressful sites, foliage should be the richest in chemical defenses because its loss to the plant should cause the most severe reduction in fitness (Janzen, 1974; McKey et *al.,* 1979) whereas in habitats at the opposite extreme, high interspecific variability in the intensity of defense is expected owing to mixes of life forms (for an example of ecogeographic patterns in alkaloids, see Levin and York, 1978).

I conclude with the comment that understanding the biology of secondary compounds requires the cooperative efforts (or at least the thoughts) of a greater variety of biologists and chemists than does any other area of biology. The new horizons lie in taking what we already know and applying it in straightforward experimental manipulations of living plants and herbivores in the field, in the laboratory, and on paper.

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