

Reprint from

• Encyclopedia of Plant Physiology  
New Series, Volume 12C

**Physiological Plant Ecology III**

Edited by O.L. Lange · P.S. Nobel · C.B. Osmond · H. Ziegler

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Springer-Verlag  
Berlin Heidelberg New York

# 16 Physiological Ecology of Fruits and Their Seeds

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## 16.1 Introduction

The function of an immature fruit is to add to the photosynthate pool and to protect the developing seed (see Chap. 17, this Vol.). Once ripe, the fruit puts the seed in the appropriate dispersal agent(s) and keeps it away from seed predators and inappropriate "dispersal agents". It is the selective pressures associated with such a diverse and often conflicting set of demands that have generated fruit physiology. To this date, the examination of fruit and seed physiology has been almost entirely directed at either the use of these structures as human food or as esoteric anatomical objects (KOZLOWSKI 1972, 1973; ROTH 1977). Here, instead of repeating the descriptive information in the above three reviews, I dwell on why fruits and seeds have the traits they do, much in the spirit of three recent reviews (JANZEN 1971, 1977a, 1979a). The physiological traits of seeds are generated by sibling rivalry, need for protection during development and dispersal, parental resource allocation considerations, dispersal agent traits, and resources needed by the young seedling. In short, a seed is a one-move time-consuming recruitment attempt by the parent plant and the fruit is its accomplice.

This attempt has a number of general traits that must be considered as philosophical background for any inquiry into the physiological ecology of fruits and their seeds.

1. The size and other resource properties of a seed are compromises between the direct needs of the parent and those of the offspring, and sibling competition for resources, in ecological and evolutionary time. Seeds are no different from any other babies in this respect.
2. There is no optimal seed or fruit for a plant species, or population, but rather a parent plant generates a distribution of seed and fruit sizes or classes that approximates the distribution that yields the highest inclusive fitness within the confines of the traits of offspring, parents and environment.
3. As with other plant parts, virtually every trait of a seed and its fruit is the product of several different and often opposing selective pressures.
4. The physiological properties of fruits and seeds are evolutionarily guided by both function of the moment (photosynthesis, herbivore repulsion, starch conversion, etc.) and by morphological-physiological preparation for some quite different future function.
5. The word "growth" is virtually meaningless in sentences that hope to approximate the rigor necessary for them to be interesting, and therefore should be avoided.
6. The function of a fruit is to add to the photosynthate pool and protect the developing seed and then, upon ripening, to put the seed into the appropriate dispersal agents.
7. The traits of fruits and seeds, even those of domesticates, must be viewed in the context of the environment that evolutionarily generated them. Elephant trunks and coconuts cannot be understood in zoos alone.

For want of space, I will restrict my discussion by and large to those fruits and seeds in some sense destined to mature. Fruit and seed abortion (KOZLOWSKI

1973) as a mechanism of parental choice of clutch size and offspring parentage (JANZEN 1977b) is well worth a similar essay. Likewise, seedlings have long wanted someone to talk about them in the context of their real worlds.

There are two terminological problems in fruit and seed biology. First, I will treat the "fruit" as that set of structures containing the seed(s) and usually developed from the ovary and its appendages (see VAN DER PIJL 1972; ROTH 1977). The fig "syconium" is thus a fruit (JANZEN 1979a), as is a strawberry. Second, we often hear of a "bird-dispersed fruit" (as linguistically analogous to a "bird-pollinated flower"). This is biological nonsense. What is meant is "bird-dispersed seeds" or "a fruit whose seeds are dispersed by birds". I have tried to avoid this semantic tangle in this essay.

## 16.2 Immature Fruits

The immature fruit is a thick layer of maternal tissue (pericarp, mesocarp, endocarp), followed by a thin layer of maternal tissue (seed coat), followed by a variously dimensioned layer of maternal and paternal tissue balanced in favor of maternal origin (endosperm), followed by an offspring related by half to its bearer. This organ, the diaspore of VAN DER PIJL (1972) and others, not only photosynthesizes, protects itself and its seeds and metabolizes the resources that flow into it and passes some on to the seed, but it abruptly transforms in part after fulfilling these functions for a long time.

### 16.2.1 Photosynthesis

Does the photosynthesis of an immature fruit contribute significantly to the resource budget of either the parent or the fruit? BAZZAZ et al. (1979) have shown clearly that extra-tropical trees can supply from 2.3% (*Quercus macrocarpa*) to 64.5% (*Acer platanoides*) of the carbon used by the fruit by photosynthesis by the green fruit. I suspect that tropical trees, with their large and very long-lived green fruits may supply even more. BAZZAZ et al. (1979) based their study on a budgetary analysis based on physiological measurements. However, it is tempting to try to approach such a question through field experimentation as well, such as by shading fruits or by removing the other sources of photosynthate in their vicinity.

The results of a shading experiment will be difficult to interpret because such an experiment involves more than a straightforward reduction in the overall resource budget of the fruit.

- a) The plant may well have the behavior of subsidizing sunlight-deprived fruits at the largely unmeasurable expense of vegetative or other sexual activities.
- b) The plant may be one of those species where fruit development is largely supported from stored reserves (e.g., mast-seeding conifers or bamboos) and therefore facultatively adjust the amount of resources fed to a fruit according to its needs. In such a case it would probably be necessary to shade most

of the fruits and know the likely size of the normal seed crop before the experimental results could be interpreted.

- c) Whether compensatory subsidy of shaded immature fruits occurs will depend not only on the physiological state of the parent, but on the proportion of the fruit crop that is shaded.
- d) Even if shading produces an immediately dramatic effect, it may simply be due to physiological confusion caused by the failure of one small component in a complex and fine-tuned system. Over evolutionary time, and perhaps even over ecological time (as with induced changes in leaf compensation points), such a dramatic effect could be eliminated with only a very small increase in subsidy from the parent.

However, shading experiments in the field are of great interest and notable for their absence from the literature. Developing fruits are often shaded by their parent's foliage and by that of adjacent plants. The general absence of fruits from somewhat shaded individuals of a species whose reproductives are generally well insolated may be due to fruit starvation rather than tree starvation, at least on an ecological time scale.

It is certain that herbivory or other natural damage to foliage often reduces fruit and seed crops and does so by perturbing the parent in many ways (see Chap. 17, this Vol.). However, it is tempting to view the removal of leaves immediately adjacent to immature fruits as a test of the hypothesis that these leaves are the direct providers of the resources used by these fruits. For example, I found that removal of the leaves immediately subtending infrutescences of Kentucky coffee bean (*Gymnocladus dioica*) reduced fruit weight, reduced seed weight, changed seed chemistry, and lowered seed survival in the fruit (JANZEN 1976a). However, this seemingly quite natural experiment is severely subject to the criticism mentioned under (d) above; Kentucky coffee bean has foliage extremely free of damage in nature and may simply never have evolved the behavior of diverting photosynthate from less damaged sets of foliage to more damaged portions of the tree crown. This brings to mind the interesting prediction that evergreen fruit crops (e.g., various Magnoliaceae, Ericaceae, Ilicaceae, conifers) should be more easily damaged by defoliation of leaves near immature fruits than would be crops of deciduous trees, provided that the selection of experimental subjects controls for the presence of mast seeding species that clearly accumulate large amounts of reserves for seed crop production (e.g., Fagaceae, Dipterocarpaceae, Pinaceae, etc.).

Given that the green of immature fruits is not merely camouflage for a visually orienting diurnal frugivore, what fruit traits may influence this photosynthetic role?

#### 16.2.1.1 Location in the Crown

Every imaginable fruit placement occurs on some plant species somewhere, but in most species the immature fruits are borne among or above the leaves. It is commonplace to assume that fruit location is dictated first by flower-pollinator interactions and second by mature fruit-dispersal agent interactions. For example, mango flowers are borne in tight clusters and then the branchlets

elongate greatly and the large fruit hang pendulously over the outer surface of the leafy crown. The usual interpretation of this behavior is that this “offers” the fruits to the large southeast Asian fruit bats (*Pteropus*). However, it also places the fruits in full sunlight rather than inside the dense foliage (and may even make them more inaccessible to arboreal seed predators such as squirrels). The price paid for cauliflory may be that the fruits are then borne in the shadiest portion of the tree crown.

#### 16.2.1.2 Fruit Size

The fruits of many species of tropical trees mature many months after flowering. The fruits of some Central American species expand to nearly full size immediately after flowering (e.g., *Hymenaea courbaril*, *Lonchocarpus costaricensis*, *Dalbergia retusa*, *Hemiangium excelsum*), while others remain tiny for several to many months (60–80% of the fruit’s developmental period) and then within a few weeks expand to full size or near it (e.g., *Cassia grandis*, *Guazuma ulmifolia*, *Enterolobium cyclocarpum*, *Pithecellobium saman*). The former pattern gains the advantage of a large photosynthetic surface throughout fruit development (as well as the opportunity for direct and gradual placement of resources in the fruit), while the latter pattern lacks this advantage (as well as requiring storage of resources for transfer into the fruit later in its development). In addition, whether the photosynthetic advantages of the former pattern are realized depends on the shape of the fruit and its placement vis a vis shade from the leaves.

In fruits that enlarge to full size immediately after flowering, but take many months to mature, the seed does not expand to full size until 2–10 months after flowering. This is especially conspicuous in flat, leaf-like wind-dispersed fruits (e.g., *Lonchocarpus* spp., *Dalbergia* spp., *Acosmium panamensis*). Since the enlarged fruit is not functioning as a resource sink, it appears that the primary function of the fruit is to be a photosynthetic surface.

#### 16.2.1.3 Fruit Shape

Given that a fruit must have moderate to great thickness to accommodate seeds and (often) rewards for dispersers, can some of the common shapes of fruits be attributed to photosynthetic ability as well as eventual dispersal agent demands? The samaras of *Hemiangium excelsum* (Hippocrateaceae) are contained in three leaf-like paddle-shaped structures which certainly have a much greater surface area exposed to the sun than would a spheroid with the same number of samaras (e.g., such as the fruits of *Cedrela odorata* and *Swietenia macrophylla*). The rock-hard immature fruits of *Luehea candida* (Tiliaceae) have ribs on their surface — are these strengthening structures or to increase the surface area of a very thick fruit? Many wind-dispersed seeds are borne in leaf-like fruits, which we assume are shaped by aerodynamic selective forces. However, it is possible that the evolution of these shapes is also driven by the photosynthetic properties of these large surfaces. The top four fruit photosynthesizers listed by BAZZAZ et al. (1979) have large wings on immature fruits.

When a young fruit is covered with long green multicellular hairs, such as *Apeiba tibourbou* (Tiliaceae), its surface area is many times greater than that of the surface of the sphere that bears these hairs. The same applies to densely tomentose or spiny fruits (e.g., the legume *Mimosa pigra*, and *Byttneria catalpaefolia* and *Triumfetta lappula* in the Sterculiaceae). Of course, these projections may also be part of the dispersal traits or serve to deter seed predators that have long beaks or ovipositors [e.g., *Castanea* fruits (Fagaceae)].

#### 16.2.1.4 Green Seeds

Many large tropical seeds have bright green cotyledons as they approach a size approximating that of the mature seed (e.g., *Caesalpinia* spp., *Enterolobium cyclocarpum*, *Pithecellobium* spp., all in the Leguminosae). They remain this way until the fruit matures (at which time the cotyledons lose the green color). Enough light is passing through the translucent fruit and seed coat for photosynthesis by the young plant. This photosynthesis is turned off when the fruit wall and/or seed becomes opaque, and is the only independent source of nutrients available to the offspring. The value of this photosynthesis to the seed should be a selective force favoring increased translucency of immature fruit walls and thereby selecting for flatter fruits rather than cylindrical ones, or the placement of seeds closer to the fruit surface than would be the case were only packaging for consumption to be considered. Immature seed coat translucency should also be selected for. Furthermore, if fruit translucency and "tenderness" or "softness" are causally correlated, then the photosynthetic needs of the seed may in part select for longer times of fruit "immaturity" than might be the case if the opacity of the mature fruit wall were of no significance.

#### 16.2.2 Fruit Dormancy

There is much more to fruit dormancy at a small size than the loss of photosynthetic surface and direct resource deposit referred to in the previous Section. The minute fruit sitting on a tree for 6 months is much less of a nutrient-rich target for herbivores than is an expanded fruit with immature seeds in it, irrespective of the rate at which the young seeds are expanding or filling. Once the seeds have filled, the immature fruit is especially valuable as a food source for herbivores such as parrots, squirrels, monkeys, moth and beetle larvae, and adult leaf-eating insects. The theoretical fruit should either delay fruit expansion, or if fully expanded, should delay seed-filling until the last possible moment. For this to occur requires that nutrients be stored in the maternal vegetative tissues and then rapidly moved to the fruit, or that photosynthate on the spot is diverted and used for rapid fruit and seed development.

The duration of immature fruit stages is especially important in view of the way vertebrate seed predators behave. Once the immature fruits reach a stage where these animals can start feeding on the seeds, the local set of parrots, sucking bugs, squirrels, etc. eat a certain number each day. The more days that the seed crop is susceptible, the greater the percent of the seeds that will

be killed. The same applies to ovipositing insect seed predators whose larvae live in the seeds, but the situation is a bit more irregular. The set of insects which arrive at a given fruit crop usually have the ability to make a fixed number of ovipositions. As long as the immature but full-sized seed crop does not last long enough for two generations of the insects, the duration of this stage can probably lengthen without the penalty of increased seed predation.

A “dormant” fruit, one in which the plant’s resources are stored or used elsewhere until the last possible moment for fruit or seed maturation, increases the resource use options open to a plant (e.g., JANZEN 1967). Likewise, if a severe biotic or weather challenge appears that knocks out the young dormant fruit crop, the as yet untransferred resources are not also lost. It is very striking that drought-stressed or severely defoliated plants often shed their crop of developing fruits.

There should be some question in the reader’s mind as to whether fruit “dormancy” is simply the outcome of developmental processes that are exceptionally time-demanding. While an avocado (*Persea*, Lauraceae) cannot develop from flower to mature fruit in a couple of days, it is clear that once developmental periods increase past more than a few weeks, then questions of strategic timing become relevant. First, there is no developmental reason to suspect that the construction of ten seeds in a large fruit should take any longer than construction of five seeds in a half-sized fruit, since each seed usually develops concurrently with its siblings. The resources for fruit and seed development are certainly always available. It is a problem in allocation. If I try to fill my swimming pool with a 1-cm diameter hose, you may say it takes a long time to fill my swimming pool because the water enters slowly. I will say no, it takes a long time to fill because I chose to use a 1 cm diameter hose to fill it. Certainly the many tropical plants that flower and mature their fruits when leafless [e.g., *Tabebuia ochracea* (Bignoniaceae), *Cochlospermum vitifolium* (Cochlospermaceae), *Ceiba pentandra* (Bignoniaceae), *Gliricida sepium* (Leguminosae)] demonstrate that the resources are by and large coming from reserves (except for those made by the green fruit), and therefore how fast they can be pumped into the fruit is largely a question of the adaptive nature of this rate. Second, many tropical (and extratropical) plants mature even very large fruits in as little as 2 months [e.g., *Andira inermis* (Leguminosae) and all the above-mentioned species], demonstrating that development does not have to take the 8–11 months encountered in many tropical trees. Third, it is clear that a plant could speed up its seed or fruit development time by making fewer of them in a given crop.

### 16.2.3 Fruit Abortion

Herbivore damage to an immature fruit usually generates one of two responses: fruit abortion or scarring. The remaining living seeds die if a fruit is aborted. If all the seeds have been killed, the fruit is always aborted. Whether a damaged fruit is aborted depends on the age of the fruit, the proportion and number of seeds living after the damage, the usual size of the seed crop, the kind of damage, the species of plant, and the health of the plant. One of the most

unambiguous and commonest types of fruit abortion from damage is caused by insects that mine in fruits and seeds. It is commonplace to find that the first fruits to fall from a large fruit crop, while appearing mature, have an insect mining in them to the degree that all or nearly all of the seeds have been killed. Here it appears that the insect waits in its attack until the fruit is old enough such that when the plant responds to seed death by fruit dehiscion (and perhaps by earlier cessation of nutrient flow to the fruit and seeds), there is still enough food to sustain the insect's development. Following autopsy, the damage is obvious in such fruits. If these fruits are censused to derive the percent pre-dispersal seed predation, however, a falsely high value will be obtained. Additionally, dispersal agents often recognize such fruits and leave them behind, thereby biasing the value for percent pre-dispersal seed predation even higher. In many plants with large seeds, it appears that the seed is filled (and therefore approximates being maximally rich in nutrients) as much as a month before the fruits are ripe. This is often enough time for a tropical insect larva to develop to maturity. Such an insect may be able to kill a seed without the parent plant being able to perceive it, and therefore abort the fruit, since the full-sized filled seed may no longer be in physiological communication with the parent.

When seeds are killed with trivial damage to the fruit, as is done by sucking Hemiptera, the parent probably uses the cessation of hormonal messages from the seed to "know" when to cut off resource flow to the fruit and abort it. This brings up the question of how many living seeds must remain in the fruit for it to be retained. This has not been the subject of experimentation with wild plants. A high percent of seeds may be killed without fruit abortion occurring if there are many seeds in the fruit and the seeds are nearly mature at the time of their death, or if seed death is a normal part of the plant's biology (as in figs, JANZEN 1979 a, b).

Extensive immature fruit damage can occur without fruit abortion if the seed is undamaged, much to the discomfort of apple growers.

When confronted with aborted fruits it is often difficult to know whether they were dehisced due to damage to the fruit or seed, or due to physiological decisions by the parent associated with matching resources with fruit crop size or optimizing genetic composition of the crop. Opening apparently undamaged fruits will reveal damage by mining insects but does not help in the case of sucking insects. Unfortunately, their damage is often recorded as physiologically aborted seeds (e.g., coreid bug damage to western U.S. conifer seeds, KOEBER 1963).

Immature fruit abortion is certainly a form of defense in that it prevents further losses of resources in developing a worthless fruit. There is, however, no evidence that it is a direct defense which can lower the intensity of insect attack for later crops on the same tree, even if fruit abortion should happen to harm the insect in the aborted fruit. However, I expect that those insect fruit and seed predators which can successfully use immature fruits and seeds are still with us, while those that were harmed by fruit abortion have gone extinct, moved to new hosts, or evolved to attack the fruit or seed at a later stage of development.

### 16.2.4 Repair of Damaged Fruits

The hole made by the proboscis of a sucking seed predator or the oviposition of a mining seed predator is often sealed with gums or resins (e.g., *Acacia collinsii*, *Hymenaea courbaril*, *Pithecellobium saman*, *Cassia emarginata*). Physiologically this is no different than sealing small holes in vegetative tissue by the same means. It usually occurs shortly after withdrawal of the offending part and is externally manifest by a small dry ball of resin or gum on the fruit wall surface. Unfortunately, the number of punctures cannot be determined by counting these balls because they fall off and not all punctures produce them.

A second type of response to a puncture of a fruit is the deposition of tannins or other antibiotic chemicals in the tissues immediately adjacent to the wound, leaving a blackened open hole at the puncture site (e.g., feeding pits in immature *Andira inermis* fruits made by *Cleogonus* weevils).

When a large piece of a fruit has been bitten off, the exposed edges are normally sealed, just as are edges of leaves chewed off by herbivores. This is one of the areas of defense against herbivores where phytoalexins come into conspicuous play. Phytoalexins are even produced when foreign objects enter the fruit locule and presumably function to stop fungal and bacterial proliferation. In many multiple-seeded fruits, the locule walls are appressed between each seed so that fungi, bacteria and dry air introduced into one portion of the locule cannot spread to other portions.

Repair of a fruit does, however, differ from repair of vegetative tissues in one major way. If the seed has been killed, this cannot be repaired in any way and therefore the fruit has lost all of its value to the parent irrespective of how well the fruit tissues are repaired. Granted, a leaf cannot replace the portion bitten off, but at least the portion remaining may still produce more photosynthate than the maintenance costs of petiole and other support functions. This difference should be reflected in the relative "willingness" of the plant to abort damaged fruits and leaves.

### 16.2.5 Protective Morphology

Immature fruits have many physical traits that appear to be protective, but none have been elaborately studied in this context. The usefulness of fruit and seed chemicals as pharmaceuticals, and the opposite for physical fruit and seed traits is reflected in our knowledge of these two defenses.

#### 16.2.5.1 Hardness

The non-nut portions of immature fruits, and especially those whose seeds or nuts will be dispersed by passage through vertebrates or burial by vertebrates, are commonly very hard compared to when they are ripe. Such hardness is generally due to high pectin levels in cell walls, pectins that are enzymatically

degraded during ripening. This hardness may protect the fruit pericarp from mechanical damage as fruit-laden branches are tossed about by wind. However, I suspect that this hardness also directly stops certain herbivores, such as those that regularly eat the leaves. Perhaps more importantly, it renders the bites relatively indigestible irrespective of the more directly toxic compounds and digestion inhibitors. Measurement of this hardness and its experimental removal are both extraordinarily difficult to conceptualize and carry out. I know of only one case where immature fruit hardness seems to be functioning to deter a fruit eater. *Rhinochenus transversalis* (Curculionidae) females cut a hole in immature *Hymenaea courbaril* (Leguminosae) fruit walls and then oviposit in them. An undescribed phyticine pyralid moth then lays a cluster of eggs in this wound and her larvae develop while feeding on the pulp of the ripening fruit. It appears that the moth, lacking a hard ovipositor, requires the beetle entry hole to get its eggs to a point where the first instar larvae can mine on into the fruit, or else the larvae require this entry point. However, even this case is ambiguous because the *H. courbaril* fruit wall is also resin-rich and the dependency of the moth on the beetle may be to pass this barrier rather than a hardness barrier.

#### 16.2.5.2 Spininess

As is the case with protective chemicals, immature fruits are often protected by the same kind of armament that is found on the foliage and more. The exploding capsules of *Cnidoscolus urens* (Euphorbiaceae) have urticating spines on them as are found on the foliage. Most cactus fruits are spiny, even if they are to be eaten largely entire by a vertebrate; those cactus species whose fruits rupture and are then eaten out by birds (e.g., most of the large columnar cacti) have even spinier fruits than stems. However, there are exceptions. The extremely spiny green fruits of *Byttneria catalpaefolia* (Sterculiaceae) and *Mucuna mutisiana* (Leguminosae) are found on spineless vines. Blackberry fruits (*Rubus*, Rosaceae) of course do not share the spines of the blackberry plant. However, spininess should be a relatively rare form of immature fruit protection because they do not easily transform to a harmless fruit on ripening and because they are not effective against insects or large molar mills.

#### 16.2.5.3 Other Rind Traits

Once we know more of the details of the interaction of insects with immature fruits, many of the surface traits of immature fruits will probably be found to influence oviposition and larval success (cf. JANZEN 1969; CENTER and JOHNSON 1974). Surface smoothness, trichome depth and density, surface expansion during growth, gross contour, fruit wall thickness, etc. all influence whether a fruit can be used by a given insect. However, it is extremely difficult to distinguish between traits selected for by fruit and seed predators and traits of direct physiological significance to the plant because they influence temperature, photosynthetic, and desiccation traits of the fruit.

## 16.2.6 Protective Chemistry

### 16.2.6.1 Fruit Tissues

While immature fruit tissue has the same two chemical functions as a leaf — to protect itself and photosynthesize — it also contains nutrient-rich materials that will make it attractive to certain vertebrates when ripe. This means that a given secondary compound may be protective (see ROSENTHAL and JANZEN 1979), precursor to an attractant or bait, attractant or bait, or any combination of the three. In addition to this complication, I expect more intense chemical defenses per unit tissue in immature fruits than in leaves for two reasons. First, the loss of an immature fruit to a herbivore is a much greater strategic and material loss than is the loss of a leaf. Second, owing to the higher nutrient content of immature fruits than leaves (owing to seeds and precursors of fruit rewards) there should be a more intense herbivore threat to them than to leaves. If you have to eat something poisonous, it might as well be the most nutrient-rich thing you can find (MCKEY et al. 1978). These statements require modification in the case of fruits whose seeds are dispersed by agents that do not take a “reward” (wind, water, burrs, explosion, etc.).

Immature fruit tissue has almost never been subject to chemical analyses. Worse, when it is, the immature seed contents are normally left in the fruit. The results then may represent what is eaten by an animal that eats entire immature fruits but are totally worthless in understanding the chemical challenges to an insect that feeds on specific fruit parts, as is usually the case.

Are immature fruit secondary compound defenses different from those in leaves? *Hymenaea courbaril* (Leguminosae) pericarp (the 4–8 mm thick “rind”) is very rich in liquid resins that ooze out when the immature fruit is cut. J. LANGENHEIM (personal communication) has shown that these are similar to, but significantly different from, those in nearby *H. courbaril* leaves. These differences may occur because of different herbivores or herbivore intensity of attack on leaves and fruits, because the fruit resins have to solidify during fruit ripening while leaf resins remain liquid during leaf life, and/or because a 2-cm-thick fruit probably has quite different heating properties than paper-thin leaves.

The tannin content of immature banana fruit (*Musa sapientum*, Musaceae) has received the most attention among the agricultural cultivars. The immature fruit pulp of bananas may be as much as 17% tannins by dry weight. Since there do not appear to be other defenses in this starch-rich immature fruit, the relative freedom of immature bananas from chewing herbivores is probably due in large part to their high tannin content. It is not hard to imagine that the extreme sourness and bitterness of immature citrus fruits is protective. There are numerous examples in entomological horticulture of fruits that abruptly become susceptible to insects and pathogens upon ripening, implying that it was green fruit chemistry that kept them out of the immature fruit.

### 16.2.6.2 Seeds in Immature Fruits

The developing seed does not contain the same proportions or kinds of nutrients and chemical defenses throughout its development. It appears that at the very

early stages of development seeds may even have almost no chemical defenses. It is very conspicuous that many seeds do not gradually accumulate nutrient content, but rather develop at nearly full size for a long time and then rather abruptly fill with storage compounds in bulk. For example, the large hard seeds of *Bursera simaruba* (Burseraceae) are present yet nearly hollow for about 6 months, and then fill within the last month before dispersal (G. STEVENS, personal communication). Protease inhibitors, which are proteases that probably serve largely a defense function (e.g., JANZEN et al. 1977) but may also function in amino acid or peptide storage, appear abruptly in *Phaseolus vulgaris* seeds just before maturation (J. HAMBLIN, personal communication). When various compounds first appear in developing seeds is of utmost importance in understanding the plant–herbivore interaction. It may be that a large number of pre-dispersal seed predators are avoiding the secondary compounds found in ripe seeds by eating the seeds at a stage before they appear, or by virtue of their damage to the seed, preventing them from ever occurring in the seed. This does not, however, apply to parrots and squirrels, major pre-dispersal seed predators that take filled and nearly mature seeds. Certainly the bulk of pre-dispersal seed predators are avoiding one of the primary defenses of many seeds — the hard seed coat. Normally, the seed coat of a seed is firm but not hard until shortly before the seed is mature.

Unfortunately, just as there has never been a detailed study of the tissue and cellular location of the array of defensive compounds in a fruit, there has likewise never been one of the location of the secondary compounds and nutrients in a developing seed. I suppose that this is because we only rarely eat immature fruits and seeds, and when we do, we eat them as entire and homogeneous units (e.g., green beans, sweet corn).

## 16.3 Fruit Ripening

### 16.3.1 Within the Fruit

Fruit maturation or “ripening” is most usefully discussed separately for two groups of fruits — those whose seeds are dispersed by animals seeking a reward, and the others. In the others, the immature fruit tissue usually dries into a hard layer with a shape, buoyancy, etc. conspicuously related to the dispersal mode (e.g., *Hura crepitans*, SWAINE and BEER 1977). Here, no protective chemicals need be neutralized or removed unless the parent plant retrieves them for resource recovery (as when withdrawing chemicals from leaves before dehiscing them). Furthermore, these “defensive” chemicals may continue to function as defenses if the seed remains in an indehiscent fruit between dispersal and germination, or even as inhibitors in the ripe fruit that delay germination until the “right” moment. Almost no studies have been made of any of these processes, except the last-mentioned.

Ripening of fruits that contain seeds accidentally dispersed by animals in return for a reward is much more complex. Here a well-protected plant tissue

is to be converted in part or totally to an object highly desirable in certain quantities to a particular subset of the “herbivores” or “frugivores” in the habitat. Most of what we know of ripening is derived from study of cultivated plants.

Nearly all of the fruit-ripening phenomena recorded as being of particular interest to the fruit industry are easily interpretable in the context of dispersal agents. For example, a major problem in avocado horticulture is that the fruits do not “ripen” until they have been picked (and it is difficult to know when to pick them). In rainforest, the large heavy fruits of *Persea americana* (Lauraceae) are dropped from a height of 20–50 m, to the animals below that will disperse the large seeds. If the fruit was soft and “ripe” when released from the tree, it would explode on contact with the ground, leaving the seed without its reward for the dispersers. The phase of increased respiration associated with very rapid conversion of starch and other carbohydrates to sweeter and more easily digested carbohydrates at the time of fruit ripening (the “climacteric” of fruit physiologists) is comfortably interpreted as an abrupt transformation from highly inedible to highly edible. This transformation should occur as rapidly as possible, at the organizational level of a single fruit, since this will minimize accidental predation on immature seeds by eager frugivores, yet have the fruits optimally attractive once the seeds are ready for their voyage. Enzymatic softening of fruits on ripening is one more way in which the reward for the disperser is increased, which is not a surprising event in view of the goal of optimizing fruit value to some animal at minimum cost to the parent plant. Grapes and other fruits which do not ripen further once picked stand in strong contrast to plums, apples and other fruits that ripen once off the tree; again, the former are normally plucked from the tree by a dispersal agent, while the latter fall to the ground and then ripen while disconnected from the parent.

In addition to the ripening of the individual fruit, the pattern of fruit ripening within the crown and within the population is of great significance to both plant and animate dispersal agent (it is hard to satiate the wind; MCKEY 1975).

### 16.3.2 Within the Crown

The primary driving force for the degree and pattern of synchrony of fruit ripening within one crown is in matching the fruit availability against the consumptive abilities of the disperser coterie. An excess of fruits may lead to seed losses through fruits rotting or falling before the appropriate animal gets to them and a shortage of fruits may lead to disinterest by those important seed dispersers for which each plant is in competition with other food sources (e.g., HOWE and VANDE KERCKHOVE 1979).

The general pattern for an animal-dispersed fruit crop is for the fruits within a crown to ripen gradually over a period of 1–3 weeks. There undoubtedly are patterns of ripening that are associated with various different types of dispersers, but there has been virtually no study of the subject. Where the seeds are dispersed by many species (and often by many individuals), there appears to have been selection for very intense fruit production over a short period.

Many of the hundreds of species of wild figs conform readily to this pattern (JANZEN 1979a). One tree of a wild fig species with 1–2 cm diameter sweet purple globose fruits may mature several million fruits over a period of 2–4 days. At the other extreme are those tropical shrubs and trees that mature a few fruits each day over weeks or months, and the crop is visited regularly by a relatively small number of species and individuals, all of which know where the tree is (e.g., MCDIARMID et al. 1977; JANZEN et al. 1976b). While this pattern is extremely common, it is almost undocumented. It is also unclear what kind of hormonal processes must occur in the plant for the selective ripening of a given number or percent of fruits each day. It may even be that the removal of a ripe fruit then leads to further ripening of branch-mates. Such a mechanism of adjusting the rate of ripe fruit appearance to the number of dispersers visiting the crop has never been experimentally examined. Extreme cases are the understory Costa Rican *Psychotria* species (Rubiaceae) that have large sprays of bright red immature fruits, in which one to three black or purple (ripe) fruits are prominently displayed for a bird to eat. In trees with large fruits, such as those of *Terminalia catappa* (Combretaceae), variation in ripening appears to be generated by exposure to direct insolation. The fruits in the sun ripen more rapidly (and are sweeter) than those in the shade. Of course, this is only one of the multitude of physiological mechanisms available to a plant to adjust its fruit ripening distribution.

### 16.3.3 Among Crowns

There is very conspicuous variation among the members of a plant population in fruit ripening times (to the joy of plant collectors and the agony of ecologists trying to document fruiting peaks with herbarium specimens). It seems safe to say that whatever the cue a plant uses to time its peak and duration of fruiting, there will be intra-population variation in its reception and interpretation (e.g., preparedness to respond). Selection for any given degree of synchronization can then occur through both the kind of cue used and the thoroughness of the response to that cue. In other words, in a population where there is a high premium on fruiting when the other members fruit, soil dryness is unlikely to turn out to be the fruit maturation cue unless the members of the population are very uniform in size and live in a very homogeneous habitat. On the other hand, in a tree species that has the highest fitness if it fruits synchronously with a minimum number of conspecifics, as is the case with many fig species (JANZEN 1979a), no cue for fruiting should be used except the internal accumulation of reserves.

Competition among crowns for dispersal agents is especially relevant to intercrown synchronization. While we know that a given dispersal agent often visits more than one plant of a species during the day or during a fruiting cycle (e.g., HOWE 1977), it is not known how much competition among plants for dispersers occurs or how it is influenced by the density and placement of conspecifics. Many educated guesses are reasonable, but futile, until some plant populations are studied with this in mind. We need many more field studies

showing that location and size of seed crops matter (e.g., THOMPSON and WILLSON 1978). It can be stated with certainty that disperser fidelity to a plant or home range, response to various size seed crops, and satiation levels will all be important in determining the intensity of selection for various patterns of inter-crown fruit maturation synchrony.

## 16.4 Ripe Fruit

When is a fruit ripe? Certainly there is no single color or chemical state that can be used inter-specifically to identify the stage when the seeds within are "ready" to be dispersed and it is best for them to be dispersed. Some fruits fall off the tree as a form of behavioral presentation of the fruit to a terrestrial disperser (e.g., *Persea americana*), *Scheelea rostrata* (Palmae), while others hang on the tree until they rot or are removed (e.g., *Cassia grandis*, *Annona reticulata* (Annonaceae). Some very ripe fruits are leaf green (e.g., *Andira inermis*), while *Casearia corymbosa* (Flacourtiaceae) fruits are bright yellow for weeks before they ripen and pop open to reveal a red aril. *Guazuma ulmifolia* (Sterculiaceae) fruits are rock hard when ripe yet avidly ground up by horses. In short, the only definition of "ripe" is that the fruits are eaten by the actual dispersal agents that create the optimal seed shadow for the parent. Of course, as humans we tend to define "ripe" as when the fruit is ready for human consumption, and this generally approximates the ripe state for wild relatives of commercial fruits. Fruits dispersed by wind, water, etc. are usually "ripe" when they blow, fall, explode, etc. off the tree. The fruit tissues are normally leathery, inert, dry, woody, etc. I will not discuss them further. I know of no analyses of dry fruits as a group.

Fruits whose seeds are dispersed by animals eating the fruits have long been of great interest as food for humans. Of what do these fruits consist? In most general terms, a ripe fruit contains the nutrients and secondary compounds that attract a certain small subset of the animals in the habitat, and contains the secondary compounds or defensive structures to cause the other animals to ignore the fruit and its seeds.

While the focus of this essay is on fruit and seed physiology, it is not complete without at least a mention of why all fruits with vertebrate-dispersed seeds do not converge on the same shape, color, seediness, nutrient content, crop size, etc. It is through the inter-specific differences in these traits that fruits compete for dispersers, guide their seeds into different subsets of the vertebrates in a habitat, avoid the wrong dispersers, avoid ripe fruit-degrading organisms, influence the rates of passage through vertebrates, avoid seed predators, etc. All frugivores are not equally good dispersers for a particular plant and its ecological requirements for recruitment. When it comes to dispersal, fruits and seeds are not selected to be eaten by the largest number of animals, but rather by specific numbers of very particular ones. Animals vary enormously in how they treat the seeds they find in fruits and where they defecate or bury them.

Horses digest many of the seeds they swallow and ruminants spit seeds when chewing their cud. Bats regularly perch far from the fruiting tree and consume a fruit while spitting or defecating its seeds (JANZEN et al. 1976b). Monkeys often eat fruits and spit seeds where they find them, but defecate seeds elsewhere. Oilbirds carry fruits to their offspring in caves (SNOW 1962), tapirs defecate seeds in water (JANZEN 1981a), and agoutis bury seeds at the bases of logs and other large objects. Mistletoe birds may even wipe the sticky seeds off their anus onto a good live branch for the seedling parasite. Ripe fruit and mature seed traits are then designed to manipulate this diverse array of animals and many more, and to make use of their traits that cannot be manipulated.

#### 16.4.1 Nutrients and Attractants

An enormous number of kinds of compounds in a fruit are of interest to an animal dispersal agent. Further, it is often difficult to know whether the compounds of interest are merely cues or if they are the actual compounds used by the animal. The system is made even more complicated by the very different nutritional interests of different species of animals. The most basic generalization is that a fruit whose seeds are dispersed by an animal is usually evolutionarily designed to be eaten by at least one or more species of animal. Within the constraints of avoiding fruit rotting and fruit consumption by other animals, a fruit will be evolutionarily designed to maximize the return to the appropriate animal once eaten. It should not be surprising to find fruit tissue to be the most easily digested of all plant parts. On the other hand, the interaction between a plant and its seed dispersers is one of exploitation. For example, in order to put the optimal number of seeds into a dispersal agent per unit time, fruit tissue may well be evolutionarily designed to create a particular digestion rate, not a maximal one. Likewise, the animal may be expected to short-circuit fruit design by spitting seeds (minimizing seediness), eating only certain fruit tissues (e.g., peeling fruits that have rinds edible to other dispersers), only partly digesting fruits, etc.

##### 16.4.1.1 Nutrients

We do not yet know enough about the nutrient traits of those fruits eaten by which seed dispersers to construct a general hierarchy of syndromes, but certain pieces of the overall network are visible (MCKEY 1975; SNOW 1965, 1971). Fruits rich in water and sugars (relatively high pulp : seed volume ratios) often have their seeds dispersed by animals that make these fruits a substantial but distinctly partial portion of their total food intake on a daily or annual basis. They may, however, obtain a major part of their carbohydrate from these fruits. Blueberries, raspberries, pineapple, bananas, peaches, and many species of wild tropical plants with juicy yellow, red, white, black or blue fruits (Rubiaceae, Moraceae, Melastomataceae, Vitaceae, Leguminosae, Phytolaccaceae, Annonaceae, Loranthaceae, Boraginaceae, Sapindaceae, Cactaceae, Passifloraceae, etc.) by and large fall into this category. Many small birds, monkeys,

squirrels, bears, bats, procyonids, canids and marsupials are commonly involved in dispersal of their seeds. The seeds usually pass quickly through the animal, are believed to be only rarely digested or chewed up (see KREFTING and ROE 1949), and are protected by and large by being relatively hard and small (as compared to the animal). Comparatively dry fruits containing bird-dispersed seeds, fruits that are rich in proteins and lipids, often have their seeds dispersed by tropical birds that are almost entirely frugivorous as adults (and even as nestlings as well), such as oilbirds, fruit pigeons, manakins, cotingas, bell-birds, toucans and hornbills (e.g., FRITH et al. 1976; SNOW 1962, 1971). On these fruits there is a relatively small fruit pulp: seed volume ratio and the fruits often contain only one large seed. The fruits are as often dull in color as bright, and the large seeds are often regurgitated after the gizzard has stripped off the pulp. The seeds are often extremely bitter but not particularly hard, and I suspect they are largely protected from the bird by secondary compounds. Most of the examples of such fruits come from tropical families: Lauraceae, Myristicaceae, Apocynaceae, Sterculiaceae, Palmae, Flacourtiaceae, Burseraceae, Simaroubaceae, etc. A third easily distinguished group of fruits are the tough and even woody large indehiscent fruits that fall to the ground and are picked up by large terrestrial mammals. The seeds (or nuts) are often large, multiple and hard, the fruit pulp is rich in proteins and carbohydrates, and the fruit colors range from dull orange to brown. A largely unknown but variable number of the seeds survive the molar mill and chemical digestion (JANZEN 1981c, 1981a). A fourth type of dispersal syndrome involves the payment of offspring as the disperser's reward. Many "nut-bearing" trees fall into this group (Pinaceae, Fagaceae, Juglandaceae, Palmae). Rodents and certain northern birds are the most common contemporary seed dispersers for these trees, as part of their seed hoarding activities (e.g., JANZEN 1971, 1978a). Successful dispersal by and large depends on the buried nuts or seeds being missed during later recovery episodes or the owner being taken by a predator. In this case, the seed chemistry must be a compromise between being protected against pure seed predators and being at least partly edible to those seed predators that will also create a high quality seed shadow. For example, the hard nut wall of black walnuts (*Juglans*, Juglandaceae) is not worth chewing through when food is abundant at the time of nut fall, but definitely is worth chewing through during periods of winter food scarcity.

As popular as is the identification of syndromes of relationships between seed dispersers and plants (e.g., VAN DER PIJL 1972), I think it is largely pointless. Those familiar with tropical animal-seed interactions will realize that all the generalizations in the previous paragraph have nearly as many exceptions as agreements. Furthermore, ecological traits are as important as is morphology in the relationship. An agouti is a seed predator to one tree species, a disperser to another, and a mix to a third. To a single species of tree, one seed swallower is a seed disperser and another seed swallower is a digestive seed predator. If the seed crop is too large, most seeds may be killed by seed predators below the parent; if it is small, most may be dispersed, and not killed. An animal that passes most consumed seeds intact may be a poor dispersal agent as compared to one that digests most of the seeds swallowed, if the later defecates

the seeds in microhabitats with much higher seedling survival than the former. The traits of the fruits whose seeds are today dispersed by agoutis may well have been evolved in response to the dietary habits of mastodonts (JANZEN and MARTIN 1982). How fearful the animal is influences what it does with the seeds it ingests (HOWE 1980).

I feel we will do much better by developing detailed field studies of fruit–seed–animal interactions than by trying to generate ecological classifications in the nomenclaturally fixated style of those fascinated by orderly hierarchies as a way to understand nature.

Given this background philosophy, what sense can be made of the nutrient chemical content of fruits? A detailed description of their contained nutrients is not relevant and will not be presented here. Suffice it to say that different species of fruits are rich in a wide variety of sugars, lipids, proteins and vitamins (as well as water, fiber and minerals). The complication comes in trying to understand what is a nutrient when nothing is known of the dietary needs of the animals that normally disperse a fruit's seeds. Is the high ascorbic acid content of some tropical fruits selected for by some bird's need for ascorbic acid or is it a trait primarily of value in reducing the susceptibility of the ripe fruit to bacterial or fungal infection? Is starch rare in ripe fruits because it cannot be tasted by potential dispersers or because it cannot be digested by potential dispersers? Are orange-colored fruits rich in orange carotenoids as coloring or as a reward for vitamin-starved animals? Even more complicated, could they also be deterrents to animals that cannot tolerate a high carotene diet and would defecate or bury the seeds in the wrong part of the habitat? Is the high water content in fruits a reward to the animal or a contaminant that the animal cannot avoid and which functions partly to determine the passage rate of the seeds through the animal?

#### 16.4.1.2 Attractants

Many fruit traits are undoubtedly functional primarily in advertisement, false or real, through vision, olfaction, taste, memory, etc. A primary problem is in knowing which are traits that arose as nutrient rewards or defenses and only became attractants through learning or evolution by the animals, and which evolved specifically as attractants.

The fruit and seed disperser interaction is rampant with opportunities for convergence in attractant traits (as well as in nutrient content). Why is orange-red such a common color for fruits whose seeds are dispersed by birds? Is it because birds are intrinsically especially sensitive to these colors (and see GOLDSMITH 1980), because these colors contrast most strongly with green foliage, because birds have exceptional carotenoid needs, or because birds have evolved sensitivity to bright colors as a consequence of fruits being these colors? Why do ripe fruits have a similar range of odors? It is commonplace for a person who has never encountered a particular species of fruit to be able to determine if it is ripe just by smelling it. Why should our odor perception converge on that of birds, for example? I suspect that the answer probably has much to do with penetrance of compounds, volatility, cost of construction, limits to perception by sensory organs, and dietary needs in common among vertebrates.

Attractants, being small molecules and generally non-nutritive, are very difficult to distinguish from protective molecules. Furthermore, many chemicals may serve in both capacities. For example, the volatile essential oils of a ripe orange rind may attract vertebrates and be bacteriocidal.

#### 16.4.2 Protective Secondary Compounds

In addition to the thousands of kinds of nutrients and attractants found in ripe fruits, the partitioning of the fruit array among the animals in a habitat is also achieved by a wide variety of more conspicuously defensive secondary compounds. In addition to protecting ripe fruits from insects, microbes and fungi, these compounds probably play the major role in keeping the “wrong” vertebrates from eating fruits. “Wrong” means those animals that do not put the seeds in the “right” place, usually because they grind them up, spit them out or defecate them elsewhere.

Secondary compounds in ripe fruit have been little searched for, but some tantalizing facts are known. *Strychnos* spp. (Loganiaceae) ripe fruit pulp contains very toxic alkaloids (brucine, strychnine) and at least elephants and langur monkeys appear to be immune to it. Since langurs are colobines with a ruminant-type stomach, the site of strychnine degradation is not hard to guess. Ripe *Terminalia chebula* (Combretaceae) and *Caesalpinia coriaria* (Leguminosae) fruit pulp contains as much as 40% dry weight hydrolyzable tannin, yet they are eaten eagerly by certain large terrestrial mammals. *Balanites* fruit pulp is rich in steroids, yet the large fruits are eagerly eaten by elephants (JANZEN 1978c). I suspect that all wild fruits with pulp of much nutrient value contain numerous compounds that render them inedible or toxic to many or most vertebrates (and insects and fungi, see below).

Secondary compounds in fruits may also lead to optimal distributions of the seeds (fruits) among the animals that do disperse them. For example, it is commonplace for a bird to remove only a few ripe fruits at a time. When I eat these ripe fruits, I develop a sore throat after eating from two to five of them; could there be chemicals in the fruit that have this effect on wild animals, thereby spreading the fruit out among the potential dispersers? When feeding fruits to pet wild animals, it is commonplace to find them satiated after eating an amount vastly less than their stomach capacity. The same occurs with foliage and it is tempting to suggest that the immediate cause is the same. Additionally the number of seeds per fruit can influence the number of seeds swallowed (JANZEN 1981 b) or killed by a seed predator (MITCHELL 1977).

### 16.5 Rotting Fruits

Once a fruit has ripened, and thereby lost many of its defenses, it should likewise be especially susceptible to attack by those insects, fungi and microbes which do not disperse seeds and which may render the fruit unattractive to dispersal agents. There should be strong selection for traits of mature fruits that deter

these organisms yet minimally deter the seed dispersers. Hard but thin rinds on ripe fruits (e.g., apple skin), defensive secondary compounds in rinds (e.g., persistent resins in ripe avocado skins), and offerings of bacteriostatic high concentrations of sugars, lipids, organic acids, etc. as rewards are all examples. Which defenses occur will depend on the traits of the dispersers. Frugivorous bats have short and microbe-poor intestinal tracts (KLITE 1965) and appear not to rely heavily on bacterial degradation of their food. Their fruits can therefore be rich in antibiotics without harming the bat (and these compounds may also deter other vertebrates from feeding on the fruits) (JANZEN et al. 1976b). The fruits with high tannin content, often eaten by grazing and browsing ruminants, may be thereby protected from rotting in their (perhaps) long sojourn on the damp ground while waiting for a large mammal to come by.

The degradation of ripe fruits by insects and microbes is probably not a simple by-product of their feeding activity. There should be strong selective pressure for these small fruit eaters to quickly convert the fruit they have found to compounds that are toxic to both other microbes and to the large animals that normally disperse the seeds. We may have the potential predation on fruit-inhabiting microbes by vertebrates to thank for beer, wine and other alcohol-containing drinks, and we may have the same process to thank at least in part for antibiotics (JANZEN 1977a, 1979c).

## 16.6 Mature Seeds

A mature seed is a seedling riding in its own bag lunch. As such, it is a spaceship that must survive dispersal, and is the focus of attention for many animals in search of high-quality food in evolutionary and ecological time. The seed as a bag lunch is a compromise between (1) the insatiable appetite of the seedling for reserves to keep it in the game until it becomes self-supporting and to allow it to attain maximum development when competing, (2) the minimum size of the container that can survive various predation and dispersal attempts, and (3) the selective pressures for large clutch size under the restriction that the more seeds in a clutch the smaller they must be. The seed as a spaceship is a compromise between the reality that the better protected the offspring, the more likely it is to survive, but the better protected, the less likely it is to be dispersed, receive germination cues, or have maximal quality reserves at minimal cost to the parent plant per seed crop. Given these two sets of strictures it is not surprising to find that one kind of molecule in a seed often serves as seed defense, seedling defense, and a source of nutrients of the developing seedling. Likewise, seeds often contain the most concentrated nutrients to be found in plants, have shapes and sizes correlated with their treatment by animals, and have edibilities to animals related to seed crop sizes and periodicity of seed crop production.

There are two sources of compounds in seeds other than directly from the parent plant. First, as mentioned earlier, the immature seed may photosynthesize (and a few seeds never lose this ability, most notably *Inga*). Second, the seed

may use raw materials from the parent to synthesize its own complex molecules (and see KOZŁOWSKI 1972).

No ecological-physiological discussion of seeds is complete without reference to the most enigmatic and poorly understood trait of all in angiosperm seeds. The endosperm is a layer of polyploid (often triploid) tissue formed from a cell that originates with a nucleus from the pollen tube and two or more egg nuclei. It is thus neither parental tissue nor seedling tissue. All nutrients moving from the parent to the developing zygote pass through the endosperm (or are even stored in it until germination). All hormonal messages from the zygote to the parent (and the sibs) passes through the endosperm. I suspect that the real function of the endosperm is that of mediating parent-offspring conflict over the all-important rate and duration of nutrient flow from the parent to the zygote in the seed.

### 16.6.1 Seed Size

As traditionally recorded, "seed size" means seed weight, and usually dormant "dry" weight with the seed coat included. Hopefully, later studies will avoid the latter sources of error; seed coats can easily constitute 20–60% of the dry weight of a seed and moisture content of dormant seeds may range from 2% to 50% (e.g., JANZEN 1977c). As SALISBURY (1942) first commented, plants of wetter and more forested sites generally have heavier seeds than do the species in drier and less forested sites. The general interpretation is that the shadier the site, the more intense the competition among seedlings and adults, and therefore the more intense the selection favoring large-seeded species (which arrive by mutation, recombination and immigration).

The largest seeds and nuts are generally found in tropical rainforest and swamp forest habitats (including mangroves) and are generally dispersed by water, or more rarely by rodents. *Mora megistosperma* (Leguminosae) with its 400–900 g seeds (dry weight 250 to 600 g) is such a tree. It grows just behind the mangrove swamps on the coasts of lower Central America. However, many seeds on islands are also exceptionally large for their family (JANZEN 1969); I interpret this as the result of the usual selection for large seedling reserves coupled with the unusual absence of seed predation on islands, which in turn lowers the need for large seed crops and seeds small enough to be carried away from the parent by whatever dispersal systems are present (JANZEN 1969).

The smallest seeds are found in orchids (much less than a milligram per seed) and many other wind-dispersed seeds. These offspring carry very little if any reserves, and are dependent on landing at a place where photosynthesis is possible and mycorrhizal associates immediately available. Associated with their small sizes, such seeds are usually members of an enormous seed crop (e.g., 1–2 million seeds from one orchid fruit) and a widespread seed shadow. This stands in striking contrast to large-seeded trees where a crop of 10–1000 seeds can be a large seed crop.

It is traditional to worry about seed size only with respect to reserves for the seedling, but seed predators and dispersal agents undoubtedly serve as part of the selective forces that determine seed size.

### 16.6.1.1 Dispersal Agents

As a general rule, the larger a seed, the more likely it is to be spit out or chewed up by an animal that would otherwise swallow and defecate the seed or regurgitate it somewhere else. However, this relationship is not likely to be linear for any particular group of seeds and animals. The seed's problem cannot be solved by merely increasing the reward in the fruit. The animal may just work harder to get rid of the seed before it swallows the higher quality fruit. Likewise, the heavier a seed, the less likely inanimate dispersal systems are to carry it far from the parent tree. The greater a seed's specific gravity, the longer it takes to go through a dispersal agent and therefore the greater the risk of seed digestion. It is probably differential responses among dispersal agents that select at least in part for a distribution of seed weights within the plant's seed crop (e.g., JANZEN 1977d, 1978d). This variation may be a particularly effective way to create a thorough seed shadow of wind-dispersed seeds.

Likewise, the larger a seed, the fewer of them there are. This relationship may either reduce the size of the fruit crop and perhaps thereby attract fewer dispersal agents to the plant, or raise the fruit/seed ratio thereby increasing the attractiveness of the fruits of a particular plant. Of course, if seed volume is what is being selected for by a particular seed dispersal system (e.g., especially floating seeds), volume can be increased at little or no cost to the parent by the inclusion of air pockets in the seed (or in an indehiscent fruit). However, seeds are quite dry in general and it will not be possible to decrease their volume greatly by further drying.

### 16.6.1.2 Seed Predators

There are at least two general ways that seed predators contribute to the selective forces that mold seed size. First, as a seed becomes smaller in evolutionary time, it either becomes too small for an internal seed predator to develop in it, or it becomes too small for a large predator to bother to search for it. The seed predator may evolve in response to these changes, but some of the directions of evolution may be to move to other prey species. Second, as seed size declines in evolutionary time, the number of seeds that the parent can make increases. This may raise the fitness of the plant in the face of seed predators which are satiated by numbers of seeds (e.g., insects with fixed ovipositional abilities) (JANZEN 1969, 1971). Viewed the other way round, as a seed increases in size, it becomes an easier and (usually) more desirable target. Furthermore, the smaller seed crop associated with larger seeds is less likely to satiate seed predators. In short, as seed size rises, protection per seed is very likely to rise as well.

## 16.6.2 Seed Shape

Seeds are blessed with a multitude of shapes, virtually none of which are understood. It seems very likely that the different possible shapes of seeds of equal volume and specific gravity could influence seed coat crushing resistance, seed

spitting, and transit times inside large dispersal agents. It is probably no accident that most seeds that pass through animals are spheres or ovoids. The flat seeds in wind-dispersed fruits are undoubtedly conforming to the fruit morphology.

### 16.6.3 Seed Coats

The mature seed coat (and nut wall) is a barrier to germination cues, a barrier to seed predators, a barrier to light, and the point of fruit pulp attachment in many vertebrate-dispersed seeds. These traits are not all compatible. The seed whose coat is so strong that it cannot be chipped or crushed by teeth (JANZEN and HIGGINS 1979), ground by a gizzard, or digested by intestinal fluids (JANZEN 1981c, 1981a) may also be impervious to germination cues and have so much of the seed volume taken up by the seed coat that the seedling's bag lunch is severely reduced in size. The cost of the very thick walls of palm nuts (they are functionally seed coats even though part of the fruit) is probably a substantial part of both fruit and seed production. The seed that has the fruit pulp firmly attached in order to avoid being spit out may make the trip through the animal gut at a much different rate than does a smooth seed.

In addition to being hard, a seed coat may be very rich in secondary defensive compounds. There is an ingredient in *Erythrina* (Leguminosae) seeds that is so toxic that it kills *Callosobruchus* first instar bruchid larvae before they can take a bite (JANZEN 1977c). If notched, *Hymenaea* seeds placed in a glass of water turn the water deep purple-red with very astringent tannins that are released from the seed coat as germination occurs. Even the very thin seed coats of walnut embryos are very rich in the toxic terpenoid juglone. The paper-thin seed coats of white cedar (*Thuja canadensis*) are sprinkled with blisters full of thujone and pinene (T. EISNER, personal communication); the blisters are conspicuously avoided by the small rodents that laboriously shell these soft seeds rather than chew them up entire. Distinguishing between compounds functional as germination inhibitors and as predator deterrents is literally impossible at this stage of knowledge of seed natural history, and in fact many compounds may regularly serve both functions. The secondary compound content of seed coats is very different from that of seed contents (as is the case with nutrients), much to the detriment of the standard analyses performed by natural-products chemists; they commonly mix coat and contents. This is detrimental because seed predators generally do not eat seed coats and because the compounds in seed coats are not metabolically available to the offspring within.

### 16.6.4 Seed Contents

It cannot be stressed too much that seedlings use seed contents and not coats, and seed predators eat seed contents and not coats, though they may have to deal with them. Chemical analyses that pool the contents of seed coats and seed contents are biologically quite meaningless.

As a general statement, seed contents normally contain from one to three small molecule toxins (alkaloids, uncommon amino acids, cyanogenic glycosides,

etc.), one to three large molecule digestion inhibitors (which may be quite toxic as well) (lectins, protease inhibitors, tannins, etc.) and storage proteins and amino acids, lipids, and carbohydrates (JANZEN 1978 b). These “storage compounds” may, however, be arranged in such a manner as to also be defensive. Thus it is that the heteropolysaccharides in *Phaseolus vulgaris* beans are highly toxic to two species of bruchids (APPLEBAUM and GUEZ 1972; APPLEBAUM et al. 1970).

#### 16.6.4.1 Where Are These Chemicals?

Seed contents (endosperm plus offspring) are not a homogeneous mix of compounds. However, their location in respect to their storage role is poorly known and their location in relation to defense is unknown. In seeds with a large proportion of endosperm (e.g., many caesalpinaceous legumes), the endosperm appears to be largely complex polysaccharides. When a *Callosobruchus* bruchid larva mines into a *Parkinsonia* or *Schizolobium* seed, neither being its normal host, it does not gain in size in the endosperm and does not remain there. Upon arriving in the embryo, it develops normally on these very different tissues (JANZEN 1977c). The tannins and alkaloids in cocoa beans (*Theobroma cacao*, Sterculiaceae) are located in enormous vacuoles in distinctive cells that are scattered uniformly through the cotyledons. The cotyledons of *Lonchocarpus costaricensis* (Leguminosae) have conspicuous resins in large pockets throughout. However, the tannin content of *Mora megistosperma* (Leguminosae) seed cotyledons is only about two thirds that of the remainder of the embryo (P. WATERMAN, personal communication). It would not be surprising to find that toxins are generally distributed throughout the seed contents while digestion inhibitors and indigestible storage compounds are concentrated where they will have the largest effects at high concentration.

#### 16.6.4.2 Seed Content Hardness

Many seeds, and especially those of very dry areas, have extremely hard contents. Since the contents fill the seed coat thoroughly, I suspect that this adds to the crushing resistance of these seeds as well as minimizing their volume (of possible value in avoiding crushing, spitting and perhaps digestion). The large seeds of *Raphia taedigera* (Palmae) are rumored to pass intact through a tapir’s molar mill and digestive system, and they have effectively no seed coat. However, the seed contents are extremely hard.

What happens to seed contents upon germination? The ordinary reserves in seeds are generally mobilized as the basic resources for the developing seedling. However, this is not necessarily the fate of the defensive compounds. HCN in germinating lima beans is moved from the cotyledons to the developing seedling parts (CLEGG et al. 1979). The canavanine in *Canavalia* seeds is partly degraded by the young seedling and partly moved into the seedling as an intact and (apparently) defensive compound (ROSENTHAL 1977). I suspect that the bulk of the lectins and protease inhibitors in seeds are treated likewise by the seedling. Tannins and other large polyphenols are probably left in the seed

or shriveled cotyledons as discarded tissue, perhaps owing to the difficulty of removing these large molecules from the vacuoles that they occupy.

There are two ways in which a secondary defensive compound such as a lectin (JANZEN et al. 1976a) can be a seedling resource. First, it may be degraded to its constituent parts, which are then used in syntheses. However, defensive compounds are often more complex than would be needed for storage purposes alone. Second, if the seedling uses the defensive compound for its own defense, the parent plant may have packed a gun in the bag lunch, something that may be much more efficient than putting in just the raw materials to construct a gun.

#### 16.6.4.3 Multiple Defenses

Each seed is challenged by two relatively different sets of potential seed predators, and it is quite likely that the multiple defensive traits of seeds have evolved in response to different arrays of predators. First, there are those that spend their life in a seed and eat only that seed; these, such as insects and some fungi, are likely to be specialists that have overcome the seed's chemical defenses or else cannot feed on it at all. Escape from these is largely behavioral or in evolutionary time. Second, there are those that eat many different seeds and kinds of seeds in their lifetime. These are likely to be able to eat some of many kinds of seeds (e.g., finches, parrots, doves, heteromyid rodents, peccaries). Escape from them is likely to be through chemical and behavioral traits in both ecological and evolutionary time. For example, legume seeds are rich in protease inhibitors, and these are probably effective deterrents to many generalist seed predators. However, bruchids appear to lack gut proteases and are thus by and large unaffected by this defense (APPLEBAUM 1964). Legume seeds also contain numerous alkaloids and uncommon amino acids, most of which are toxic to any specific bruchid. However, one or a few of these can be resisted by each species of bruchid. The plant's only escape is through inter-plant and inter-seed crop spacing. In short, protease inhibitors in legume seeds probably evolved as a general protection, and then bruchids radiated onto this food source (APPLEBAUM 1964), while selecting for protective traits in their own more specific interactions. It is evident that none of these traits will stop a large frugivore from digesting a relatively small volume of seeds. Here an impermeable seed coat or nut wall has to be the other defense of the seed.

#### 16.6.4.4 Chemically Defenseless Seeds

All wild seeds have some chemical defenses, but it is evident that at least several taxonomic groups and one ecological group are exceptionally poorly defended. Monocots as a group have seeds whose contents are generally chemically poorly defended — it is no accident that grass seeds, bamboo seeds and palm nuts are major human foods. Monocots also tend to live in circumstances or have fruit types that are correlated with poor chemical defense — supra-annually mast-fruited stands (JANZEN 1976b), hard nut walls around the seed. Which came first is hard to divine. I suspect than an original poorly defended seed

among monocot prototypes led to strong selection for monocot behaviors and habitat occupations where escape by satiation of generalist seed predators works fairly well. The same generalities apply to Dipterocarpaceae, gymnosperms and Fagaceae, three other taxonomic groups that usually have highly edible seeds (JANZEN 1971, 1974). The evolution of dicots from monocots may even have been in part a break away from this pattern by plants whose seeds were by and large protected from generalists by the plants' behavior. This then allowed survival of isolated individuals that seeded at annual intervals in habitats that were not particularly hard on their animal populations.

The ecological group that displays the defenseless seed content so glaringly is the set of (largely) extra-tropical trees that grow in very low species-richness stands and produce large synchronized crops of generally edible seeds (nuts) at supra-annual intervals (gymnosperms, bamboos, Dipterocarpaceae, Fagaceae, *Strobilanthes*, etc.). Again, it is not clear if the high edibility of their seeds should be viewed as an evolutionary outcome of having trees growing in stands with low species richness and thereby selecting for seeding behavior leading to population- or community-level seed-predator satiation as a primary means of seed escape, or whether trees with highly edible seeds are especially prone to evolve the remainder of the syndrome. There is, of course, no reason why both evolutionary pathways could not have led to the mast-seeding outcome.

The central process operating in mast-seeding, be it produced by iteroparous or semelparous woody perennials, is that large seed crops produced synchronously by many members of a dense tree population satiate both the local and immigrant seed predators, many of which are able to digest the seeds in bulk. This occurs because the seed predators are generally at a low level for one of many reasons, such as community-level highly pulsed seed input, harsh climatic conditions between seed crops, long intervals between seed crops, and low harvestable productivity at the site. Satiation also occurs because the seed crops of individuals are very large. This is probably due to long periods of reserve accumulation between seed crops, to putting a minimum into individual seed defenses (and thereby making as many seeds as possible), and to putting almost nothing into pollination (virtually all of these plants are pollinated by wind or insects that act like wind) and dispersal (these plants are dispersed by wind or by the seed predators).

#### 16.6.4.5 Overcoming Seed Content Defenses

The animals that prey on seeds are bypassing, degrading, using or sequestering a wide variety of secondary compounds, and these are often at quite high concentrations when compared to vegetative parts. We know next to nothing of the specifics of how they do it. In the only insect seed-predator example worked on in detail, bruchid beetles apparently avoid the protease inhibitors by not using proteases in their gut physiology. One species has smart RNA-transferase that can avoid the uncommon and toxic amino acid canavanine in protein synthesis, can degrade canavanine to ammonia, and apparently can use this ammonia in its own amino acid synthesis (ROSENTHAL et al. 1976, 1977, 1978;

ROSENTHAL, personal communication). First, the beetle larva degrades the canavanine  $[\text{H}_2\text{N}-\text{C}(=\text{NH})-\text{NH}-\text{O}-\text{CH}_2-\text{CH}_2-\text{CH}(\text{NH}_2)\text{CO}_2\text{H}]$  to L-canaline  $[\text{H}_2\text{N}-\text{O}-\text{CH}_2-\text{CH}_2\text{CH}(\text{NH}_2)\text{CO}_2\text{H}]$  and urea  $[\text{H}_2\text{N}-\text{C}(=\text{O})-\text{NH}_2]$  by hydrolyzing the canavanine with ordinary arginase. The urea is subsequently degraded to  $\text{CO}_2$  and ammonia ( $\text{NH}_3$ ) with a urease that is found in the larva at concentrations approximating that found in *Canavalia* seeds, the usual commercial source of urease. The canaline, a compound highly toxic to insects, is then reductively deaminated to homoserine  $[\text{HO}-\text{CH}_2-\text{CH}_2-\text{CH}(\text{NH}_2)\text{CO}_2\text{H}]$  and ammonia.

## 16.7 In Summary: A Case History

Rather than yet further condense a severe condensation, I will describe the ecological physiology of the fruits and seeds of *Enterolobium cyclocarpum*, and their interactions with animals, as are emerging from an ongoing study of this large legume tree in the lowland deciduous forests of Santa Rosa National Park in northwestern Costa Rica. A guanacaste tree (*E. cyclocarpum*) produces a large crop of white moth-pollinated flowers (W. HABER, personal communication) in March–April during the second half of the 5-month dry season. The new immature fruits grow to about 6 mm in length and 3 mm in diameter and then remain dormant at this size well into January (i.e., until the beginning of the following dry season). During this period a large number of the young “fruits” are spheroid tiny dormant galls that contain a dormant egg of a cecidomyiid fly *Asphondylia enterolobii* (GAGNE 1978) that was laid in the floret in March–April. In January–February the galls and the fruits enlarge rapidly, the former into spheres 15 mm in diameter and the latter into 5–20 seeded 6–10 cm diameter bright green immature fruits. Trees that are heavily galled produce few fruits. I suspect that this is due in part to the galls taking up resources needed for fruit development and in part to the flies attacking the florets that would have become fruits. The adult flies emerge from the galls about the time of the next year’s flowering and the time of mature fruit drop.

The seeds in the green full-sized fruits attain full size within a month. These are solidly filled with green and apparently photosynthesizing tissue, even though they are buried 3–6 mm below the mildly translucent fruit surface. At this time, the immature fruit pulp is rich in saponins (and probably other compounds) and not fed on by any herbivore. Since the tree is largely to entirely leafless at this time, all fruit development is based on some combination of stored reserves, photosynthetic stem epidermis, and photosynthesis in the fruit and seed. About the time that the seeds are full-sized and solidly filled with tissue, the large *Amazona ochrocephala* parrots fly to the tree crowns and, with their powerful beak, cut into the center of the seed and remove the seed contents. They often leave the soft seed coat behind, still imbedded in the immature fruit. These birds often kill as much as 50% of the seed crop before the seeds harden to the point where they are no longer attacked.

About March–April, the indehiscent fruits mature (turn brown and dry out). They fall directly to the ground below. In contemporary natural forests, the majority lie below the tree and rot or have their seeds removed by small rodents (see below). Some are eaten by tapirs (*Tapirus bairdii*) and collared peccaries (*Dicotyles tajacu*). The peccaries remove the seeds and crush them between their molars. This requires 70 to 200 kg, depending on the orientation of the seed in between the molars (JANZEN and HIGGINS 1979; and see KILTIE 1980). They are seed predators. The tapir, as based on observations of a single captive animal, spit out about half of the seeds in the two to six guanacaste fruits they will eat in a meal, and swallow the remaining seeds without breaking them. About 80% of those swallowed are killed by the digestive process, I suspect because the hard seeds germinate and then become able to be digested (JANZEN 1981c, 1981a). The remaining seeds are defecated in water (puddles, streams), a trait that may make the tapir of much greater importance as a dispersal agent than would appear from the number of seeds it defecates (see below).

However, contemporary natural forests differ strongly from the megafaunal-rich habitats in which guanacaste trees evolved, and up until about 10,000 years ago it seems likely that a fruit crop of a guanacaste tree was rapidly eaten by mastodons, ground sloths, horses, and other large mammals which then probably generated a wide-spread and relatively thorough seed shadow (JANZEN and MARTIN 1982). This inference is supported not only by logic, but by observations on introduced cows and horses. When cows encounter a guanacaste fruit crop, they avidly consume the fruits and pass nearly all the seeds intact in 5–10 days. Horses also avidly eat the fruits but spit out 40–60% of the seeds while chewing up the fruits and digest 70–95% of the seeds they swallow (JANZEN 1981c, 1981b).

Return to the fruits below the tree. If they are not picked up by large mammals, they are chewed open by small heteromyid mice (*Liomys salvini*) that remove the seeds. If the seed is hard and ungerminated (the usual case), the mouse eats some seeds directly and cuts a small notch in the seed coat of others. These germinate immediately on moist soil and a caged *L. salvini* will eat 10–15 per 24 h and maintain its body weight on a pure diet of this food for a month (HALLWACHS and JANZEN 1982). These mice will harvest at least 99% of the guanacaste seeds left below the parent tree during the first 6 months after fruit fall. However, they also avidly harvest guanacaste seeds directly from newly defecated horse and cow dung. These seeds have the same fate as those taken directly from fruits.

Being able to eat a large amount of ungerminated or germinated guanacaste seed tissue is a general trait of rodents. When the other common small terrestrial rodent (*Sigmodon hispidus*) in the habitat is given a pure diet of germinated guanacaste seeds, it eats a little and then starves to death at about the same rate as if it were given no food at all. However, it can survive indefinitely on a pure diet of boiled newly germinated guanacaste seeds. Mature guanacaste seeds contain a high concentration of three potentially toxic compounds — a protease inhibitor (C. RYAN, personal communication) and two uncommon amino acids (albizzine, pipercolic acid, E.A. BELL, personal communication);

boiling should denature the protease inhibitor and leach out the uncommon amino acids.

Return to the large mammals that disperse the seeds (horse, cow, tapir, mastodont, etc.). It is evident that where they defecate the guanacaste seeds will be very important. *L. salvini* is a forest rodent; *S. hispidus* is a grassland rodent. Guanacaste trees are normally found along the edges of open areas, along water courses, and in swamps. When artificial dung piles containing guanacaste seeds are placed in open grassland far from the forest, many seeds survive to a seedling stage old enough to be ignored by the rodents, even though there is a high *S. hispidus* density at the site. In the forest, there is virtually no survival to the seedling stage, and this is due to seed predation by *L. salvini*.

The forest *L. salvini* may be responsible for a current enigma. In Panama guanacaste fruits lie around long enough to rot open and the exposed seeds are oviposited on by the bruchid *Stator generalis*. The larvae develop in the seeds (C.D. JOHNSON, personal communication). The beetle does not oviposit on the fruit. Why has it not extended its range up the continuous population of guanacaste trees from South America to northern Mexico? If these beetles are offered Costa Rican guanacaste seeds in the laboratory, they develop very well on them. I suspect that between modern livestock and mice, the bruchids never have the chance to develop a population on fallen guanacaste seeds.

*Acknowledgements.* This study was supported by NSF DEB 77-04889, EEI (Belmont, Massachusetts), and Parques Nacionales de Costa Rica. The manuscript was constructively criticized by W. HALLWACHS.

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