I should like to mention only generalized pseudoasymmetric cases with pseudoasymmetric axes and planes, models of which are shown in Fig. 16. Examples of stereoisomeric molecules represented by these models have been prepared by Günter Helmchen (*23*) in our laboratory (Figs. 17 and 18). It is noteworthy that many bilateral organisms including men are examples of planar pseudoasymmetry.

I have limited the discussion to three-dimensional basic figures with four ligands because they are typical for organic stereochemistry. The same procedures can be applied to produce catalogs based on figures with five or more vertices, but the multiplicity of models so obtained is larger and therefore more difficult to deal with in a brief lecture or article.

The need for brevity also prevents me from dealing with the manifold biochemical and biological aspects of molecular chirality. Two of these must be mentioned, however briefly. The first is the fact that, although most compounds involved in fundamental life processes, such as sugars and amino acids, are chiral and although the energy of both enantiomers and the probability of their formation in an achiral environment are equal, only one enantiomer occurs in nature; the enantiomers involved in life processes are the same in men, animals, plants, and microorganisms, independent of their place and time on Earth. Many hypotheses have been conceived about this subject, which can be regarded as one of the first problems of molecular theology. One possible explanation is that the creation of living matter was an extremely improbable event, which occurred only once.

The second aspect I would like to touch, the maintenance of enantiomeric purity, is less puzzling but nevertheless still challenging to chemists. Nature is the great master of stereospecificity thanks to the ad hoc tools, the special catalysts called enzymes, that she has developed. The stereospecificity of enzymic reactions can be imitated by chemists only in rare cases. The mystery of enzymic activity and specificity will not be elucidated without a knowledge of the intricate stereochemical details of enzymic reactions. The protagonist in this field is John Warcup Cornforth.

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Plant Defense Guilds

Many plants are functionally interdependent with respect to their herbivores.

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It is generally agreed that herbivores exert strong selectional pressures on plant populations and that chemistry (including nutrition), morphology, and escape in time and space are the plant's primary means of defense (*1–4*). Research on antiherbivore mechanisms has naturally focused on the individual's own suite of protective characteristics. This approach generally neglects an important facet, that the probability of a plant being fed upon depends not only on its inherent quality and quantity, but on the chemistry, morphology, distribution, and abundance of alternative prey and nonprey as well. Only a few protective traits are lethal deterrents, whereas the majority function by influencing the feeding behavior of potential herbivores, causing the animal to exclude certain plants or plant parts from its optimal diet (*5*). When traits are marginally protective, their deterrent value is highly conditional on a variety of stimuli produced by other plants. The literatures of ecology, entomology, pathology, and agriculture have long noted the effects of specific kinds of plants in reducing herbivory; in this article we bring together these examples in developing the concept of "guild" defense against herbivores. We wish to emphasize the ways in which plant associates can function as antiherbivore resources in ecological time and discuss the possible selective value of defense "guilds" through evolutionary time.

The term guild has been used botanically to describe groups of plants in some way dependent on other plants, such as the epiphytes, saprophytes, parasites, or climbing vines. More recently the term has been used in a broader sense to characterize ecologically unified, functional groups of organisms (*6*). Our usage denotes individuals that are functionally dependent or interdependent with respect to their herbivores, and does not necessarily imply spatial association. Although close spatial relationships are often important, functional guild bound-

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aries are in each case defined by herbivore feeding behavior and dispersal capacity.

Guild members function as antiherbivore resources in three major ways: (i) as insectary plants that aid in the maintenance of herbivore predators and parasites, (ii) as repellent plants, either directly or indirectly causing the herbivore to fail to locate or reject its normal prey, and (iii) as attractant-decoy plants causing the herbivore to feed on alternative prey. In most cases the chemical or physical influence of these plant associates causes a lowered herbivore functional or numerical response (or both) (*7*). Guilds of potentially alternate prey may have the additional long-term effect of increasing the functional life of plant defense genes. We find the last-mentioned hypothesis particularly interesting and devote most of our discussion to its exploration.

Insectary Plants

Floral and extrafloral nectaries provide an important alternative energy source for herbivore predators and parasites. When nectar production by neighboring (insectary) plants is synchronized with egg laying by herbivore predators and parasites, the efficiency of these insects may be significantly higher, causing a lowered herbivore numerical response. Parasitization of tent caterpillar pupae in trees growing near nectar-producing plants can be 18 times greater than in trees lacking associated nectar sources (*8*). Species of *Phacelia* grown in orchards greatly increase the parasitization of *Prospaltella perniciosi* by its parasite *Aphytis proclia* (*9*). Chumakova's data also show that the efficiency of tachinid and ichneumonid parasites is substantially higher in cabbage fields when they are grown near flowering umbelliferous plants. Allen and Smith (*10*) report that parasitization of the alfalfa caterpillar by *Apanteles medicaginis* is far greater where adjacent weeds are in bloom than where they are absent. Similarly, more beneficial insects can be found in cotton growing immediately adjacent to sorghum than in cotton growing without sorghum (*11*).

Insectary plants also function as nursery plants by supporting alternate hosts for predators and parasites (*12*). *Macrocentrus ancylivorus* is an effective parasite against the oriental fruit moth in southern New Jersey, where strawberries are frequently grown near peach orchards and support alternate hosts for

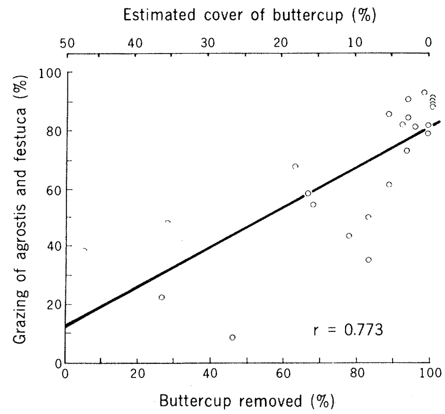

Fig. 1. Selective grazing by cattle of *Agrostis* and *Festuca* in the presence of differing densities of the buttercup *Ranunculus bulbosus* [Data from (*15*)]

the overwintering of the parasite (*13*). An outstanding example of a single parasitoid species functioning on two separate leafhopper hosts on two separate plant genera has been described (*14*). In central and northern California the wild grape, *Vitis californica*, is attacked by the grape leafhopper *Erythroneura elegantula*. The egg parasite *Anagrus epos* is particularly effective in controlling the grape leafhopper, but must have an alternate host (the leafhopper *Dikrella cruentata*), which occurs on wild blackberries (*Rubus ursinus*). Wild grape and blackberries grow in the same riparian habitat and are often intertwined. Early each year, usually in February, the *Dirkrella* females are stimulated to oviposit by the rapid flush of new blackberry leaves. The parasitoids quickly respond and their numbers increase enormously, reaching their peak in late March. The outpouring of adult *Anagrus* from blackberry thickets coincides effectively with the first appearance of grape leaves and the initial deposition of eggs by overwintering grape leafhoppers. The phenology may be accelerated or delayed depending on temperature, but the same factors that govern the appearance of new blackberry growth also seem to influence the time of appearance of the grape leaves and the first oviposition by *Erythroneura*. Selection may have favored grape plants with a delayed leaf production synchronized with the availability of egg parasites "cultured" on blackberries.

Although grape plants derive maximum protection by growing adjacent to or intermixed with blackberries, dispersal of *Anagrus* individuals produced early in the spring provides effective control of the grape leafhopper at least 4 miles from blackberries. The dispersal capacity of herbivores and their predators or parasites warns against the expectation that defense guild members will always occur in close spatial proximity.

Repellent Plants

Repellent neighbors primarily lower herbivore functional response via spines, toxins, odors, and shade, causing the herbivore to reject or fail to locate its normal prey. The physical protection derived from a cactus patch or a spiny shrub is often readily apparent, whereas interference by a chemically repellent neighbor is not so obvious. In one such case, Phillips and Pfeiffer (*15*) have shown that forage grasses such as *Agrostis* and *Festuca* gain considerable protection from cattle when associated with the noxious buttercup *Ranunculus bulbosus*. This species contains the lactone ranunculin (*16*), a powerful irritant of skin and mucous membranes. Our plot of their data (Fig. 1) shows the general correlation between decreasing buttercup density and increased intensity of grazing. A similar but unquantified example is found in southern Arizona rangelands, where the presence of poisonous burroweed (*Haplopappus tenuisectus*) conveys considerable protection to its associated perennial grasses (*17*). In other cases of increased resistance in mixed species stands, the specific cause is unknown. Two closely related species of *Trifolium*, *T. repens* (white clover) and *T. fragiferum*, are commonly found as wholly intermingled swards in lowland and riverside grasslands in Britain. When plots of these species were grown as pure stands and as mixtures at Oxford (*18*), white clover was ignored by hares, which, however, completely defoliated the plots of *T. fragiferum*. In mixed stands *T. fragiferum* was ignored by the hares and the species persisted together. Similarly, the grass grub *Costelytra zealandica* and the porina caterpillar damage white clover in pure stands, but susceptibility is decreased in stands mixed with perennial ryegrass (*19*).

The well-documented principle of warning coloration for visually orienting predators predicts the operation of warning odor for chemotactically orienting herbivores. Levin (*3*) advances the hypothesis that volatile components of trichome exudates serve the plant as an outer line of defense by advertising the presence of substances that insects would find repellent should they sample the host. Volatile chemical deterrents

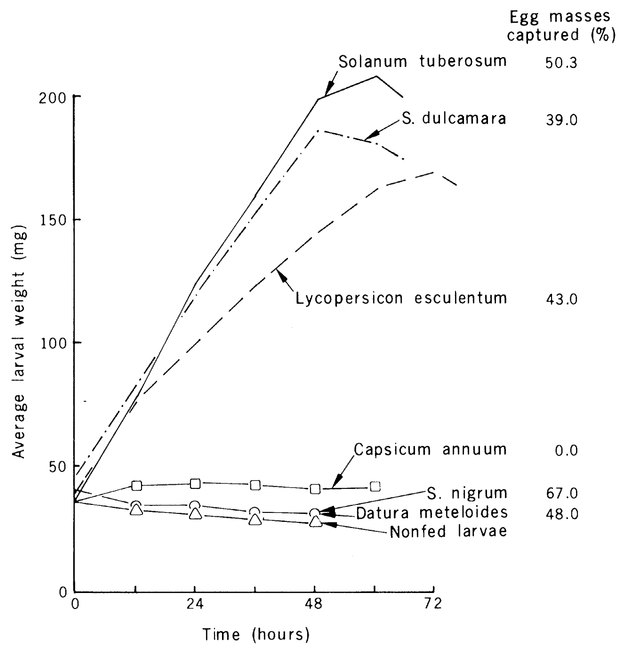

Fig. 2. Growth response of the Colorado potato beetle on six Solanaceous species, contrasted with the percentage of egg masses captured by these plants in the presence of equal amounts of the normal host, *Solanum tuberosum*. [Modified from Hsiao and Fraenkel (*33*)]

may also modify feeding behavior on neighboring plants by acting as a general repellent or by the masking and antagonism of feeding cues. Significant data on repellent-interference have been marshalled through studies of plant-insect associations in simple and diverse communities (*20, 21*). These investigations and others (*22*) establish the pattern that plants grown in monoculture may suffer a higher herbivore load than conspecifics grown in floristically diverse habitats. Field experiments by Tahvanainen and Root (*21*) suggest that the presence of nonhost plants interferes with herbivore orientation and host utilization. On the basis of the hypothesis that some plants produce repellent or masking chemical stimuli, choice experiments were used to test the influence of nonhost plants on the feeding behavior of a specialized herbivore, *Phyllotreta cruciferae*. In all cases, collard (*Brassica oleracea* var. *acephola*) that was kept alone was preferred over collard associated with the nonhost test leaves (tomato and *Ambrosia artemisiifolia*). The experiment indicated that interference was effective on the olfactory level and possibly was due to direct repulsion rather than merely to feeding inhibition. Root (*23*) concluded from these studies that ecosystems in which plant species are intermingled possess an "associational resistance" to certain types of herbivores.

The principle of odor masking is further supported by the fact that host-finding by the parasites of herbivores often depends on cues produced by both the herbivore larvae and by their food plants (*24*). Monteith (*25*) demonstrated that the differences in the percentage of parasitism by *Bessa harveyi* of the larch sawfly *Pristiphora erichsonii* in different sections of its food tree were primarily due to the masking effect of the odors from shrubs beneath the *Larix laricina* trees and by the close proximity of *Picea glauca* and other species of trees.

The shade produced by plant canopies can also be an effective herbivore deterrent (*26*). At the time of its introduction into North America, the Klamath weed *Hypericum perforatum* grew best on open, sunny, well-drained slopes, and grew poorly in the shade. In a biological control effort, two leaf-eating beetles (*Chrysolina quadrigemina* and *C. hyperica*) were introduced into California from France and England. The beetles prefer to lay their eggs in sunny areas, and consequently the weed was eliminated best from open habitats. Klamath weed now occurs more frequently under trees than in sunny areas (*27*). The crucifer *Dentaria diphylla* is apparently protected from at least three flea beetles by growing in shady woodland habitats (*28*). Herbivore pressure may also confine the hemiparasitic plant *Pedicularis densiflora* largely to growth in the shade of oak trees (*29*). Larvae of the nymphaline butterfly *Euphydryas editha* feed on this plant, but ovipositing females at Jasper Ridge do not fly into the shade, even on hot days (*30*). This flight behavior tends to keep them out of contact with *Pedicularis*, although they frequently fly within 3 to 4 meters of large stands of the plant. Shade is, of course, produced by a variety of abiotic objects, but in many habitats plant foliage is the only available source of this potential herbivore deterrent.

Attractant-Decoy Plants

We now consider plants that can potentially serve as alternative prey and examine how feeding and oviposition behavior is influenced by relative quality. Each food plant has an absolute quality defined by its chemical, morphological, temporal, spatial, and numerical effects on herbivore fitness, but also has a relative quality that is a function of its abundance and its chemical, morphological, temporal, and spatial distance (quality distance) from other known prey. Attractant plants and decoy plants represent the two extremes in this spectrum of relative quality. Both draw off herbivores and dilute their impact, but have opposite effects on herbivore fitness.

Many attracting plants are not what they advertise, and function as decoys, causing mortality or reduced fecundity because of the presence of toxins or because of the absence, deficiency, or imbalance of certain nutritional materials. Although some animals select food primarily in a negative way and eat everything not containing deterrent chemicals (*1, 31*), the presence of feeding excitants may be the stimulus for oviposition "mistakes" that lead to larval death in many specialized insects (*32*). Herbivores dependent on specific oviposition or feeding cues are susceptible to the presence of similar stimuli in associated species of variable nutritional value, as illustrated by the study of Hsiao and Fraenkel (*33*) on host selection and growth response of the Colorado potato beetle, *Leptinotarsa decemlineata* (Fig. 2). In the presence of equal amounts of the normal host, *Solanum tuberosum*, species from several genera in the Solanaceae each capture a large proportion of the available egg masses. Growth response, and presumably fecundity, differs markedly, with one of the most lethal decoy plants (*Solanum nigrum*) drawing the highest percent of egg masses. These data and others (*34*) suggest that coexisting toxic and nontoxic plants with similar attractant chemistry represent a selectional paradox for would-be host-specific herbivores. In agricultural systems, the proper management of decoy plants might produce effective control of some crop pests. The argument that similar ovipositional and feeding "mistakes" would not be expected in natural coevolved systems neglects the occurrence of rapid changes in plant quality. We discuss later a variety of factors that produce such variability.

Plant attractiveness is often relative and changes with the availability of other choices. The amount of bracken fern eaten by cattle is a function of the relative palatability of neighboring plants (*35*). In pastures where highly palatable species are available, bracken fern is rarely grazed (20 grams per head daily), while in pastures with moderately palatable species available cattle consume up to 200 g per head each day. Bracken consumption jumps to 2 kg per head per day in pastures with many unpalatable species. Neighbor-controlled relative preference is equally operative within polymorphic populations. In the presence of alternative prey, the slug *Agriolimax reticulatus* rejects strongly cyanogenic *Lotus corniculatus* individuals, but readily consumes this chemical morph in the absence of the preferred intermediate and acyanogenic phenotype (*36*).

Attractant plants function as sinks for insect herbivores and may permit a less preferred species, race, morph, or age-class to exist at high absolute abundance or to escape during a critically susceptible growth stage. In agricultural systems, the lygus bug attacks both cotton and alfalfa, but shows a decided preference for alfalfa. Stern *et al.* (*37*) interplanted 160 acres (1 hectare = 2.47 acres) of cotton with strips of alfalfa totaling 8 acres. In June, July, and August the average number of *Lygus* adults per 50 sweeps was 100, 96, and 198 per month in the alfalfa strips, and only 2 per month in the cotton. Cotton is normally sprayed for *Lygus* when densities reach 10 to 15 adults per 50 sweeps; and in the absence of alfalfa, as many as four chemical treatments of cotton may be required during the season. Changes in the relative abundance of prey did not alter preference; when an adjacent 160-acre field of alfalfa was cut, the number of adults in the neighboring alfalfa strips increased from 198 to 439 immediately after cutting. At the same time, adult *Lygus* bugs in the interplant cotton only increased from two to four per 50 sweeps. In a similar case (*38*), the sorghum shoot fly damages exotic and Indian varieties of sorghum equally when there is no choice for oviposition, but manifests a strong preference for exotic varieties in a choice situation. Counts of eggs per plant averaged 7.3 on the exotic variety as compared with a range from 1.4 to 2.5 on four Indian varieties. Attractant plants are thus at a selective disadvantage and would tend to maintain this status in regimented agricultural systems. The reverse may be true in natural ecosystems, where a variety of perturbations and natural cycles alter the relative attractiveness of alternative prey.

Gene Conservation Guilds

In the adaptation-counteradaptation view of plant-herbivore coevolution it is assumed that plant gene pools are sufficiently diverse and that recombination is sufficiently effective to meet most new herbivore breakthroughs. Pathologists seeking to control plant disease in agricultural systems have in the past made analogous assumptions, as Van der Plank (*39*) humorously describes:

> The plant breeder incorporates into a new wheat variety a gene for resistance to a rust fungus. Sooner or later the fungus responds with a gene or genes that allow it to attack the new variety. The breeder then adds more genes, the fungus overcomes them, etc. To ensure a continuous supply of genes for defense the breeder establishes an international wheat collection to discover all available genes in *Triticum*, and to make doubly sure he is missing nothing, he draws on *Aegilops* and *Agropyron* as well. If only he can find enough defense genes to match every one the fungus can throw into the battle, and then have one to spare when the fungus has exhausted itself, the battle will go to the breeder. Victory, in this view, goes in the end to the side with the remaining gene.

This notion of "winning the arms race" has proved unrealistic in agricultural systems and is equally invalid in natural ecosystems. Decades of experience with crop protection have led to the general conclusion that actions delaying the demise of existing defenses are often more beneficial than an endless search for new weaponry (*40*). The most interesting prediction arising from our consideration of defense guilds is that gene conservation should also play an integral role in the defensive posture of natural populations.

If gene conservation is a principal factor in successful long-term defense against herbivores, selection should favor individuals living in environments that effectively "cultivate" herbivore susceptibility. Susceptibility can best be maintained through host nonuniformity that disrupts evolutionary tracking or specialization by herbivores. Individuals occurring within feeding environments (guilds) that provide acceptable options of similar but distinctive quality should have greater fitness than those in feeding environments offering little or no choice. The requisite variability in plant quality may be generated within populations via age-class differences, genetic polymorphisms, and variable growth conditions, or by guild formation between populations, races, closely related species, and unrelated but chemically similar species.

Herbivore susceptibility may be enhanced either by selection against virulent individuals, or by decreasing the exposure frequency of susceptible genotypes. The latter event takes advantage of herbivore behavioral sensitivity to variable food quality. Georghiou (*41*) argues that selection for behavioristic resistance to pesticides (the ability to detect, escape to nontreated areas, and survive) operates in favor of individuals with physiological susceptibility to the pesticide. If the "irritated" insects do not have an escape opportunity (alternate nontoxic areas), selection will favor physiological resistance. Analogously, if herbivores are "irritated" by their food but have no feeding alternatives, selection will favor physiological resistance.

The second model of direct selection against "virulent" genotypes requires temporal cycling of the herbivore population between resistant and nonresistant hosts. It also assumes that herbivore races with the "virulence" necessary to counter a particular resistance gene are less fit to compete successfully on host types without this gene. Evidence for loss of fitness by organisms carrying unnecessary virulence is well documented (*42*), particularly for plant pathogens. Van der Plank (*39*) contrasts the ability of the stem rust *Puccinia graminis* to overcome resistant wheat under conditions approaching monoculture, with its inability to do so with alternating exposure to nonresistant varieties. In North America, *P. graminis* cycles between spring wheat, which is protected by the resistance gene Sr_6, and winter wheat, substantially without the Sr_6 gene. *P. graminis* spends about 2 months of the year in varieties with the Sr_6 gene and the remaining 10 months of the year in varieties without this gene. Races of *P. graminis* able to attack varieties with the gene Sr_6 have been present in North America for many years, but spring wheat continues to remain relatively free from attack. Van der Plank calculates that, during the 10 months or 30 generations *P. graminis* is on winter wheat, the relative abundance of races with the necessary virulence to attack spring wheat drop to 2.6×10^{-7} of its initial value.

Puccinia graminis is completely capable of flourishing on the genotype Sr_6. This genotype (variety Eureka) was released in Australia in the late 1930's and soon became widely grown in Queensland and northern New South Wales. The rust utilized grasses and self-sown wheat as alternate hosts when it was not in the planted wheat fields. As the Eureka variety increased in popularity, the self-sown wheat also became largely of the same genotype. Without relaxation of selection for Sr_6 resistance, the Eureka variety was quickly destroyed. Van der Plank emphasizes that, although there is no substitute for strong genetic resistance, it is a common misconception that a resistance gene is a resistance gene per se, wherever it may be.

Many insect populations use several hosts of variable quality but, over a period of time, they may be exposed to additions, deletions, and changes in the proportion of each type of host. For example, from a population sample of the African Queen butterfly, *Danaus chrysippus*, collected in Ghana, Brower and his associates (*43*) concluded that 6 percent of the caterpillars fed on *Calotropis procera*, 10 percent on *Pergularia daemia*, and 84 percent on *Leptadenia hastata*, three species of the Asclepiadaceae with markedly differing cardenolide concentrations. At a series of sites in Colorado, larvae of the flower-feeding lycaenid butterfly *Glaucopsyche lygdamus* feed on a suite of perennial herbaceous legumes: four *Lupinus* species, *Thermopsis montana*, and *Vicia americana* (*44*). Oviposition choice among the lupine species is related to pubescence; when *G. lygdamus* has a choice, it lays eggs preferentially on the inflorescences of the least hairy *Lupinus* present. Dolinger and co-workers (*45*) have shown that three of the *Lupinus* species have distinctly different alkaloidal patterns, "low," "high variable," and "high constant." They hypothesized that within-population variability in alkaloids is an antispecialist chemical defense mechanism which may impede selection for pest strains capable of detoxifying these compounds. They suggest that plant population variability may be maintained by frequency-dependent selection, since, as an alkaloidal type becomes most common, it will also, after several butterfly generations, become the most susceptible to predation. Their view of the significance of intrapopulation variability is analogous to our concept of gene conservation guilds, and frequency-dependent selection is one mechanism, among others, that could force herbivore cycling between guild members, whether they be intra- or interspecific associates.

Herbivores exhibiting a flexible search image influenced by learning have the ability to switch prey, that is, to concentrate their attacks disproportionately on a new prey type (*46*). Conditions that favor switching behavior in general predators may include (i) prey that are patchy in distribution in both space and time with respect to the search range of the predator, (ii) mobile searching behavior in the predator, and (iii) use of sensory detection systems that work at a distance. Although clear cases of switching remain to be observed, many herbivore-plant systems satisfy these general conditions. The checkerspot butterfly, *Euphydryas editha*, from Gardisk Lake, California, will oviposit on either *Penstemon heterodoxus* or *Castilleja nana* if no choice exists, but in the presence of *C. nana* the insect must reach a high state of oviposition motivation before *P. heterodoxus* becomes an acceptable alternative. Singer (*30*) suggests that the probability of this state being reached would depend on the relative densities of both species, and on their distribution relative to that of *E. editha* females. In populations where adult nectar sources, oviposition plants, and larval food plants are all abundant and share similar distributions in space, oviposition motivation would only rarely rise to the point at which secondarily preferred oviposition plants are accepted. In contrast, when nectar sources are dispersed and favored oviposition plants are less abundant, the frequency of oviposition on secondarily preferred plants should increase (*30*). Accordingly, a chemotactically preferred host such as *C. nana* should increase its fitness by growth at low frequency, intermixed with an acceptable alternative host, and away from potential nectar sources.

Events that induce or force changes in herbivore feeding behavior are poorly understood. The availability of preferred prey can be altered by changes in the physical environment, by herbivore competitors (*47*), by interplant competition that may result in cycles of alternating high and low population densities (*48*) and by repellent neighbors. The introduction or immigration of new plant species and races can cause temporal host diversion of some phytophages (*37, 38, 49*). In situ changes in plant quality are facilitated by "open" recombination systems (*4, 50*) and by the fact that many defense compounds also have important metabolic functions and respond to stimuli other than predation (*51*). More rapid and less predictable phenotypic changes in secondary chemistry are caused by diverse environmental factors such as photoperiod, season, temperature, drought, nutrient availability and ultraviolet light (*51, 52*). Mattson and Addy (*53*) emphasize the sensitivity of forest insects to changes in plant quality and conclude that factors such as plant age, stressful climatic conditions, low fertility of the site, and bottlenecks in the flow of certain nutrients interact to cause significant increases in host quality and decreases in host resistance. A dramatic example is found in Australian grasslands where levels of tryptamine alkaloids in the grass *Phalaris tuberosa* rise with increasing temperature, light intensity, and nitrate nitrogen, converting this palatable food plant into a toxic decoy plant that causes neurological disorders and sudden death in sheep (*54*). Even this environmentally mediated change is neighbor-related; pastures on which sudden deaths occur are invariably those on which nitrogen-fixing clover has been grown for some years.

A growing number of investigators (*23, 55, 56*) have argued that diversity per se does not increase stability in plant-herbivore systems. The concept of gene conservation guilds supports the alternative idea that "a little powerful diversity" of the right kind (*55*) is a key component of stability. Validation of the gene conservation hypothesis will require long-term genetic and demographic studies of herbivore feeding patterns and greater awareness of the food quality variability achieved by abiotic environmental factors, by population polymorphism, and by the association of races, closely related species, and chemically similar, unrelated species. The common phenomenon of cohabitation by closely related, theoretically competitive plant species can be viewed with new perspective under this model. Gene flow may also be viewed as an important means of retaining functional quality distance between species of diverging secondary chemistry. Sterile hybrids, often seen as energetically superfluous, may function as attractant-decoy plants that contribute significantly to the cultivation of herbivore susceptibility.

Summary

Optimal plant defense should incorporate any mechanisms that influence the feeding behavior of potential pests. From a diverse collection of examples suggesting that the defense of a plant may be improved in the company of specific neighbors, we discuss a framework of operational mechanisms that begin to clarify some aspects of the recognized influence of species diversity on herbivory. Neighbors serve as insectary plants for herbivore predators and parasites, and influence herbivore feeding behavior by repelling, masking, attracting, and decoying. Insectary plants lower the numerical response of herbivores by increasing the efficiency of their predators and parasites. Repellent plants primarily lower functional response by causing the predator to fail to locate or reject its normal prey. Attractant-decoy plants

dilute herbivore impact by drawing off herbivores, either increasing or decreasing their numerical and functional response (or either).

The concept of gene conservation guilds adds diversionary and delaying tactics to the adaptation-counteradaptation view of plant-herbivore coevolution. The useful life of a given gene for resistance may best be extended by mechanisms that disrupt genetic tracking (specialization) by herbivores. Some plants may remain inedible not because their chemistry or morphology represents an evolutionary impasse, but because they live in an environment that provides acceptable options of variable quality. Feeding environments that provide little or no choice promote specialization by forcing physiological adaptation. Conversely, the evolutionary momentum of specializing herbivores may be lowered by enhancing their susceptibility, either by selection against virulent individuals, or by decreasing the exposure frequency of susceptible genotypes. The latter mechanism of conserving susceptible individuals takes advantage of herbivore behavioral sensitivity to variable plant quality. Direct selection against virulent genotypes requires temporal cycling of the herbivore population between resistant and nonresistant hosts. Both events may occur within defense guilds that provide acceptable feeding options of similar but distinctive quality.

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