Exploring Plant Resistance to Insects

Plants are not helpless when confronted with insect herbivores; they have evolved many different ways to fight back

The evolution of new instruments of war has typically been accompanied by a corresponding, if somewhat slower, evolution of defensive strategies. The discovery of the sword was followed by the shield and body armor. The development of the gun led inevitably to the development of the tank, the intercontinental missile to the antiballistic missile, and the spy satellite to the particle beam weapon. Attacker and attacked have managed to maintain a rough parity, even while a significant proportion of their vitality is sapped by an arms race.

This is no less true in the ceaseless war between plant and pest. As pests grew more rapacious, plants evolved subtle toxins to poison them. As pests developed enzymes to detoxify the poisons, plants developed other defensive strategies. This coevolution of attacked and attacker has led to a delicately balanced ecosystem in which plants, for the moment at least, seem to have the upper hand. Even the most "susceptible" plants manage quite well. Cutworm larvae raised on an artificial diet, says John C. Reese of the University of Delaware, gain six times as much weight as those raised on tissues from "susceptible" corn leaves. Chemicals produced by plants, adds Jack C. Schultz of Dartmouth College, "may be more important than any other single factor in controlling insects in nature."

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The mechanisms by which plants resist insect attacks were the subject of a 2-day symposium at the recent Las Vegas meeting of the American Chemical Society. Some of the ways that plants avoid being eaten alive are not only unusual but quite sophisticated.

Schultz reported that a single sugar maple tree, for example, produces adjacent leaves that differ quantitatively in many chemical and physical traits important to insects trying to eat them. One group of leaves may be high in tannins and other metabolites that are toxic to insect herbivores while another section may have below-normal concentrations of nitrogen-containing nutrients desired by the insects. The concentrations of these materials may change on a regular basis, or in response to destruction by insects. New oak leaves that grow back in areas defoliated by pests, Schultz notes as an example, have high concentrations of tannins that discourage further defoliation.

"It is as if the tree presents its insects with a 'shell game' in which good quality food is scattered about the plant, effectively hidden, or is even shuttled about by constant chemical change," says Schultz. Insects must thus "hustle about searching for high-quality leaves," thereby exposing themselves to predators much more frequently.

A similar response in alder and Sitka willow trees has been observed by David F. Rhoades of the University of Washington. Attack on the trees by tent caterpillars and webworms leads to increased concentrations of tannin and resins and decreased concentrations of nutrients in the leaves of the attacked trees—as well as in the leaves of nearby trees. Mechanical defoliation produces the same results. Rhoades speculates that the effect may be mediated by substances released by the destroyed leaves. "Most plants do in fact release low levels of terpenes and other volatile compounds for unknown reasons," he says, and these may be detected by adjacent trees.

One way in which a protective response may be mediated within a plant was described by Clarence E. Nelson and his colleagues at Washington State University. They found that tomato and potato plants produce at least two different proteinase inhibitors in response to attack by chewing insects. These inhibitors interfere with the insects' digestion of the plant and reach high concentrations in a tomato leaf within 4 hours after a single, severe wound; the concentrations remain constant for another 5 hours or so before decreasing rapidly. A second wound at the 9-hour mark, however, triples the rate of accumulation of the inhibitors. This accumulation is initiated by the release of a putative wound hormone called proteinase inhibitor-inducing factor. This hormone may stimulate defenses throughout the plant.

Other chemicals are involved in defenses of other plants. Douglas firs from Montana that produce the greatest quantities of the sesquiterpene cadinene and the diterpene myrcene are the most resistant to budworm attack, according to Rex G. Cates of the University of New Mexico. Budworms on New Mexican firs that produce above-average amounts of bornyl acetate and other monoterpenes are smaller and less fecund than normal.

Limonoids, the bitter tetranortriterpenes found in citrus fruits, are relatively potent antifeedants that stunt the growth of the fall armyworm and the cotton bollworm, according to Isao Kubo and James A. Klocke of the University of California at Berkeley. Large amounts of these products could become available for commercial use: Kubo speculates that more than 300 tons of limonoids could be extracted annually from grapefruit seeds alone. Kubo and Klocke have also isolated a naphthoquinone from the tropical medicinal shrub, *Plumbago capensis*, that inhibits molting in several lepidopterous agricultural pests. The chemical also inhibits an enzyme involved in the synthesis of chitin, the insect's hard covering. The two investigators have previously isolated other chemicals that also inhibit molting (*Science*, 24 April 1981, p. 430).

A new class of natural products, steroid glycosides known as withanolides, are apparently unique to members of the family Solanaceae, according to Jon Bordner of North Carolina State University. Bordner and his colleagues have isolated withanolides that stimulate egg-laying and feeding in the tobacco hornworm, which feeds on many members of the Solanaceae. They have also isolated another withanolide, nicandrenone, that is an antifeedant for the same pest. Another species of Solanaceae, a wild tomato, produces a potent chemical, 2-tridecanone, that inhibits feeding by the tobacco hornworm and certain other

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pests. Bordner and his colleagues are attempting to breed commercial tomatoes that would also produce the chemical, but the tomatoes they have obtained so far do not turn red when they ripen.

Many plants produce chemicals that are toxic only when the insects are exposed to light, says J. Thor Arnason of the University of Ottawa. Synthetic photosensitizers such as xanthine dyes have long been known to be toxic to insects, but it is only recently that naturally occurring photosensitizers have been observed by investigators such as May Berenbaum of the University of Illinois and G. H. Neil Towers of the University of British Columbia.

Work by several investigators has shown that there are two general pathways for photosensitization. Dyes such as methylene blue and rose Bengal are excited to the singlet state by ultraviolet light; the singlet state decays to the triplet state, which interacts with oxygen in its ground (triplet) state to produce singlet oxygen and triplet dye. Singlet oxygen is a highly reactive species that literally burns up insect tissues. Naturally occurring photosensitizers such as the furanocoumarins, which are found in wild parsnips and members of the carrot family, are also excited to the singlet state. These interact directly with the insect's DNA, however, to form lethal chromosomal abnormalities. Four different agriculturally important orders of insects have been studied so far and all—even hard-bodied insects like boll weevils—are susceptible to photosensitizers.

Arnason and Towers have been studying polyacetylenes isolated from members of the family Compositae, which includes daisies, black-eyed Susans, marigolds, and fleabane. They studied 14 different polyacetylenes and found that nine were toxic to mosquito larvae, their test species. Three of these—phenylheptatriyne, α-terthienyl, and 2-[non-*trans*-1′-en-3′,5′,7′-triynal]-furan—are especially potent and have potential commercial application. α-Terthienyl, in particular, is more potent than DDT in insects exposed to light.

Some insects have evolved defenses against even these compounds. Certain microlepidopteran larvae that feed on Compositae species roll themselves in the leaves while they are eating. The reason for this behavior was not clear before, says Arnason, but it now seems likely that the larvae are simply avoiding light, which is necessary for the chemicals to have effect.

Another unusual defense against pests involves a class of chemicals known as phytoalexins (*Science*, 28 May 1976, p. 874). These are lipid-like antimicrobial chemicals synthesized by plants in response to fungal and bacterial infections; their synthesis can also be initiated by ultraviolet radiation and leaf damage. They are in many ways analogous to interferon, an antiviral chemical produced in humans in response to viral infections.

The complete mechanism of phytoalexin activity is not known. Some can inhibit the germination of disease-causing fungal spores, while others may inhibit fungal and bacterial enzymes that degrade the cell walls of plants. There have been only isolated reports of phytoalexin activity against insects, and some investigators think these are artifacts. Marcos Kogan of the University of Illinois reported that the phytoalexins in soybeans deter feeding of the Mexican bean beetle, an important pest of soybeans. The primary phytoalexin of soybeans, glyceollin, had no effect, however, when added to an artifical diet fed to another pest, the soybean looper. The looper, like many other insects that have developed specific ecological niches, has apparently developed a defense against the toxin.

The synthesis of phytoalexins is known to be stimulated by specific substances known as elicitors. Work by a number of investigators, particularly Peter Albersheim of the University of Colorado, has shown that many of these elicitors are complex carbohydrates formed by the breakdown of the bacterial or fungal cell wall. Many such naturally occurring elicitors are being studied experimentally in hope that they can be used to turn on a plant's defenses before an actual attack—a process analogous to vaccination in humans.

Because these naturally occurring elicitors are expensive to produce, it would be useful if synthetic elicitors could be developed. Robert J. Kaufman and his colleagues at Monsanto Agricultural Products Company of St. Louis reported the synthesis of two different types of artificial elicitors. The first group are highly branched aryl cluster glycosides produced by cyclotrimerization of alkynyl sugar derivatives. The second group comprises fluorinated carbohydrates prepared with the fluorinating agent diethylaminosulfur trifluoride. Both types of compounds can be prepared relatively easily in high yield, and both stimulate production of phytoalexins in a soybean cotyledon assay about ten times as effectively as naturally occurring elicitors. Production of the phytoalexins is very detrimental to the soybeans, however: Kaufman terms it a "suicide response" that the plant might use only as a last resort against overwhelming infection.

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Death trap?

Daisies contain chemicals toxic to insects exposed to light.

The use of elicitors, or any other materials that might stimulate a plant's natural defenses, must thus be approached very carefully. Plants generally produce defensive substances only in response to an attack because that production represents a drain on their energy reserves and their synthetic capacities. Increased resistance to insects and other pests can come only at the cost of a decreased yield or decreased production of biomass. If that decrease is more than the loss resulting from infestation, the process becomes self-defeating.

—Thomas H. Maugh II