Current Status of Breeding for Resistance to Insects[1]

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The major objectives of this paper are to acquaint nematologists with the current progress in developing resistant cultivars of major commodity crops to key insect pests, to discuss briefly the role of resistant varieties in pest management strategies, and to examine what we currently know about the chemical and physical causes of resistance and insect-plant interactions.

The study of plant resistance to insects dates back to the earliest days of applied entomology. The early literature contains several significant examples of differences in response of cultivars to insect attack. Havens' (12) report that the 'Underhill' variety of wheat was resistant to the Hessian fly, *Mayatiola destructor,* is generally considered the earliest documentation of an insect-resistant variety. The development of the science of plant resistance can be divided roughly into three areas: the pre-World War II era, the immediate post-World War II era, and the present era of environmental awareness. Before World War II, initial observations by scientists had led to cooperative efforts by plant breeders and entomologists to develop improved cultivars to control insect pests. The postwar years showed a significant shift from studies in insect biology and insect-host interactions to the exploitation of the newly developed organic chemical pesticides. New pesticides were identified and synthesized with spectacular results when applied to insect populations. Research and control strategies shifted toward the new chemical-control approach. Research and development in insect biology and insect resistant plants languished during this period. Since the late 1960s, there has been a shift toward the development of integrated systems of pest control. This change was conditioned by two major factors—the development of insect resistance to insecticides and the concern for environmental pollution stemming from the use of chemical pesticides.

The development of the specialty of plant resistance to insects can also be viewed from the accumulation of knowledge in its published form. The first review of the subject (33) listed 567 references, of which only 37 were published prior to 1920. Publications increased considerably after that. The first book on insect resistance in crop plants was published by Painter in 1951 (28), and it had more than 1,000 works cited. Subsequently, significant review papers have been published by Painter (29), Beck (5), National Academy of Sciences (26), Maxwell et al. (24), and Gallun et al. (8). The comprehensive treatment of the field in the text *Breeding Plants Resistant to Insects,* edited by Maxwell and Jennings (25) and underwritten by the Rockefeller Foundation, represents the latest efforts to provide a textbook and major reference work in the field.

Categorization of resistance in plants to insects has differed from that found in the phytopathological and nematological literature which has used the terms *vertical* (specific), *horizontal* (general), and *hypersensitive* resistance. Painter (28) provided a workable compromise between mere categorization of resistance phenomena and the basic study of causative factors or processes. He proposed three categories of *mecha-*

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nisms of resistance: nonpreference, antibiosis, and tolerance.

Nonpreference includes the insects' responses to plants that lack the characteristics to serve as hosts. These range from negative reactions to total avoidance during search for food, oviposition sites, or shelter. Nonpreference is often projected as a property of the plant, which is not congruous with the process to be described. For this reason, Kogan and Ortman (17) proposed to substitute *antixenosis* for the term nonpreference. It is parallel to antibiosis and conveys the idea that the plant is avoided as a "bad host."

Antibiosis includes all adverse effects exerted by the plant on the insect's biology —its survival, development, and reproduction.

Tolerance includes all plant responses resulting in the ability to withstand infestation and to support insect populations that would severely damage susceptible plants.

PROGRESS WITH CROPS

Space does not permit more than a summary of major progress in several of the world's major commodity crops.

Alfalfa: The development of insect resistant alfalfa cultivars through selection and breeding methods has had unprecedented success in the United States during the past quarter century. Much of this success can be attributed to the spotted alfalfa aphid, *Therioaphis maculata.* The introduction of this aphid into the United States in 1954 caused the initiation of the research that led to the development and release of more than 30 alfalfa cultivars, many of which have multiple pest resistance and high forage yields. Primary varieties being utilized against the spotted alfalfa aphid today are Lahontan, Moapa, Zia, Cody, Sonora, Caliverde 65, Mesa-Sirsa, Washoe, Bonanza, Dawson, Mesilla, WL-504, CX UC-Cargo, and CUF 101. The selection and breeding techniques developed to combat the spotted alfalfa aphid have also speeded the production of cultivars resistant to the pea aphid, *Acyrthosiphon pisum* (i.e., Apex, Washoe, Dawson, Mesilla, Kanza, WL 512, PA-1, CUF 101, and Paine), the blue aphid, *Acyrthosiphon kondoi* (i.e., CUF 101 and WL 514), alfalfa weevil, *Hypera postica* (i.e., Team, Weevlchek, and Arc), alfalfa spittle bug, *Philaenus spumarius* (i.e., Culver), and potato leafhopper, *Empoasca fabae* (i.e., Cherokee). As indicated, several of the cultivars carry resistance to all three of the primary aphids that attack alfalfa.

Cotton: The bulk of the research on plant resistance to insects has been done within the last 15–20 years. Prior to the mid-1950s, research on insect resistance was quite limited; Painter (28) noted that, except for the breeding of varieties resistant to certain leafhoppers, no extended efforts had been made to develop genetic resistance to cotton insect pests. Extensive efforts from the early 1960s to the present, primarily in Texas, Mississippi, Arkansas, and Louisiana, have led to the identification and incorporation of a number of resistant characters into advanced breeding lines and into currently grown varieties. Table 1 summarizes the traits found in cotton and the insect to which the trait confers a measurable amount of resistance. Table 2 indicates how traits are being combined to provide resistance to multiple pests as well as building higher levels of resistance to single insects through incorporation of different resistant characters under different genetic control which, when combined, confer higher levels of resistance. Primary factors affecting various cotton insect pests are nectariless, high gossypol, frego bract, high tannins, glabrousness, heavy pubescence, red plant color, okra leaf, oviposition-suppression, plant bug suppression factor, and early-rapid fruiting. Early fruiting types with combinations of the above factors are offering many advantages in Texas, especially in cotton pest management programs.

Maize: In recent years, breeding for resistance to insects in corn has largely been concentrated at four locations: CIMMYT outside of Mexico City; Southern Grains Insect Laboratory, Tifton, Georgia; Mississippi State University; and the USDA European Corn Borer Laboratory, Iowa State University, Ames, Iowa. Considerable effort on corn rootworms has been concentrated in South Dakota at the Northern Grain Insect Laboratory. Early work on European corn borer (ECB), *Ostrinia nubilalis,* was conducted by Penny and Dicke (30) and others. Resistance to first-brood leaf feeding

Table 1. Insect resistance characteristics of cotton*.

Trait	Boll weevil	*Heliothis* spp.	*Lygus* spp.	Cotton fleahopper	Spider mites	Pink bollworm	*Empoasca* spp.	Thrips	Aphids	Cotton leaf perforator	Whitefly
Frego bract	R	N	S	S	N		S	N	N		
Nectarilessness	N	R	R	R		R	R	N	N		
Glabrousness	N	R	(?)	R(?)		R	S	S	(?)		
Terpenoids (high sqare gossypol, heliocides)	N	R	R	R			R	S	R(?)		S
High tannins	N	R	N	N	R	R	N	N	(?)	R	(?)
Heavy pubescence	R	S	(?)	R	N	R	R	(?)	(?)	R(?)	(?)
Red plant color	R	N	N	N					N		
Okra leaf	N										R
Oviposition—suppression factor	R										
Plant bug suppression factor			R	R							
Early—rapid fruiting	E	E				E					

*R = resistance; S = susceptible; E = escape; N = neutral; (?) = conflicting evidence or not verified.

Table 2. Resistant characters used as building blocks for higher and multiple resistance to insect and spider mite pests in cotton.

Trait*	Pests resisted	Status of breeding program
ne + e	Plantbugs, Boll weevil, Pink bollworm	Commercial
ne + sm	Bollworms	Commercial
ne + e + fg	Plantbugs, Boll weevil	Commercial
ne + sm + fg	Plantbugs, Bollworms, Boll weevil	Commercial
ne + sm + hg	Plantbugs, Bollworms, Spider mites	Advanced lines
ne + sm + fg + e	Plantbugs, Bollworms, Boll weevil	Commercial, Advanced lines
ne + sm + fg + r	Plantbugs, Bollworm, Boll weevil	Advanced lines
ne + sm + fg + e + ok	Plantbugs, Bollworm, Boll weevil, Whiteflies	Advanced lines
ne + sm + fg + ok + hg	Plantbugs, Bollworms, Boll weevil, Whiteflies, Spider mites	Experimental lines
ne + sm + fg + ok + hg + r	Plantbugs, Bollworms, Boll weevil, Whiteflies, Spider mites	Experimental lines

*ne = nectariless, e = earliness, sm = smoothleaf (glabrous), fg = frego bract, hg = high gossypol, r = red color, ok = okra leaf.

was found and subsequently incorporated in most of the hybrids in the north central area of the United States and other areas where the borer is a major problem. Resistant hybrids are estimated to be grown on 12–13 million hectares, with a value of $150–175 million annually. The continuing program, centered out of Ames, has subsequently identified new sources of resistance to first-brood borers, and more recently to second-brood borers (3,11).

The biochemical basis of resistance to first-brood ECB has been identified as 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA). Levels of DIMBOA are high in most seedling-stage maize plants, but these decrease as plants mature. At the mid-whorl stage of development, some lines retain high DIMBOA levels and are resistant to ECB. DIMBOA levels are low in all lines at the time of second-brood infestation; hence DIMBOA is not related to stalk-boring resistance.

Some Latin American germplasm has been screened and selected for both first- and second-brood resistance. DIMBOA is not responsible for resistance in these varieties.

Leadership for developing resistance to Southwestern corn borer, *Diatraea grandiosella,* is centered out of Mississippi State with a USDA team. Excellent progress has been obtained over the past 5 years, and a number of resistant inbred lines have been released.

Progress in breeding for resistance to corn earworm, *Heliothis zea,* has been disappointing over the years. Although important resistant mechanisms have been identified, most of these have not as yet become important in commercial hybrids. The most valuable characteristics that have contributed to the ability to raise corn in the south have been the long, tight husks and long silk channels. Husk cover is greatly affected by moisture stress and therefore is variable. Silk and kernel antibiosis factors have not proven to be useful thus far. The highest resistance to corn earworm has been found in the Mexican strain, 'Zapalote Chico'; apparently it is due to long tight husks and a growth inhibitor. However, the tight husks are agronomically undesirable in sweet corn; this limits the use of Zapalote Chico as a resistant donor for commercial varieties.

Fall armyworm is becoming a more serious pest in the southern United States. It is a limiting factor in successful production of corn in many parts of Mexico and Central and South America. Initial screening efforts for resistance have been concentrated at the Southern Grains Insect Laboratory. A number of resistant genetic materials have been reported, many with the 'Antigua' germplasm (36).

Resistance to corn rootworm, *Diabrotica* spp., has been found in lines having a high potential for root regeneration and growth despite moderate attack. The best source of resistance to corn rootworm larval feeding has been an inbred line, 'SD 10.' In addition, several moderately tolerant lines have been identified. To date however, there are few commercial hybrids carrying any measurable degree of resistance to the rootworm complex.

Rice: Although this crop is now important in five states in the United States (Louisiana, Arkansas, Mississippi, Texas, and California), there is very little being done to develop resistant varieties. Some effort is underway in Louisiana and Texas, primarily against the rice water weevil, *Lissorhoptrus oryzophilus,* which is the most serious pest in the southern states. The major thrust for breeding for insect resistance is at the International Research Institute, Manila. Resistant varieties have been released for striped rice borer, *Chilo suppressalis;* yellow rice borer, *Tryporyza incertulas;* green rice leafhopper, *Nephotettix virescens;* brown planthopper, *Nilaparvata lugens;* white-backed planthopper, *Sogatella furcifera;* rice delphacid, *Sogatodes orizicola;* rice gall midge, *Orseolia oryzae;* rice whorl maggot, *Hydrellia phillippina;* and rice stem maggot, *Chlorops oryzae.* Sources of resistance to many other major pests of rice have been identified, and breeding programs are at various stages of evolution toward released varieties.

Sorghum: Early work on breeding for resistance in the United States was centered around chinchbug, *Blissus leucopterus leucopterus.* 'Atlas,' a cultivar resistant to chinchbug, was released in the late 1930s. After the advent of sorghum hybrids, chinchbug declined in importance as a pest of sorghum. The threat to sorghum from greenbug, *Schizaphis graminum,* Biotype C, was recognized in 1968. However, resistant hybrids became commercially available by 1976. The primary resistance mechanism is tolerance, which is ecologically advantageous and increases the value of resistant sorghum as a component in pest management. The recent discovery of greenbug, Biotype E, which is not affected by the resistance to Biotype C, has necessitated the incorporation of other sources of resistance in sorghum hybrids. Fortunately, sources of resistant germplasm were available and new commercial hybrids containing resistance to Biotype E will soon be available.

The most important pest of sorghum is the dipterous sorghum midge, *Contarinia sorghicola.* The primary means of reducing midge damage in the United States is uniform regional early planting. As a result of a major team effort at Texas A&M University, good sources of resistance to this pest have been located and incorporated in advanced breeding lines. Resistant inbreds have been released to the seed industry. Ovipositional nonpreference and antibiosis are the primary mechanism of resistance. There has been some effort with the Banks spider mite, *Oligonychus pratensis,* and the corn leaf aphid, *Rhopalosiphum maidis,* in locating resistance, but this has not been utilized in breeding programs to date.

Wheat: Major programs to develop resistance in wheat to insect pests have been started throughout the world and resistant wheat varieties have been developed for protection against the Hessian fly, *Mayetiola destructor;* cereal leaf beetle, *Oulema melanopus;* and wheat stem sawfly, *Cephus cintus.* Resistance to greenbug, *Schizaphis graminum,* was set back in 1980 by the discovery of Biotype E greenbug which was able to overcome the major source of resistance that was cytogenetically transferred to wheat from rye.

In summary, wheat has the longest existing program in breeding for resistance, beginning with Hessian fly work in the 1920s and extending to the present. The use of wheat resistant to insect pests is a major control measure, with an annual value of approximately $250 million in the United States. The Hessian fly and wheat stem sawfly are controlled solely by resistant varieties, whereas the greenbug and cereal leaf beetle are also controlled by insecticides. To date, 42 wheat varieties resistant to one or more biotypes of Hessian fly have been released. Most of these varieties were grown in the United States in 1974, accounting for a total of about 20 million acres. In the same year, five varieties resistant to the wheat stem sawfly were grown on 1-1/2 million acres in the United States, providing the sole protection against this insect pest. 'Downey' wheat, the first variety developed and released that has resistance to the cereal leaf beetle, was grown in Indiana, Michigan, and Ohio for the first time in 1977. It can also be used in conjunction with parasites and chemical control.

Soybeans: Important sources of resistance have been identified to some major species of insects attacking soybeans, particularly Mexican bean leaf beetle, *Epilachna varivestris;* bollworm, *Heliothis zea;* velvet bean caterpillar, *Anticarsia gemmatalis;* soybean looper, *Pseudoplusia includens;* beet armyworm, *Spodoptera exigua;* and fall armyworm, *Spodoptera frugiperda.* While efforts are underway in North Carolina, South Carolina, Louisiana, and Illinois, no resistant varieties have been released.

INTEGRATED CONTROL SYSTEMS

Resistant varieties ideally should provide complete and permanent control of the major crop pests. However, such high levels of resistance are present in only a few crop varieties. High resistance also has the disadvantage occasionally of providing high selection pressure resulting in the development of biotypes capable of feeding on the resistant varieties.

Fortunately, high levels of resistance are not necessary for a crop variety to have value in an integrated control system. Varieties with low or moderate levels of resistance, or those that may be grown to evade pest attack, can be used to good advantage for pest suppression. The key to success lies in their incorporation into management systems involving other control measures such as regulated planting dates, early harvesting and crop residue disposal, manipulation of alternate hosts, host-free periods, and destruction of overwintering pest insects. The system devised should suppress pest numbers and conserve their natural enemies. If this is achieved, insecticides can be used more selectively and less frequently for crop protection.

Resistant varieties, even those with low and moderate levels of resistance, offer a number of advantages to an integrated control system. The reduction in pest numbers achieved through resistance is constant, cumulative, and practically without cost to the farmer. The reduction in pest numbers makes control by chemical and cultural methods easier, and the level of natural biological control required to hold pest numbers below crop-damaging levels need not be so great (1,6,14,23,32).

NATURE OF RESISTANCE

Behavioral considerations: Functional behavior, such as host selection by an insect, is composed of a sequence of simple behavioral responses. Each activity in the sequence brings the insect into a situation in which an appropriate stimulus will release the next activity. These temporal patterns of behavioral components are associated with internal drives, such as the need to oviposit or feed.

Volatile chemicals are frequently involved in orientation of insects to plants (attractants) from a distance (olfactory stimuli), but these chemicals are also known to stimulate biting, probing, and oviposition after the insect is in physical contact with the plant. The final recognition process leading to acceptance or rejection of the plant is usually mediated by nonvolatile chemicals (feeding stimulants, incitants, repellents) acting on contact chemoreceptors.

Orientation to potential host plants and the discrimination of host from nonhost requires a highly developed sensory system. Usually the insect must respond to the odor of a plant located in a stand of mixed vegetation. Specific plant odors are seldom single compounds, but are usually complexes of several volatile substances. The attraction scent of potato plants for example, is made up of a particular combination of leaf alcohols and aldehydes that are, individually, not unique to potato. The Colorado potato beetle, *Leptinotarsa decemlineata,* is attracted to the combination of compounds produced by the potato plant. Similarly, the cotton boll weevil is attracted to cotton by a complex of aromatic compounds. In other cases a single compound may be predominant in the attraction process. For example, α-pinene, one of the terpenoids produced by conifers, elicits a strong response in most conifer-inhabiting insect species, and most insects attacking cruciferous plants are strongly attracted to mustard oils. Once the insect has made physical contact with a plant, contact chemoreceptors located on the tarsae, antennae, mouthparts, or ovipositor receive stimuli related to the chemical characteristics of the plant surface. Probing is usually in response to chemical factors that act as incitants. Initial feeding and continued feeding are responses that also result from stimulants. If stimuli received on initial testing indicate an unacceptable plant, the behavior pattern is interrupted and the insect abandons the plant. Many important feeding stimulants are general nutrient substances, such as sugars and amino acids, rather than host-plant specific compounds.

Chemicals imparting resistance: Phytochemicals conveying plant resistance to insects include inorganics (e.g., selenium), primary and intermediary metabolites (e.g., citric acid, cysteine, and certain aromatic amino acids), and secondary substances such as allellochemics (e.g., alkaloids). Studies in recent years show that chemicals affecting insects fall into the following major categories: isoprenoids, acetogenins, aromatics derived from shikimic acid and acetate, alkaloids, protease inhibitors, and nonprotein amino acids and glycosides (27).

Two classes of allelochemicals of particular importance in insect-plant interactions are allomones and kairomones. Allomones are chemicals tending to confer an adaptive advantage on the producing organism (host plant), and kairomones are chemicals tending to give an adaptive advantage to the receiving organism (phytophagous insect) (35).

Isoprenoids: This group of phytochemicals has been found to be very important in affecting insect behavior and survival. It includes the full range of terpenes (i.e., from hemipterpenes through polyterpenes). Allomones have been found especially among the monoterpenes, sesquiterpenes, triterpenoids, saponins, and various steroids. Research has shown several points in regard to isoprenoids as allomones in plants. The monoterpenoids are dominant components in the volatile oils of plant species. Research findings in recent years (e.g., α-pinene and 3-carene with pine beetles, gossypol with blister beetles and boll weevil, and cucurbitacin with *Diabrotica* spp.) has shown the importance of these materials in allomonic responses to these species of insects.

Another exciting element discovered in recent years is the ability of isoprenoids from certain plants (e.g., *Pteridium aquilinum, Achyranthes* sp., *Abies balsamea,* and others containing isoprenoidal hormones) to affect insect developmental rates, metamorphosis, fecundity, and longevity.

Acetogenins: These are chemicals generated from acetate units. Acetate units have been found to have important roles in the defense chemistry of plants as components of benzoquinones, flavonoids, cerain coumarins, condensed tannins, and stilbenes. The allelochemical, juglone in hickory (*Carya* sp.), repellent to elm bark beetle, *Scolytus quadrispinosus* (10), and DIMBOA and other benzoxazolinones from *Zea mays,* repellent to ECB, are two extensively studied groups of acetogenins. Research on aceogenins as bases for plant defense is promising because many of these molecules possess unusual abilities to exchange electrons and protons with their environments. Thus they possess the attributes deemed especially important in a chemical messenger. Their extraordinary abilities enable them to function at multiple sites of action in insects.

Aromatics derived from shikimic acid and acetate: This group includes flavonoids, benzophenones, some coumarins, lignans, condensed tannins, and stilbenes. They constitute one of the more important groups of plant defense chemicals against insects.

Flavonoids have been most explored as allomones against insects. Quercetin, for example, has been shown to stimulate boll weevil development and is also one of the chemicals involved with feeding stimulation. On the other hand, Quercetin has been shown to reduce development of the pink bollworm, *Pectinophora gossypiella;* cotton bollworm, *Heliothis zea;* and cotton budworm, *Heliothis virescens.* Hedin (13) and Norris and Kogan (27) have summarized a number of other effects of the group on specific insect and mite species.

Alkaloids: About 20 percent of all vascular plants contain alkaloids. The toxic and medicinal powers of alkaloids have been known to pharmacologists since botanically based medications originated. The alkaloid nicotine in *Nicotiana* functions as an allomone against many insect species. Its unusual insecticidal powers resulted in its wide-spread agricultural use as one of the early organic pesticides, and it is still used commercially. However, despite marked toxicity to many insects, the tobacco budworm, *Manduca sexta,* copes with the nicotine in *Nicotiana* (16).

Entomological research into the roles of alkaloids in plant defense have centered primarily with the steroidal pseudoalkaloids. The best-known work is that of Kuhn and Gauhe (18) who conducted extensive studies on the role of alkaloids deterring the Colorado potato beetle, *Leptinotarsa decemlineata,* from potato plants. Major identified compounds included solanine, tomatine, and demissine; observed effects were deterrence of larval and adult feeding, and inhibition of the growth rate of larvae. Another well-known example of alkaloidal defense is that of pilocereine and lephocereine in the cactus *Lophocereus schotti.* These alkaloids repel or deter *Drosophila* spp. from using the cactus as a host plant; *D. pachea* which uses the cactus as a host, tolerates these alkaloids (15). For more information on other specific alkaloidal allomones known in plants, and species of insects involved, see Hedin et al. (13) and Kogan (16).

Protease inhibitors and nonprotein amino acids: Research into the effects of protease inhibitors on insects has concentrated on grain feeders. Lipke et al. (20) discovered that a highly acidified extract of raw soybeans contained an inhibitor of the proteolytic enzymes of *Tribolium confusum* and *Tenebrio molitor.* Applebaum and Birk (4) have demonstrated that three proteinaceous fractions from soybean strongly inhibit the growth of *T. castaneum* larvae. In addition, they isolated several proteolytic enzymes from wheat and lima beans. Walker-Simmons and Ryan (34) demonstrated that damage by the Colorado potato beetle to potato and tomato leaflets caused the release of a protease inhibitor inducting factor (PIIF) which was rapidly transported throughout the plant causing accumulation of a potent inhibitor of several proteases of both insects and microbes. The discovery of wound-induced accumulations of protease inhibitors in many plant species may open possibilities in terms of plant resistance. There may be the possibility of inducing immune reactions in plants by controlled methods not unlike the vaccination of animals.

Glycosides: Glycosides are asymmetrical mixed acetals. The sugar component may be mono-, di-, or trisaccharids. Glucose is the most commonly involved sugar. A glycone may come from any number of different biosynthetic pathways. There are more phenolic aglycones than any other type involved with affects on insects. A few specific plant glycosides or their aglycones are implicated as allomones against insects. Lichenstein et al. (19) found that the aglycone 2-phenyethyl isothiocyanate from *Brassica rapae* deterred *Drosophila melanogaster* from feeding and at higher concentrations killed the fly. However, many insects using crucifers as hosts utilize such isothiocyanates as kairomones. Sinigrin in crucifers is a feeding deterrent to the aphid, *Myzus persicae* (7). The feeding of four species of *Epicauta* was inhibited by cis-o-hydroxycinnamic acid glucoside, which apparently occurs in *Melilotus officinalis* and *M. alba* (21).

RESISTANCE CHARACTERS

Morphological (physical) resistance factors interfere physically with locomotor mechanisms, and more specifically, with the mechanisms of host selection, feeding, ingestion, digestion, mating, and oviposition, as opposed to those factors affecting the chemically mediated behavioral and metabolic processes. Much of the existing man-enhanced practical resistance in crop plants involves morphological factors.

The primary morphological factors studied in connection with effects on insects are thickening of cell walls, increased toughness of tissues, proliferation of wounded tissues, solidness and other characteristics of stems, trichomes (hairs), accumulation of surface waxes, incorporation of silica, and anatomical adaptations of nonspecialized organs and protective structures. Of these, solidness and other characteristics of stems and trichomes have been used most extensively in breeding for insect resistance.

Solidness and other stem characteristics: There are numerous examples of slight or profound changes in a stem feature that decrease its fitness for insect attack. Resistance to certain stem borers is related to the nature of the stem tissues. Solid stems are responsible for the resistance of several wheat varieties to the wheat stem sawfly, *Cephus cinctus.* On sugarcane the denticles on the midrib of leaves, number of vascular bundles, lignification of cell walls, and number of layers of sclerenchymatous cells play important roles in the resistance to first and second instars of *Diatraea saccharalis.* As older larvae bore into the stalk, hardness of the rind and fiber content of stalks are key factors of resistance (2,22). In the hard woody stems of *Cucurbita* spp. the closely packed, tough, vascular bundles are the main resistance factors against the squash vine borer, *Melittia cucurbita.*

Trichomes: Trichomes are unicellular or multicellular outgrowths from the epidermis of leaves, shoots, and roots. The collective trichome cover of the plant surface is called pubescence. Insect species respond differently to the presence of plant hairs. Pubescence as a resistance factor interferes with insect oviposition, attachment of eggs to the plant, feeding, and ingestion. Glaborous forms of plants may be more resistant to some species (e.g., bollworm on cotton and soybeans). The mechanical effects of trichomes or pubescence on insects depends on density, erectness, length, and shape. In some cases trichomes possess associated glands that exude secondary plant metabolites that may be toxic to insects or serve as a sticky exudate to trap certain species. In the case of sucking insects like aphids and leafhoppers, trichomes may prevent the proboscis from reaching the mesophyll or the vascular bundles.

Pubescence in wheat greatly reduces cereal leaf beetle oviposition and has been used as the principle resistant factor in the development of varieties resistant to this serious pest.

Certain varieties of bean plants possess hooked trichomes, and leafhoppers and other soft-bodied arthropods such as aphids are impaled on these hooks. The efficacy of these hair defenses was more fully revealed by the use of the electron microscope (31). Gibson (9) observed that when cell walls of trichomes on three species of wild potatoes (*Solanum polydemium, S. berthaultii,* and *S. tariyense*) were ruptured by contact with the aphids *Myzus persicae* or *Macrosiphum euphorbiae,* the exudate hardened around the aphids' legs causing death.

The action of glandular hairs demonstrates the close interaction of physical and biochemical plant defenses to insects. Although repellent to many insects, glandular hairs serve as cues in host-plant finding for a few species that have evolved the mechanisms to utilize such resources. The diverse arthropod fauna associated with odorous pubescent plants is evidence of such adaptation.

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