PLANT-INSECT BEHAVIORAL STUDIES:
EXAMPLES WITH HELIOTHIS AND MANDUCA SPECIES

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ABSTRACT

A thorough understanding of the behavioral repertoire of an insect pest species is a key element in the establishment of a successful program for the development of plant cultivars resistant to insect attack. Behavioral components are especially important during the host finding and host acceptance phases of a pest’s biology. The behavior of an insect pest is affected by the physical and chemical characteristics of its potential host plant. Breeders may modify plant characteristics that affect the behavior of pest species so they are less damaging. Avoidance or rejection of an unsuitable plant as food or as an oviposition substrate represents one of the primary modalities, nonpreference or antixenosis, of plant resistance to insects. The behavioral adaptations of insects in relation to their host plants and the impact this has on host plant resistance are reviewed here. In particular, the behaviors of the polyphagous Heliothis spp. (Lepidoptera: No-
tuidae) and the oligophagous *Manduca* spp. (Lepidoptera: Sphingidae) are emphasized, as these are two important pest complexes in the southeastern United States for which insect-resistant germplasm has been developed.

**RESUMEN**

Un entendimiento completo del repertorio del comportamiento de una especie de plaga de insecto es un elemento clave en el establecimiento de un programa exitoso para el desarrollo de variedades de plantas resistentes a ataques de plagas de insectos. Los componentes de comportamiento son especialmente importante durante la fase de la búsqueda del hospedero y la aceptación de la biología de la plaga. El comportamiento de una plaga de insectos es afectada por las características físicas y químicas de la potencial planta hospedera. Estas características pueden modificar las características de la planta que afectan el comportamiento de una especie de plaga para que sean menos dañinas. El evitar o rechazar una planta no adecuada como alimento o como un substrato de oviposición representa una de las modalidades primarias, no-preferencia o antixenosis, de resistencia de plantas a insectos. Se revisan aquí las adaptaciones de comportamiento de insectos en relación a sus plantas hospederas y su impacto en las plantas hospederas. En particular se le da énfasis al comportamiento de las especies polífagas *Heliothis* (Lepidoptera: Noctuidae) y a las especies olífagas *Manduca* (Lepidoptera: Sphingidae), puesto que éstas son dos complejos de especies muy importantes en el sureste de los Estados Unidos para las cuales se ha desarrollado germoplasma resistente a insectos.

An intimate understanding of the behavior of a pest species is a basic component of a breeding program for the development of insect-resistant crop cultivars (Painter 1951). Behaviors associated with host finding, host recognition, and host acceptance are especially important, as they determine whether a plant is initially attacked by an insect pest. There are also behavioral components associated with an insect determining the host's suitability as an oviposition substrate or as a food source. The physical and chemical interactions between an insect and its host plant help determine the behavior of that pest. Thus, we are often concerned with modifying various physical or chemical characteristics of the plant in order to alter an insect's behavior to less destructive ends. Also our experimental procedures for evaluating insect-resistant germplasm are almost always dictated by some portion of the behavioral repertoires of insects. Also included in their behavioral repertoires are activities that do not directly affect host finding or host acceptance, such as mating activities, dispersal flights, avoidance of adverse weather conditions or predators, and construction of pupal cells. However, these activities may interrupt host finding or host recognition processes, or they may be necessary to put the insect in the proper physiological state before orientation behaviors can occur. Thus, we should not lose sight of the fact that we must deal with the insect as a whole, and not become excessively concerned over one portion of its behavior.

This paper reviews some examples of insect-host plant interactions that affect insect behavior, and relates how these interactions may impact programs for breeding plants resistant to insect pests. This discussion will primarily be concerned with examples from the polyphagous *Heliothis* spp. and the oligophagous *Manduca* spp. because: (1) these insects are major pests of field crops in the southeastern United States; (2) insect-resistance germplasm has been developed against these species; and (3) they provide convenient examples that easily illustrate certain principles.

**IMPORTANCE OF HELIOTHIS AND MANDUCA SPECIES**

Worldwide, *Heliothis armigera* (Hubner), *H. virescens* (F.) and *H. zea* (Boddie) are the most damaging *Heliothis* species (Reed & Pawar 1982, Fitt 1989). Other *Heliothis*
species are of lesser importance due to restricted host ranges, limited geographic distributions, or inconsistent damaging populations (Pitt, 1989). The two economically important Heliobia species in the United States (H. zea and H. virescens) are polyphagous, and they attack several families of plants including many cultivated crops. In the southeastern United States, crops damaged by these two pests include corn, cotton, tobacco, soybeans, peanuts, tomatoes, and edible peas and beans (Neunzig 1969, Schneider et al. 1986, Pitt 1989).

There are two economically important Manduca species in North America. Manduca sexta (L.), the tobacco hornworm, is more southern in distribution than the tomato hornworm, Manduca quinquemaculata (Haworth) (Madden & Chamberlin 1945). However, their geographic ranges overlap widely, and in the middle Atlantic States both species commonly occur. Hornworms are economically important only on tobacco and tomato in the United States.

FACTORS AFFECTING HOST PLANT SELECTION

Host plant location and acceptance by an insect involves a sequence of encounters that elicit either positive or negative responses. The term “encounter” is used here as the initial reception of sensory information (Miller & Strickler 1984, Singer 1986). Acceptance or rejection of a host plant depends on the interactions of both the external host stimuli and the internal state of the insect (Dethier 1982). Olfactory, gustatory, mechanical, or visual receptors transmit sensory inputs to the central nervous system (CNS). These contain both positive and negative information about a plant, and its acceptability is in part a function of the ratio of positive to negative factors. The insect’s response is further modulated by the summation of positive and negative internal inputs (Dethier 1982).

Although plant discrimination by specialist insects may be mediated by specific key stimuli (Stadler 1986, Visser 1986), it has been shown that for both specialist and generalist herbivores of cabbage, the decision to reject or accept a plant is not uniquely based on a few key stimuli, but rather on a chemical image of a large variety of stimulatory and inhibitory plant chemicals acting together (Sehon et al. 1986). This concept of a chemical “Gestalt” of a plant that constitutes the signal that is perceived by insect herbivores is now widely accepted (Dethier 1982, Stadler 1983). However, specific repellent or deterrent compounds from avoided plants may be important for host discrimination by generalist herbivores (highly polyphagous species) (Jermy & Szentesi 1975).

Insect-host plant relationships are affected by both abiotic factors, and by biotic characteristics of the plant (Kogan 1975). Abiotic factors include the time of day, light intensity, photoperiod, soil conditions, and weather phenomena such as temperature, wind speed, relative humidity, and barometric pressure (Tingey and Singh 1980). All of these factors must be considered when designing bioassays for measuring insect behaviors. Just as important are the general characteristics of the plants to be evaluated. Besides the genetic considerations of a breeding program (Gallun and Khush 1980), the plant must be in the proper phenological stage, and growing conditions should be regulated to produce healthy plants. The visual, mechanical, and chemical cues provided by such leaf characteristics as size, color, shape, trichome density, and cuticular chemistry may affect the behavior of the insect.

Insects are affected throughout their lives by chemicals in the environment. Chemical diversity among plants is the principal factor underlying host specificity in phytophagous insects (Schoonhoven 1981, Visser 1983). Chemical cues mediate many aspects of insect behavior including host finding, host acceptance, avoidance of danger, and mate location. Chemical nutrients and secondary plant components also determine
the suitability of a particular host plant for development and survival. Besides chemicals, other environmental stimuli such as temperature, humidity, visual cues, and tactile stimuli also contribute to the total sensory input to the insect's central nervous system.

Behaviors such as host finding and host selection consist of sequences of simpler behavioral responses (Kogan 1975, Beek & Schoonhoven 1980). The sequential nature of these behaviors is significant since each activity in the sequence conditions the insect for the next behavioral state, which is achieved when the appropriate stimuli are received. When the sequence is broken because the releasing stimulus for the next behavior is not received, the insect often reverts to earlier behaviors in the sequence (Miller & Stickler 1984, Ramaswamy 1988).

NONPREFERENCE CONSIDERATIONS

Of Painter's (1951) three general modalities of resistance, nonpreference (or antixenosis [Kogan and Ortman 1978]) is most closely associated with the behavior of insects (Smith 1989). Such insect behaviors as non-recognition, avoidance, or rejection of a plant may all be viewed as nonpreference responses. Several examples of behavioral variations that encompass nonpreference are cited here. First, a plant may not be attacked simply because pests are unable to find it. Although certain pseudoresistance phenomena (as defined by Painter 1951) may sometimes cause a plant to remain pest-free, insects may also fail to locate plants because they lack certain attractant qualities found in susceptible plants. For example, a resistant cultivar may have a slightly different shape, color, or odor than a susceptible one, and thus it may not be as attractive. Plants which are not recognized by ovipositing moths, may or may not support larval growth; and they have been termed acceptable non-hosts or unacceptable non-hosts, respectively (de Boer & Hanson 1984).

Secondly, a resistant plant may be just as attractive over a distance as a susceptible cultivar but it lacks specific stimuli that cause it to be recognized or accepted for oviposition or feeding. These characteristics are often determined upon contact. For example, moths of *H. virescens* are stimulated to lay eggs on commercial tobacco cultivars due to the proper physical texture of the leaf and due to contact ovipositional stimulants (Jackson et al. 1983, 1984, 1986, Ramaswamy 1988). Thus, the near absence of cuticular constituents normally found on commercial tobacco cultivars causes the tobacco introduction (TI) 1112 to be resistant to oviposition by *H. virescens* due to nonpreference (Jackson et al. 1983, 1984). Female moths of *H. virescens* may land on TI 1112, but they apparently do not recognize it as a suitable host, and they do not lay as many eggs on it as they do on a typical flue-cured tobacco cultivar such as NC 2326 (Jackson et al. 1983).

A third example of nonpreference has to do with insects rejecting a host due to specific deterrent or repellent plant characteristics. Many non-host plant species have chemical repellents or deterrents that prevent oviposition or feeding by lepidopterans (Schoonhoven 1972, 1982, Jermy & Scsontei 1978, Renwick & Radke 1981, Tingle & Mitchell 1984). The host ranges of larvae of *Heliothis* spp. and *Manduca* spp. are broader than the actual host ranges determined by ovipositing moths. This phenomenon is not unusual for lepidopterans, and it is likely that ecological pressures other than merely feeding suitability restrict their host ranges (Schneider et al. 1980).

The remainder of this paper will consider the behavioral processes of insect herbivores as they occur in sequence from hatching or eclosion through host utilization. Included in this discussion will be the host finding, host recognition and acceptance, and host suitability phases of an insect's behavior.
HOST FINDING

In most insect pest species the host finding process is not entirely random. Also, the immature stages of most insect pests are incapable of long-range movement, so they seldom move from a host plant until fully developed. Thus, it is crucial that adult females place their eggs (or nymphs) on or near a suitable host plant. For example, neonate larvae of Heliothis and Manduca spp. do not wander far from their egg shells before they begin to feed. If young larvae try to leave a plant, their chances of finding another suitable host are slim. Larvae of Manduca spp. only leave plants under conditions of severe crowding, and then usually as fifth instars (McFadden 1968).

An insect must be in the proper developmental, physiological and behavioral state, and environmental conditions must be suitable, before that insect will initiate searching for a host plant. Theoretically, cross wind flight is an efficient appetitive searching strategy for flying insects, since it increases the probability of encountering a windborne host odor (Cardé 1984). However, this may apply more to male orientation to female-produced pheromones than to host plant finding. Downwind flight is a more efficient way of searching for plants because insects travel for longer distances, and thus they have a higher probability of encountering suitable hosts. This might account for the daily short-range, downwind flights of Heliothis adults before they feed (Lingren & Wolf 1982). Unfortunately, appetitive searching behavior of insects has not been extensively studied (Cardé 1984).

Relatively little is known about how insects locate field crops over a long distance. Some pests, such as aphids, are passively carried to fields by the wind. Landing by aphids is fairly nonspecific with orientation only to color and light reflections (Van Emden et al. 1969). Host discrimination takes place after alate aphids have probed a plant, and they will leave unacceptable hosts. Many other insect species, such as lepidopteran moths, use air-borne chemicals and visual cues to orient to plants (Miller and Strickler 1984).

Olfactory, visual, and contact stimuli may all be utilized by ovipositing female moths during the orientation process. Olfactory and visual cues are used for orientation to the plant surface, but contact chemoreception and mechanoreception are typically necessary before eggs are deposited (Ramawamy 1988). Thus, behavioral experiments must be carefully designed in order to determine the exact role plant-produced chemicals have on ovipositional behavior. A particular chemical may act as an attractant, repellent, arrestant, excitant, stimulant, deterrent, or have some other function (Singh 1986).

Orientation of flying insects to volatiles has been studied most extensively with regard to the response of moths to pheromones (Cardé 1984), but many of the same principles apply to orientation by insect herbivores to plant-produced chemicals (Finch 1986). Volatiles travel downwind from point sources in filamentous plumes whose concentrations and shapes are determined by such factors as the amount of chemical released, wind speed, height of the odor source above the ground, turbulent diffusion, and interference caused by objects in the pathway. The concentration gradient of chemicals in an odor plume varies comparatively little along the windward axis, but has rather sharp variation laterally (Elkinton & Cardé 1984). Within a few meters from an odor source the filament becomes a chaotic tangle, and insects usually encounter pulses of the volatiles in various dilutions (Murlis & Jones 1981, Kramer 1986).

Insects probably do not orient toward point sources of odors using concentration gradients (Kramer 1986). This is especially true for plant-produced volatiles in the field that do not emanate from point-sources. Instead, moths orient upwind toward odor sources using an optomotor anemotactic mechanism in conjunction with counterturning movements which may be either self-steered (Kennedy 1986) or provoked by transverse chemo-klinotaxis (Cardé & Carlton 1985). Other behavioral mechanisms for the chemical orientation of insects to plants have been proposed, but the optomotor anemotactic
mechanism is supported by most data and is widely accepted (Cardé 1984). Some insects orient by visual rather than by chemical cues, and there are examples of plants becoming resistant to pests after the color of their foliage was genetically altered (Smith 1989). Prokopy (1986) also stressed the importance of the interactions between visual and olfactory stimuli in insect orientation to resources.

Yamamoto et al. (1969) proposed a generalized scheme of oviposition by moths of *M. sexta*. They divided the orientation to plants into a non-discriminatory approach in which visual and olfactory cues are utilized, and a discriminatory landing utilizing olfactory stimuli. They also suggested that separate kairomones were involved in the attraction and ovipositional phases. Contact chemoreception is then required to elicit egg deposition.

Chemoreception by insects may be divided into contact chemoreception (or gustation) and olfaction, based on the characteristics of the stimuli, the transport mechanism, and the morphology of the sense organs (Stadler 1984). However, the distinction between olfaction and gustation may sometimes become unclear, especially when insects enter the boundary layer of a leaf where concentrations of plant volatiles may be high. For example, the “gustatory” receptor cells of larvae of *M. sexta* respond to olfactory cues of their host plants at close range (Städler & Hansson 1975). For the most part, however, long-range olfaction and contact chemoreception are quite distinct.

It is likely that separate plant-produced kairomones mediate such adult behaviors as orientation to food sources, orientation to oviposition substrata, initiation and continuation of feeding, and stimulation of oviposition. In general, oviposition stimulants and deterrents are different from chemicals that elicit or inhibit feeding responses of larvae (Renwick 1983). For example, contact ovipositional stimulants can be separated from larval feeding stimulants for *M. sexta* from extracts of dried tomato leaves and horseradish (Yamamoto & Fraenkel 1960a, Bordner et al. 1983). Alcohol or water extracts and steam distillates from fresh or dried leaves of several solanaceous species elicit strong ovipositional activity by moths of *M. sexta* (Yamamoto & Fraenkel 1960a, Yamamoto et al. 1969). Electrosensorygram (EAG) analyses showed that the steam distillates stimulated antennal chemoreceptors of *M. sexta*. Further fractionation by gas chromatography yielded several isolates with EAG activity, but ovipositional behavior with individual components was lost (Tichenor & Seigler 1980). These tests indicate that moths are attracted by specific mixtures of components and not by individual compounds.

Female moths of *Heliothis* spp. prefer to lay eggs on or near the flowering or fruiting portions of many of their host plants, but in the absence of flowers, vegetative structures are chosen (Hardwick 1965). For example, eggs may be found on all portions of nonflowering tobacco plants, but they are concentrated on the first few leaves below the leaf bud (Jackson et al. 1983).

The upwind orientation of moths of *H. virescens* toward nectar sources and ovipositional sites suggests the presence of air-borne feeding and oviposition attractants being emitted by the plants (Lingren & Wolf 1982). *Heliothis subflexa* (Gueneé) exhibits positive flight responses to odors extracted from the leaves of its host, ground cherry, *Physalis* spp. (Tingle et al. 1989). Mitchell et al. (1990) reported a positive anemotactic response by female moths of *H. virescens* toward volatile materials extracted from the leaves of tobacco, cumin, and Florida beggarweed, *Desmodium tortuosum* (Swartz) de Candolle, a wild host plant of *Heliothis* spp. In contrast, Ramaswamy (1988) was unable to find any odor-mediated, upwind orientation by female moths of *H. virescens* to either cotton (a host) or ground cherry (a nonhost). He argues that highly polyphagous insects such as *H. virescens* and *H. zea* do not depend on olfactory cues for host location. Instead, he suggests that they orient more randomly by upwind anemotaxis to nonspecific olfactory cues.
HOST RECOGNITION AND ACCEPTANCE

Once an insect locates a plant using visual and olfactory cues, contact with the plant surface is usually essential before feeding or oviposition is initiated. Both contact chemoreceptors and mechanoreceptors are used to evaluate the plant surface. Many phytophagous insects choose their host plants without perception of the leaf interior. This is certainly the case with many lepidopteran pests whose adult females lay eggs on undamaged plants. It is unlikely that the leaf surface provides much information about the nutritional quality of the plant. Lepidopteran pests more likely utilize physical characteristics and secondary plant metabolites (stimulants or deterrents) to identify potential hosts for oviposition.

The initiation of feeding (tasting) also is mediated by stimulatory cues from the leaf surface, but the continuation of feeding depends on a sensory analysis of the consumed material. Both nutrients and secondary plant compounds are important in host identification by chewing and by sucking insects (Schoonhoven 1981, 1987).

Plant compounds may have immediate effects on insect behavior or they may have delayed actions and affect physiological processes. Plant chemicals may adversely affect insects by being directly toxic without affecting feeding, or by altering behavior and reducing food intake. However, the results may be the same with each of these modalities, and that is reduced growth or death of the insect. It is not easy to determine whether a plant compound is a feeding deterrent and/or a toxin, thus, deterrence and toxicity must be measured separately to determine which caused an insect's demise (Bernays 1982). Some compounds may have more than one effect on insects. For example, Chinaberry extract was reported as both a feeding deterrent and growth inhibitor for H. zea (McMillian et al. 1969). Pyrethroids have repellent, antifeedant, and toxic properties (Ruscoe 1977). Azadirachtin from the Neem tree acts as a feeding deterrent and an insect growth regulator that affects a wide range of insects including M. sexta and Heliothis spp. (Schulte et al. 1985, Barnby & Klocke 1987).

Lepidopteran larvae normally first encounter an undamaged plant surface after hatching, and they must recognize that surface as a host before feeding is initiated. Hatching larvae may simply refuse to feed on plants selected by their mothers, due to the lack of necessary sensory inputs needed to identify the plant, or due to the presence of specific feeding deterrents. Larvae of M. sexta have olfactory and gustatory receptors, which are both used to discriminate hosts (Hanson & Dethier 1973). The stimulation of either receptor may result in normal discrimination among acceptable hosts, but gustatory reception alone appears to play a role in rejecting unacceptable plants (Hanson & de Boer 1986).

Lepidopteran larvae use their subtle sense of taste to select the best part of the plant and to avoid high concentrations of deterrents. When a larva tastes a food source, receptor cells are stimulated and coded by the CNS. Each cell possesses its own sensitivity spectrum, and each plant tasted evokes a unique overall response pattern in these cells. These external stimuli are weighed by the CNS against internal satiety signals (i.e., stretch receptors in the alimentary canal) and also against the general physiological state of the insect that includes feedback from nutritional factors, nutritional deficiencies, and toxins (Schoonhoven 1987). When both olfactory and gustatory chemoreceptors are removed by amputation of the antennae and maxillae, tobacco hornworm larvae will feed on plants normally rejected (Waldbauer & Fraenkel 1961).

Both polar and nonpolar compounds stimulate feeding by larvae of M. sexta (Bordner et al. 1983, de Boer and Hanson 1988). Extracts, from leaves of tomato, tobacco, and jimson weed, when applied to nonhost plants or to paraffin sheets, elicit feeding responses by hornworm larvae (Morgan & Crumb 1928). An active glycosidic substance isolated from a crude ethanol extract of tomato leaf powder, in combination with various sugars, is necessary to elicit maximal feeding by hornworm larvae on agar diets.
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(Yamamoto & Fraenkel 1960b). This illustrates the importance of both feeding stimulants and nutritional factors in mediating the feeding response of these insects.

Yamamoto & Fraenkel (1960a) first demonstrated the induction of a host preference as the result of a prior feeding experience for hornworm larvae. As early as the second instar, larvae prefer to feed on host plants on which they had previously fed. Host plant induction for M. sexta is chemically based (Stadler & Hanson 1976).

Moths of Heliothis spp. prefer to oviposit on pubescent rather than smooth surfaces (Callahan 1957). Even in no-choice situations, few eggs are laid on cotton, corn, tobacco, or tomatoes, with smooth leaves (Robinson et al. 1980, Jackson et al. 1988). The surface texture is probably determined by mechanoreceptors on the tarsi and especially on the ovipositor. Proper leaf moisture is also required by moths of H. virescens for oviposition (Navasero & Ramaswamy 1990).

Ramaswamy (1988) presented an ethographic representation of moth ovipositional behavior using H. virescens as a model. Visual, tactile, olfactory, and contact chemosensory cues are all involved in the host finding and host acceptance processes. Oviposition occurs as a series of 3 - 6 "major bouts" each consisting of 8 - 20 "minor bouts" where moths lay 5 - 10 eggs. Between bouts, moths fly from plant to plant and/or rest. Moths rely primarily on contact chemosensory and mechanosensory information and not olfactory or visual information for close-range discrimination of host plants (Ramaswamy 1988, 1990, Ramaswamy et al. 1987).

After landing on a plant surface, moths of tobacco budworms exhibit "wing fanning while walking" followed by "abdomen bending", "dragging of the ovipositor", then egg laying. Other behaviors observed include "antennal movement", "wing buzzing", and periods of inactivity. Walking over the plant surface, antennal tapping, and ovipositor dragging all bring sensilla in contact with the plant surface, and provide moths with sensory information (Ramaswamy et al. 1987). On inanimate surfaces, moths do not exhibit "ovipositor dragging" before laying eggs, and they have more "no egg" (non-oviposition) bouts. Cage screens do not provide appropriate chemical ovipositional cues, but because screens provide acceptable tactile cues and they lack ovipositional deterrents, some Heliothis eggs are typically laid on them, especially in the absence of more suitable plant substrata (Ramaswamy 1988, 1990). The repetition of behavior probably influences the internal state of the insect and lessens the intensity of external cues necessary to elicit oviposition. The ovipositor drag observed for females on plant surfaces is utilized by the female to get a final sensory reconfirmation of the suitability of the leaf (Ramaswamy 1988, 1990).

In paired choice tests with a typical flue-cured tobacco, NC 2326, less than 25% of the eggs from H. virescens are deposited on TI 1112 in small field cages (Jackson et al. 1983). Commercial tobacco cultivars have glandular trichomes that secrete exudates, whereas TI 1112 has simple trichomes that lack glands and the trichome exudates. Certain components of trichome exudates from commercial tobaccos, especially dianthrienediols, dianthrienediols, and succrose esters, are ovipositional stimulants (Jackson et al. 1986, 1988). TI 1112 is not oviposited on to the same degree as NC 2326 due to its near absence of ovipositional stimulants found on the commercial tobacco cultivar. Thus, resistance in TI 1112 to tobacco budworms is due, in part, to ovipositional nonpreference related to the near absence of the ovipositional stimulants from trichome exudates.

Oviposition by H. virescens on TI 1112 is somewhat analogous to oviposition by them on cage screen as described by Ramaswamy (1988, 1990). TI 1112 has simple trichomes, and thus the proper tactile cues are present and there are no chemical deterrents, but ovipositional stimulants are nearly absent. Whole leaf washes from 6-week-old flue-cured tobacco stimulate oviposition by tobacco budworms when sprayed on TI 1112 (Jackson et al. 1984).

Evidence that dianthrienediols are perceived by adult females of H. virescens upon contact was gathered from a series of experiments (Jackson et al. 1989) using I-35, a
glandless breeding line developed from TI 1112 (Miles et al. 1980). In one experiment, duvatrienediols were sprayed onto whole I-35 plants, and two treated plants were bioassayed against two unsprayed I-35 plants in field cages. In another experiment, duvatrienediols were applied to every other leaf of four plants, and these were bioassayed in a no-choice test. Interestingly, the same percentage of eggs (ca. 65%) was laid on the duvatrienediol-treated leaf surfaces regardless of the treatment, indicating that the close proximity of a treated leaf does not increase oviposition onto an untreated leaf (Jackson et al. 1989). Similarly, the infestation levels of Heliothis spp. and Manduca spp. on NC 2326 and TI 1112 in 1000-plant blocks in the field were the same whether the plants were in pure stands of each tobacco type, or whether every other plant type was alternated within rows (Jackson et al. 1988).

Tingle & Mitchell (1984, 1986) found ovipositional deterrents for moths of H. virescens from aqueous extracts of several nonhost plant species. Deterrent compounds may prevent Heliothis spp. from ovipositing on these plants in the wild. In generalist species such as Heliothis, the acceptance of a host plant for oviposition is governed to a large extent by the absence of deterrents (Renwick 1983, Ramaswamy 1988).

Nonpreferred plant species may have deterrent chemicals that prevent moths from ovipositing on them, but that cause no harm to larvae feeding on that species. In the field, moths of M. sexta oviposited exclusively on solanaceous host plants (Yamamoto & Fraenkel 1960c). In the laboratory, however, they oviposit on Petunia, which is toxic to their larvae, and on Nicandra physalodes (L.) Persoon, which is repellent to their larvae (Yamamoto & Fraenkel 1960c, Thurston 1970, Dethier & Yost 1979). In both laboratory and field experiments, females preferred to oviposit on tomato over several other solanaceous species, including tobacco (Yamamoto & Fraenkel 1960b,c). However, ovipositional preferences by Manduca spp. for host plants appear to be regionalized and dependent on the predominantly available host plant species. In areas where tobacco is widely grown, it may be the preferred host (Madden & Chamberlain 1945).

**Host Suitability**

It is often difficult to determine whether a larva dies from starvation because it rejects a plant as unsuitable (a behavioral response) or whether it accepts that plant and dies due to some antibiotic factor (a physiological response). This difficulty is especially acute with first instar larvae that hatch directly on undamaged plants. This is further complicated by the fact that larvae will sometimes initiate feeding, but consume very little before moving on. Do such larvae die of starvation or do they receive a lethal dose of a plant allelochemical? Antibiotic factors also include physical plant characteristics that entrap or injure insects as well as allelochemicals that poison insects, offset their development, or reduce digestibility of their food. For example, some tobaccos, such as TI 163 and TI 165, have high levels of cuticular durance diterpenes and sucrose esters, and they are very susceptible to oviposition by H. virescens (Jackson et al. 1988). However, poor survival of larvae results in little damage to these tobaccos in the field (Johnson & Severson 1984). This resistance is due to both feeding nonpreference and antibiotic factors. Feeding preference tests showed that newly hatched, 4-, 7-, and 10-day old larvae preferred NC 2326 over TI 165. Neonate larvae will initiate feeding on TI 165, but they do not feed normally and they often move to other portions of the leaf. Methanol-water soluble fractions from leaf extracts from both NC 2326 and TI 165 pipetted onto artificial diet were also toxic to first instars of H. virescens (Severson et al. 1985).

Sticky trichome exudates may be a physical deterrent or an antibiotic factor that prevents small larvae or nymphs from becoming established by entangling them on the leaf surface or by gluing their mouthparts shut (Duffy 1988). Extremely villous surfaces may also limit establishment by small insects.
Although some toxic allelochemicals may be perceived before food is ingested and cause it to be rejected (feeding deterrents), others apparently are not detected; or if they are detected they do not deter feeding. Their deterrence may not be apparent until feeding is initiated or it may be hidden by counteracting feeding stimulants. Insects may therefore ingest lethal or sublethal doses of secondary plant compounds.

Waldbauer et al. (1984) proposed that insects can, to varying degrees, select a favorable nutrient balance from their natural foods by consuming different plant structures that vary in their nutritive values. Larvae of *H. zea* can select an optimal nutrient balance from two nutritionally deficient diets, one lacking only casein and one lacking only sucrose. Larvae regulate their nutrient balance by switching back and forth between diets and by varying the length of feeding bouts on each one. In this fashion, larvae consume both diets until they reach a 80:20 ratio of casein:sucrose, which is the optimal ratio of these nutrients for larval growth (Waldbauer et al. 1984, Cohen et al. 1987).

Many insects optimize their intakes of protein. Given the opportunity, larvae of *Heliotris* spp. will feed on the protein-rich fruiting structures or seeds of several crops, and they selectively feed on different plant parts of tomato, cotton, corn, and tobacco (Neunzig 1969). However, this may be due to the influence of environmental factors, escape from predators, or the avoidance of secondary plant compounds, rather than to nutrient self-selection. But, at least for fifth instar *H. zea* feeding on corn, larvae are able to increase their intake of protein-rich germ over carbohydrate-rich endosperm (Cohen et al. 1988). Larvae also regulate the amount of food eaten to provide adequate nutritional requirements. Insects may also compensate for a deterioration in food quality (such as leaf senescence) by increasing their consumption (Slansky 1981).

**Conclusions**

Breeding programs for the development of insect-resistant crop cultivars typically involve the efforts of scientists from several disciplines, including plant breeders, geneticists, chemists, ecologists, and entomologists. The primary roles of entomologists in these programs are to identify sources of resistant germplasm and to determine the modalities and mechanisms of resistance to insect pests. These tasks are achieved only after the biologies of the pest species are thoroughly studied. To completely understand the mechanism of resistance, an entomologist must understand the behavior of the pest and the interactions between the plant and the insect.

Understanding insect behavior is an important element in a program for breeding pest-resistant cultivars, because genetic alterations in the physical or chemical characteristics of a plant may alter the behavior of pests and thus reduce the plant's susceptibility to insect attack. This paper has reviewed insect-plant interactions that affect the host finding, host recognition, host acceptance, and host utilization behaviors of certain lepidopteran pests. Breeders can alter plant characteristics to make a cultivar less attractive over a distance or to make it less recognizable or acceptable as an oviposition substrate or food source once insects have found it.

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