INSECT NUTRITIONAL ECOLOGY AS A BASIS FOR STUDYING HOST PLANT RESISTANCE

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ABSTRACT

The links between food attributes, food consumption and utilization, and subsequent insect performance are a primary focus of insect nutritional ecology. Development of effective host plant resistance (HPR) tactics requires an understanding of these links to successfully manipulate insect pest performance. Thus, the principles of insect nutritional ecology provide a logical basis for research in HPR. Nutritional, allelochemical and morphological attributes of crop plants may be altered through selective breeding, biotechnology and cultural practices to affect target pest biochemistry, physiology and behavior, including food consumption, digestion and absorption, conversion to biomass, metabolism, detoxication, sequestration and excretion. These actions are designed to reduce crop damage by deleteriously affecting insect performance; lowered consumption, slowed growth and reduced weight gain increase mortality and decrease reproduction in survivors. Responses by the target pest (e.g., detoxication enzyme induction and increased food consumption) may act to counter certain HPR tactics, but additional tactics may derive from manipulating these responses. Use of a single plant attribute to cause heavy mortality associated with a genetically simple mechanism in the target insect (e.g., an allelochemical toxin in the plant acting analogous to a synthetic insecticide applied to the crop), is likely to lead to relatively rapid evolution of resistance in the pest population to the HPR tactic. A better strategy for maintaining long-term effectiveness of resistant crop varieties (i.e., slowing the development of resistance in the target pests to our HPR efforts) should probably involve multiple HPR tactics, especially if deployed within a genetically diverse crop variety (such that the plants in a crop field differ in the extent of expression of the various attributes serving as resistance factors) and/or by alternating in subsequent plantings crop varieties manifesting different resistance factors. Also, HPR tactics should be used which require genetically complex alterations in physiology and behavior for an insect to evolve resistance.

RESUMEN

El eslabón entre los atributos de alimentos, consumo de comida y utilización, y el subsecuente comportamiento del insecto, son el foco principal de la ecología nutricional del insecto. El desarrollo de tácticas efectivas de un programa de resistencia de plantas hospederas requiere un entendimiento de estos calabazos para manipular con éxito el comportamiento de la plaga de insecto. De aquí que los principios de la ecología nutricional de insectos provee una base lógica para hacer investigaciones sobre resistencia de plantas hospederas. Atributos nutricionales, alleloquímicos y morfológicos de plantas de cultivo pueden ser alterados por fitomejoramiento selectivo, la biotecnología o por prácticas culturales que afectan la bioquímica, la fisiología y el comportamiento, incluyendo el consumo de alimentos, la digestión, y la absorción, la conversión a masa biológica, el metabolismo, detoxificación, reducción y excreción, de la plaga señalada. Estas acciones están diseñadas para reducir los daños al cultivo por la acción dañina al comportamiento del insecto; el consumo menor, el crecimiento retardado y el reducido aumento de peso, aumenta la mortalidad y disminuye la reproducción en los sobrevivientes. La reacción de la plaga escogida (tal como la inducción de enzimas detoxicantes y el aumento del consumo de alimentos) pueden actuar para contrarrestar ciertas tácticas de resistencia de plantas hospederas, pero se pudieran derivar otras
tácticas manipulando esas reacciones. El uso de un solo atributo de la planta que cause una gran mortandad asociada con un mecanismo genético simple en el insecto escogido (tal como una toxina aleloquímica en la planta que actúa análoga a un insecticida sintético aplicado al cultivo), es probable que lleve a una evolución rápida el desarrollo de resistencia en la población de la plaga hacia la táctica de resistencia de planta hospedera. Una estrategia mejor para mantener una efectividad más duradera de las variedades resistentes (tal como demorando el desarrollo de resistencia de la plaga escogida como blanco de nuestros esfuerzos en la resistencia de plantas hospedadoras) probablemente deben de incluir varias tácticas de resistencia de plantas hospedadoras, especialmente si es desplegada dentro de una variedad genéticamente diversa (tal como las plantas en el campo difieren en la expresión de los varios atributos que sirven como factores de resistencia) y/o alterando la siembra de variedades que manifiestan distintos factores de resistencia. También deben de usarse tácticas de resistencia de plantas hospedadoras que requieran complejas alteraciones genéticas fisiológicas y de comportamiento para impedir que el insecto desarrolle resistencia.

"A study of the resistance of crop plants to insect attack has served to emphasize the great importance of food habits in the biology and evolution of plant feeding insects" (Painter 1996)

With the above quoted sentence, Reginald Painter began his seminal 1996 paper "The Food of Insects and its Relation to Resistance of Plants to Insect Attack". The ideas expressed in that paper were the seeds for his classic book "Insect Resistance in Crop Plants", in which, 15 years later (Painter 1951), he formulated the basic principles of host plant resistance (HPR) that continue to provide the foundation underlying our current HPR research and application efforts. As indicated by the above quote, Painter also was one of the pioneer insect nutritional ecologists, for he early recognized the importance of the interactions of food attributes and other environmental factors with food consumption and subsequent post-ingestive performance. Understanding these interactions is a primary goal of nutritional ecology, because the consumption of food is a necessity for all other aspects of insect performance (i.e., growth and development, reproduction, defense, movement and survival; Slansky & Rodriguez 1987). Food consumption is also the main cause of crop injury due to pest insects, either directly through feeding damage or indirectly through vectoring of disease agents during feeding. Attempts to reduce such damage by manipulating insect performance through alteration of crop plant characteristics form the crux of research on host plant resistance (HPR) and its application (Painter 1951, Maxwell & Jennings 1980, Hedin 1983). Thus, the principles of insect nutritional ecology provide a logical basis for choosing particular plant attributes in the development and use of resistant crop varieties (Gould 1983, Hare 1983, Slansky & Rodriguez 1987).

In order to effectively manipulate the biochemistry, physiology and behavior of pest insects through use of HPR tactics, we must understand the links between the various attributes of the insects’ food, their food consumption and utilization, and subsequent performance (Figure 1). In this paper I first describe some of the main plant attributes that affect insect performance. Many of these plant characteristics can be altered through selective breeding and cultural practices (Maxwell & Jennings 1980, Hare 1983, Borlaug 1983, Osborn et al. 1988), and some are now (and others undoubtedly will soon be) modifiable through bioengineering (Barton & Brill 1983, Gasser & Fraley 1989). Thus, these plant attributes comprise key components of existing and future HPR tactics. I then outline the consumption and processing of food by insects, suggesting potential “weak links” in the chain of events leading from host plant to insect that might be exploited through HPR tactics, toward achieving the goal of improved crop pest
management. I next indicate the importance of understanding the mode of action of the various plant attributes used as HPR tactics, and delineate the impact of HPR tactics on insect performance. I continue by discussing some possible biochemical, physiological and behavioral responses by insects that may act to counter certain HPR tactics, and indicate how these responses might be used as additional HPR tactics. Finally, I discuss the development of resistance by insect pests to our HPR efforts, and suggest how this phenomenon might be slowed or prevented. Throughout this paper I concentrate on immature insects, although the ideas expressed also pertain to adults (e.g. Orthoptera, Hemiptera, Homoptera and Coleoptera) that require nutrient intake. These concepts fall primarily within the “antibiosis” component of Painter’s (1951, p. 25) “threefold basis of resistance”. The ability of insects to locate and choose their host plants is also an important link in the chain and is susceptible to modification through HPR [Painter’s “preference” component; more recently termed “antixenosis” (Kogan & Ortman 1978)], but this topic is generally beyond the scope of the present paper, as is the third component of the HPR triad, “plant tolerance”.

**PLANT ATTRIBUTES**

Two main categories of plant attributes relevant to plant-feeding insects are nutritional and non-nutritional factors, the latter being comprised of at least two sub-categories: allelochemicals and morphological features. Nutrients can be defined generally as substances that are necessary or useful for the metabolic functioning of an organism (i.e., proteins, amino acids, carbohydrates, lipids, vitamins, minerals, water, etc.); the basic nutritional requirements of insects and vertebrates overlap substantially,
with a few key differences, and there are various differences among insect species as well (Hagen et al. 1984, Dadd 1985, Reinecke 1985).

Allelochemicals are defined as non-nutritional compounds "by which organisms of one species affect the growth, health, behavior, or population biology of organisms of another species" (Whittaker & Feeny 1971, p. 164; see also Reese 1979). Allelochemicals comprise a diverse group of substances (i.e., alkaloids, phenolics, glucosinolates, terpenoids, etc.) and may be beneficial to either the organism producing them (e.g., by repelling enemies) or the organism receiving them (e.g., a foodplant attractant); the former are termed allomones, and the latter, kairomones (Whittaker & Feeny 1971, Rosenthal & Janzen 1979). Morphological plant attributes form a broad group including texture, "toughness", color, size, shape, growth form, etc. While morphological attributes typically affect insects at the "preference" level (especially adult oviposition), some of them (e.g., "toughness" and pubescence) also may function through "antibiosis" (Norris & Kogan 1980).

This classification of plant attributes is based primarily on functional considerations relative to the insects consuming the plant; thus a particular component may occur in more than one category depending on the situation. For example, an allelochemical toxic to one insect species may serve as an attractant or nutrient to another, and some of the chemicals contributing to a leaf's toughness may also have allelochemical activity (see next section). In developing insect-resistant plant varieties, it is important to know the functional mode of action of the different plant attributes relative to the target insects, for several reasons as described below (see Importance of Understanding HFR Mechanisms).

FROM HOST PLANT TO INSECT: WEAK LINKS IN THE CHAIN

Food consumption. The initial interaction between insect and crop plant of concern to the present discussion is feeding. Certain nutrients and allelochemicals (as defined previously) serve as feeding stimulants for insects, whereas others (especially allelochemicals) function as antifeedants (Hanson 1983, Stadler 1984, Miller & Strickler 1984, Hsiao 1985). Thus, we could select for reduced amounts or the absence of the stimulating chemicals to decrease the propensity of the target insect to initiate feeding, and/or for the presence or increased amounts of antifeedant chemicals to repel or deter pest insects from feeding (Bernays 1983, Frazier 1986, Smith 1986). For several different crops grown in the southeastern United States, there are varieties exhibiting antibiosis-based resistance, apparently due at least in part to antifeedant effects (e.g., Kleyla et al. 1978, Lynch et al. 1981, Jackson et al. 1985, Peterson & Schalk 1986, Smith 1986, Wiseman & Widstrom 1986, Wiseman et al. 1986, Chang et al. 1987, Isenhour & Wiseman 1987, Jones et al. 1987, Beach & Todd 1988, Jackson et al. 1988, Niemeyer 1988, Parrott et al. 1989).

In many cases, the factors presumably responsible for the observed resistance have been delineated only recently. Most remain unknown, and often it has not been determined if the resistance results from a direct antifeedant effect or from a less direct, toxic effect on growth which subsequently reduces feeding. Indeed, it can be difficult to distinguish antifeedant versus toxic effects; time-intensive quantification and manipulation of feeding rate are often required (Blau et al. 1978, Dimock et al. 1986, Puttick & Bowers 1988). In addition to chemical compounds, physical factors such as greater toughness of plant tissues associated with increased fiber may interfere with feeding. For example, tough leaves wear down the cutting surface of the mandibles of adult Plagioderma more so than tender leaves, reducing the beetles' feeding rate, which in turn would cause fecundity to decline (Raupp 1985).

Along with sensory information from taste receptors, feeding by insects is regulated through several mechanisms, including feedback from stretch receptors and from nutri-
ent levels in the hemolymph, with obvious involvement of the neurohormonal system (Bernays 1985, Simpson & Simpson 1990). Thus, HPR tactics may be designed to influence neurotransmitters, etc., in the target insect to alter feeding behavior in the desired manner. For example, consumption of an inhibitor of the neurotransmitter serotonin altered feeding behavior in Heliothis zea (Boddle) caterpillars (Cohen et al. 1988a; see Menn & Borkovec 1989, for a review of insect neuropeptides from an insect control perspective). In some cases, it might be appropriate to stimulate feeding by a pest insect, at least initially, if this results in an overall reduction in feeding damage (see Insect Responses to HPR Tactics below).

Digestion and absorption. After food has been ingested, it must be digested and absorbed by the insect. Certain allelochemicals, such as protease inhibitors, can hinder these processes (Reese 1979, Ryan 1983, Shukle & Murdock 1983, Applebaum 1985, Turunen 1985, Broadway & Duffey 1986, Osborn et al. 1988). These compounds occur in certain crop plants, especially those in the Gramineae (e.g., corn), Leguminosae (e.g., soybean and alfalfa) and Solanaceae (e.g., potato and tomato), and their production by the plant often seems to be increased (i.e., induced) in response to plant damage (Ryan 1988, Broadway et al. 1986). Thus, there seems to be good potential for their use in HPR.

The activity of some of these inhibitory compounds, of certain insect pathogens and of the digestive enzymes themselves, is pH dependent, and gut pH can vary among insect species as well as with the food eaten (Berenbaum 1980, Applebaum 1985). For example, the virulence of nuclear polyhedrosis virus (NPV) tends to be highest at neutral to acidic pH, whereas that of Bacillus thuringiensis (Bt) occurs in the basic range; the effectiveness of these pathogens against various insect species therefore may depend in part on an insect’s gut pH, and the use of microbial chitinase (which is active at acidic pH) to facilitate the penetration of pathogens through the peritrophic membrane/gut wall of caterpillars may be more effective for NPV (e.g., Shapiro et al. 1987) than for Bt (Schultz 1988). Thus, if some factor acting at the digestion/absorption level is considered for use as an HPR tactic, it is important to confirm that it functions adequately within the gut pH range of the target insect, or alternatively, plant quality would need to be modified to create the appropriate pH level.

The fibrous component of plant cell walls (a chemically diverse mixture of cellulose, hemicellulose, lignin and other substances occurring in various proportions depending on plant species and variety, age and growing conditions) can interfere with food digestibility in vitro and in vivo in cattle (Van Soest 1982), but our knowledge of the impact of fiber on the digestion of food by insects is limited (Mattson & Scriber 1987). Few insects can digest cellulose (Martin 1983), thus the dry weight digestibility of food generally declines as this substance increases in the diet (Peterson et al. 1988, Timmins et al. 1988, Slansky & Wheeler 1990). However, there seems to be no unequivocal evidence for insects indicating that digestion/absorption of the nutrient component of the food is reduced by the presence of fiber. For example, although the digestive efficiency of dry weight declined with an increase in the cellulose content of an artificial diet for the velvetbean caterpillar (Anticarsia gemmatalis Hübner) (Slansky & Wheeler, 1990), fall armyworm [Spodoptera frugiperda (J. E. Smith)] (Wheeler & Slansky, unpublished data) and southern armyworm [Spodoptera eridania (Cramer)] (Peterson et al. 1988), the efficiency of digestion/absorption of the nutrient portion of the diet either did not decline or increased. Of course, adding powdered cellulose to an artificial diet is a radically different situation from increasing the cell wall fiber in a plant leaf; thus the relevance of these data to caterpillars consuming plant leaves is questionable. We are not aware of any studies determining the impact of increased fiber in plant leaves on nutrient utilization by insects, but the dry weight digestibility of bermudagrass varieties for S. frugiperda did not appear to show a negative relationship to the fibrous components of the foliage (Jamjanya & Quisenberry 1988). Thus, at pres-
ent we cannot conclude that increased fiber can be used to interfere with nutrient digestion in insects; however, because an increase in plant fiber would most likely result in a dilution of the nutrient portion of the food, which in turn would probably affect insect feeding behavior, and for other reasons [see Food consumption above, and Norris & Kogan (1980)], fiber may nonetheless be useful in HPR.

Decreased dietary water may reduce nutrient digestion/absorption because the lower water level interferes with these processes (see Turunen 1985). In addition, the increased concentration of nutrients associated with low dietary water may force the insect to excrete excess nutrients that have been absorbed (see next section). Because quantitative food utilization studies of insects often measure only the dry mass of the food ingested and feces egested (rather than also measuring uric acid, etc., in the feces), the separate contributions of decreased digestion/absorption and increased excretion of metabolic wastes to a decline in the calculated value of the “digestion/absorption” efficiency are seldom distinguished. Data compiled for the caterpillars of 25 species of Lepidoptera indicate that the maximum values exhibited for dry mass digestion/absorption efficiency decline with a reduction in both leaf water (% fresh weight) and nitrogen (% dry weight) (Slansky & Scriber 1985).

Conversion to biomass, metabolism, detoxication and excretion. After the nutritional precursors have been absorbed from the gut, the insect allocates a portion of them to growth and nutrient accumulation; much of the remaining portion is used to supply energy and nutrients for metabolic processes. Interconversions and metabolism of nutrients, often associated with nutrient imbalances, result in the production of metabolic waste products requiring excretion. Potentially deleterious allelochemicals may also be absorbed, which the insect may detoxify and excrete, whereas some insects sequester allelochemicals from their food for use in defense from their enemies or as pheromones. Many of these physiological events are regulated through the neurohormonal system. Thus, there is considerable potential to use HPR tactics to manipulate these metabolic processes to affect deleteriously insect performance, as briefly discussed in the remainder of this section.

One obvious possibility is to alter the nutritional composition of crop plants to reduce or eliminate nutrients, or otherwise create nutritional imbalances. It would seem especially important to reduce the level of essential nutrients that are required but cannot be synthesized by the target insect. For example, linolenic (C18:3) acid, which may be synthesized rarely by insects, if at all (Downer 1978; see also Stanley-Samuelson et al. 1988), seems to be especially important for certain Lepidoptera; poor adult emergence and wing deformities occur if the level of this fatty acid is too low in the diet, and thus artificial diets are often supplemented with it (Bracken 1982, Turunen 1983). Soybean lines low in linolenic acid in the seeds have been selected to improve seed oil quality (Hammond & Fehr 1984), but levels of this fatty acid in the foliage are not closely correlated with those in the seeds (Martin & Rinne 1985). Whether the performance of soybean seed-feeding insects is affected on these lines, and whether a level of linolenic acid in the foliage low enough to deleteriously affect leaf-feeding insects can be achieved, has apparently not been investigated.

In addition to fatty acids, variation in sterols (Thompson et al. 1980, Al-Izzi & Hopkins 1982; but see Grunwald & Kogan 1981), amino acids (Prestidge & McNeill 1983, Brodbeck & Strong 1987, Feilhau et al. 1988) and probably other nutrients may contribute to HPR. Unless a certain level of non-essential (“dispensable”) amino acids is present in insect diets, the essential amino acids may be depleted and growth slowed (Dadd 1985); thus, altering both essentials and non-essentials in a crop plant may be appropriate in some situations. Amino acids are a typical source of nitrogen for plant-feeding insects, but nitrogen fixation by rhizobial bacteria occurring in legume root nodules (e.g., soybean plants) produces nitrogen-containing ureides (i.e., allantoin and allantoin
acid) which are transported in the plant. Wilson & Stinner (1984) found that these compounds seem to be a poor source of nitrogen for certain crop pests; ureide production can be manipulated by altering the amount of nitrogen fertilizer given to the plant. In addition to direct reduction in growth due to nutrient limitation, the additional metabolic interconversions and excretory demands of nutrient imbalances and excesses (e.g., Van't Hof & Martin 1989) could divert nutrients and energy from growth to greater enzyme activity associated with the increased metabolic demands, further contributing to a deleterious impact on insect performance.

Nutrient analogs, such as non-protein amino acids, are substances generally similar enough in chemical structure to nutrients that they enter the metabolic pathways, but they are different enough to not function properly and thus interfere with metabolism (Reese 1979). Various non-protein amino acids have deleterious impacts on several insects (Rosenthal & Bell 1979), although some insects are not affected (Srivastava et al. 1988) and at least one beetle species is able to utilize a non-protein amino acid (i.e., canavanine) as a source of nitrogen (Rosenthal et al. 1982).

Anti-nutrients bind with certain vitamins or minerals (Reese 1979), possibly in the gut or after absorption, reducing the availability of these nutrients. For example, phytic acid, which occurs in several plant species (e.g., grains and legumes, especially in the seeds), may bind with vitamin D, proteins and certain minerals (Reese 1979, Jaffe 1981). In apparently the only study examining the impact of phytic acid on an insect, Rowen & Slansky (unpublished data) found that this chemical prevented egg hatch when added to an artificial diet at 2% dry weight (dw) and prevented egg production at 5% dw, when fed to adult southern green stinkbugs (Nezara viridula L.).

A low level of water in the food may divert absorbed nutrients away from the synthesis of biomass and to the production of metabolic water or to energy costs associated with excreting excess nutrients; in addition, low water may slow growth by more directly limiting the rate at which hydrated tissue can be synthesized (Scriber 1977, Martin & Van't Hof 1988, Van't Hof & Martin 1989). High water content in the food may increase an insect's energy costs if the insect increases its feeding rate sufficiently in response to the dilution of the nutrients; it also may interfere with growth in other ways, possibly by overriding the insect's hemolymph and by requiring extra metabolic activity to maintain an appropriate water balance (Slansky & Wheeler 1989).

Many allelochemicals are toxins, affecting various components of metabolism, nerve impulse transmission, etc. (Reese & Holyoke 1987, Holyoke & Reese 1987). Insects possess detoxification enzymes with which they metabolize certain allelochemicals to generally less toxic metabolites (Ahmad et al. 1986), and the activity of these enzymes is often induced by allelochemicals and pesticides (Yu 1986). Relevant HPR tactics could involve the use of naturally occurring chemicals that inhibit detoxification enzymes (e.g., certain lignans and other compounds found in many economically important plants, including black pepper, blueberry, nutmeg, sesame, soybean, tomato and various umbellifers), and substances that, rather than being detoxified, are activated to more potent forms (Ahmad et al. 1986, Berenbaum & Neal 1987).

Many insects rely on sex pheromones as an essential component of the mating process, and these are commonly synthesized de novo by the insects; in such cases pheromone quality or quantity does not seem to be greatly influenced by larval food quality, although associated processes (e.g., age at which pheromone release occurs) may be altered significantly (McNeil & Delisle 1989). In species in which allelochemicals are sequestered from the larval food, either to be used directly or as precursors for sex pheromones or defensive agents against the insects' natural enemies, food quality can have a substantial impact on these aspects of insect performance (Schneider et al. 1982, Smiley et al. 1985, Brattsten 1986, McNeil & Delisle 1989). In such interactions involving insect pests of crops, manipulation of these compounds could be used in an HPR program.
Regulation of the various metabolic processes involves neurotransmitters and neurohormones (Steele 1985), and thus HPR tactics may be used to interfere with this regulation (see Menn & Borkovec 1989). Naturally occurring chemicals with juvenile hormone or ecdysteroid activity can have deleterious impacts on insects (e.g., Kubo et al. 1989, El-Ibrahimi 1987). Knowledge of the hormonal regulation of diuresis (Spring et al. 1988) and uric acid excretion (Buckner 1982) may lead to manipulation of these processes through HPR.

**Importance of Understanding HPR Mechanisms**

Although resistant plant varieties can be (and have been) developed without knowing the specific mechanisms involved in conferring resistance, a more directed approach to HPR, involving crop plant design and implementation within an integrated pest management scheme, necessitates an understanding of the mode of action of the plant attributes, for several reasons. First, as mentioned previously, the effects of plant attributes depend on the insect species involved. Thus, unless we know the mode of action of a particular attribute relative to the key pests, we may be making a crop variety more susceptible to one pest species while attempting to make it more resistant to another.

Second, there may be interactions among the various plant traits, and between them and other pest management tactics, which either enhance or diminish the success of an HPR effort. For example, in the previous section possible interactions between insect gut pH and the functioning of certain allelochemicals and insect pathogens were described. Some plants, through their effect on insect detoxication enzymes, may make an insect either more or less susceptible to synthetic insecticides (Yu 1986). Other examples of interactions involve natural enemies, which may be a key part of an integrated pest management scheme involving HPR (see next section). For example, an alteration in a plant attribute that slows growth of the target insect may be advantageously coupled with augmentation of a predator species, if the slower growth increases the pest’s exposure to the predator. However, there probably would be little need for predator augmentation if a toxic allelochemical either killed off the early stages of the target pest or if the compound were accumulated in the target insect, rendering it unsuitable to the predator (see Bergman & Tingey 1979, Doethel & Eikenbarry 1986 and Barbosa & Letourneau 1988 for detailed discussions of such interactions). Thus, we need to know the effects of the plant attributes to promote or avoid such interactions, as appropriate.

Third, in practical terms, it is obviously necessary to identify a particular resistance factor before it can be introduced into a crop variety via gene-transfer. In regard to traditional breeding programs, these may be simplified and streamlined through knowledge of the underlying mechanisms of resistance. For example, if a crop variety is being bred to increase an allelochemical in the foliage to a particular level previously determined in laboratory and limited field experiments to reduce feeding of the target pest by 50%, then plants in each generation of the breeding program can be analyzed more rapidly and possibly less expensively through chemical techniques to assess their allelochemical concentration. If, however, the plants were being bred to increase their resistance to the insect pest without knowing the role of the allelochemical, then each generation of plants would have to be field tested to determine which individuals to choose for the next cycle of breeding. Such field work, involving the arrangement, planting and maintenance of field plots, and monitoring of insect numbers and damage levels, would undoubtedly be more time-consuming and expensive. Of course, even in the former situation, once the desired level of allelochemical was achieved, field work would have to be carried out to confirm the previous experimental results, to assess natural enemy interactions, etc., before full scale production and release of the variety.
Finally, an important consideration in the creation and implementation of insect-resistant crop varieties is their long-term effectiveness; that is, whether and how rapidly the target pest will develop resistance of its own to the HPR tactics (see Insect Responses to HPR Tactics below). If we are to understand the situations in which insects evolve such resistance so that we can devise ways to avoid or slow this process, we need to know which mechanisms and combinations thereof the insects have and have not been able to overcome.

**Effects on Insect Performance**

The ultimate goal of using HPR tactics to impact the consumption and utilization of food by a target pest as described previously usually is to maintain crop damage below economic injury levels. This can be done by killing the target pest outright, such as through use of a potent toxin or antifeedant (the latter causing death through starvation). Prevention of feeding may be necessary in a situation in which the target insect is a vector of a disease agent or in other cases with a very low economic injury threshold. However, heavy mortality caused by a single plant attribute, especially if a genetically simple mechanism in the pest insect is involved, should probably be avoided because the strong selective pressure imposed may lead to relatively rapid development of resistance in the target insect population (see next section).

As discussed previously, there are many potential HPR tactics, and these can be used to alter the performance of crop pests to exert deleterious effects on their fitness, even if mortality caused directly by the plant attributes is low and food consumption is not directly or immediately reduced. Many of the tactics described previously can result in slowed development and reduced weight gain by the immature target insects, which in turn may reduce overall feeding damage and help prevent a subsequent increase in the pest population.

Slowed development will prolong an insect’s exposure to the environment, including rain, pathogens, parasitoids, predators and other potentially harmful agents, and thus increase its probability of mortality prior to reaching the adult (reproductive) stage. For example, an insect may be forced to remain longer in early instars, which might be the only stages attacked by certain arthropod predators or parasitoids. Similarly, a requirement for additional feeding (e.g., because digestion/absorption of the food is partially inhibited by a protease inhibitor in the crop foliage) might result in greater mortality if movement to a feeding site and during feeding increases the insect’s exposure to natural enemies, or if the increased consumption leads to ingestion of an infective dose of a pathogen or lethal dose of a toxic allelochemical. Increased mortality of pest insects feeding on resistant versus susceptible crop varieties caused by natural enemies has been documented (Hare 1983, Price 1986, Isenhour et al. 1989); however, each crop variety/insect pest/ natural enemy interaction of concern will probably need to be evaluated prior to drawing any conclusions, because certain plant attributes may either enhance or interfere with particular natural enemies (Bergman & Tingey 1979, Boethel & Elkenbury 1986, Barbosa & Letourneau 1988).

If the target insect survives to the adult stage, slowed development may alter its synchrony with important temporal features of the environment, including both abiotic (e.g., the need to diapause or migrate prior to a killing frost) and biotic (e.g., foodplant phenology) components, thereby reducing its fitness (Taylor 1980, 1981). Reduced weight gain resulting in a sub-normal sized adult can decrease fitness by interfering with mating success, by reducing fecundity and by making the adult less able to cope with stresses (Slansky & Scriber 1985); in some cases, however, flight activity or migratory ability may increase in smaller individuals (Angelo & Slansky 1984). In addition, stress during the immature stage (e.g., the presence of a particular non-lethal allelochemical in their food) may affect the ability of the next generation immatures to
cope with stress (Gould, 1988). Thus, there is considerable potential to impose significant deleterious effects on target pest performance associated with manipulation of crop plant attributes, whether or not the HPR factor directly causes mortality of the target insect pest.

Insect Responses to HPR Tactics

Painter (1951, p. 85) recognized two important concerns regarding the use of resistant crop plants: "Research in insect resistance in plants requires a knowledge of the possible plasticity of insect behavior and of the possible rate of change of insect biotypes and species." Indeed, insects are not passive creatures totally at the mercy of their environment; their biochemical, physiological and behavioral activities are regulated through neuroendocrine and other feedbacks, allowing adaptive responses to the changing environments in which they exist (Slansky 1982, Slansky & Rodriguez 1997). Thus, individual insects may have the capacity to respond to certain of our HPR tactics, possibly counteracting or mitigating them. Assessing these types of responses experimentally is a major task of research in nutritional ecology; without such knowledge, altering a food attribute as an HPR tactic might not have the intended effect of reducing performance of the target insect, and could even increase feeding damage. In addition, the genetic variability of insect populations, coupled with the differential impact on the fitness of the target pests exerted by a resistant crop variety, may lead to the evolution of resistance in the target species to an HPR tactic. These two issues are discussed in this section.

Biochemical, physiological and behavioral responses. As mentioned previously, one biochemical/physiological response exhibited by insects is the induction of detoxication enzyme activity by allelochemicals, which may allow the insect to tolerate higher doses of these potentially toxic compounds, as well as of certain insecticides. Habituation and aversive learning in response to feeding deterrents have also been demonstrated in insects (Jermy et al. 1982). A response by some insects to nutritionally variable food is the phenomenon of "self-selection", in which individuals consume the most nutritionally suitable tissue or a combination of tissues or foods to obtain an adequate balance of nutrients (Waldbauer & Friedman 1988). For example, last instar Heliothis zea caterpillars feed preferentially on the germ of maize kernels (Cohen et al., 1988b).

Several insect species alter food consumption in response to changes in food quality, for example by increasing the feeding rate if their level of nutrients in the food declines (Table 1). Such responses may eliminate or limit the impact of variation in food attributes on insect performance. For example, dilution of an artificial diet with water, which reduced the nutrient level from 35% to 21% fw (fresh weight), caused little reduction in weight gain or relative growth rate (RGR) by A. gemmatalis caterpillars, associated with their increase in food consumption (Slansky & Wheeler 1989). Although both weight gain and RGR declined significantly with further dilution to 11% fw nutrients, the continued increase in feeding mitigated the deleterious impact of diet dilution; for example, on the latter diet, RGR would have been reduced about 40% more without the increased-feeding response.

These physiological and behavioral responses do not necessarily have to be liabilities to our HPR tactics; indeed, we might use them to further manipulate insect performance. For example, if a pest caterpillar is more susceptible to natural enemies while feeding, then decreased foliage nutrient level could be used to increase feeding and the insect’s exposure to natural enemies. The increased-feeding response could also be used to cause insects to consume sufficient doses of pathogens (Richter & Fuxa 1984) or allelochemicals. For example, A. gemmatalis caterpillars were made to ingest a lethal dose of a toxic allelochemical (i.e., the methylxanthine alkaloid caffeine) by diluting the
TABLE 1. VARIATION IN FOOD CONSUMPTION EXHIBITED BY SELECT INSECTS FEEDING ON DIFFERENT NATURAL OR ARTIFICIAL DIETS, INDICATING SUBSTANTIAL CAPACITY FOR ALTERATION IN FEEDING, SUCH AS IN RESPONSE TO DIETARY DILUTION.

<table>
<thead>
<tr>
<th>Species</th>
<th>Food</th>
<th>X-fold range in consumption</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>LEPIDOPTERA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cabbage butterfly</td>
<td>Crucifer var &amp; spp</td>
<td>2.2</td>
<td>Slansky &amp; Feeny (1977)</td>
</tr>
<tr>
<td>Fall armyworm</td>
<td>Peanut var &amp; spp</td>
<td>1.8</td>
<td>Lynch et al. (1981)</td>
</tr>
<tr>
<td>Bermuda-grass clones</td>
<td>Diluted art diet</td>
<td>1.4</td>
<td>Quisenberry &amp; Wilson (1985)</td>
</tr>
<tr>
<td>Green cloverworm</td>
<td>Soybean: grnhs vs field grown</td>
<td>2.2</td>
<td>Hammond et al. (1979)</td>
</tr>
<tr>
<td>Southern armyworm</td>
<td>Alfalfa var</td>
<td>3.4</td>
<td>Scriber (1979)</td>
</tr>
<tr>
<td>Tobacco hornworm</td>
<td>Diluted art diet</td>
<td>2.6</td>
<td>Timmins et al. (1988)</td>
</tr>
<tr>
<td>Velvetbean caterpillar</td>
<td>Legume spp</td>
<td>2.0</td>
<td>Waters &amp; Barfield (1989)</td>
</tr>
<tr>
<td><strong>COLEOPTERA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mexican bean beetle</td>
<td>Soybean var</td>
<td>2.3</td>
<td>Barney &amp; Rock (1975)</td>
</tr>
<tr>
<td><strong>ORTHOPTERA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locusta</td>
<td>Diluted diet</td>
<td>1.7</td>
<td>Dadd (1960)</td>
</tr>
<tr>
<td><em>Melanoplus</em></td>
<td>Diluted diet</td>
<td>6.9</td>
<td>McGinnis &amp; Kasting (1967)</td>
</tr>
<tr>
<td><em>Schistocerca</em></td>
<td>Diluted diet</td>
<td>3.1</td>
<td>Dadd (1960)</td>
</tr>
</tbody>
</table>

Nutrients in an artificial diet with water, even though the concentration of caffeine (as a % of diet fresh weight) was the same in all the diets (Slansky and Wheeler, unpublished data). Because feeding rate increased with dilution of nutrients in the diet, the ingested dose of the allelochemical increased, eventually to a toxic level. If the increased-feeding response is a short-term phenomenon, resulting in reduced growth or death such that the total damage done by a pest insect is reduced, then it has potential for use as an HPR tactic.

Evolution of resistance. Several hundred cases are known of insects having evolved resistance to insecticides acting as direct agents of mortality (Rush & McKenzie 1987); common mechanisms of resistance are enhanced detoxication activity and target site alterations that prevent insecticide binding, although behavioral avoidance also occurs (Lockwood et al. 1984, Brattsten et al. 1986). Thus, use of a single plant attribute intended to cause heavy mortality of an insect pest (e.g., an allelochemical toxin in the plant acting analogous to a synthetic insecticide applied to the crop) may create strong selection pressure leading to relatively rapid evolution of resistance in the target pest population to the HPR tactic, especially if the tactic can be overcome by a genetically relatively simple change in biochemistry, physiology or behavior. A better strategy for maintaining long-term effectiveness of resistant crop varieties should probably involve multiple HPR tactics, especially if deployed within a genetically diverse crop variety or by changing the resistance factors in varieties planted in succession. In addition, it
would probably be desirable if genetically complex alterations in physiology and behavior were necessary for an insect to evolve resistance (see below).

Painter (1961) recognized the interrelationships among the HPR triad, indicating that various combinations of antibioticomas, non-preference and plant tolerance within a crop variety could achieve the desired level of plant resistance. He also suggested ways of dealing with the development of resistance in pest insects to HPR tactics, stating (p. 105) that "A change in genetic factors for resistance [i.e., primarily behavioral modes of action] is more effective at limiting the development of insect resistance than use of a single factor has apparently received little research attention, although there is some evidence, based on a genetic model, that this dual approach may slow the development of resistance in the target pest to the HPR tactics (Gould 1984). Empirical research is clearly needed to confirm this.

Lockwood et al. (1984), in a discussion of insect resistance to insecticides, make the valid point that behavior is "observable physiology" and thus there is really no fundamental difference between "behavioral" and "physiological" resistance in terms of insects having the capacity to evolve either or both of these in response to selective pressure from a toxicant (from an HPR perspective, these would be equivalent generally to resistance to "non-preference" and "antibiosis" tactics, respectively). However, resistance mechanisms in insects that require modification of more complex behaviors than mere avoidance of a toxicant (the primary behavioral response discussed by Lockwood et al. 1984]) would nonetheless seem to provide a means of slowing the development of resistance (see below). Thus, it is important to broaden the traditional view of HPR mechanisms: not only does behavioral "non-preference" have an underlying physiological component, but biochemical/physiological "antibiosis" has a behavioral component. This latter fact has become especially evident as research in insect nutritional ecology uncovers the interactions between feeding behavior (i.e., alterations in the rate and duration of food consumption, movement to and from feeding and resting sites, searching for suitable food, etc.) and food utilization/alloocation, as impacted by food attributes (Slansky & Rodriguez 1987). From this perspective, there is substantial potential to diverge from the traditional "antibiosis" tactics which attempt to use plant attributes in a manner analogous to synthetic insecticides (e.g., allelochemical toxins as "natural insecticides"), to instead manipulate a variety of biochemical, physiological and behavioral components of pest insect performance in an effort to employ effective HPR tactics that slow development of insect resistance to the tactics.

As an example of manipulating the performance of an insect pest in a way that may slow the development of resistance, I present the following scenario. A crop variety is bred with a reduced level of nutrients in the foliage (e.g., by increasing the water or fiber contents), which forces the target caterpillars to spend twice as much time feeding to obtain adequate nutrient intake for growth. During feeding, the cryptically colored caterpillars are exposed to a certain arthropod predator, and this predator species is augmented in the crop field to bring about a level of mortality adequate to maintain the target pest below the economic injury threshold.

Several possibilities exist for the insect species to develop resistance to this HPR tactic, including evolution of:

1. reduced requirements for many different nutrients such that the caterpillars would not need to increase their feeding in response to nutrient dilution (and thus not increase their exposure to the predator);

2. insensitivity to nutrient dilution such that the caterpillars would not respond via
increased feeding, which would reduce nutrient intake, requiring in addition the evolution of increased food utilization efficiencies and/or a smaller body size;

(3) and altered temporal activity pattern, such that the caterpillars feed when the predator is inactive; and/or

(4) defensive mechanisms against the predator.

To the extent that these evolutionary alterations require a complex of biochemical, physiological and/or behavioral changes, each is probably more-or-less unlikely to occur. A more likely occurrence might be the evolution of a shift to a related host plant species (see Diehl & Bush 1984), such that the insect would no longer become a pest of the target crop. Indeed, generalized predators may be very important selective agents leading to food plant specialization (Bernays 1988). Simultaneous use of various plant attributes that differ substantially in mode of action (e.g., an inhibitor or stimulant of the synthesis of a neuropeptide involved in regulation of feeding, a digestion blocker acting in the lumen of the gut, and an inhibitor of detoxication enzymes), may also slow the evolution of resistance in the target pest population, because there would probably be few individuals in the population resistant to all of the diverse modes of action even though there may be greater frequencies of individuals resistant to any one factor. A somewhat analogous suggestion has been made for use of a mixture of insecticides to help manage the development of insecticide resistance in insects (Brattsten et al. 1986). Maintaining genetic diversity in a crop variety, such that different plants in a field express differing degrees of the various attributes serving as resistance factors, and/or alternating crop varieties manifesting different resistance factors in subsequent plantings, may also slow or even prevent the development of resistance in the target pest (see Donno & McClure 1983, Whitham 1989), because the selective pressures for resistance in the target pest will be inconsistent (i.e., a particular insect genotype exhibiting a certain resistance mechanism may be selected for on one plant or in one generation but not on a neighboring plant or in the next generation).

The development of resistance in pests and its management are complex issues, as yet poorly understood (for discussions, see Tabashnik & Croft (1983), Gould (1983, 1984), Lockwood et al. (1984), Pluthero & Singh (1984), Brattsten et al. (1986) and Koush & McKenzie (1987)). Much of this discussion of the development of resistance in target insect pests to our HPR efforts has been speculative, in part because of a lack of experimental data. Clearly, there appears to be a variety of strategies to discourage the development of insect resistance, but much additional research is required before we will understand this phenomenon sufficiently to be able to limit or prevent it.

Conclusions

Research in insect nutritional ecology has uncovered many links between food attributes, food consumption and utilization, and subsequent insect performance. These interactions can be manipulated in diverse ways through HPR tactics, especially as part of an integrated pest management strategy, toward the goal of managing insect crop pests to maintain crop damage below economic injury thresholds. In addition to attaining effective short-term control, it is important to utilize HPR tactics in a manner which impedes the evolution of resistance in the target pest population to the tactics. Traditional plant breeding programs, as well as more recent biotechnological advances (e.g., gene-transfer between plant species), allow crop plants to be “designed” with specific resistance mechanisms directed at particular insect pests. Future research should concentrate on determining the mode of action and impact of plant attributes on key crop pests, the interactions among multiple HPR tactics and between HPR and other man-
agement tactics (in particular, natural enemy augmentation), the implementation of laboratory results to manipulating insect performance in the field, and the most effective ways to restrict the development of resistance in insect pests to our HPR efforts.

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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: Noc-