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Hervibors hosts influence on insecticide resistance: a review

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La influencia del hospedero en la resistencia de hervíboros a insecticidas: una revisión

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Abstract

Resistance is a worldwide problem, which if ignored or improperly managed, will significantly reduce worldwide agricultural production and public health. Resistance is influenced by genetic factors but also there is an environmental effect, which in the case of phytofagas diseases is partially represented by the chemicals found in the host plants. Species with an evolutionary history of feeding on heavily chemically defended plant structures should have elevated levels of enzymes that detoxify defensive chemicals, and therefore an enhanced ability to evolve resistance to synthetic toxins. The role of host plant chemistry on the expression and evolution of pesticide resistance is reviewed from the perspective of understanding the non-genetic factors influencing pesticide resistance. This perspective is important since environmental factors may have relatively important effects influencing the activity of detoxification enzymes in animals, and hence, susceptibility to xenobiotics. Research on non-genetic factors influencing pesticide resistance must be undertaken if we are to increase our confidence in proposed management strategies.

Key words :detoxification enzymes, pesticide resistance, non-genetic factors, susceptibility to allelochemicals.

Resumen

La resistencia de hervíboros a insecticidas es un problema a nivel mundial, que si es ignorado o manejado inadecuadamente, reduciría significativamente la producción agrícola mundial y la salud pública. La resistencia está influenciada por factores genéticos pero también existe un efecto del medio ambiente, que en el caso de las plagas fitófagas está en parte representado por sustancias químicas

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presentes en las plantas hospederas. Las especies que se alimentan de estructuras de plantas muy bien defendidas químicamente deberían tener elevados niveles de enzimas que detoxifiquen las sustancias químicas usadas por las plantas para defenderse, y por lo tanto muestran una habilidad mejorada para desarrollar resistencia a las toxinas sintéticas. Se revisa el rol de la química de la planta hospedera, desde el punto de vista de entender el efecto de los factores no-genéticos que influyen en la resistencia a plaguicidas de los insectos herbívoros. Esta perspectiva es importante ya que los factores del medio ambiente pueden llegar a tener un importante efecto en la actividad enzimática de detoxificación de los animales, y por lo tanto, la respectiva susceptibilidad a los xenobióticos. Investigación de los factores no-genéticos que influyen en la resistencia a plaguicidas debe ser llevada a cabo si queremos incrementar nuestra confianza en las estrategias de manejo propuestas.

Palabras clave: enzimas, detoxificación, resistencia, plaguicidas, factores no-genéticos, susceptibilidad, aleloquímicos.

Introduction

The evolution of resistance to pesticides is an example of the evolutionary process. The pesticide is the selection pressure, which creates a very strong fitness differential between susceptible and resistant genotypes. The survival and subsequent reproduction of resistant individuals leads to a change in the frequency over time of alleles conferring resistance. Widespread application of pesticides has led to a global resistance problem (12, 13). Resistance compromise crops, animal production and human health (through pesticide resistance in vectors of animal and human diseases and, drug resistance in the pathogens and parasites). While selection pressure acts to change allele frequencies within pest populations, the phenotype upon which selection operates is a function of both the genotype and the environment. Relatively little research has focused on the influence of environmental factors on the evolution of pesticide resistance. In the case of plant pests, the chemical constituents of plants are a significant part of the environment, a part that has been shown to affect the action of many resistance mechanisms. We review the role of host plant chemistry on the expression and evolution of pesticide resistance and show that this interaction must be considered if we are to develop rational pest management strategies for safe and efficient crop production.

Relationship between detoxification (Enzymatic Mechanisms) and host plants (Allelochemicals)

It became obvious relatively early in the history of insecticide use that polyphagous species develop high levels of insecticide resistance rather rapidly. Gordon (15) suggested that the natural exposure of polyphagous species to a wide variety of plant allelochemicals had resulted in high capacities for their detoxification, which would now enable the insects to develop resistance to synthetic insecticides. This idea directly implicated plant allelochemicals as the natural substrates for insecticide detoxifying enzymes for the first time.

Plant allelochemicals modify levels of detoxifying enzymes in herbivores and, therefore, their susceptibility to insecticides (4, 6, 26, 29, 34, 41, 45). Insects have detoxification mechanisms to deal with plant chemicals and also often the same mechanisms are involved in pesticide resistance. It is important to understand the interaction of plant allelochemicals with the detoxification system.

Three systems of detoxification enzymes (i.e., polysubstrate monooxygenases (PSMO), general esterases (GE), and glutathione S-transferases (GST) are commonly regarded as the most important biochemical mechanism for the metabolism of xenobiotics (7, 45) including allelochemicals (53) and pesticides (17). Xenobiotics may act as inducers by stimulating enzyme synthesis (53). Insects induced by dietary allelochemicals or host plants apparently increase metabolism of several synthetic pesticides, as demonstrated by their increased tolerance to these compounds (17). Insecticide resistant strains of insects often have greater detoxifying enzyme activities (43), and in at least one example, enzyme inducibility was greater than in a susceptible strain (37).

Esterases. This is a very large family of related enzymes. Included in the esterases are acetylcholinesterase, important in the proper transmission of nerve signals, and juvenile hormone esterase, which helps to regulate the process of metamorphosis. These enzymes work, in general, by breaking carboxylester and phosphorotriester bonds. They are active against many types of insecticides, especially organophosphates and pyrethroids. Much of the evidence for a role of esterases in insecticide resistance comes from assays of general esterase activity using model substrates. However, this is only an indirect measure of the role of esterases. Some studies with synergists have also implicated esterases. Esterase genes associated with insecticide resistance have been identified in mosquitoes and aphids.

Mullin and Croft (33) for example, found large differences in general esterase activity relative to snapbean (ranging from 0.4-fold on a mint to 2.4-fold on umbellifers) for *Tetranychus urticae* fed 13 different host-adapted strains.

Lindroth (25) studied the effects of food plant on larval performance and midgut detoxification enzymes in larvae of the luna moth, *Actias luna*. He found that larval food plants (black cherry, cottonwood, quaking aspen, white willow, red oak, white oak, tulip tree, paper birch, black walnut, butternut, shagbark hickory) affected the activities of soluble esterases and were 1.8-fold higher in larvae fed walnut, than in larvae fed birch. Microsomal esterases exhibited an opposite trend in activity, with lowest values in larvae fed walnut, and highest in those fed birch.

Activities of microsomal *cis*- and *trans*-epoxide hydrolase in northern corn rootworm, *Diabrotica barberi* Smith& Lawrence, were significantly increased by diet shifts from corn ear to squash blossom and sunflower inflorescence, while levels of these enzymes in the western corn rootworm, *D. virgifera virgifera* LeConte were unaffected (42).

Susceptible larvae from artificial diet had significantly higher nonspecific esterase activity than susceptible larvae fed apple, gorse, broom, and blackberry. Furthermore, activity of nonspecific esterases of resistant larvae fed blackberry was significantly lower than activities in resistant larvae fed artficial diet, gorse, apple, or broom, and not significantly different from nonspecific esterase activities of susceptible larvae reared on artificial diet, gorse, apple, blackberry, or broom (40).

Esterases afford protection from phenolic glycosides to *Papilio glaucus canadensis*, and general esterase activity was elevated 22% after consumption of a phenolic glycoside diet (27). The induction capacity of hydrolytic enzyme systems (e.g., esterases, epoxide hydrolases) is generally marginal in comparison to that of PSMOs and glutathione transferases (28).

Cytochrome P450-dependent monooxygenases (PSMO). These enzymes are linked to the electron transport system of the cell. They add oxygen to the substrates, and the substrate is then more easily excreted. There is usually a family of cytochrome P450-dependent monooxygenase enzymes present in each individual organism to deal with many types of reactions and many substrates. Each particular enzyme has a broad, but unique, pattern of substrate specificity. Most of our knowledge of the monooxygenase system comes from studies on mammalian liver. However, some recent genetic studies in insects are beginning to add to our understanding. It is now clear that a specific cytochrome P_{450}-dependent monooxygenase is responsible for the ability of black swallowtail butterfly caterpillars to deal with certain chemicals in their diet. In the case of many organophosphate insecticides, certain monooxygenase enzymes actually make the insecticide more toxic to the insect by substituting an oxygen for a sulfur atom. Even so, this enzyme family appears to be responsible for a number of cases of resistance to insecticides, based upon synergism studies. Monooxygenase activity appears to be partially responsible for Colorado potato beetle resistance to abamectin.

The first evidence that plant allelochemicals could induce the PSMO system was reported by Brattsten *et al.* (8). They found that larvae of the polyphagous southern armyworm were induced rapidly by a variety of allelochemicals. The larvae with induced enzymes were less susceptible to the toxic tobacco alkaloid nicotine. That induced activity did provide general protection was indicated by the fact that allelochemical-mediated induction often reduced the susceptibility of insects to insecticides (6).

A study with 35 species of herbivorous Lepidoptera larvae (23) gave rise to the idea that polyphagous caterpillars had higher detoxification enzyme activity than oligophagous and monophagous species. The need for higher PMFO level was in agreement with the greater risk for generalists in contacting plants potentially richer in allelochemical diversity and concentration compared with specialists, which usually are well-adapted via a single detoxification mechanism to the host's specific defensive chemicals.

In another lepidopteran, the variegated cutworm, *Peridroma saucia* (Hubner), feeding on peppermint induced midgut PSMO activity up to 45-fold compared with activity in larvae fed a basic control diet (54). Mint-fed larvae were more tolerant of the insecticide, carbaryl, than were bean-fed larvae. Yu *et al.* (54) suggested the possibility that plant species differ in the degree to which they stimulate such enzymes and that an insect's ability to detoxify insecticides may depend on the nature of its host plant.

In a similar study, Berry *et al.* (4) investigated the influence of peppermint, alfalfa, snap beans, garden beets, curly dock, and artificial diet on the midgut microsomal oxidase activity of variegated cutworm larvae and on its susceptibility to different insecticides. They found that tolerance to acephate, methomyl, and malathion was greater when larvae were fed peppermint leaves than in those fed bean leaves. Midgut enzyme activity was increased up to 9 times when larvae fed on peppermint leaves.

With last instar cabbage looper, *Trichoplusia ni* (Hubner), larvae fed peppermint, alfalfa, broccoli, cabbage, or artificial diet, only peppermint-fed larvae had a four-fold increase in midgut aldrin epoxidase activity. Bioassays of induced larvae indicated that tolerance to carbaryl and methomyl was greater than with larvae fed the other plants (11).

Yu (48) demonstrated PSMO induction by plants in fall armyworm larvae. Alfalfa, sorghum, peanuts, cabbage, cowpeas, cotton, Bermudagrass and corn all stimulated enzyme activity, with corn being the strongest inducer. Millet and soybean leaves induced no more activity than the artificial diet control. In tests with eight insecticides, fall armyworm larvae were more tolerant after feeding on corn than on soybean leaves.

Glutathione S-transferases (GST). Glutathione transferases work by adding the tripeptide glutathione to a substrate. The subsequent cleavage of the substrate leads to easier excretion. As with the other detoxification enzymes, there are multiple genes for glutathione transferase proteins, and each protein has a unique specificity. Many studies suggesting a role for glutathione transferase in insecticide resistance have used enzyme assays with model substrates. However, in house flies, conjugation of glutathione to insecticides has been demonstrated. Also, DDT dehydrochlorinase, a mechanism of resistance in house flies, has been shown to be a glutathione transferase.

Plants and plant allelochemicals also induced glutathione transferase activities in fall armyworm (49, 52). Parsnip caused a 39-fold increase compared with activity in fall armyworm larvae fed artificial diet. Marked induction of this enzyme was also observed in larvae fed on turnip and cowpeas, but nine other host plants (peanuts, cotton, corn, cucumber, potato, Bermudagrass, millet, sorghum, soybean) caused little or no effect compared to artificial diet. Fall armyworm larvae fed for two days on cowpeas were twice as tolerant to diazinon, metamidophos, and methyl parathion as those fed on soybeans, one of the less active plant inducers of the enzyme.

Induction of GST also occurs in deciduous tree-feeding insects. Lindroth (25) have demonstrated that GST activities in the luna moth (*Actias luna*) larvae fed black walnut, butternut and shagbark hickory were 2 to 3-fold higher than in those fed paper birch.

Several allelochemical inducers of GST in fall armyworm larvae (51, 52) did not induce GST in diamondback moth larvae. Among the host plants investigated, rape was most active in inducing GST in diamondback moth larvae (53).

GST activity was significantly higher in cereal aphids, *Sitobion avenae* (F.), fed on the moderately resistant wheat variety, Grana, than in those fed on the susceptible variety, Emika (24). Furthermore, the activity of GST in aphid tissues was significantly correlated with the concentration of allelochemicals in the wheat on which they had fed (24).

Host plant did affect larval detoxification enzyme activity in both the resistant and susceptible strain of *Platynota idaeusalis*. Glutathione transferase and esterase activities, both implicated in *P. idaeusalis* resistance to azinphosmethyl, varied significantly between strains and among hosts. Diets of apple and plantain appeared to inhibit both enzyme systems compared to artificial diet in both insect strains (10).

Hunter *et al.* (19) determined that an apple allelochemical, phloridzin, influenced detoxification activities of larval *P. idaeusalis*. Phloridzin decreased GST activity in both susceptible and resistant *P. idaeusalis*. Also, phloridzin inhibited esterase and aniline hydroxylation of the susceptible larvae, but induced higher esterase activity in resistant larvae.

Relationship between insecticide toxicity and host plants (Allelochemical variation)

Detoxification mechanisms discussed in previous section are often very important for insecticide resistance. Because of the interaction of those plant chemical with detoxification mechanisms it is important to review the evidences that plant chemicals can change patterns of insecticide resistance. Furthermore, due to the rapidly accelerating cost and difficulty in discovering and registering new pesticides, plus the danger that the few pesticides that are presently available will become ineffective because of resistance, preserving pest susceptibility to currently available pesticides is valuable until we have other IPM-compatible control measures. Thus, it is important to consider what factors influence the loss of pesticide susceptibility and to obtain a basic understanding of non-genetic influences (e.g., diet, age, development, temperature, nutrients) on the expression of insecticide resistance. For instance, plants can influence the toxicity of insecticides to herbivorous insects indirectly by inducing higher activities of insecticide-detoxifying enzymes or inhibiting these enzymes by limiting the energy available to the insects to perform detoxification reactions (6). Furthermore, the diversity and variability in composition and concentration of plant allelochemicals (e.g., plant variety, growth condition, plant part, and season) may impose a corresponding phenotypic and genotypic diversity and flexibility on detoxifying capabilities of the insects (6).

It has long been known that feeding on certain host plants can alter the susceptibility of the herbivore to insecticides (4, 54). This altered response to insecticides is often due to a direct induction of the insect's detoxification system by exposure to plant chemicals. There is evidence that herbivorous insects metabolize and detoxify insecticides using the same enzymes that are involved in the metabolism of ingested plant allelochemicals (2, 5). Furthermore, induction of a detoxification enzyme system as a result of feeding on particular host plants can alter the susceptibility of insects to pesticides (4, 5, 8, 11, 30, 38, 48, 49, 54).

Brattsten *et al.* (8) reported that some naturally occurring substances in host plants increased the activity of mixed function oxidases, thereby reducing the susceptibility of larvae of southern armyworm, *Spodoptera eridania* (Cramer), to insecticides. Plant secondary chemicals have been shown to have an effect on toxicity of azinphosmethyl (4, 53). The concentration of phloridzin, a major apple allelochemical (18, 20), in artificial diet changed *P. idaeusalis* susceptibility to azinphosmethyl (19). Susceptible third instar larvae fed artificial diet were even more susceptible to azinphosmethyl in the presence of phloridzin, while resistant larvae fed artificial diet with or without phloridzin did not change in their responses to azinphosmethyl (19).

The susceptibility of the southern armyworm to arsenicals was influenced when different host-plant foliage was treated and fed to larvae (30, 44). Brattsten *et al.* (8), working with the same species, found that mixed-function oxidases were induced rapidly by a variety of allelochemicals. Larvae with induced activity were less susceptible to the toxic tobacco alkaloid nicotine.

Feeding on peppermint induced the midgut polysubstrate monooxygenase (PSMO) activity of the variegated cutworm, *Peridroma saucia* (Hubner), up to 45-fold compared with activity in larvae fed a basic control diet (54). Larvae given peppermint leaves for 2 days were less susceptible to a 0.5% carbaryl treatment than bean leaf-fed larvae exposed to a 0.1% dose. They suggested the possibility that plant species differ in the degree to which they stimulated such enzymes and that an insect's ability to detoxify insecticides may depend on the nature of its host plant (54). Berry *et al.* (4) reported that tolerance to acephate, methomyl, and malathion was greater in variegated cutworm larvae fed peppermint leaves than in those fed bean leaves.

Larvae of fall armyworm, *Spodoptera frugiperda* (J. E. Smith), reared on millet were 6-fold more susceptible to trichlorfon than larvae reared on bermudagrass, corn, cotton or soybean, while larvae reared on bermudagrass and millet were more susceptible to carbaryl and permethrin than larvae reared on corn, cotton, or soybean (47). In tests with eight insecticides, Yu (48) found that fall armyworm larvae were more tolerant after feeding on corn, the strongest inducer among ten hosts tested, than on soybean leaves, one of the least active inducers. In addition, fall armyworm larvae fed for two days on cowpeas were twice as tolerant to diazinon, methamidophos, and methyl parathion as those on soybeans. Among last instar cabbage looper, *Trichoplusia ni* (Hubner), larvae fed peppermint, alfalfa, broccoli, cabbage, or artificial diet, only peppermint fed larvae had a four-fold increase in midgut aldrin epoxidase activity. Bioassays of induced larvae indicated that tolerance to carbaryl and methomyl was greater than with larvae fed the other plants (11).

Experiments conducted by Kennedy (21) with corn earworm, *Helicoverpa zea* (Boddie), larvae and one tomato allelochemical (2-tridecanone), which plays an important role in the resistance of wild tomato to *Manduca sexta* (L.) and Colorado potato beetle, *Leptinotarsa decemlineata* (Say), showed an induction of mixed function oxidase activity in corn earworm larvae in the presence of this compound. Bioassays of induced larvae indicated an enhanced ability of the insect to metabolize carbaryl (21). He demonstrated an adverse interaction between plant resistance and chemical control wherein the phytochemical responsible for resistance to one pest species, at concentrations present in resistant plants, induces insecticide tolerance in another pest species on the same crop. Moreover, treatment of the tobacco budworm, *Heliothis virescens* F., larvae with 2-tridecanone resulted in increased tolerance to diazinon (39). They also found that tobacco budworm larvae were over four-fold more tolerant to diazinon when fed leaves of wild tomato than when fed artificial diet (39).

Third instar corn earworm larvae fed on a haricot bean diet were significantly less susceptible to topically applied cis-cypermethrin than larvae fed a wheat germ diet (31). Larvae fed on an alfalfa diet were of intermediate susceptibility. Likewise, larvae fed on the wheat germ diet were approximately twice as susceptible to topically applied carbaryl as those fed on the haricot been diet. Furthermore, sixth instar corn earworm larvae fed on diet containing coumarin required 7.5 times as much carbaryl to achieve the same LD_{50} as those fed on a control diet (31).

Muehleisen *et al.* (35) investigated the effects of cotton plant allelochemicals fed to corn earworm larvae on their response to insecticides and levels of detoxifying enzymes. They reported increased tolerance to methyl parathion in 6-day-old corn earworm larvae fed a cotton flower bud diet. Their data suggested that the response of insects to insecticides may be greatly modified by the presence and concentration of host plant allelochemicals (35).

Abd-Elghafar *et al.* (1) found that third-and fifth-instar tobacco budworm larvae became less susceptible to methyl parathion after one day of feeding on wild tomato or peppermint plants compared to larvae fed on artificial diet. Furthermore, fifth-instar budworm larvae fed wild tomato leaves were more tolerant to methyl parathion than those fed peppermint leaves, whereas, overall, third-instar larvae were less tolerant than fifth-instar larvae (1).

Susceptibility of western corn rootworm, *Diabrotica virgifera virgifera* LeConte, adults to aldrin increased seven or nine-fold when maintained on squash blossom and sunflower, respectively, instead of corn (42). Northern corn rootworm, *Diabrotica barberi* Smith & Lawrence, exhibited only slight modification of aldrin susceptibility among the three host diets (corn, squash, sunflower) (42).

In another coleopteran, the toxicity of permethrin was significantly greater to Colorado potato beetle reared on eggplant than to those reared on tomato (14).

Berry *et al.* (3) determined that larvae of gypsy moth, *Lymantria dispar* (L.), reared on Douglas-fir were significantly more tolerant to both topically and orally administered diflubenzuron than were those raised on white alder.

Hinks and Spurr (19) found that host plants can significantly affect the susceptibility of neonate migratory grasshoppers, *Melanoplus sanguinipes* (F.), to deltamethrin and dimethoate. The ratios between the highest and lowest LD_{90}'s among the cereal cultivars examined were 3.5:1 for deltamethrin in grasshoppers reared on 'Cascade' oats and 'Gazelle' rye, and 1.6:1 for dimethoate in grasshoppers fed 'Bonanza' barley and 'Fidler' oats; such differences would represent substantial differences in the amount of insecticide required in the field.

Robertson *et al.* (40) examined the effects of host plants and moth genotypes on susceptibility to azinphosmethyl in the light brown apple moth, *Epiphyas postvittana* (Walker). Their results demonstrated that resistant larvae fed black raspberry and susceptible larvae fed on artificial diet were similar. Moreover, resistant larvae fed black raspberry were significantly less resistant than resistant larvae fed apple, artificial diet, broom, or gorse, whereas susceptible larvae reared on artificial diet were significantly more tolerant compared with susceptible larvae reared on any of the host plant species.

Platynota idaeusalis is a highly polyphagous species, which utilizes at least 17 plant families (32). Larval populations have been found on a wide variety of herbaceous plant species beneath host apple, pear, peach, nectarine, and cherry trees (22). Therefore, there is a high probability for this insect to encounter and deal with an abundance of plant allelochemicals. Knight and Hull (22) noted that knowledge of *P. idaeusalis* biology outside of apple, on ground cover within orchards, would be extremely useful in an IPM program. If the same enzymes that are involved in the metabolism of plant allelochemicals are also involved in metabolism and detoxification of pesticides (2, 19, 35), then this maybe a major non-genetic influence on resistance. Non-overlap of 95% confidence limits at the LD_{50} level suggested that the overall effect of host plants on toxicity of azinphosmethyl to *P. idaeusalis* was significant (9, 10). When susceptible larvae of *P. idaeusalis* were fed different hosts, they were subsequently found to have different levels of susceptibility to azinphosmethyl.the resistant strain responded to artificial diet and plantain with a large increase in the level of resistance compared to the susceptible strain, demonstrating that resistance in *P. idaeusalis* was genetically based. Resistant larvae appear resistant if they eat plantain or dandelion, but appear susceptible if they eat black raspberry or, to some extent, apple. In contrast, susceptible larvae appear susceptible if they eat black raspberry or plantain, but appear resistant if they eat dandelion; apple is intermediate in effect (9). The results of this study differ in part from those of a similar study by Robertson *et al.* (40) on another tortricid species, light brown apple moth. They found that susceptible larvae reared on artificial diet were significantly more tolerant compared with susceptible larvae on any of the natural host plant species they tested. Because of the many differences between these experiments, however, comparisons between studies must be approached cautiously. Among many factors that could explain the different results are the following: different insect species, weight and instar of the larvae at the time bioassays, variety and root stock of apple trees, growth stage of plants, nutrients, number of days that the larvae were allowed to feed on the hosts, temperature, and composition of artificial diet (19, 28, 36, 46, 50, 55). If environmental factors have relatively important effects, as these results suggest, then differences in susceptibility between larvae or adults collected from different field populations must be based on genetic and/or environmental differences. Thus, bioassays of field-collected adults, which eliminate laboratory rearing, may not provide useful information and could produce misleading conclusions about resistance (19, 40). Since assays of field-collected insects are efficient and widely used to monitor resistance, the potential types of environmental effects, environment x genotype interactions, and their effect on resistance merit further consideration (36). Choice of larval host plant could have a dramatic effect on the apparent OP resistance of *P. idaeusalis*. It appears that feeding on apple and black raspberry plants may be inhibiting the genetic resistance present in the resistant *P. idaeusalis* strain. In contrast, susceptible *P. idaeusalis* appear resistant if they feed on apple or dandelion (9).

Hunter *et al.* (19) studied the effect of phloridzin, a major apple allelochemical (18, 19) on the toxicity of azinphosmethyl to susceptible and resistant *P. idaeusalis*. In their assay of third instar resistant and susceptible *P. idaeusalis* strains by diet incorporation of azinphosmethyl, they showed that mortality of third instar susceptible larvae was higher in the presence of phloridzin in the diet. Third instar resistant larvae reared on artificial diet with or without phloridzin were not significantly different in their responses to azinphosmethyl.

The effects of genotype, host plant, and age on susceptibility to acephate in the B biotype of sweetpotato whitefly, *Bemisia tabaci* (Gennadius) were examined by Omer *et al.* (36). In contrast to studies discussed above, they found that differences in susceptibility to acephate between the resistant and susceptible colonies were genetically based and that responses of each colony were not significantly affected by differences in the three host plants studied (pole bean, tomato, zucchini).

Conclusions

Differencial toxicity of particular allelochemicals to phytophagous insects can now be explained on the basis of differences in the enzyme activity of insects (28). Differences in enzyme activity may be genetically linked, but may also occur due to changes in individual insects as a consequence of a host of intrinsic and extrinsic factors. The role of particular enzyme systems in the detoxication and comparative toxicity of specific allelochemicals needs further study. We know little about how all enzyme systems are altered by extrinsic factors such as diet (28). In order to be able to reduce the problem of resistance it is important to monitor pest populations for evidences of resistance. Accurate results require the control of many variables as possible when conducting bioassays. The examples discussed above demonstrate the potential effect of plant chemicals in the insect diet on patterns of insecticide resistance. Therefore, whenever possible we should attempt to control for this diet effects. For many pests it is difficult to control the diet. Even in cases where we got the bioassay from just one plant species, the chemical variation among the individual host plant could affect resistance. Thus, bioassays of field-collected adults, which eliminate laboratory rearing, may not provide useful information and could produce misleading conclusions about resistance (19, 40). Since assays of field-collected insects are efficient and widely used to monitor resistance, the potential types of environmental effects, environment and genotype interactions, and their effect on resistance merit further consideration (36). Deriving appropriate rates of insecticides for one host plant species and extending these rates to related host plants, as is current practice, probably results in instances of excessive or inadequate use of pesticides. The efficacy of insecticides might be increased by adjusting rates of application to match pest species response on specific host plants (16).

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