plant enzyme (Rexova-Benkova and Markovic, 1976). The spectrophotometric assay would thus be set up at lower pH and an indicator dye with the appropriate pK_a selected. For example, those forms of PME with optimal activity at pH 5 could be conveniently assayed with bromocresol green as the indicator dye (Rexova-Benkova and Markovic, 1976; Waser, 1966). The potential adaptibility of the spectrophotometric assay should make it useful for characterizing the fungal pectin degrading enzymes important in plant disease (Cooper, 1983).

Registry No. PME, 9025-98-3; pectin, 9000-69-5.

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Influence of Extracts from Soybean (*Glycine max* (L) Merr.) Leaves on Hydrolytic and Glutathione *S*-Transferase Activity in the Soybean Looper (*Pseudoplusia includens* (Walker))

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Methanol extracts of a resistant (PI227687) and a susceptible (Davis) soybean variety were incorporated into artificial diets that were fed to larvae of the soybean looper *Pseudoplusia includens* (Walker). Homogenates of insects fed on the diet containing the PI227687 extract generally had significantly lower rates of hydrolysis of *cis*-permethrin and fenvalerate, and significantly higher rates of conjugation of 1-chloro-2,4-dinitrobenzene relative to those insects fed on diets containing the Davis extract. Minor differences were noted for *trans*-permethrin and α-naphthyl acetate hydrolysis for insects fed on the two extract diet types. The rate of hydrolysis of acephate to methamidophos changed slightly and varied according to the leaves from which the extracts were made. Incorporation of coumestrol, a flavonoid occurring in the PI227687 extract, into the diet also resulted in lower rates of hydrolysis of *cis*-permethrin, fenvalerate, and acephate that were similar to those found for insects fed on diets containing the PI227687 extract.

INTRODUCTION

Host plant resistance and insecticide treatment are frequently combined as a strategy for insect control in integrated pest management programs (Adkisson and Dyck, 1980). However, the type of host plant fed upon by insects prior to treatment can affect insecticide toxicity (Maxwell, 1972). One possible explanation for this occurrence involves the modification of detoxification enzyme activity by plant allelochemicals. Plants have been shown to contain compounds that can either induce (Brattsten et al., 1977; Berry et al., 1980; El-Sebae et al., 1981; Farnsworth et al., 1981; Moldenke et al., 1983; Yu, 1982, 1983; Yu et al., 1979) or depress (Dowd et al., 1983a; Yu (1983) enzyme systems that may be involved in insecticide metabolism. Results of both laboratory (Dowd et al., 1983a) and field (Kea et al., 1978) studies have suggested that larvae of the soybean looper *Pseudoplusia includens* (Walker) fed on resistant soybean varieities may have altered levels of enzymes involved in insecticide metabolism.

While the effects of plant toxins on the induction or repression of microsomal mixed-function oxidases have received a great deal of attention, studies on the action of these plant toxins on hydrolytic and conjugative systems have been relatively limited (for review, see Dowd et al., 1983b). Hydrolytic and conjugative enzymes play a variety of roles in the metabolism of many insecticides, including pyrethroids and organophosphates (Dauterman, 1976; Yang, 1976). Therefore, we examined how the metabolism of several insecticides, and related substrates, was influenced by feeding larvae of *P. includens* on extracts of resistant and susceptible soybean varieties.

PROCEDURE

Chemicals. Radiolabeled *cis*- and *trans*-permethrin and 3-phenoxybenzyl alcohol (^{14}C label on the methylene carbon of the 3-phenoxybenzyl alcohol, sp act. 57 mCi/mmol) were a gift from FMC. Radiolabeled acephate (^{14}C label on the *S*-methyl group, sp act. 4.77 mCi/mmol) was

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provided by Chevron Chemical Co. Fenvalerate (^{14}C label on the chlorophenyl group of the acid moiety, sp act. 8.2 mCi/mmol) and unlabeled fenvalerate were provided by Shell Development Co. The radiolabeled fenvalerate acid was produced by enzymatic hydrolysis and separated by reversed-phase thin-layer chromatography (TLC) (C-18, Whatman) using methanol as a solvent. Fenvalerate (Shell) and the 2-(*p*-chlorophenyl)-3-methylbutyric acid (acid moiety of fenvalerate) (Frinton Laboratories) were used as TLC standards. The α-naphthyl acetate (ANA) was from Sigma, the 1-chloro-2,4-dinitrobenzene (CDNB) was from Aldrich, and the coumestrol was from Kodak. All other chemicals were of reagent-grade quality.

Insects and Diets. Insect rearing and diet preparation were performed as described previously (Dowd et al., 1983a). Methanol extracts were prepared from mature leaves of susceptible (Davis) and resistant (PI227687) soybean varieties (Kilen et al., 1977; Luedders and Dickerson, 1977), for the first field season (referred to as "total leaf extracts"), and from those leaves shown to contain the greatest amount of resistance (fully unfurled leaves L4 and older; Reynolds and Smith, 1985) the second season (referred to as "selected leaf extracts"). Methanol extracts of PI227687 and Davis were used for this study, since the methanol extracts of PI227687 contain the resistance factors (Smith and Fischer, 1983). After the methanol was evaporated and the extract redissolved in water, the extracts were incorporated into warm diet, as reported previously (Dowd et al., 1983a). Coumestrol was added to diets (in Me_2SO) at a rate approximating the level that occurs in resistant varieties (0.01%) (Smith, 1985). Newly hatched *P. includens* larvae were introduced onto each diet and feeding last instar larvae (day 2; Shour and Sparks, 1981) were used for all assays.

Enzyme Assays. Whole-body homogenates, used for all studies, were prepared by homogenizing larvae (1/mL) in phosphate buffer (0.1 M, pH 7.4), and then centrifuging the homogenate at 1000*g* (5 min). The resulting supernatant was diluted and then used for the acephate and ANA assays or filtered (0.45-μm filter) prior to use (Dowd and Sparks, 1984) for the pyrethroid and glutathione *S*-transferase assays. The pyrethroids (5 μM in 100 μL) were incubated at 35 °C for 20 min with homogenates containing ca. 0.05 mg of protein for the *cis*-permethrin and fenvalerate assays and 0.01 mg of protein for the *trans*-permethrin assays. The amount of hydrolysis of the radiolabeled *trans*-permethrin, *cis*-permethrin, and fenvalerate was determined by solvent partitioning using methanol and dodecane (Dowd and Sparks, 1984, as described for *trans*-permethrin and the phenoxybenzyl alcohol product). The effectiveness of the partition for *trans*-permethrin, *cis*-permethrin, and fenvalerate in the dodecane phase was 86.8 ± 1.5%, 96.1 ± 0.2%, and 95.0 ± 0.8%, respectively. The effectiveness of the partition for the 3-phenoxybenzyl alcohol and the fenvalerate chlorophenyl acid (2-(*p*-chlorophenyl)-3-methylbutyric acid) in the methanol buffer phase was 81.2 ± 1.9% and 75.9 ± 1.9%, respectively. Simultaneous equations were used to determine the amount of pyrethroid metabolites that were produced in each case. The hydrolysis of acephate to methamidophos was determined by a modification of the method of Rose and Sparks (1984). Acephate (5 μM) was incubated with the homogenate (0.5 mg of protein) for 1 h at 35 °C. The reaction was terminated by the addition of cold ethanol (100 μL, 4 °C) followed by vortexing. Aliquots (50 μL) were spotted on TLC plates (Whatman LK5DF) and developed in ammonium hydroxide–benzene–2–propanol (1:6:12). The plates were scraped, and metabolism was quantitated by liquid scintillation counting. Acephate and methamidophos were used as chromatographic standards. General esterase and glutathione *S*-transferase activity was monitored with use of ANA (2.5 mM in 1.1 mL for 20 min at 35 °C, ca. 0.01 mg of protein) and CDNB (1 mM in 2 mL for 10 min at 35 °C, ca. 0.01 mg of protein) as substrates, respectively (Sparks et al., 1979; Habig et al., 1974). For all assays, the homogenates were appropriately diluted so that the rate of hydrolysis or conjugation was linear during the course of the assays. All assays were run on pooled samples of three larvae replicated three times on each of two separate occasions. Protein concentration was determined by using the Bio-Rad packaged assay, which is based on the method of Bradford (1976).

Table I. Effects of Diets Containing Extracts from Resistant (PI227687) and Susceptible (Davis) Soybean Varieties on the Metabolism of Compounds by Homogenates of *Pseudoplusia includens* Larvae

compd	metabolism[a] Davis	metabolism[a] PI227687	% change[b]
	Total Leaf Extracts		
trans-permethrin	64.8 ± 3.2	73.2 ± 1.6	+13.0
cis-permethrin	1.9 ± 0.1	1.4 ± 0.1	−26.3*
fenvalerate	2.1 + 0.1	1.5 + 0.1	−28.6*
acephate	2.2 ± 0.4	2.6 ± 0.3	+18.2*
ANA[c]	1293.3 ± 37.2	1309.5 ± 10.5	−1.3
CDNB[c]	27.1 ± 0.6	39.7 ± 1.2	+46.5*
	Selected Leaf Extracts		
trans-permethrin	47.6 ± 1.5	47.5 ± 0.8	+0.2
cis-permethrin	3.5 ± 0.1	2.8 ± 0.3	−20.0*
fenvalerate	2.2 ± 0.1	1.8 ± 0.1	−18.2
acephate	1.5 ± 0.1	1.3 ± 0.1	−13.3
ANA[c]	1143.0 ± 37.8	1196.1 ± 54.3	+4.6
CDNB[c]	29.1 ± 0.3	37.4 ± 0.3	+28.5*

[a] Values for hydrolysis are mean ± standard error for two trials of three pooled larvae of two replicates each; values for all pyrethroids and acephate hydrolysis are in terms of pmol/min per mg of protein, while ANA and CDNB metabolism are in terms of nmol/min per mg protein. [b] Percentages followed by an asterisk indicate means in rows are significantly different at $p \leq 0.05$ by t-test analysis. [c] ANA = α-naphthyl acetate, CDNB = 1-chloro-2,4-dinitrobenzene.

RESULTS

The rates of hydrolysis of *trans*-permethrin and ANA were similar for larvae fed on the diets containing extracts of the Davis and PI227687 soybean varieities, for both the diets containing total leaf extracts and those containing selected leaf extracts (Table I). The rate of hydrolysis of both *cis*-permethrin and fenvalerate was lower in homogenates of larvae fed on diets containing PI227687 leaf extract than in homogenates of larvae fed on diets with Davis extract, in both total leaf and selected extract studies (Table I). The rate of hydrolysis of acephate was higher in homogenates of larvae fed on total leaf diets containing PI227687 extract than in homogenates of larvae fed on diets with Davis extract (Table I). However, the opposite trend was noted when the extracts were from selected leaves. Conversely, the rate of conjugation of CDNB was higher in homogenates of larvae fed on diets containing PI227687 extract than in homogenates of larvae fed on diets with Davis extract, in both total and selected leaf extract studies (Table I).

The rates of hydrolysis of *trans*-permethrin and ANA were similar in homogenates of larvae fed on control and coumestrol-containing diets (Table II). However, the rates of hydrolysis of *cis*-permethrin and fenvalerate were lower in homogenates of larvae fed on the diets with coumestrol

Table II. Effects of Diets Containing Coumestrol on the Metabolism of Compounds by *Pseudoplusia includens* Larvae

compd	rate of metabolism[a] control	+coumestrol	% change[b]
trans-permethrin	36.6 ± 3.0	34.7 ± 5.5	-5.2
cis-permethrin	1.7 ± 0.1	1.4 ± 0.1	-17.6*
fenvalerate	2.1 ± 0.1	1.8 ± 0.1	-14.3
acephate	1.9 ± 0.1	1.4 ± 0.1	-26.3*
ANA[c]	873.9 ± 20.3	908.9 ± 44.3	+4.0
CDNB[c]	30.1 ± 0.9	26.6 ± 0.7	-11.6

[a] Values are in terms of pmol/min per mg of protein for the pyrethroid and acephate hydrolysis and nmol/min per mg of protein for ANA and CDNB; values are means of three replicates of assays performed on four separate occasions (two for acephate) (pools of three larvae) ± the standard errors. [b] Percentages followed by asterisks indicate means in rows are significantly different at $p \leq 0.05$ for t-test analysis. [c] ANA = α-naphthyl acetate and CDNB = 1-chloro-2,4-dinitrobenzene.

than for larvae fed on the control diets (Table II). These differences are of a nearly equal magnitude to those seen for both of the extract studies when insects were fed on diets containing PI227687 vs. Davis extracts. As observed with the selected leaf extracts, the rate of hydrolysis of acephate was lower in homogenates of larvae fed on the diets containing coumestrol than for larvae fed on the control diets (Table II). In contrast to both leaf extract studies, the rate of conjugation of the glutathione *S*-transferase substrate was lower in homogenates of larvae fed on diets with coumestrol than for larvae fed on the control diets (Table II).

DISCUSSION

The rate of hydrolysis of *trans*-permethrin was greater than that of *cis*-permethrin in all cases in this study, which is the typical pattern for insects (Casida, 1983; Soderlund et al., 1983). In contrast to the results for *trans*-permethrin, the rates of hydrolysis of *cis*-permethrin and fenvalerate were lower by 18.2–28.6% for larvae feeding on diets containing PI227687 extract than for larvae feeding on diets containing Davis extract (Table I). Compared to *trans*-permethrin, hydrolysis is typically of lesser overall importance in total metabolism of *cis*-permethrin by insects (Casida, 1983; Soderlund et al., 1983). Therefore, the effect of the insect-resistant soybean variety on the hydrolysis, and hence toxicity of cis–trans mixtures of permethrin typically used in the field, may be expected to change only slightly. Indeed, little difference in the toxicity of permethrin (cis–trans (40:60) has been noted between *P. includens* larvae fed on leaves of PI227687 and the insect-susceptible soybean variety Bragg (Rose et al., 1985). Like *cis*- and *trans*-permethrin, fenvalerate is also subject to ester hydrolysis in *P. includens* (Dowd and Sparks, 1986). Thus, desirable increases in the toxicity of fenvalerate to *P. includens* feeding on PI227687 could potentially occur. However, given the limited decrease in the rate of hydrolysis seen herein, the effect should be slight. Indeed, only a slight increase in the toxicity of fenvalerate to *P. includens* larvae fed on leaves of PI227687 vs. Bragg have been noted (Rose et al., 1985).

Little change in the rate of hydrolysis of the general esterase substrate ANA was noted for larvae fed on diets containing either Davis or PI227687 extracts. This trend is in contrast to the slight decrease (ca. 18%) in *p*-nitrophenyl acetate (NPA) hydrolysis reported for midgut homogenates of *P. includens* larvae fed on similarly prepared diets (Dowd et al., 1983a). Thus, the enzymes involved are likely to be different, either for the substrates (ANA vs. NPA) and/or for midgut vs. whole-body homogenates. However, increases in the rate of hydrolysis of ANA have been reported for larvae of *Spodoptera eridania* fed on different host plants and on diets containing plant toxins (Yu, 1983) and for the rate of hydrolysis of NPA by midguts from larvae of *Trichoplusia ni* fed on diets containing extracts from PI227687 (Dowd et al., 1983a).

Acephate owes its insecticidal activity to its conversion to methamidophos (Magee, 1982; Rose and Sparks, 1984). This activation occurs by hydrolysis of the amide linkage of acephate. It is difficult to monitor changes in the hydrolytic metabolism of many organophosphorus compounds since they may potentially inhibit the enzymes responsible for their own metabolism (e.g., malaoxon (Dauterman, 1976)). Thus, changes in acephate hydrolysis are of interest since it is a hydrolytic reaction that can be monitored, and it is also an activation reaction involving an organophosphate. The rate of hydrolysis of acephate (and hence its activation) was significantly higher for larvae fed on diets containing total leaf extract from PI227687 than for larvae fed on diets with Davis extract. Conversely, activity was lower for larvae fed on selected leaf extracts of PI227687 as opposed to the Davis and for those larvae fed on the coumestrol vs. untreated diets. Thus, there can be a large variation in the effects of host plants, possibly due to different levels of allelochemicals that may be present, depending on which leaves are used. The efect on toxicity may also vary, depending on which leaves are fed upon.

In the present study, the greatest effect of host plant variety on enzyme activity was noted for glutathione *S*-transferase as indicated by conjugation of CDNB. A 46.5% higher rate of conjugation was noted for *P. includens* larvae fed on diets containing total leaf extract from PI227687 than for larvae fed on diets with Davis extract. Similarly, a 28.5% higher rate of conjugation was noted for larvae fed on diets with selected leaf extract from PI227687 than for larvae fed on diets with Davis extract. Changes in the activity of glutathione *S*-transferases have also been prompted by feeding on different host plants and on diets containing plant toxins (Yu, 1983). This form of insecticide metabolism is of widespread overall importance, since it may serve in both primary (initial metabolism) and secondary (conjugation of primary metabolites) (Yang, 1976) detoxification. Of all the reactions investigated herein, increased glutathione *S*-transferase activity has the greatest potential for unfavorably altering the toxicity of insecticides used in combination with insect-resistant soybean varieties.

The differences in responses of *P. includens* enzyme systems responsible for acephate hydrolysis in total vs. selected leaf extracts studies suggest that plant compounds influencing insecticide metabolism by *P. includens* may not necessarily be related to those conferring resistance to soybean insects. Although the increased coumestrol content of PI227687 does not appear to be responsible for the observed resistance to insects (Smith, 1985), the similarity in the patterns of response for the hydrolysis of *cis*-permethrin and fenvalerate in the leaf extract studies to those of the coumestrol study suggests that the coumestrol may be at least partially responsible for the observed changes in ester hydrolysis. Thus, both the results with acephate in total vs. selected leaf extract studies, and the similarities in the response of *cis*-permethrin and fenvalerate hydrolysis when insects were fed on diets with PI227687 extracts and coumestrol, suggest that plant allelochemicals in resistant plant varieities that are not directly responsible for conferring resistance in insects may influence the metabolism of xenobiotics. In addition, while

a number of compounds found in plants are known to induce enzymes responsible for insecticide metabolism, as discussed above, this study demonstrates that some plant allelochemicals such as coumestrol that occur at higher levels in an insect-resistant plant variety (PI227687) may not only influence enzymes that metabolize substrates that an insect is not likely to encounter (such as ANA or CDNB) but also influence the metabolism of specific insecticides (here *cis*-permethrin and fenvalerate).

It has previously been suggested that the combination of host plant resistance and insecticide treatment is of benefit since insects often become more susceptible to insecticides (Maxwell, 1972). The results presented herein suggest that changes in the rates of metabolism of insecticides may, in part, be responsible for changes in toxicity of insecticides that have been described for insects feeding on resistant varieties of host plants. The decreases in metabolism may potentially be the result of inhibitory effects of plant toxicants on insecticide metabolizing enzymes or disruption of regulatory mechanisms responsible for the synthesis or degradation of these enzymes.

Information from this study indicates that no generalizations can be made concerning the response of hydrolytic or conjugative enzymes in insects feeding on insect-resistant host plant varieties. The differential response is to be expected, since apparently minor structural differences can substantially alter the susceptibility of a compound to metabolism by an enzyme. For example, cis and trans isomers of permethrin appear to be hydrolyzed by different enzymes (Abdel Aal and Soderland, 1980; Ishaaya and Casida, 1980). A variety of responses have been reported for the inducton of different forms of monooxygenases, which are also important in insecticide metabolism (Nakatsugawa and Morelli, 1976). Investigation of monooxygenase activity in insect species where they play a major role in insecticide metabolism (such as *S. eridania*) would also be of interest. However, as suggested by the present study, factors conferring plant resistance may not necessarily be responsible for changes in insecticide metabolism. An understanding of the interactions between plant resistance and insecticides, with regard to both possible effects of plant toxins on insecticide metabolism or the effects of insecticides on plant toxin metabolism, may provide useful insights into past and future efforts directed at improving integrated pest management strategies.

Abbreviations Used: ANA = α-naphthyl acetate; CDNB = 1-chloro-2,4-dinitrobenzene; NPA = *p*-nitrophenyl acetate.

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Registry No. ANA, 830-81-9; CDNB, 97-00-7; *trans*-permethrin, 61949-77-7; *cis*-permethrin, 61949-76-6; fenvalerate, 51630-58-1; acephate, 30560-19-1; coumestrol, 479-13-0; esterase, 9013-79-0; glutathione *S*-transferase, 50812-37-8.

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