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**EFFECTS OF DIET ON SUSCEPTIBILITY TO
AZINPHOSMETHYL OF THE TUFTED APPLE BUD MOTH
PLATYNOTA IDAEUSALIS (LEPIDOPTERA: TORTRICIDAE)**

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Abstract. We determined the effect of diet on insecticide resistance in two genetically similar strains (one susceptible and one resistant to azinphosmethyl) of the tufted apple bud moth (*Platynota idaeusalis*). Susceptibility to azinphosmethyl was studied by bioassay of larvae fed a synthetic diet and four different host plant species: apple (*Malus domestica*), cv Red Yorking; black raspberry (*Rubus occidentalis*); broad-leaved plantain (*Plantago major*); and dandelion (*Taraxacum officinale*). Susceptible-strain larvae fed dandelion were significantly more tolerant to azinphosmethyl than those fed with other diets. Resistant-strain larvae reared on black raspberry were not significantly different from apple-fed larvae, but were more susceptible than those raised on plantain, dandelion, or artificial diet. Analysis of dose-mortality regressions suggests that different mechanisms may be induced by hosts in the susceptible strain, but the resistant strain responds to host chemistry by using different activity levels of the same enzymatic mechanism. Overall effect of host plants on toxicity of azinphosmethyl to *P. idaeusalis* was significant. To preserve susceptibility of *P. idaeusalis* to azinphosmethyl, abundance and number of host plants present in orchard ground cover should be taken into account.

Key Words: Apple, azinphosmethyl, diet, host-insect interaction, host-plants, plant allelochemicals, Lepidoptera, *Platynota idaeusalis*, resistance, Tortricidae, toxicity, tufted apple bud moth.

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EFECTOS DE LA DIETA EN LA SUSCEPTIBILIDAD AL AZINPHOSMETHYL DE LA POLILLA DE LA MANZANA *PLATYNOTA IDAEUSALIS* (LEPIDOPTERA: TORTRICIDAE)

Resumen- El efecto de la dieta sobre la resistencia a un insecticida por dos razas similares genéticamente (una susceptible y una resistente a azinfosmetil) de la "polilla de la manzana" *Platynota idaeusalis* (Walker) fue examinada. La susceptibilidad a azinfosmetil fue estudiada mediante bioensayos de larvas alimentadas separadamente con una dieta artificial y cuatro diferentes especies de plantas hospederas: manzana, *Malus domestica* cv Red Yorking; mora, *Rubus occidentalis*; llantén, *Plantago major*; y diente de león, *Taraxacum officinale*. Las larvas de la raza susceptible alimentadas de diente de león fueron significativamente más tolerantes a azinfosmetil que las larvas que se alimentaron con otras dietas. Las larvas de la raza resistente criadas en mora no fueron significativamente diferentes de las larvas alimentadas en manzana, pero fueron más susceptibles que las larvas criadas en llantén, diente de león, o dieta artificial. Los análisis de regresión de dosis-mortalidad sugieren que diferentes mecanismos enzimáticos pueden ser inducidos por los hospederos en la raza susceptible, pero que la raza resistente responde a lo aleloquímicos de la hospedera con diferente niveles de actividad del mismo mecanismo enzimático. El efecto global de las plantas hospederas en la toxicidad de azinfosmetil a *P. idaeusalis* fue significativo. El presente estudio sugiere que es necesario tener en cuenta la abundancia y el número de plantas hospederas presentes en la cobertura vegetal de la plantación, para preservar la susceptibilidad de *P. idaeusalis* al azinfosmetil.

Palabras clave: Aleloquímicos-plantas, interacción hospedera-insecto, manzana, polilla de la manzana, resistencia, toxicidad, plantas-hospederas.

INTRODUCTION

Development of resistance to the organophosphate (OP) insecticide azinphosmethyl, used in apple orchards for the past 30-40 years, is believed to be one of the major causes of the insurgence of the tufted apple bud moth to a pest status (Meagher Jr. and Hull 1986, Biddinger 1993).

The tufted apple bud moth (*Platynota idaeusalis*) is a highly polyphagous species, which feeds on at least 17 plant families (McPheron and Carlini 1992). Larval populations have been found on a

wide variety of herbaceous plant species commonly found beneath crop hosts such as apple, pear, peach, nectarine, and cherry trees (Knight and Hull 1988). Therefore, there is a high probability that this insect will encounter and deal with an abundance of plant allelochemicals. It is important to consider which factors influence loss of OP susceptibility and to obtain a basic understanding of non-genetic influences (i.e., varying with 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 (Brattsten 1988).

If the same enzymes involved in metabolism of plant allelochemicals are also involved in metabolism and detoxification of pesticides, then this may be a major non-genetic influence on resistance (Ahmad *et al.* 1986, Rosenheim *et al.* 1996). Feeding on certain host plants can alter the susceptibility of the herbivore to insecticides (Yu *et al.* 1979, Tan and Guo 1996). This altered response to insecticide 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 (Brattsten 1979). Furthermore, induction of a detoxification enzyme system, as a result of feeding on particular host plants, may alter the susceptibility of insects to pesticides (Markos and Campbell 1943, Yu 1982a, b).

Robertson *et al.* (1990) examined the effects of host plants and moth genotypes on susceptibility to azinphosmethyl in the light brown apple moth (*Epiphyas postvittana*). Their results demonstrated that resistant larvae fed black raspberry and susceptible larvae fed an artificial diet were similar. Moreover, resistant larvae fed black raspberry were significantly less resistant than resistant larvae fed apple, an artificial diet, broom, or gorse, whereas susceptible larvae reared on an artificial diet were significantly more tolerant compared with susceptible larvae reared on any of the host plant species.

The concentration of phloridzin, a major apple allelochemical, in artificial diets changed *P. idaeusalis* susceptibility to azinphosmethyl (Hunter and Hull 1993, Hunter *et al.* 1994b). Susceptible third instar larvae fed an artificial diet were even more susceptible to azinphosmethyl in the presence of phloridzin, while resistant larvae fed artificial diets with or without phloridzin did not change their response to azinphosmethyl (Hunter *et al.* 1994a). However, there is no information about the change of susceptibility of *Platynota idaeusalis* fed with different host plant species to azinphosmethyl. The purpose of this work is to examine the interactions between different host plants and azinphosmethyl resistance.

MATERIALS AND METHODS

HOST-PLANTS

The host-plant species Apple (*Malus domestica* Bork: Rosaceae), black raspberry (*Rubus occidentalis* L.: Rosaceae), broad-leaved plantain (*Plantago major* L.: Plantaginaceae), and dandelion (*Taraxacum officinale* Wiggers: Asteraceae), were raised in the greenhouse at Pennsylvania State University, University Park, USA. Apple is an economically important host of *P. idaeusalis*, but the other three species are often present in apple orchards and surrounding vegetation. The apple trees were cultivar Red Yorking on root-stock EMLA7. Black raspberries were obtained from cuttings. The remaining host species were grown from seed in potting soil.

All plants were transplanted to pots filled with Terra Lite Metro-Mix 250R Growing Medium (E. C. Geiger, Harleysville, Pennsylvania). Plants were fertilized every two months with water-soluble 15-30-15 N-P-K fertilizer (4.0 g/L). Plants were watered as needed and grown under a 16-h photophase and ambient relative humidity (60%). Whitefly, thrips, mite and aphid infestations in the greenhouse were controlled by using 2.5% Safer insecticidal soap (50.5% potassium salts of fatty acids, AgroChem, Jamul, California). As a precaution, all host species were treated at the same time. Test plants were selected arbitrarily from a group of individual plants similar in height and phenology. For comparison with previous studies, *P. idaeusalis* larvae were also reared

on a lima bean-based artificial diet under identical environmental conditions (Meagher 1985).

INSECT CULTURES

Two genotypes of *P. idaeusalis* were employed in this experiment. One of them, susceptible to azinphosmethyl, has been maintained in continuous culture on a lima bean-based artificial diet for over ten years without insecticide selection. The second genotype, resistant to azinphosmethyl, is a near isogenic line derived from resistant larvae collected in an apple orchard in Adams County, Pennsylvania, USA, which shares approximately 97% the same genetic background with the susceptible strain. To generate the resistant strain, we used the protocol for diet-incorporated azinphosmethyl selection bioassay of neonates followed by Biddinger (1993). Briefly, formulated azinphosmethyl was applied (0.5 mL) in diluted aqueous solution to the surface of 7-10 mL of lima bean-based synthetic diet in plastic cups and allowed to air-dry for 2–3 h. Test larvae were introduced into diet cups in groups of four. Larval exposure period to the treated diet was until pupation or death.

TREATMENT OF INSECTS

Twelve-day-old fourth instar larvae were used for bioassays. Larvae from the resistant strain were generation 16. Larvae had been maintained since hatching on a lima bean-based artificial diet at 26.7°C, 60% relative humidity with a photoperiod of 16:8 (L:D) h in the Department of Entomology, Pennsylvania State University. Twelve-day-old larvae were removed from artificial diet and transferred to one of four host plants: apple, black raspberry, plantain, or dandelion or artificial diet for seven days.

Sleeve cages, (5–10 larvae per cage) were placed on the top of the plant, made of fine pore nylon mesh. Sleeve cages were sealed with parafilm to prevent larval escape. Plants raised in the greenhouse were moved to a walk-in type growth chamber at the Department of Entomology, Pennsylvania State University, set at 26.7°C, day length: 16:8 (L:D) h and 50-80% relative humidity. After 7 days, larvae were removed from their respective diets for insecticide bioassays.

AZINPHOSMETHYL BIOASSAYS

Ten bioassays (2 strains x 5 diets) were done by topical application using technical grade azinphosmethyl (91% active ingredient) (Miles Company, Kansas City, Missouri) dissolved in acetone. Test larvae were removed from each diet and weighed individually. A minimum of 20 larvae were tested at each dose of azinphosmethyl within each bioassay. The larvae were placed in a petri dish in groups of five doses of azinphosmethyl in acetone to generate dose-response curves. Because larval weight of susceptible ($F = 39.1$; $df = 4, 48$; $P < 0.0001$) and resistant ($F = 77.9$; $df = 4, 48$; $P < 0.0001$) strains differed significantly among hosts, each concentration was converted to a body weight basis (micrograms per milligram body weight) using an average weight among replicates for each bioassay. A minimum of 20 larvae were tested at each dose of azinphosmethyl within each bioassay. One μL of insecticide-acetone solution was applied to the dorsum of each individual using a Hamilton microapplicator. Control larvae (no fewer than 20 larvae per bioassay) were treated with acetone only. Mortality was recorded at 24 h post-treatment. Larvae were considered dead if they were unresponsive to gentle prodding with a pin.

STATISTICAL ANALYSES

LD50 values were calculated using pesticide concentration-mortality data transformed with the probit option of POLO-PC. The difference between two LD50s was considered significant if the 95 % confidence limits did not overlap. Resistance ratios between hosts were calculated by dividing the LD50 of the resistant colony by the LD50 of the susceptible colony on the same host. A likelihood ratio (LR) test of equality for each strain fed different diets was calculated. The test of equality evaluates whether the slopes and intercepts of each line are significantly different (Robertson and Preisler 1992).

RESULTS

Azinphosmethyl toxicity data for susceptible and resistant *P. idaeusalis* larvae reared on different diets are presented in Table 1. A resistance ratio of 3.4 on artificial diet provided baseline evidence of

inter-strain differences. Variation in insecticide susceptibility among diets using the susceptible *P. idaeusalis* strain was significant, as indicated by the non-overlap of 95% confidence limits at the LD50 level. The LD50 values for susceptible *P. idaeusalis* larvae varied by a maximum of about 2.8 fold (LD50 dandelion/LD50 artificial diet). Larvae reared on dandelion were significantly more tolerant than any of the susceptible larvae reared on other diets. Susceptible strain larvae fed dandelion had a LD50 equivalent to resistant larvae on artificial diet. Those susceptible larvae reared on artificial diet were comparable in susceptibility to those reared on black raspberry and plantain. They were only more susceptible than those reared on apple and dandelion. Susceptible larvae fed on apple, black raspberry, or plantain had intermediate LD50 values, but only apple was significantly greater than artificial diet. Even greater variation in resistance to azinphosmethyl was evident in the resistant strain.

LD50s for resistant larvae varied by a maximum of about 3.8 fold (LD50 artificial diet/LD50 black raspberry). Larvae reared on black raspberry were significantly more susceptible to topically-administered azinphosmethyl than were those reared on plantain, dandelion or artificial diet, but were not significantly different from larvae fed apple. Although not significantly different from apple (due to wide confidence limits around the apple LD50), larvae fed on artificial diet, dandelion, or plantain had an LD50 approximately 2.5 times that of apple-reared larvae. Resistant larvae reared on artificial diet, dandelion, and plantain had the highest LD50 values. Resistant strain larvae fed on dandelion or plantain were not different, and resistant strain larvae fed on black raspberry and apple had a LD50 equivalent to the susceptible strain on artificial diet. Of even greater interest is the resistance ratio comparing response of the two different strains on a common diet (Table 1). The resistant strain responded to plantain similarly to larvae fed on artificial diet; there was an increase in the level of resistance compared to the susceptible strain as expected. Apple, black raspberry, and dandelion were similar in their host effects; these host plants seem to reduce the expression of resistance. The likelihood ratio test (Table 1) indicated that the probit regression lines for the susceptible strain feeding on different host plants were neither parallel nor had equal intercepts. The

Table 1. Toxicity of azinphosmethyl applied topically to susceptible (S) and resistant (R) *Platynota idaeusalis* larvae fed different diets.

Host	Strain- Generatin	No. Insects	Slope $\pm$ SE	LD ₅₀ (95CL) ¹ ug (AI)/mg larva	Resistance ratio ²
Apple	S	113	3.8 $\pm$ 0.9	0.008 (.069–.108) b	-
Black raspberry	S	113	3.1 $\pm$ 0.7	0.059 (.033–.081) ab	-
Plantain	S	125	4.5 $\pm$ 0.8	0.058(.034–.077) ab	-
Dandelion	S	109	8.4 $\pm$ 1.8	0.133 (.119–.148) c	-
Artificial diet	S	163	3.1 $\pm$ 0.6	0.047 (.035–.057) a	-
Apple	R-18	139	1.3 $\pm$ 0.2	0.064 (.035–.127) ab	0.7
Black raspberry	R-16	117	1.9 $\pm$ 0.3	0.042 (.020–.081) a	0.7
Plantain	R-16	171	1.6 $\pm$ 0.3	0.155 (.095–.245) b	2.7
Dandelion	R-16	169	2.1 $\pm$ 0.3	0.158 (.087–.262) b	1.2
Artificial diet	R-16	171	1.1 $\pm$ 0.3	0.160 (.098–.288) b	3.4

¹LD₅₀ values followed by the same letter are not significantly different based on overlap of 95% confidence limits.

² LD₅₀ of the resistant strain/LD 50 of the susceptible strain on the same host.

probit regression lines for the resistant strain feeding on different host plants were parallel but had different intercepts.

DISCUSSION

Non-overlap of 95% confidence limits at the LD50 level suggested that overall effect of host plants on toxicity of azinphosmethyl to *P. idaeusalis* was significant. When susceptible larvae of *P. idaeusalis* were fed different hosts, they were subsequently found to have different levels of susceptibility to azinphosmethyl (Domínguez-Gil *et al.* 1994). The use of two isogenic strains in this study, one susceptible and another resistant to azinphosmethyl, enabled us to attribute any differences in response to azinphosmethyl to resistance mechanisms (or possibly, closely-linked genes) rather than

unrelated strain differences. 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 either plantain or dandelion, but appear susceptible if they eat either black raspberry or, to some extent, apple. In contrast, susceptible larvae appear susceptible if they either eat black raspberry or plantain, but appear resistant if they eat dandelion; apple is intermediate in its effect on the larvae.

The lower mortality of susceptible larvae fed apple is not consistent with the higher mortality of third instar susceptible-strain larvae on diet containing phloridzin (plant allelochemical) found by Hunter *et al.* (1994a) in apple leaf. This disagreement may result from differences in the weight and/or instar of larvae at the time of the bioassays, or the number of days that larvae were allowed to feed on the diet (Wells *et al.* 1983). Hunter *et al.* (1994a) used smaller larvae than were used in this study, and larvae were fed for a longer period on diet containing only phloridzin as opposed to the 7-day feeding period on intact apple foliage in this study. Apple leaves contain a much richer secondary chemistry than simply phloridzin, and different chemicals could have contradictory effects on insecticide toxicity.

The data also suggest that unknown allelochemicals within dandelion or apple may cause an increase in the ability of the susceptible larvae to detoxify azinphosmethyl. As indicated by the LR test results (Table 1), entirely different enzymes may be linked with this change in susceptibility. This strain has been maintained in the absence of azinphosmethyl and plant chemicals for more than 120 generations. Several enzyme systems may be involved in detoxification of plant allelochemicals and azinphosmethyl in *P. idaeusalis*, and it is difficult to predict how they would interact with xenobiotics (Wells *et al.* 1983, Carlini *et al.* 1991, Carlini 1992, Carlini *et al.* 1995, Hunter *et al.* 1994a). Resistant larvae reared on black raspberry foliage were significantly (3.8 times; LD50 artificial diet/LD50 black raspberry) more susceptible to azinphosmethyl than resistant larvae fed artificial diet. These results are consistent with those of Robertson *et al.* (1990),

who reported a similar resistance ratio comparing resistant light brown apple moth larvae raised on artificial diet and blackberry (*Rubus laciniatus* Wild). These similar results may suggest that chemistry of the genus *Rubus* can affect the detoxification mechanisms responsible for azinphosmethyl resistance in these insect species.

In this study, resistant larvae of *P. idaeusalis* were more tolerant to azinphosmethyl when reared on plantain or dandelion than when reared on black raspberry. Robertson *et al.* (1990) postulated that resistant larvae fed black raspberry might be mistakenly identified as being genetically susceptible, because they are significantly more susceptible to azinphosmethyl compared with resistant larvae fed any of the other three hosts (apple, broom, gorse). Our results suggest that testing of field-collected insects could produce misleading conclusions about resistance, similar to the findings of Robertson *et al.* (1990). If environmental factors have relatively important effects, as these results suggest, then differences in susceptibility between larvae or adults collected from different field populations may 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 (Robertson *et al.* 1990, Hunter *et al.* 1994a). Because assays of field-collected insects are efficient and widely used to monitor resistance, the potential types of environmental effects, environment $\times$ genotype interactions, and their effect on resistance merit further consideration (Omer *et al.* 1993). 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. 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. This study indicates that efficacy of insecticides might be increased by adjusting rates of application to match pest species response on specific host plants similar to the findings of Hinks and Spurr (1989), in cases where eliminating some weeds (e.g., dandelion) may be too

difficult. The present study suggests that it is necessary to take into account the abundance and number of host plants present in orchard ground cover and surrounding vegetation, if we want to preserve the susceptibility of *P. idaeusalis* to azinphosmethyl.

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