Effects of linear furanocoumarins on the herbivore *Spodoptera exigua* and the parasitoid *Archytas marmoratus*: host quality and parasitoid success

Stuart R. Reitz & John T. Trumble
Department of Entomology, University of California, Riverside, CA 92521–0314, USA

Abstract

We assessed the effects of three photoactivated linear furanocoumarins, secondary plant metabolites present in *Apium* spp. (Apiaceae) and other taxa, on the larval-pupal parasitoid, *Archytas marmoratus* (Townsend) (Diptera: Tachinidae) and the host *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), in the presence and absence of ultraviolet radiation. These results then were compared with previously described responses of *Archytas marmoratus* and other hosts to different plant allelochemicals. Ultraviolet radiation had no consistent detrimental effects. Increasing concentrations of linear furanocoumarins (from 0 to 0.029% of fresh weight) increased mortality of both the host and parasitoid. Increasing linear furanocoumarin levels also prolonged larval development of surviving *S. exigua*, but had no effect on pupal developmental time or pupal mass. Consequently, there was no effect of increasing linear furanocoumarin levels on surviving parasitoid development time (from the time of host pupation) or size. These results indicate the effects of linear furanocoumarins are mediated through effects on the host. Because reported responses of *Ar. marmoratus* to other allelochemicals (e.g., flavones, methyl ketones) are mediated through host effects, these results support the hypothesis that *Ar. marmoratus* displays a generalized response to plant allelochemicals that are predictable based on host mediated effects.

Introduction

Many factors influence the physiological interactions between herbivorous insects and their parasitoids. Host plant nutritional quality (Karowe & Martin, 1989) and secondary chemical composition (Barbosa et al., 1986; Price, 1986; Hare, 1992) are among the primary factors mediating herbivore-parasitoid interactions. Secondary plant chemicals can affect parasitoids directly, where the parasitoid exhibits responses that differ from those of the herbivore, or indirectly, where effects on the parasitoid are mediated through allelochemical effects on the host herbivore. Clearly, interspecific variation in life histories can account for differential responses of parasitoids to the same allelochemical (Barbosa et al., 1986; Farrar et al., 1992). Although such tritrophic interactions have been documented frequently, information to determine if the response of an individual parasitoid species to different types of plant secondary chemicals is predictable is scarce (see Barbosa et al., 1991). Therefore we examined a parasitoid, whose responses to two different classes of plant defenses are host-mediated, to determine if its responses to a third type of plant allelochemicals could be predicted on the basis of host responses to plant chemistry.

The system we studied consists of the parasitoid *Archytas marmoratus* (Townsend) (Diptera: Tachinidae), the herbivore *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), and three allelochemicals found in celery, *Apium graveolens* L. (Apiaceae). Previously, different herbivore-mediated effects of host plants on *Ar. marmoratus* have been documented. For example, *Ar. marmoratus* adult mass, development time, and survival are reduced when reared from *Helicoverpa zea* fed a resistant maize variety (*Zea mays* L. 'Zapalote Chico') possessing antibiotic factors (Mannion et al., 1994). The antibiosis in this maize variety has been attributed to the flavone, maysin (Waiss et al., 1979; Snook et al., 1993). These effects on the parasitoid

parallel those on two host species, *H. zea* and *Spodoptera frugiperda* (Wiseman et al., 1983; Wiseman & Widstrom, 1986). In another system, *Ar. marmoratus* reared from *H. zea* fed the methyl ketone, 2-undecanone, found in wild tomato *(Lycopersicon hirsutum* f. *glabratum* Mull. accession PI 134417), did not have altered development time but did have increased mortality (Farrar et al., 1992). These responses again indicate indirect allelochemical effects on *Ar. marmoratus* because 2-undecanone in diet caused mortality among *H. zea* pupae (Farrar & Kennedy, 1987; 1988). Unfortunately, these studies did not address effects on the host and parasitoid simultaneously.

Ar. *marmoratus* is a polyphagous larval-pupal parasitoid of numerous Noctuidae. Females oviposit on foliage, and planidial-type larvae attach to passing host larvae (Hughes, 1975). Larvae remain as first instars until the host pupates. *S. exigua* is a polyphagous herbivore of a wide variety of host plants, including celery (Van Steenwyk & Toscano, 1981). *Ap.* spp. contain several classes of allelochemicals that can be detrimental to *S. exigua* (Trumble et al., 1991; Meade et al., 1994). Among these compounds are linear furanocoumarins whose production is thought to be induced by environmental stresses (Beier & Oertli, 1983; Dercks et al., 1990), including herbivory (Zangerl, 1990), and whose activity is enhanced by ultraviolet radiation (Berenbaum, 1991).

In the present study, we extend those previous findings for *Ar. marmoratus* by comparing its development and that of the host *S. exigua* when the host consumes diets containing linear furanocoumarins. The presence of linear furanocoumarins can impact *S. exigua* fitness by slowing larval development (Trumble et al., 1991) and increasing mortality, although there is no effect on pupal mass of surviving individuals (Diawara et al., 1993; Brewer et al., 1995). In contrast, *Trichoplusia ni* (Hübner) had slower larval development, but experienced only minimal mortality with increasing concentrations of linear furanocoumarins (Reitz & Trumble, 1996). In this latter study, the egg-larval parasitoid *Copidosoma floridanum* suffered significantly greater mortality with increasing linear furanocoumarin concentration in the host diet, suggesting a direct allelochemical effect on the parasitoid.

Given that *Ar. marmoratus* shows host-mediated responses to different plant allelochemicals but that linear furanocoumarins can have direct toxic effects on higher trophic levels, we examined the hypothesis that responses of *Ar. marmoratus* to linear furanocoumarins are host-mediated, and propose that responses of this parasitoid to plant allelochemicals are predictable on the basis of host-herbivore effects.

Materials and methods

Experimental insects. Spodoptera exigua were obtained from a laboratory colony originally established from material collected in Orange County, California, and to which new genetic material was added annually. *S. exigua* were reared according to methods described by Patana (1969). *Ar. marmoratus* were obtained from a colony collected from maize in southern Georgia and northern Florida, and maintained at the USDA laboratory in Tifton, Georgia. Our colony of *Ar. marmoratus* was reared from *S. exigua*.

Experimental procedures. All tests were conducted in a walk-in environmental chamber maintained at $27 \pm 2\,°C$, with a L14:D10 photoperiod. The three phototoxic linear furanocoumarins present in *Apium* spp., psoralen, bergapten (5-methoxypsoralen) and xanthotoxin (8-methoxypsoralen) were obtained from Sigma Chemical Co. (St. Louis, MO). The effects of these three linear furanocoumarins on the host-parasitoid relationship were tested at four different concentrations through diet incorporation assays. The linear furanocoumarin mixtures comprised 0%, 0.0008%, 0.0050%, and 0.0290% of the fresh weight of the diets. We tested diets containing linear furanocoumarin concentrations at the levels present in the inner leaves of celery cultivar 'Tall Utah 5270-R' ('Low' treatment: $0.001\ \mu M\ g^{-1}$ fresh weight psoralen, $0.022\ \mu M\ g^{-1}$ bergapten, $0.0138\ \mu M\ g^{-1}$ xanthotoxin, Diawara et al., 1995), in the outer leaves of 'Tall Utah 5270-R' celery ('Medium' treatment: $0.021\ \mu M\ g^{-1}$ fresh weight psoralen, $0.130\ \mu M\ g^{-1}$ bergapten, $0.083\ \mu M\ g^{-1}$ xanthotoxin, Diawara et al., 1995), and in the leaves of the celery breeding line 87A 147-2, *Ap. graveolens* × *(Ap. graveolens* × *Ap. chilense* Hook and Arn.) ('High' treatment: $0.183\ \mu M\ g^{-1}$ fresh weight psoralen, $0.782\ \mu M\ g^{-1}$ bergapten, $0.416\ \mu M\ g^{-1}$ xanthotoxin, Trumble et al., 1990). In addition to these three treatments, a control diet that contained no linear furanocoumarins was tested.

The linear furanocoumarins were dissolved in acetone and then adsorbed onto a nonnutritive fiber (alphacel, ICN, Costa Mesa, CA) by evaporating the acetone (Chan et al., 1978). The mixture was then resuspended in distilled water (1:5 alphacel:water, w/w). Warm, liquid lima bean-based diet was added

to the linear furanocoumarin mixture and then blended for five minutes. The amount of alphacel constituted 3% of the final diet mass. The diet mixture was then dispensed into individual 30 ml plastic cups (approximately 10 mg per cup), and allowed to solidify.

To examine differential effects on the herbivore and parasitoid, unparasitized and parasitized *S. exigua* were included in experiments. Neonate *S. exigua* larvae were placed individually in diet cups ($n = 60$ per linear furanocoumarin treatment level, each replicated two times). One half of the larvae for each linear furanocoumarin treatment were randomly assigned to receive ultraviolet radiation (UV) exposure, and the other half received no UV exposure. Diet cups were covered with Teflon FEP Fluorocarbon Film (E. I. DuPont de Nemours & Co., Wilmington, DE) to permit penetration of ultraviolet radiation (Trumble et al., 1991). Ultraviolet radiation was provided by fluorescent lights (40 W Sylvania Blacklight, General Electric, Cleveland, OH) with an emittence peak of 350 nm (UV-A). Wavelengths of 300 to 400 nm are the most active for linear furanocoumarins (Musajo & Rodighiero, 1962). The lights provided ultraviolet radiation at an intensity of approximately 500 μW cm^{-2}, for 6 h per day during the photophase. This level of ultraviolet radiation approximates the intensity found in the canopy of celery fields in southern California (J.T.T., unpublished data). Ultraviolet radiation was measured with a System 371 Optical Power meter with a 268 detector head (United Technologies, Hawthorne, CA).

Parasitization. Larvae ($n = 20$, per linear furanocoumarin $\times$ UV treatment replicate) were parasitized two days after their final larval molt. Two - three *Ar. marmoratus* planidia (< 24 h old) were placed on the thorax of each larva. Planidia were transferred with a camel-hair brush. Because only one parasitoid survives per host (Reitz, 1995), survivorship data are based on one *Ar. marmoratus* per host. The remaining *S. exigua* larvae were left unparasitized ($n = 10$ per replicate). Because *S. exigua* pupate in the soil, all individuals were removed from UV exposure following pupation.

Data collection and analysis. *Spodoptera exigua* larval mass was determined nine days after hatching. Because no larvae were parasitized until this time, data for parasitized and unparasitized individuals were pooled. Nine days after hatching corresponds to the feeding stage of ultimate instar *S. exigua* when reared on artificial medium containing no allelochemicals (S.R.R., unpublished data). *S. exigua* larvae were inspected daily to determine time of pupation. Daily inspections also were made to determine the time of *Ar. marmoratus* pupariation, and adult eclosion. Putatively parasitized *S. exigua* that did not produce adult *Ar. marmoratus* were examined to determine the fate of parasitoid immatures. Pupal mass was recorded for *S. exigua* one day after pupation. Times from host pupation until parasitoid pupation and adult eclosion were recorded. Only measurements from unparasitized *S. exigua* surviving to adulthood, or from hosts producing adult *Ar. marmoratus* were included in these analyses. To determine if the size of flies differed among treatments, the metathoracic tibial length was measured, with a microscope fitted with an ocular micrometer (Bai et al., 1992; Reitz & Adler, 1995).

The experiments with parasitized and unparasitized *S. exigua* were designed as factorial experiments with two factors, linear furanocoumarin concentration (at four levels) and ultraviolet exposure (at two levels). Host and parasitoid survival data were analyzed by log linear models (Agresti, 1990). Host and parasitoid size and development data were subjected to analyses of variance. Data were examined first for the presence of significant interactions between the factors. If a significant interaction occurred, the joint effects of the two factors were analyzed. If no significant interaction was present, the main effects of linear furanocoumarin concentration and ultraviolet radiation were analyzed (Neter et al., 1990). Transformed data were back-transformed to their original scales for presentation purposes.

Results

Herbivore and parasitoid survival. Both *Ar. marmoratus* and *S. exigua* showed similar patterns of mortality across treatments. Correlations between linear furanocoumarin levels (expressed as a percentage of fresh weight of diet) and survival were -0.87 for *S. exigua*, and -0.94 for *Ar. marmoratus*. Survival of unparasitized *S. exigua* decreased significantly at the two highest linear furanocoumarin concentrations compared with the control and low treatments ($X^2 = 27.2$, P < 0.001, 3 df, Figure 1). There were no significant differences in *S. exigua* survival between UV treatments ($X^2 = 2.57$, P > 0.10, 1 df). The majority of mortality occurred between the larval-pupal metamorphosis and adult eclosion.
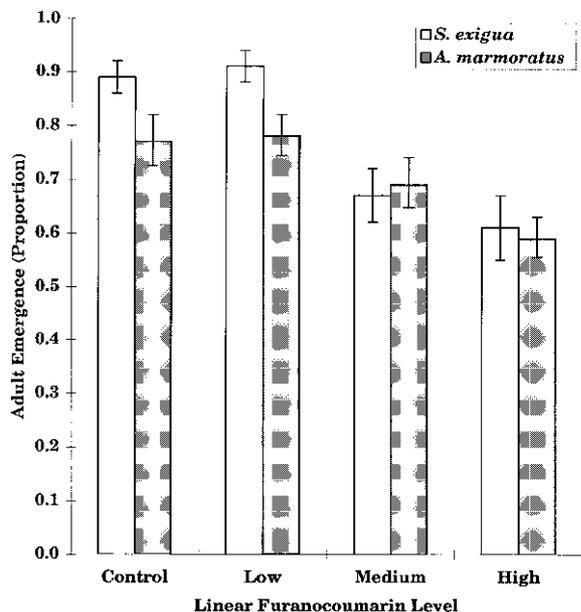
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Figure 1. Proportion of unparasitized *Spodoptera exigua* and *Archytas marmoratus* surviving to the adult stage, when *S. exigua* were reared on diets containing mixtures of linear furanocoumarins. Bars represent standard errors.
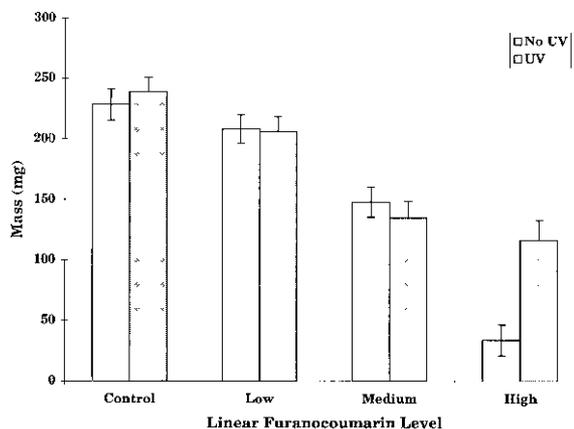

Figure 2. Mean larval mass of *Spodoptera exigua*, nine days after hatching, when reared on diets containing mixtures of linear furanocoumarins. Open bars represent larvae reared in the absence of ultraviolet light, and shaded bars represent means of larvae reared in the presence of ultraviolet radiation. Bars represent standard errors of the means.

Ar. marmoratus survival also decreased at the highest linear furanocoumarin level ($X^2 = 10.27$, P < 0.012, 3 df, Figure 1). As with unparasitized *S. exigua,* there were no significant differences in survival between UV and no UV exposures ($X^2 = 0.35$, P > 0.55, 1 df). The majority of *Ar. marmoratus* mortality occurred after host pupation. Fewer than 10% of *Ar. marmoratus* died prior to host pupation.

Herbivore and parasitoid development. Among surviving *S. exigua*, increasing furanocoumarin concentrations slowed larval development. This slower development is reflected in larval mass at nine days after hatching (Figure 2). There was a significant interaction between furanocoumarin concentration and UV treatment ($F = 6.67$, P = 0.0002), which is attributable largely to the significantly lower mean mass for *S. exigua* in the high furanocoumarin × no UV treatment group. The length of the larval stage for unparasitized *S. exigua* further corroborates the slower development of the herbivore with increasing furanocoumarin concentration (Table 1). There was a significant interaction between furanocoumarin treatment and UV exposure (P < 0.03) indicating that linear furanocoumarins and UV exposure were acting antagonistically to the developmental rate of *S. exigua* (Table 1 and

Figure 2). This interaction resulted from the lack of developmental time differences between control and low treatments while UV exposure actually resulted in slightly faster larval development for *S. exigua* in the two highest linear furanocoumarin treatments.

Whereas, the linear furanocoumarins slowed larval development, they did not have a significant impact on the final pupal mass of surviving *S. exigua* (P = 0.20; Table 1). In a similar manner, there was no effect of linear furanocoumarin concentration on size of surviving *Ar. marmoratus* (P > 0.07; Table 2). Developmental constraints of linear furanocoumarins were observed only during the feeding stage of *S. exigua*. There was no significant variation in time from pupation until *S. exigua* adult eclosion (<0.5 day among linear furanocoumarin treatments, Table 1); nor was there a treatment effect on pupal mass (Table 1). In accordance with this result, there was no significant treatment effect on the development time of *Ar. marmoratus* from the time of host pupation until adult eclosion (Table 2).

Discussion

Our results confirm previous studies that indicate (1) linear furanocoumarins have detrimental impacts on the generalist herbivore *S. exigua*, and 2) support the hypothesis that the parasitoid, *Ar. marmoratus*, is affected indirectly by allelochemicals ingested by

Table 1. Growth and developmental responses of *S. exigua* when reared on diets containing linear furanocoumarins, and under different ultraviolet radiation exposures

Furanocoumarin	UV exposure	*S. exigua* larval development time (days)[a]	*S. exigua* pupal development time (days)[b]	*S. exigua* pupal mass (mg)[c]
Control	No	11.6 ± 0.3a	6.1 ± 0.2	106.9 ± 4.09
	Yes	11.7 ± 0.3a	6.5 ± 0.2	118.5 ± 3.87
Low	No	11.6 ± 0.3a	6.7 ± 0.2	120.2 ± 3.67
	Yes	11.9 ± 0.3a	6.6 ± 0.2	122.6 ± 3.74
Medium	No	13.2 ± 0.4b	6.5 ± 0.2	111.0 ± 3.98
	Yes	12.3 ± 0.4a	7.0 ± 0.2	120.3 ± 4.40
High	No	16.1 ± 0.4d	6.8 ± 0.2	113.2 ± 4.40
	Yes	14.5 ± 0.5c	6.8 ± 0.3	118.2 ± 4.78

[a] Furanocoumarin $\times$ UV interaction: $F = 3.08$, P $= 0.03$, means followed by the same lower case letter are not significantly different (P $= 0.05$, least squares means t-tests).
[b] Furanocoumarin $\times$ UV interaction: $F = 2.47$, P $= 0.06$; Furanocoumarin main effect: $F = 2.2$, P $= 0.09$; UV main effect: $F = 3.47$, P $= 0.06$.
[c] Furanocoumarin $\times$ UV interaction: $F = 0.62$, P $= 0.60$; Pupae reared in the presence of supplemental UV radiation were significantly heavier than those reared in the absence of supplemental UV radiation ($F = 6.56$, P < 0.012). There were no significant differences among furanocoumarin treatments ($F = 1.58$, P $= 0.20$).

Table 2. Growth and developmental responses of *Archytas marmoratus* when reared from *Spodoptera exigua* feeding on diets containing linear furanocoumarins, and under different ultraviolet radiation exposures

Furanocoumarin	UV exposure	*Ar. mamoratus* development time (days)[a]	*S. exigua* larval development time (days)[b]	*Ar. marmoratus* tibial length (mm)[c]
Control	No	13.8 ± 0.4	11.2 ± 0.5a	2.08 ± 0.038
	Yes	14.4 ± 0.3	11.5 ± 0.4ab	2.07 ± 0.032
Low	No	13.7 ± 0.4	12.3 ± 0.4abc	2.02 ± 0.029
	Yes	12.9 ± 0.4	12.7 ± 0.5bc	2.01 ± 0.033
Medium	No	14.0 ± 0.3	14.4 ± 0.4d	1.99 ± 0.030
	Yes	14.5 ± 0.4	13.4 ± 0.5cd	2.07 ± 0.034
High	No	13.6 ± 0.3	16.8 ± 0.4e	1.95 ± 0.029
	Yes	13.6 ± 0.4	14.9 ± 0.6d	1.98 ± 0.041

[a] Time from host pupation until adult *Ar. marmoratus* eclosion. Furanocoumarin $\times$ UV interaction: $F = 2.11$, P > 0.10; Furanocoumarin main effect: $F = 2.03$, P > 0.11; UV main effect: $F = 0.05$, P > 0.82.
[b] Time from hatching until pupation of *S. exigua*. Furanocoumarin $\times$ UV interaction: $F = 3.42$, P > 0.019, means followed by the same lower case letter are not significantly different (P > 0.05, least squares means t-tests).
[c] Furanocoumarin $\times$ UV interaction: $F = 1.06$, P > 0.36; Furanocoumarin main effect: $F = 2.33$, P > 0.07; UV main effect: $F = 1.07$, P > 0.30.

its host. As linear furanocoumarin content increased, *S. exigua* experienced increased mortality and extended larval development time. Similarly, *Ar. marmoratus* experienced increased mortality as its host consumed greater quantities of linear furanocoumarins, but surviving parasitoids did not appear adversely affected. The observed responses for the *Ar. marmoratus – S. exigua* system do not represent a uniform effect of linear furanocoumarins on herbivores and parasitoids (e.g., Bull et al., 1984; Nitao, 1989; Zangerl, 1990; Reitz & Trumble, 1996), but suggest that *Ar. marmoratus* responses to plant allelochemicals are predicated on herbivore-mediated effects.

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Apparently, toxic amounts of linear furanocoumarins or metabolites (Bull et al., 1984) are retained in *S. exigua* pupae. Before host pupation, first instar *Ar. marmoratus* feed and develop very little relative to final adult size (Bratti et al., 1993). Therefore, it is unlikely that during this period *Ar. marmoratus* larvae ingested potentially toxic amounts of linear furanocoumarins or metabolites. When feeding on linear furanocoumarin containing diets, considerable *S. exigua* mortality occurs during the pupal stage (see also Diawara et al., 1993), and dissections of hosts that did not produce adult *Ar. marmoratus* revealed that most parasitoids died as third (ultimate) instars. Although we could not determine if host death preceded parasitoid death in these cases, Tachinidae larvae feed the greatest amount and grow the most during the third stadium (Reitz, 1996).

Although few data exist on how *S. exigua* metabolize such allelochemicals (see Brewer et al., 1995), evidence from other generalist Noctuidae suggests that low levels of xanthotoxin are slowly metabolized by larvae (Smirle & Isman, 1992) through the action of P450 cytochrome monoxygenases (Lee & Berenbaum, 1989). However, toxic compounds may accumulate in the body as larvae consume larger amounts of allelochemicals, because furanocoumarin detoxification activity does not appear to be induced in these generalists (Lee & Berenbaum, 1989; Bull et al., 1984).

The lack of a consistent negative impact of UV exposure on *S. exigua* was unexpected. Linear furanocoumarins are generally considered to have greater activity in the presence of UV (Berenbaum, 1991). However, not all effects of linear furanocoumarins are dependent on photoactivation (Berenbaum, 1978; Berenbaum & Neal, 1985), and Zangerl (1990) has suggested *T. ni* may physiologically compensate for UV-induced toxicity. Given that these plant-herbivore-parasitoid systems are normally exposed to UV, our results from treatments in the UV exposure would be more biologically relevant.

The effects of linear furanocoumarins on the eventual size of the host and parasitoid was not unexpected. Previously, Diawara et al. (1993) and Brewer et al. (1995) found no effect of linear furanocoumarin on host pupal mass, and *Ar. marmoratus* size is correlated with host pupal mass (Reitz, 1995). Nonetheless, this effect would be important to the population dynamics of the two species because body size tends to be correlated with fecundity for *Spodoptera* (Rothschild, 1969; Janssen, 1994; but see Brewer et al., 1995) and numerous parasitoids (Bai et al., 1992; Reitz & Adler,

1995). Another important consideration for population dynamics is the effect on development time. Any effect of linear furanocoumarins on the development time of *Ar. marmoratus* would result from increasing the time from parasitism until host pupation.

Our results, in concert with other studies, support the hypothesis that *Ar. marmoratus* responses to plant allelochemicals are mediated through host responses to those allelochemicals. In the case of linear furanocoumarins, we do not mean to imply that the linear furanocoumarins *per se* are detrimental to *Ar. marmoratus*, but their effects may be mediated through metabolized products or physiological disruption of the host pupa rendering it unsuitable for complete *Ar. marmoratus* larval development. *S. exigua* pupal mortality increased with linear furanocoumarin concentrations, but there was no effect on pupal size. Consequently, *Ar. marmoratus* survival was reduced with increasing linear furanocoumarin levels, but of those parasitoids surviving to adulthood, no discernible effects of linear furanocoumarins were found.

Although the responses of *Ar. marmoratus* to allelochemicals were different in two previously studied systems, all of these results are consistent given the life history of *Ar. marmoratus*. The methyl ketone 2-undecanone fed to *H. zea* larvae caused pupal mortality (Farrar & Kennedy, 1988). Consequently, *Ar. marmoratus* reared from *H. zea* under such conditions could not complete their larval development (Farrar et al., 1992). Diets containing silks of *Z. mays* 'Zapalote Chico' result in smaller host pupal size (Mannion et al., 1994). Consequently, the parasitoid has reduced size and development time. These results suggest that host dietary history is critical in determining the success of *Ar. marmoratus* parasitism. Whereas the particular allelochemicals consumed by an herbivore are significant to understanding the ecology of plant-herbivore-parasitoid interactions (Barbosa et al., 1991), so too are the specific life histories of the herbivores and parasitoids involved.

Acknowledgments

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