Tritrophic Interactions Among Linear Furanocoumarins, the Herbivore *Trichoplusia ni* (Lepidoptera: Noctuidae), and the Polyembryonic Parasitoid *Copidosoma floridanum* (Hymenoptera: Encyrtidae)

STUART R. REITZ AND JOHN T. TRUMBLE

Department of Entomology, University of California, Riverside, CA 92521

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ABSTRACT Secondary plant metabolites can affect parasitoids directly or indirectly through their action on the parasitoid host. We assessed if the linear furanocoumarins, psoralen, bergapten and xanthotoxin, secondary plant metabolites present in *Apium* spp. and other taxa, exerted direct or indirect effects on *Copidosoma floridanum* (Ashmead), a polyembryonic parasitoid of *Trichoplusia ni* (Hübner), through diet incorporation bioassays. Because linear furanocoumarins are photoactivated, we tested for these effects in the presence and absence of UV radiation. Increasing concentrations of linear furanocoumarins prolonged larval development of *T. ni*, but resulted in greater pupal mass. Furthermore, increasing concentrations of linear furanocoumarins increased *T. ni* mortality, but only marginally. However, increasing concentrations of linear furanocoumarins in the host diet significantly increased mortality of the parasitoid. There were no significant differences in the number of reproductive parasitoid larvae among treatments, indicating that linear furanocoumarins did not interfere with polyembryonic development of *C. floridanum*, but exerted toxicity after the parasitoid larvae began feeding on host tissue. Supplemental UV radiation slowed development, but it did not affect survival of either *T. ni* or *C. floridanum*. Because of the differential effects on the host and parasitoid, linear furanocoumarins, at naturally occurring concentrations, can mediate this host–parasitoid relationship through direct effects on the parasitoid, and not merely as a consequence of their effect on the host.

KEY WORDS tritrophic interactions, *Apium*, linear furanocoumarins, UV radiation

SECONDARY PLANT METABOLITES are capable of altering the suitability of host plants for insect herbivores and consequentially affecting plant–herbivore interactions. Although specialist herbivores may sequester such compounds and use them to defend against natural enemies (e.g., Thurston and Fox 1972), many secondary plant compounds act as feeding deterrents or toxins against generalist insect herbivores, and are one of the bases of host plant resistance (Berenbaum and Zangerl 1992). The assessment of such deleterious effects on herbivores can be documented by examining herbivore performance in relation to intraspecific variation in metabolite content of host plants. Beyond the plant–herbivore interface, secondary plant metabolites can also exert influences on higher trophic levels by modifying host suitability for parasitoids (Hare 1992) or through biomagnification (Barbosa et al. 1986). Host-plant chemistry can mediate host–parasitoid interactions indirectly, through actions on the herbivore, or directly where the compounds exert differential effects on the herbivore and its natural enemies. However, differentiating between such indirect and direct effects on natural enemies has seldom been examined.

The linear furanocoumarins psoralen, bergapten, and xanthotoxin, present in celery (*Apium graveolens* L.) (Apiacaea) and related species, are photoactive plant metabolites that are thought to be induced by environmental stresses (Beier and Oertli 1983, Nitao 1989, Dercks et al. 1990). However, concentrations of these compounds in healthy plants vary widely among celery cultivars and accessions (Trumble et al. 1990), among different plant structures (Diawara et al. 1995), and with plant phenology (Trumble et al. 1992). Although not necessarily evolved as defenses against herbivores, linear furanocoumarins can affect herbivore fitness by deterring feeding (Yajima and Munakata 1979, Berenbaum et al. 1989), increasing development time, reducing growth, or causing mortality (Berenbaum 1978, Berenbaum and Feeny 1981, Trumble et al. 1991, Diawara et al. 1993b, Brewer et al. 1995). Despite the presence of these potentially deleterious linear furanocoumarins, the polyphagous herbivore *Trichoplusia ni* (Hübner) can develop successfully when feeding on celery foliage (Van Steenwyk and Toscano 1981, Meade and Hare 1991).

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Copidosoma floridanum (Ashmead) is a polyembryonic egg–larval parasitoid of plusiine Noctuidae (Noyes 1988). Females oviposit in host eggs; the parasitoid eggs then undergo polyembryonic development during the larval stage of the host (Strand 1989a). Two larval phenotypes, termed precocious and reproductive, are produced. Precocious larvae eclose throughout the host larval stage and defend their reproductive siblings from interspecific (Cruz 1986) or intraspecific competitors (Grbic et al. 1992). These precocious larvae die before pupating. Reproductive larvae eclose from the egg during the ultimate larval stadium of the host, and consume the host. At this point, reproductive larvae pupate within the host carcass, which is termed a mummy (Doutt 1947). These reproductive larvae develop into adult wasps. More than 1,000 adult wasps may develop from one egg. However, host plant antibiosis can affect survival and emergence of *C. floridanum* (Orr and Boethel 1985, Beach and Todd 1986).

Our objectives were to determine the impact that linear furanocoumarins in the diet of an herbivore have on a parasitoid, and establish whether observed effects are direct consequences that linear furanocoumarins have on the parasitoid, or if they are indirect consequences of the impact that linear furanocoumarins have on the host herbivore. We chose the *Apium–T. ni –C. floridanum* system as a model to examine the direct and indirect effects of linear furanocoumarins, based on their life histories. *T. ni* larvae feed on foliage, which contains the highest concentrations of furanocoumarins (Diawara et al. 1993a, 1995), and because *C. floridanum* is an egg–larval parasitoid, it is exposed to linear furanocoumarins, or their metabolites, throughout the entire feeding stage of the host.

Specifically, we determined if linear furanocoumarins, present in naturally occurring concentrations in the host diet, affect the development time, clutch size, or adult size of *C. floridanum* and compared those data with data for unparasitized *T. ni*. Because linear furanocoumarin activity is enhanced by UV radiation (Scott et al. 1976), we tested for these effects in the presence and absence of UV light. Linear furanocoumarins slow development of generalist herbivorous insects (McCloud and Berenbaum 1994, Brewer et al. 1995); therefore, a corresponding effect should occur with parasitoids that develop during the host larval stage. Because *C. floridanum* would be exposed to these mutagenic linear furanocoumarins (Song and Tapley 1979) throughout its development, polyembryonic development could be disrupted, resulting in fewer individuals being produced per host. In addition, high concentrations of linear furanocoumarins can be fatal to *T. ni* (McCloud and Berenbaum 1994), but through biomagnification, sublethal doses tolerated by herbivores may be toxic to parasitoids. If such biomagnification occurs, *C. floridanum* mortality should increase more precipitously with linear furanocoumarin levels than mortality for *T. ni*. Finally, plant allelochemicals can affect body size of parasitoids (Campbell and Duffey 1979), which for many parasitoids (Bai et al. 1992, Reitz and Alder 1995) is an indicator of potential fecundity. Therefore, we examined the impact of linear furanocoumarins on *C. floridanum* body size.

Materials and Methods

Insects and Parasitization Methods. *T. ni* were derived from a laboratory colony originally established from material collected from cabbage in Orange County, California, and to which new material has been added on a regular basis. *T. ni* were maintained in an environmental chamber at 27 ± 1°C, and a photoperiod of 14:10 (L:D) h. Females were allowed to oviposit on paper towels. Adults received a 20% honey in water solution, and larvae were reared on a lima bean-based artificial medium (Patana 1969).

Copidosoma floridanum were derived from parasitized *T. ni* collected from tomatoes, *Lycopersicon esculentum* Mill., in Riverside County, California, and from celery in Ventura County, California. The colony of *C. floridanum* was maintained in sleeve cages with the top glass streaked with honey. Newly oviposited (< 24 h old) *T. ni* eggs were parasitized by exposing them to small groups of wasps (24–72 h old).

Experimental Procedures. The 3 phototoxic linear furanocoumarins present in celery, psoralen, bergapten (5-methoxypsoralen), and xanthotoxin (8-methoxypsoralen) were obtained from Sigma (St. Louis, MO). The effect of these 3 linear furanocoumarins was tested at 4 different concentrations on the host–parasitoid relationship, through diet incorporation assays. We tested diets containing furanocoumarin concentrations at the levels present in the inner leaves of celery 'Tall Utah 5270-R' (low treatment: 0.168 μg/g fresh weight psoralen, 4.791 μg/g bergapten, 2.988 μg/g xanthotoxin) (Diawara et al. 1995), the concentrations present in the outer leaves of Tall Utah 5270-R celery (medium treatment: 3.936 μg/g fresh weight psoralen, 28.002 μg/g bergapten, 17.899 μg/g xanthotoxin) (Diawara et al. 1995), and the concentrations present in the leaves of the celery breeding line 87A 147-2 (*A. graveolens* × [*A. graveolens* × *A. chilense* Hook and Arn.], high treatment: 34.09 μg/g fresh weight psoralen, 168.98 μg/g bergapten, 89.85 μg/g xanthotoxin) (Trumble et al. 1990). These levels reflect naturally occurring constitutive amounts of linear furanocoumarins found in *Apium* foliage. In addition to these 3 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 alpha-

cel:water, wt:wt). Warm, liquid lima bean-based diet was added to the furanocoumarin mixture and then blended for 5 min. The amount of alphacel constituted 3% of the final diet mass. The diet mixture was then dispensed into individual 30-ml plastic cups (≈10 mg per cup) and allowed to solidify.

Neonate *T. ni* were placed individually in diet cups (n = 30 per treatment replicate, experiments were replicated 2 times). Parasitized hosts were obtained by exposing newly oviposited *T. ni* eggs to groups of ≈10 female wasps, and observed to verify that oviposition occurred. We attempted to include only eggs that were superparasitized and therefore produce mixed sex broods (Strand 1989b). Diet cups were covered with Teflon FEP Fluorocarbon Film (DuPont, Wilmington, DE) to permit penetration of UV radiation (Trumble et al. 1991). UV 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 300–400 nm are the most active for furanocoumarins (Musajo and Rodighiero 1962). The lights provided UV radiation at an intensity of ≈500 μW/cm^2, for 6 h/d during the photophase. This level of UV radiation approximates the intensity found below the canopy of celery fields in southern California (unpublished data). UV radiation was measured with a System 371 Optical Power meter with a 268 detector head (United Technologies, Hawthorne, CA).

Data Collection and Analysis. The experiments with parasitized and unparasitized *T. ni* were designed as factorial experiments with 2 factors, linear furanocoumarin concentration (at four levels) and UV exposure (at 2 levels). Data were subjected to analysis of variance (ANOVA). The presence of significant interactions between the factors was tested for first. If a significant interaction occurred, the joint effects of the 2 factors were analyzed. If no significant interaction was present, the main effects of furanocoumarin concentration and UV radiation were analyzed (Neter et al. 1990). Means separation was achieved by least squares means t-tests (PROC GLM, least squares means option, SAS Institute 1989). Mass and *C. floridanum* count data were log-transformed before analysis, and proportions were arcsine square-root transformed before analysis. Transformed data were back-transformed to their original scales for presentation purposes.

Both parasitized and unparasitized *T. ni* larvae were weighed 9 d after hatching. This time corresponds to the feeding stage of ultimate instar *T. ni* when reared on artificial medium (Strand 1989a; S.R.R. unpublished data). Pupal mass, and time until pupation and adult eclosion were recorded for unparasitized *T. ni*. Individuals were sexed following eclosion. Time from hatching until host mummy formation (Doutt 1947) was recorded for parasitized *T. ni*. Time until adult eclosion was recorded for *C. floridanum*. The time interval between host mummy formation and adult eclosion was taken as the pupal development period of *C. floridanum*. Only measurements from unparasitized *T. ni* surviving to adulthood, or from hosts producing adult *C. floridanum* were included in these analyses. The total number of progeny per host was determined by counting the numbers of adults and reproductive immatures that did not eclose as adults, for 20 randomly selected hosts per factor combination. To determine if the size of wasps differed among treatments, the metathoracic tibial length was measured, with a microscope fitted with an ocular micrometer, for 5 female *C. floridanum* from each host for which clutch size was counted.

Table 1. Mean ± SEM survival, pupal mass, and development time of unparasitized *T. ni* reared on diets containing different concentrations of linear furanocoumarins, and exposed to different levels of UV radiation

Furanocoumarin concn	UV treatment	Survival, %[a]	Days to pupation	Days to adult eclosion[b]
Control	No	98.3	11.4 ± 0.1a	17.4 ± 0.1ab
	Yes	90.0	11.6 ± 0.1ab	17.7 ± 0.1bc
Low	No	96.2	11.5 ± 0.1ab	17.4 ± 0.2ab
	Yes	98.2	11.7 ± 0.1b	17.9 ± 0.2c
Medium	No	88.3	11.9 ± 0.1b	17.8 ± 0.1c
	Yes	93.3	12.2 ± 0.1c	18.5 ± 0.1d
High	No	87.0	13.5 ± 0.1d	19.5 ± 0.2e
	Yes	88.2	14.7 ± 0.1e	21.0 ± 0.2f

Means, within a column, followed by a common letter are not significantly different ($P > 0.05$, least squares means t-test).

[a] Percentage surviving to adulthood. There was no significant interaction among linear furanocoumarin and UV treatments. Survival differed significantly among furanocoumarin levels ($\chi^2 = 9.3$, df = 3, $P < 0.03$) as follows: control = low = medium > high. Survivorship did not differ between UV treatments ($\chi^2 = 0.2$, df = 1, $P > 0.9$; log-linear ANOVA).

[b] Mean time for adult eclosion was significantly longer for males than for females ($P < 0.001$, data not shown).

Results and Discussion

Linear furanocoumarin-containing diets and UV radiation had pronounced effects on both *T. ni* and *C. floridanum*. The effects on *T. ni* varied with parasitism treatment, suggesting that consumption of linear furanocoumarins, in concert with UV exposure, mainly affect development rate of unparasitized *T. ni*, whereas the parasitized larvae and their parasitoids are more adversely affected. Although the linear furanocoumarins were an additional stress on parasitized larvae, the differential effects between *T. ni* and *C. floridanum* indicate that the direct effects of linear furanocoumarins on *C. floridanum* are more important than effects mediated through the host.

Effects on *T. ni*. UV radiation did not affect the survival of unparasitized *T. ni*. Survivorship was not significantly impacted by exposure to the low or medium furanocoumarin concentrations (Table 1). Survival for unparasitized *T. ni* was lower for the high treatment compared with the other treatments although the high concentration represented a 36-fold greater concentration than the low

treatment level and survivorship still exceeded 85%. In contrast, the proportion of parasitized larvae surviving and producing parasitoids was substantially lower than survival of unparasitized *T. ni* to adulthood (Tables 1 and 2). These results suggest that the furanocoumarins had an additive effect on *T. ni* already stressed by the presence of the parasitoid.

Linear furanocoumarins and UV radiation had dramatic, albeit differential, effects on the developmental rate of unparasitized and parasitized *T. ni*. For unparasitized *T. ni*, there was a significant interaction between furanocoumarin and UV exposure on larval mass ($F = 6.77$, $P = 0.0002$), indicating that the decreased growth rate resulting from increased furanocoumarin concentrations were enhanced by UV radiation (Fig. 1A). There were no differences among larvae reared on the lowest concentration of furanocoumarins in diets, but those reared on the medium level in the presence of UV radiation, and the high level had significantly lower mean masses than the others.

Although there was no significant interaction between linear furanocoumarin concentration and UV radiation on parasitized larval mass ($F = 1.31$, $P = 0.27$), increasing furanocoumarin concentrations ($F = 11.5$, $P < 0.0001$) and UV exposure ($F = 33.02$, $P < 0.0001$) slowed development of these larvae (Fig. 1B; Table 2). There is indirect evidence that the furanocoumarin and UV exposure had greater effects on parasitized than unparasitized *T. ni*. Although parasitized *T. ni* in our tests did not undergo a supernumerary molt, the similarity of larval weights between parasitized and unparasitized *T. ni* indicate that hyperphagy, typically evident by 9 d after hatching (Strand 1989a), did not occur until later in the larval development of parasitized *T. ni*.

Relative consumption rates probably decreased with increasing concentrations of linear furanocoumarins (Fig. 1), but overall, linear furanocoumarins acted more as digestibility reducers than as feeding deterrents. Increasing concentrations of furanocoumarins resulted in a concomitant extension in the time necessary for unparasitized *T. ni* to pupate or for mummification of parasitized larvae (Table 2). Had the furanocoumarins acted as feeding deterrents, we would have expected mean pupal mass to decrease with increasing furanocoumarin concentration. Yet, the exact opposite occurred, with the heaviest pupae coming from the highest furanocoumarin concentration and the lightest from the control group (Fig. 2A). Meade and Hare (1991) suggest that *T. ni* could compensate for nutritionally inferior diets by increasing consumption, and may do the same with respect to linear furanocoumarin-containing diets (Lee and Berenbaum 1989). As the ability of *T. ni* to detoxify compounds increases with larval age (Ahmad 1992), larvae may compensate by increasing consumption with age.

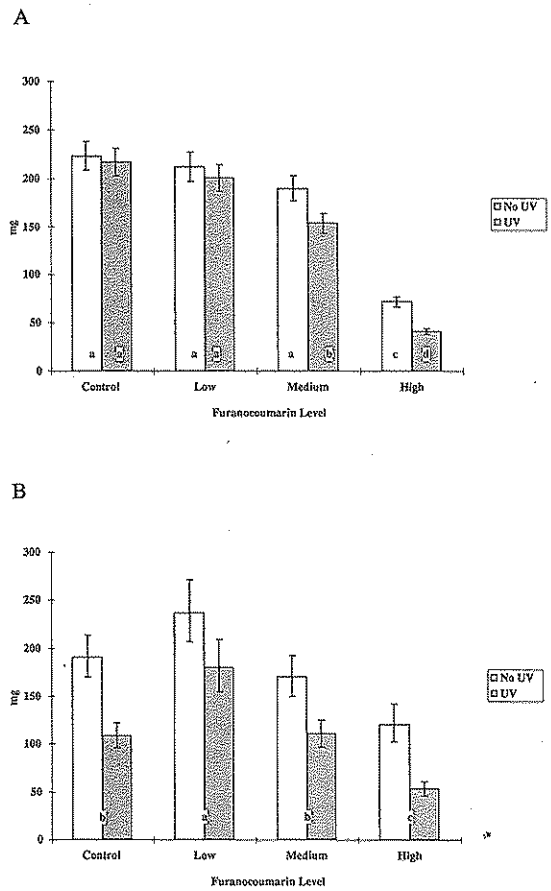

Fig. 1. (A) Larval mass (mean ± 95% CI) of unparasitized *T. ni* 9 d after hatching, when reared on artificial diet containing different concentrations of linear furanocoumarins, and in the absence (open bars) and presence (shaded bars) of UV radiation. The interaction between linear furanocoumarin concentration and UV radiation was significant ($P < 0.001$). Treatment means with the same letter within bars are not significantly different ($P > 0.05$, least squares means *t*-test). (B) Larval mass (mean ± 95% CI) of parasitized *T. ni* 9 d after hatching, when reared on artificial diet containing different concentrations of linear furanocoumarins, and in the absence (open bars) and presence (shaded bars) of UV radiation. There was no significant interaction between linear furanocoumarin and UV radiation treatments ($P > 0.27$). The linear furanocoumarin main effect was significant ($P < 0.0001$). Linear furanocoumarin means with the same letter below bars are not significantly different ($P < 0.05$). The mean mass of larvae exposed to supplemental UV radiation was significantly less than that of larvae not exposed to supplemental UV radiation ($P < 0.0001$). Linear furanocoumarin treatment means with the same letter within bars are not significantly different ($P > 0.05$, least squares means *t*-test). All data were analyzed after log-transformation and are presented following transformation to their original scale.

Effects on *C. floridanum*. Linear furanocoumarins present in the host diet affected the larval stage of *C. floridanum*, but not its polyembryonic or pupal stages. UV radiation had less of an impact

Table 2. Mean ± SEM progeny production and development time of *C. floridanum* from *T. ni* larvae reared on diets containing different concentrations of linear furanocoumarins, and exposed to different levels of UV radiation

Furanocoumarin concn	UV treatment	Host survival, %[a]	Total progeny	Adults[b]	Immatures	Progeny survival, %[c]	Days to host mummification[d]	Days to adult eclosion[e]
Control	No	76.9	1,282.9 ± 65.3	1,148.6 ± 87.0	134.3 ± 45.2	87.2 ± 5.3	13.0 ± 0.5	21.9 ± 0.3
	Yes	72.0	1,136.6 ± 63.9	1,082.1 ± 85.1	54.5 ± 44.3	95.1 ± 5.2	14.4 ± 0.5	23.4 ± 0.3
Low	No	63.0	1,167.3 ± 65.0	985.3 ± 86.5	182.0 ± 45.0	83.0 ± 5.3	11.3 ± 0.7	22.0 ± 0.3
	Yes	63.6	1,145.1 ± 75.8	1,068.5 ± 100.9	76.7 ± 52.5	93.5 ± 6.1	12.5 ± 0.9	22.3 ± 0.4
Medium	No	64.7	1,064.3 ± 65.3	868.7 ± 87.0	195.7 ± 45.2	75.0 ± 5.3	13.3 ± 0.5	22.4 ± 0.3
	Yes	57.7	1,165.2 ± 65.3	911.6 ± 87.0	253.6 ± 45.0	73.6 ± 5.3	14.4 ± 0.6	23.4 ± 0.3
High	No	53.1	1,093.8 ± 70.6	868.8 ± 94.0	225.0 ± 48.9	77.0 ± 5.7	14.2 ± 0.4	23.2 ± 0.4
	Yes	75.0	996.6 ± 66.7	771.2 ± 88.8	225.3 ± 46.2	74.6 ± 5.4	15.7 ± 0.4	25.0 ± 0.3

[a] Percentage of parasitized hosts producing *C. floridanum* progeny. There were no significant differences among treatments ($P > 0.15$; log-linear ANOVA).

[b] There was no significant interaction among linear furanocoumarin and UV treatments ($P > 0.50$). Number of adults per host differed significantly among furanocoumarin levels ($P < 0.01$) as follows: control = low > high = medium ($P > 0.05$, least squares means *t*-test). Number of adults per host did not differ between UV treatments ($P > 0.75$).

[c] There was no significant interaction among linear furanocoumarin and UV treatments ($P > 0.50$). Percentage of survival differed significantly among furanocoumarin levels ($P < 0.01$) as follows: control = low > medium > high ($P > 0.05$, least squares means *t*-test). Percentage of survival did not differ between UV treatments ($P > 0.30$).

[d] There was no significant interaction among linear furanocoumarin and UV treatments ($P > 0.90$). Time until host mummy formation differed significantly among furanocoumarin levels ($P < 0.01$) as follows: high > control = medium > low ($P > 0.05$, least squares means *t*-test). Supplemental UV significantly increased time until host mummy formation ($P < 0.001$).

[e] There was no significant interaction among linear furanocoumarin and UV treatments ($P > 0.20$). Time until adult eclosion differed significantly among furanocoumarin levels ($P < 0.001$) as follows: high > control = medium > low ($P > 0.05$, least squares means *t*-test). Supplemental UV significantly increased time until adult eclosion ($P < 0.001$).

on *C. floridanum* development than on *T. ni* development. Based on the results for development of *T. ni*, we expected furanocoumarin level and UV radiation to slow development of *C. floridanum*. Because *C. floridanum* reproductive larvae do not hatch from the egg until the host enters its ultimate stadium (Strand 1989a), slower host development (Fig. 1B; Tables 1 and 2) suggests that increasing furanocoumarin concentration indirectly affected the development of *C. floridanum* evidently by delaying the time of parasitoid egg hatch. In addition, the time until host mummy formation increased with furanocoumarin concentration ($F = 8.43$, $P < 0.0001$, Table 2) and exposure to UV radiation ($F = 11.47$, $P < 0.001$; Table 2). However, although the prolonged host development resulted in a longer overall development time for *C. floridanum*, the pupal development time of *C. floridanum* did not differ with respect to furanocoumarin concentration ($F = 1.84$, $P > 0.14$) or UV treatment ($F = 3.27$, $P > 0.07$). These results indicate that linear furanocoumarins consumed by the host exert their effect on the larval stage of *C. floridanum*.

Had the linear furanocoumarins affected *C. floridanum* before hatching (i.e., interfered with polyembryonic development), the total number of reproductive progeny produced per host should have been lower with increasing furanocoumarin treatment. However, we found no significant differences in total number of reproductive progeny per host (Table 2). The linear furanocoumarins clearly affected developing parasitoid larvae as the number of adults per host was lower with increasing furanocoumarin concentrations (Table 2).

Although increasing linear furanocoumarin concentrations increased parasitoid mortality, *C. floridanum* females from hosts reared on the highest furanocoumarin level were significantly larger than those from the other treatment groups (Fig. 2B). Given the results of previous studies examining the impact of linear furanocoumarins on arthropods, this result is somewhat anomalous. However the trend of *C. floridanum* sizes resembles the pattern seen for pupal mass of unparasitized *T. ni* and could reflect surviving *C. floridanum* larvae having more host resources available as a result of reduced intraspecific competition. McCloud and Berenbaum (1994) did not observe any differences in pupal mass of *T. ni* reared on furanocoumarins although larger pupae were obtained when larvae were exposed to shorter-wave UV-B radiation. Although furanocoumarins may be detoxified or at least metabolized by an herbivore before reaching the hemolymph, Bull et al. (1984) found the polyphagous *Spodoptera frugiperda* (J. E. Smith) passes large amounts of unmetabolized xanthotoxin into the body. Lee and Berenbaum (1989) also suggest that unmetabolized furanocoumarins collect in *T. ni* tissues and produce toxic oxyradicals before being detoxified later in larval development (Ahmad 1992). Therefore, *C. floridanum* mortality might result from larvae feeding on host tissues where such oxyradicals may accumulate.

Our results confirm and extend previous findings that plant chemistry can affect herbivore-parasitoid interactions. In our study, the secondary plant metabolites acted directly on the parasitoid. The contrast between our results and those of previous studies of *C. floridanum* (Orr and Boethel 1985,

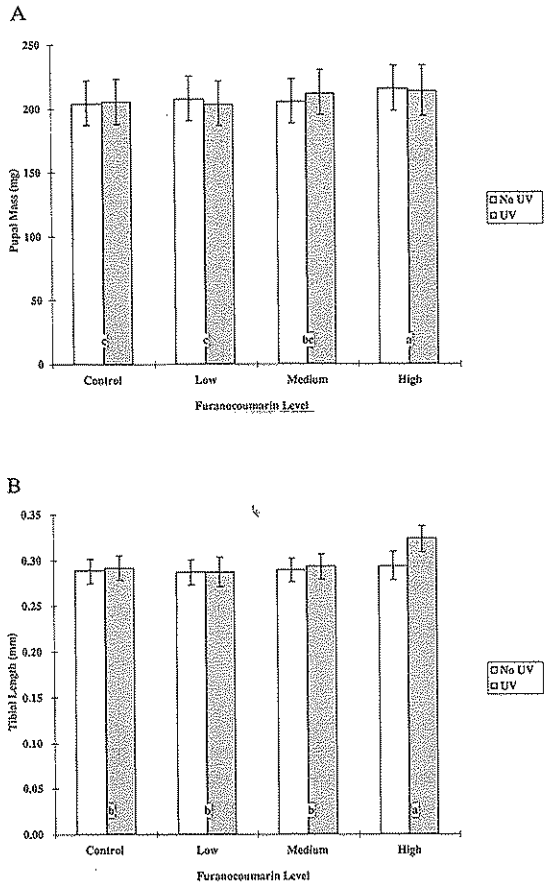

Fig. 2. Effects of linear furanocoumarin containing diets and UV radiation on body size of unparasitized *T. ni* and *C. floridanum* reared from *T. ni*. (A) Pupal mass (mean ± 95% CI) of *T. ni* when reared on artificial diet containing different concentrations of linear furanocoumarins and in the absence (open bars) and presence (shaded bars) of supplemental UV radiation. There was no significant interaction between linear furanocoumarin and UV radiation treatments ($P > 0.05$). The linear furanocoumarin main effect was significant ($P < 0.001$). Linear furanocoumarin means with the same letter within bars are not significantly different ($P > 0.05$, least squares means *t*-test). The mean mass of larvae exposed to supplemental UV radiation was not significantly different from that of larvae not exposed to supplemental UV radiation ($P > 0.8$). Mean mass of male pupae was significantly greater than that of female pupae ($P < 0.001$, data not shown). (B) Metathoracic tibial length (mean ± 95% CI) of female *C. floridanum* from *T. ni* reared on artificial diet containing different concentrations of linear furanocoumarins and in the absence (open bars) and presence (shaded bars) of supplemental UV radiation. There was no significant interaction between linear furanocoumarin and UV radiation treatments ($P > 0.05$). The linear furanocoumarin main effect was significant ($P < 0.02$). Linear furanocoumarin treatment means with the same letter within bars are not significantly different ($P > 0.05$, least squares means *t*-test). The mean tibial length of wasps from *T. ni* larvae exposed to supplemental UV radiation was not significantly different from that of wasps from *T. ni* larvae not exposed to supplemental UV radiation ($P > 0.07$). All data were analyzed after log-transformation and are presented following transformation to their original scale.

Beach and Todd 1986) also demonstrate that different host plant traits exert differential influences on *C. floridanum*. In these previous studies, parasitoid mortality resulted when hosts, *Pseudoplusia includens* (Walker), fed on resistant soybeans, *Glycine max* (L.). Although the mechanism of host plant resistance was not identified, their results indicate the host plant effects on the parasitoid were mediated indirectly through effects on the host. Although *C. floridanum* can complete development when hosts feed on linear furanocoumarin-containing diets, the overall impact of the photoactivated linear furanocoumarins found in celery on *C. floridanum* populations could be quite severe given that the number of putatively parasitized hosts surviving to produce parasites, and the number of parasitoids per surviving host decreases with increasing linear furanocoumarin content.

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