Host Plant Resistance and Linear Furanocoumarin Content of *Apium* Accessions

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ABSTRACT Linear furanocoumarin contents and antibiotic resistance to *Liriomyza trifolii* (Burgess) were documented for *Apium* species being investigated in a celery breeding program. In no-choice tests, *L. trifolii* fed more, produced more offspring, and had the highest pupal and adult productivity on the widely planted cultivar 'Tall Utah' 52-70R (*Apium graveolens* L.). Antibiotic effects of the commercial cultivar 'Tall Utah' 52-70 HK and University of California families 87A-147 and 87A-338, derived from *A. chilense* Hook and Arn., were intermediate. Only *A. nodiflorum* (L.) Lag (accession 87A-236) did not allow survival beyond the larval stage. Concentrations of the carcinogenic and mutagenic linear furanocoumarins varied by location within plants (leaves usually > petioles), by specific compound (trend: psoralen < xanthotoxin < bergapten or isopimpinellin), and between accessions. *A. nodiflorum* had the lowest foliar levels of phototoxic furanocoumarins (11.8 μg/g fresh weight) and the best potential for use in the breeding program. Foliar levels of phototoxic furanocoumarins (psoralen, bergapten, and xanthotoxin) in plants 87A-147-3 (406 μg/g), 87A-147-2 (292.9 μg/g), and the family 87A-338 (265.9 μg/g) were 22.6, 16.3, and 14.8 times higher, respectively, than the concentration known to produce contact dermatitis (18 μg/g). Even with such variability in concentration, the foliar content of linear furanocoumarins (individually or total) and *L. trifolii* adult production were not correlated.

KEY WORDS Insecta, *Liriomyza trifolii*, furanocoumarin, phototoxicity

PHOTOTOXIC DERMATITIS caused by contact with celery infected with a *Sclerotinia* fungus has been reported since the early 1900s (Austad & Kavli 1983, Ashwood-Smith et al. 1985). Since the mid-1970s, the causal agents of the dermatitis have been definitively identified as the phototoxic linear furanocoumarins psoralen, bergapten, and xanthotoxin. When exposed to longwave ultraviolet light, the phototoxic linear furanocoumarins rapidly alkylate DNA (Scott et al. 1976). These chemicals have proven lethal and carcinogenic in in-vitro bioassays of bacterial and mammalian cells (Ashwood-Smith et al. 1980), shown substantial toxicological risks for humans (Scott et al. 1976), been recognized as causally related to skin cancer by the World Health Organization (International Agency for Research on Cancer 1983), and been shown to cause cataract formation in animals and humans (Lerman 1986). The presence of high concentrations of linear furanocoumarins in other *Apium* L. species and in related genera in the Apiaceae (Umbelliferae), also have been reported by Berenbaum (1981a,b) and Chaudhary et al. (1986). In addition, the furanocoumarins confer insect resistance (Berenbaum 1978). Therefore, the potential presence of these compounds is of concern to those seeking to breed new cultivars of celery.

In a celery breeding program in California, where >50% of the celery produced in the United States is grown (Ivey & Johnson 1986), more than 150 *Apium* species have been evaluated for resistance to a key insect pest, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) (Trumble & Quiros 1988). Foliar mining by this species not only reduces the photosynthetic capacity of the leaves (Trumble et al. 1985), which results in yield losses, but also decreases marketability and increases production costs (Leibee 1984, California Celery Research Advisory Board 1985).

Our studies evaluated crosses between commercial celery cultivars and resistant *Apium* species to determine the inheritance of resistance and to determine if any observed plant resistance was based on potentially hazardous concentrations of linear furanocoumarins.

Materials and Methods

No-Choice Experiments. To determine if selected species and backcrosses were actually unsuitable for *L. trifolii* population maintenance or development, we conducted no-choice challenges. The F_1 hybrids of *A. graveolens* × *A. chilense*, confirmed by isozyme electrophoresis (Ochoa & Quiros 1986), were backcrossed once with *A. grave-*

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olens to produce three plants designated University of California (UC) Davis family number 87A-147. These plants had low fertility and were cloned to produce adequate numbers for testing. The clones have been reported as 87A-147-1, 2, or 3, depending upon the plant from which they were cloned. Family 87A-338, consisting of approximately 15 plants, was obtained by backcrossing one of the the 87A-147 plants with *A. graveolens* a second time. Most of the plants in family 87A-338 then regained fertility and cloning was not necessary. The cultivars 'Tall Utah' 52-70 HK and 'Tall Utah' 52-70R (*A. graveolens*) were included to provide comparative data from commercially available plants. *A. nodiflorum* (UC #87A-236, PI 279829), which had appeared promising in preliminary laboratory experiments, also was tested.

The plant materials used in the experiment were standardized to the extent possible. All plants were germinated concurrently. They were exposed to the same nutrient, moisture, and light regimes in a greenhouse equipped with charcoal filters to remove air pollutants. Test plants were transplanted into 1-liter pots in UC soil mixture (Matkin & Chandler 1957) and fertilized twice weekly with one-half strength Hoagland's nutrient solution (Downs & Hellmers 1975). Plants were held in a greenhouse for at least 2 mo before experiments. Leaf area on the test plants was standardized to 200–300 cm^2 per plant (Li-Cor 3000 Portable Leaf Area Meter, Li-Cor, Lincoln, Nebr.) by removing the youngest leaves and any visibly senescent foliage. This left several of the largest (approximately 25–30 cm) and most attractive petioles for oviposition and larval development (Tryon & Poe 1979). The larger leaves trimmed from each plant then were weighed, frozen in liquid nitrogen, and stored at −65°C until analysis for linear furanocoumarin content.

Although this minor trimming of the plants might induce production of defensive chemicals, structural damage caused during transplantation (i.e., stripping of excess petioles or mowing of the top 6 to 8 cm of foliage), by feeding of leafminers or lepidopterous larvae, or by common cultural practices, such as side dressing of fertilizer, also would stimulate induced responses. Thus, the advantages associated with standardizing plant size outweighed possible interference of induced responses for the no-choice feeding tests.

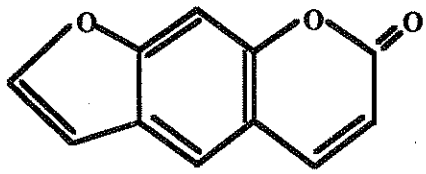
Adult *L. trifolii* used in these trials were obtained from a celery field in Orange County, Calif., and maintained in a laboratory colony reared on 'Tall Utah' 52-70R celery. All *L. trifolii* adults used in this study were 3 d old and had been fed only a 20% honey solution before exposure to the test plants. Although Tavormina (1982) and Via (1984a,b) demonstrated that closely related species of *Liriomyza* developed a preference for the host species from which they had been reared, Via found no differences in average responses (pupal weight, developmental time) to different host species. Thus, 'Tall Utah' 52-70R was chosen for laboratory maintenance, because this is the most common celery cultivar planted in California, and *L. trifolii* will be forced to make a similar transition to alternative hosts under field conditions if new accessions become widely used.

Plants were placed individually in 11.4-liter cylindrical containers and exposed to five pairs of adult *L. trifolii* for 2 h. Ten replicates were evaluated, with each consisting of one plant from each of six accessions. Plants were held in an environmental chamber set for a photoperiod of 16:8 (L:D) and 26.7 ± 1°C. After 3 d, feeding and oviposition punctures were counted. The numbers of mines per plant were counted after 4–5 d. Plants then were tilted on their sides so that larvae emerging from the leaves would drop into a tray filled with sand. Numbers of larvae and pupae were recorded daily until no live larvae remained in the foliage. Pupae from each plant were held in the environmental chamber for at least 2 wk, at which time the numbers of males and females successfully reaching the adult stage were recorded. Developmental data were analyzed with ANOVA and Student-Newman-Keuls test (ANOVA procedure, Clear Lakes Research 1986) ($P < 0.01$). Ratios of feeding punctures/mines, pupae/mines, adults/pupae, and females/males were analyzed similarly following an arcsine transformation.

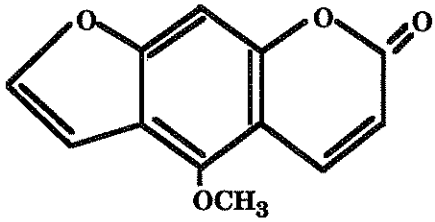
Extraction of Linear Furanocoumarins. Extraction of the linear furanocoumarins psoralen, bergapten, xanthotoxin, and isopimpinellin was modified from a technique reported by Beier (1985) and Beier et al. (1983a,b). *Apium* accessions and cultivars examined were those reported for the no-choice experiments. Foliage and petioles from each of eight plants were extracted and analyzed (three times from each plant). The frozen plant material was immersed in liquid nitrogen and crushed to a fine powder with a mortar and pestle. The powder was transferred into a 40-ml Ten Broeck homogenizer and further ground in 15 ml of deionized H_2O. The homogenate was poured into centrifuge tubes, the volume brought up to 25 ml with deionized H_2O, and the samples centrifuged for 6 min at 570 × *g*. The supernatant was passed into separatory funnels through several layers of cheesecloth and the sediment was discarded.

The aqueous phase was extracted once with 20 ml and three times with 10 ml of diethyl ether. Ether fractions were combined, centrifuged at 110 × *g* to break emulsions, and decanted into a round-bottom flask. The samples then were reduced to dryness by rotary evaporation. The residue was dissolved in 0.6 ml acetonitrile and 0.4 ml H_2O was added; this flask washing step was repeated four times.

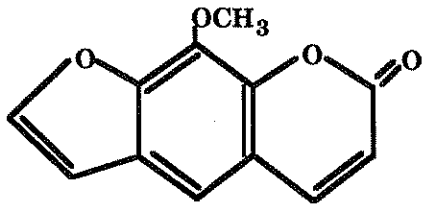
To remove unpolar impurities, the combined flask rinses were passed through a C18 SEP-PAK cartridge (Waters Associates, Milford, Mass.), which was previously washed with 15 ml MeOH and rinsed with 15 ml H_2O); and the eluate was collected. The



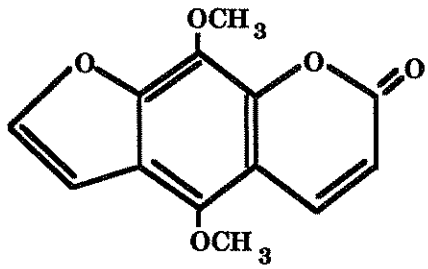
Psoralen



Bergapten



Xanthotoxin



Isopimpinellin

Fig. 1. Chemical structures of the four linear furanocoumarins found in celery.

SEP-PAK cartridge then was washed with 8 ml 60% acetonitrile in water and the eluates were combined. Fifteen ml of anhydrous EtOH was added to the sample to facilitate azeotropic distillation of the water, and the sample subsequently was reduced to approximately 1 ml by rotary evaporation. The remaining water was poured into a test tube and extracted twice with 5 ml ethyl acetate by vigorously shaking the tubes.

After phase separation the ethyl acetate layers were drawn off with a Pasteur pipette, combined, and passed through a silica SEP-PAK cartridge (previously washed with 15 ml chloroform) to remove polar impurities. The SEP-PAK cartridge was then eluted with 8 ml of 7.5% ethyl acetate in chloroform and the combined eluates were concentrated to dryness by rotary evaporation. The samples were taken up to 1 ml in chloroform and stored at −65°C until analyzed. In all cases, extraction recoveries of standard solutions were equal to or greater than 83%.

Mass Spectrometry. Elutants were identified using mass spectrometry. Psoralen, bergapten, and isopimpinellin analyses were performed on a 70-250 Mass Spectrometer (MS) (VG Analytical, Wythenshawe, England). The MS source was directly coupled to an HP5890 Gas chromatograph (GC). The MS source block was kept at 190°C. The GC/MS interface was 260°C and the GC injector temperature was 250°C. GC/MS determinations were done with a fused silica capillary column (SPB-1) at a length of 30 m and an inside diameter of 0.25 mm with a 0.25 μm coating (Supelco, Bellefante, Pa.). Samples were injected into the HP 5890 GC in the spitless mode. The injector was purged after 30 s into each run. The carrier gas was helium at 11 kg/cm² head pressure. The GC temperature program started at 40°C for 3 min, then elevated at 10°C/min until 210°C, and was held at 210°C for 20 min. Data were recorded on a VG 11-250 data system. Xanthotoxin was analyzed using a 7070E Mass Spectrometer (VG Analytical) with a solid probe (200–250°C) under electron ionization conditions (70 eV, source temperature = 150°C). A mass range of 100–300 daltons was scanned. The standards used in this study were psoralen, bergapten (5-methoxypsoralen), and xanthotoxin (8-methoxypsoralen), and isopimpinellin (5,8-methoxypsoralen) (Fig. 1). The first three were purchased from Aldrich Chemical Company (Milwaukee, Wis.), and the last was isolated from *Ammi majus* L.

Linear Furanocoumarin Concentrations. Linear furanocoumarins were resolved using high-performance liquid chromatography (HPLC) on a 25 cm Beckman Ultrasphere 5 μm spherical 80Å pore silica column (Beckman, Fullerton, Calif.), preceded by an Ultrasphere 5 μm Guard Column on a Beckman 334 Liquid Chromatograph. The solvent system was 100% chloroform pumped by a Beckman 110B Solvent Delivery Module at a flow rate of 1.5 ml/min. Samples were injected with a Beckman 210A Sample Injection Valve equipped with a 20-ml loop. Eluting components were monitored with a Beckman 160 Absorbance UV Detector set at 254 nm. Sample peaks were recorded and integrated with a model 3392A Integrator (Hewlett Packard, Avondale, Pa.).

Retention times were 5.59, 5.96, 7.95, and 9.32 min for psoralen, bergapten, xanthotoxin, and isopimpinellin, respectively (Fig. 1). With some chloroform, addition of methyl alcohol (not exceeding 0.2%) was required to achieve similar retention times. Standard curves for the four furanocoumarins, which were generated over a concentration

Table 1. Influence of *Apium* accession on oviposition, development, and survival of *L. trifolii*

Celery plant[a]	No./plant[b]				Ratio per plant[c]	
	Feeding punctures	Mines	Pupae	Adults	Pupae/mines	Adults/pupae
52-70R	212.0a	31.3a	25.5a	15.0a	0.87a	0.67a
147-2	106.0b	23.5ab	17.4b	10.7a	0.73a	0.62a
52-70 HK	43.1b	17.6bc	8.3c	4.8b	0.72a	0.68a
338	91.8b	15.2bc	8.9c	5.4b	0.78a	0.66a
147-3	55.2b	9.8cd	2.0c	0.8b	0.11b	0.51a
236	46.8b	2.5d	0.0c	0.0b	—[d]	—[d]

[a] University of California–Davis, Department of Vegetable Crops accession/plant numbers.
[b] Means within columns followed by the same letter are not significantly different ($P > 0.05$, Student-Newman-Keuls test [Clear Lakes Research 1986]).
[c] Means within columns followed by the same letter are not significantly different ($P > 0.05$, arcsine transformation, Student-Newman-Keuls test [Clear Lakes Research 1986]; untransformed data are presented).
[d] Division by zero precludes analysis.

range of 0.05 (detection limit) to 150 μg/ml by direct injection of the furanocoumarin standards into the HPLC column, produced linear correlation coefficients >0.999 in each case. Means comparisons of furanocoumarin contents among accessions were made using the ANOVA procedure of SAS (SAS Institute 1985) with the plant within variety as the mean square error term; the F values all were significant at the $P < 0.05$ level. Use of the ANOVA procedure was followed with Duncan's multiple range test (SAS Institute 1985). Correlations between resistance level (as measured by numbers of emergent adults) and individual and total linear furanocoumarin content in each accession were performed with Stat View II (Abacus Concepts, Berkeley, Calif.). Significance ($P = 0.05$) of the correlation coefficients was determined by a t test (Rohlf & Sokal 1981).

Results and Discussion

No-Choice Tests. The commercial celery cultivar 'Tall Utah' 52-70R was more suitable for *L. trifolii* feeding and development than the other accessions tested (Table 1). Leafminers released on this cultivar fed significantly more, generated the highest number of mines, produced significantly more pupae, and yielded the highest numbers of adults. In contrast, accession 236 (*A. nodiflorum*), demonstrated substantial antibiosis; few mines were observed and no larvae survived to the pupal stage. The other accessions were intermediate in effect, but all allowed some insects to complete development to the adult stage. Of these the *A. chilense* derivative 147-2 was notable for allowing high levels of adult production, whereas 147-3 was distinguished by relatively low adult emergence and the lowest ratio of pupae to mines. Thus, the relative suitability of the accessions for *L. trifolii* population maintenance and development was variable, with suitability following the pattern 52-70R > 87A-147-2 > 87A-338 > 52-70 HK > 87A-147-3 > 87A-236.

As was observed in a previous study (Trumble & Quiros 1988), the potential for leafminer population development was generally lower on hybrids than on the parental accessions (*A. graveolens* > 87A-147-2 > 87A-147-3). This suggests that the antibiotic trait is dominant and that hybrid vigor may be a useful tool for breeding celery resistant to *L. trifolii*. Because resistant accessions with antibiotic properties have considerable potential for slowing the growth rates of pest populations (Kennedy et al. 1987), and because *L. trifolii* is broadly polyphagous (Minkenberg & van Lenteren 1986), regional use of the more resistant accessions identified in our study should help reduce the destructive intercrop movements reported for this pest (Zehnder & Trumble 1984).

Mass Spectrometry. Psoralen, bergapten, xanthotoxin, and isopimpinellin were the only linear furanocoumarins detected. The presence of these four compounds is in agreement with previously published reports for healthy celery (Beier et al. 1983b, Dercks et al. in press). The most important fragment ions for psoralen included: m/z 187 (12%), 186 (100%), 159 (10%), 158 (74%), 130 (14%), 129 (9%), 103 (11%), and 101 (27%). Key fragment ions for bergapten included: m/z 217 (12%), m/z 216 (100%), 201 (29%), 188 (12%), 173 (43%), 173 (94%), 145 (20%), 144 (20%), 102 (22%), and 100 (19%). Identifying fragment ions for xanthotoxin included: m/z 217 (26%), 216 (72%, $[M]^{+\cdot}$), 201 (60%), 188 (45%), 174 (40%), 173 (100%), 158 (22%), 145 (92%), 129 (37%), 117 (21%), 116 (23%), 102 (25%), and 101 (21%). Key fragment ions for isopimpinellin included: m/z 247 (16%), 246 (100%), 232 (12%), 231 (91%), 203 (12%), 188 (12%), 175 (10%), and 160 (12%).

Linear Furanocoumarin Concentrations. Linear furanocoumarin content varied by location within plants, by specific compound, and among accessions (Table 2). Petioles generally had lower concentrations than leaves. In some cases (psoralen, plant 87A-147-3), the differences exceeded 100-fold. More typically, the variation in concentrations averaged 1.5- to 10-fold. With the exception of accession 87A-236, a general trend in our study for linear furanocoumarin concentrations occurred such that psoralen < xanthotoxin, < isopimpinellin or

Table 2. Linear furanocoumarin content (μg/g freshweight) of selected *Apium* accessions[a]

Celery plants	Psoralen		Bergapten		Xanthotoxin		Isopimpinellin	
	Petioles	Leaves	Petioles	Leaves	Petioles	Leaves	Petioles	Leaves
147-3	0.39bc	44.79a	41.67ab	273.28a	12.38ab	87.91ab	62.27abc	199.20a
147-2	2.71a	34.09ab	135.53ab	168.98ab	47.63a	89.85ab	110.99a	115.63a
236	1.59ab	1.59d	4.46b	8.53c	0.73b	1.73b	1.93c	4.82d
338	0.00c	17.08c	154.20a	144.19b	43.34ab	104.62a	90.87ab	97.11bc
52-70R	0.00c	21.75bc	16.77ab	57.90bc	3.80ab	18.35ab	12.43c	21.43cd
52-70 HK	0.15c	0.00d	18.62ab	9.49c	8.18ab	12.78ab	20.53bc	14.63cd

Means within columns followed by the same letter are not significantly different ($P > 0.05$, Duncan's multiple range test [SAS Institute 1985]).

[a] University of California–Davis, Department of Vegetable Crops accession/plant numbers; 52-70 HK and 52-70R are commercial cultivars.

bergapten. Although the potential effects of the non-phototoxic isopimpinellin on mammals may be less than the effects of other furanocoumarins that are phototoxic, the observed differences in relative concentrations of isopimpinellin between accessions may be important.

Concentrations of total linear furanocoumarins in petioles was highest in plant 87A-147-2 (296.7 μg/g fresh weight), family 87A-338 (288.4 μg/g) and plant 87A-147-3 (116.7 μg/g). Levels were lower in the commercial varieties (52-70 HK = 47.3 μg/g; 52-70R = 33.0 μg/g), and were lowest in accession 87A-236 (8.71 μg/g). Concentrations of the phototoxic linear furanocoumarins followed a similar trend such that 87A-338 (197.5 μg/g) > 87A-147-2 (185.7 μg/g) > 87A-147-3 (54.4 μg/g) > 52-70 HK (26.9 μg/g) > 52-70R (20.6 μg/g) > 87A-236 (6.7 μg/g). The phototoxic linear furanocoumarin levels in petioles of 87A-338, 87A-147-2, and 87A-147-3 justify concern because concentrations of 18 μg/g fresh weight in celery cause contact dermatitis (Austad & Kavli 1983). Data presented by Seligman et al. (1987) suggest that repeated exposure to celery with concentrations as low as 7 to 9 μg/g fresh weight in the petioles can result in phytophotodermatitis.

The accession 87A-236 (11.8 μg/g) had the lowest levels of the phototoxic linear furanocoumarins of any of the accessions tested. Given that this accession also demonstrated effective antibiosis (100% mortality) against the leafminer, 87A-236 should be a suitable plant line to attempt backcrossing with commercial celery varieties to develop a commercially acceptable resistant cultivar. Because our study provides no evidence that the linear furanocoumarins alone were providing any antibiotic effects, the mechanism for resistance to the leafminer in accession 87A-236 should be the subject of additional research. However, we can not eliminate the possibility that the linear furanocoumarins were acting in a synergistic fashion with other plant compounds (see Neal 1989).

The levels of psoralen, bergapten and xanthotoxin (phototoxic furanocoumarins) from control plants in our test were six times higher in leaves and stems than observed by Beier et al. (1983a) (mean from leaves or petioles for psoralen ≤ 0.15, bergapten ≤ 1.5, xanthotoxin 3.5 μg/g), but were similar (approximately 1.4 times greater) to the concentrations reported by Berkeley et al. (1986) (phototoxic furanocoumarins, 11.2 μg/g in petioles and 20.4 μg/g in leaves) and were equivalent to or less than levels observed by Dercks et al. (in press) on the same control accession (two tests with different age plants; phototoxic furanocoumarins in leaves, 25–69.5 μg/g; and in petioles, 12.6–29.2 μg/g). Such increases may be due to varietal effects (Berkley et al. 1986), but direct comparisons with previous studies were not possible because all the cultivars tested were not reported.

The high foliar concentrations of the phototoxic linear furanocoumarins observed in our study are of considerable importance given a new trend in marketing intact celery (leaves not trimmed) rather than the more common "topped" celery (most leaves removed). The common practice of topping the celery before sale also removes the distal portions of the petioles, which have the highest concentrations of phototoxic furanocoumarins (R.C.B., unpublished data). Foliar concentrations reached the highest and most dangerous levels in plants 87A-147-3 (406.0 μg/g fresh weight), 87A-147-2 (292.9 μg/g), and family 87A-336 (265.9 μg/g). To our knowledge, these levels of linear furanocoumarins are the highest reported from any botanical source. These accessions clearly are not suitable or appropriate for release for commercial use. However, 87A-338 was a heterogeneous family segregating for traits from its wild parent *A. chilense*. Therefore, the progeny are likely to include plants with a wide range of linear furanocoumarin concentrations and, potentially, suitability for leafminers. Thus, selection from these progeny plants characterized by leafminer resistance and low concentrations of furanocoumarins may be possible.

Concentrations of the linear furanocoumarins in the foliage of the commercial varieties 52-70 HK (22.3 μg/g) and 52-70R (98.0 μg/g) were substantially lower and less hazardous than in the aforementioned plants. Because contact dermatitis in celery handlers is common (19 cases out of 48 handlers in the most recent study [Seligman et al. 1987]),

we suspect that the concentrations of phototoxic furanocoumarins observed in the commercial cultivars included in our study are not unusual.

The linear furanocoumarin concentrations reported in our study may be conservative. None of the plants used in this study exhibited symptoms of disease or were subjected to mechanical damage or air pollutants which can increase furanocoumarin content (Beier & Oertli 1983, Ashwood-Smith et al. 1985, Chaudhary et al. 1985, Dercks et al. in press). Also, because the plants were not yet at the commercially harvestable stage, an increase in linear furanocoumarin content could be expected with increases in plant size (Austad & Kavli 1983).

Correlation analyses of adult emergence versus psoralen, bergapten, xanthotoxin, isopimpinellin, or total linear furanocoumarin content of the accessions indicated that increasing concentrations of these compounds did not confer resistance to the leafminer. The correlation coefficients generally were not significant ($P > 0.05$, df = 5), with values of −0.207 ($t = -2.19$), 0.174 ($t = 1.91$), −0.110 ($t = -2.43$), and 0.004 ($t = -2.44$) for isopimpinellin, psoralen, bergapten, and xanthotoxin, respectively. The correlation coefficient for total furanocoumarin content was significant at 0.101 ($t = -2.6$, df = 5, $P > 0.048$), but provides little predictive value. This contrasts with earlier reports for other insects, which implicated these compounds in host plant resistance (Berenbaum 1981a,b). However, at least one other insect species has been shown to detoxify linear furanocoumarins, and a mechanism for the detoxification has been documented (Ivie et al. 1983). Clarification of the mechanism by which leafminers detoxify these compounds merits further study.

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