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Resistance to *Spodoptera exigua* in *Apium prostratum*

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Abstract

Two *Apium* accessions were compared with the commercial cultivar 'Tall Utah' 52-70R (*A. graveolens* [L.]) for resistance to *Spodoptera exigua* (Hübner)(Lepidoptera: Noctuidae). Oviposition rate was not significantly different between the three genotypes. In all accessions, eggs were usually placed on the upper half of the plants. Implications of this oviposition pattern on *S. exigua* management in celery are discussed. The wild species *A. prostratum* ssp *prostratum* var filiform (A230) showed a significantly higher resistance to *S. exigua* than 52-70R. The levels of carcinogenic and mutagenic linear furanocoumarins in the commercial cultivar 52-70R (1.41 μg/g in the petioles; 5.85 μg/g in the leaves) and in the plant accession *A. nodiflorum* (5.40 μg/g in the petioles; 2.99 μg/g in the leaves) were far below the concentration reported to produce acute contact dermatitis (18.0 μg/g). The levels of furanocoumarins in *A. prostratum* petioles (186.14 μg/g) and leaves (326.45 μg/g) were 10 and 18 times higher, respectively, than the concentration known to cause contact dermatitis. However, resistance in *A. prostratum* was primarily due to non-preference and the linear furanocoumarins did not induce non-preference. Therefore, the resistance shown by this plant accession does not appear to be furanocoumarin-based and may be suitable for transfer to commercial celery for use in *S. exigua* management.

Introduction

The beet armyworm, *Spodoptera exigua* (Hübner), and the leaf miner *Liriomyza trifolii* (Burgess) are currently the major insect pests of celery (*Apium graveolens* [L.]) in the United States (Van Steenwyk & Toscano, 1981; Trumble *et al.*, 1990). Jones & Granett (1982) reported that *S. exigua* caused important economic damage to celery, especially late in the growing season. The insect feeds on both leaves and petioles of celery (Jones & Granett, 1982; Griswold & Trumble, 1985). The first two to three instars feed on the leaves while later instars attack the leaves, petioles, and even the plant heart, which can prevent production of new petioles. Feeding on the petiole causes cosmetic injury and results in reduced product marketability (Jones & Granett, 1982).

Efforts to control *S. exigua* with chemicals have resulted in increased *L. trifolii* infestations due to the destruction of their natural enemies (Oatman & Kennedy, 1976; Johnson *et al.*, 1980; Trumble, 1984). Reliance on insecticides as the primary insect control system in celery also has caused the development of insecticide resistance (Trumble, 1990) and resulted in the use of maximum rates

of insecticides (Trumble & Toscano, 1983). Trumble & Parrella (1987) reported that heavy reliance on chemicals has increased legislation restricting insecticide registration. Alternatives to pesticides are necessary to sustain economically viable celery production. One of the best alternatives to chemicals in integrated pest management is the use of pest resistant plant cultivars (Kennedy *et al.*, 1987).

Trumble & Quiros (1988) reported resistance to *L. trifolii* in celery *Apium nodiflorum* (L.) Lag (PI 1279829 from Ethiopia). Our preliminary studies indicated potential resistance to *S. exigua* in *A. prostratum* ssp *prostratum* var. filiform (A. Rich). The research reported herein was initiated to investigate these two plant species for resistance to *S. exigua* by comparing them with the widely grown commercial celery cultivar 'Tall Utah' 52-70R (*A. graveolens* [L.]). Previous studies (Trumble *et al.*, 1990) revealed hazardous concentrations of the phototoxic linear furanocoumarins psoralen, bergapten and xanthotoxin in some *Apium* accessions. These compounds have been shown to be carcinogenic, mutagenic (Scott *et al.*, 1976; Ashwood-Smith *et al.*, 1980), and to cause contact dermatitis (Austad & Kavli, 1983; Seligman *et al.*, 1987). Consequently, the different celery lines were tested for linear furanocoumarin content.

Materials and methods

The commercial celery 'Tall Utah' 52-70R, the accession *A. nodiflorum* (PI 1279829 from Ethiopia), and the wild species *A. prostratum* spp *prostratum* var. filiform (A230 from Australia) were obtained from germplasm resources held at the University of California, Davis, Department of Vegetable Crops. *S. exigua* larvae were from a laboratory colony maintained on artificial diet (Shorey & Hale, 1965) at 27 ± 2 °C and 16:8 (L:D) photoperiod. Test plants were seeded on 15 October 1990, transplanted into 1-liter pots in University of California soil mixture (Matkin & Chandler, 1957) on 30 November 1990, and maintained under the same moisture, light, and nutrient regimes in a greenhouse equipped with charcoal filters to remove air pollutants. Elimination of ozone and related pollutants was necessary to reduce the potential for induction of linear furanocoumarin production (Dercks *et al.*, 1989). A one-half strength Hoagland's nutrient solution (Downs & Hellmers, 1975) was used to fertilize the plants twice per week. All plants were 4 mo old when experiments started. Four experiments were conducted.

Oviposition substrate preference experiment. This study was designed to determine the preference/non-preference of *S. exigua* for oviposition among the three celery test entries. We used two $135 \times 90 \times 95$ cm transparent plastic cages with a wooden frame. The cages were maintained in a greenhouse and ventilated through two $24 \times 90 \times 26$ cm windows made at the lower part of the two opposite long sides. Two plants of similar size for each test entry were placed 35 cm apart in each cage in a circular pattern with the two plants of the same test entry on opposite sides of the circle diameter. Placement of the initial plant of each entry was chosen randomly. Moths (9 males and 9 females) that had been fed a 20% sugar:water solution were released into the center of the cage. A small bottle of sugar water was placed in the center of the cage. Plants were examined 3 d later and the number of egg batches per plant and the number of eggs per batch were recorded. Sampling was done at 3 d because Smits *et al.* (1986) reported that very few eggs hatched in 3-5 d and the insect laid most of its eggs during this time period. The experiment was repeated three times, giving a total of six replications.

Free-choice feeding experiment. S. exigua larval feeding preference for the three lines was tested using 15×2 cm lidded glass petri dishes as bioassay chambers. A moistened filter paper disc was placed in each dish and leaves (one leaf from each cultivar) of similar size were equidistantly placed along the outer edge of the dish. Fifty first instar larvae were placed directly onto the center of the dish which was immediately covered with

the lid. The dish was then wrapped in dark paper to avoid influence of light and placed in an incubator at 27 ± 2 °C and 75% RH. After 24 h the number of larvae found on or under each test entry was recorded. A total of 21 replications were used. Fourth instar larvae were tested using the same procedures, but the number of larvae per dish was reduced to 5, and the dishes included both leaves and petioles. Larvae were deprived of food for 10 h before starting the experiment.

No-choice feeding experiments. Two suitability tests were conducted to compare *S. exigua* differential development on leaves and petioles of the three celery genotypes. In the first test, 7 ml of 5% agar:water solution were dispensed into 30 ml plastic cups and allowed to cool at ambient temperature. Fresh tissue of each celery genotype was harvested, and leaves and petioles were separated. The cups then were filled with fresh plant parts of each celery genotype and one neonate *S. exigua* was placed in each cup, which was then capped with a plastic lid with pin-holes. We used the agar solution because preliminary tests showed that this new method preserved plant material better than the filter paper alone. The plant tissue was renewed daily and the agar solution weekly. Treatment cups were arranged as a split-plot design with three replications of 30 cups per replicate. The first replicate was conducted when celery was 4 mo old. Replicates 2 and 3 were conducted 3 weeks later. In each replication the three celery lines were the main plots and the plant parts (leaves and petioles) were the subplots. Larvae were confined on the plant material until pupation. Pupae were then moved to a new cup to monitor adult emergence. All treatments were maintained in environmental chambers at 27 ± 2 °C, 75% RH, and 16:8 (L:D) photoperiod. The developmental variables measured were weight of larvae at 7, 8, and 9 d, duration of the larval stage, weight of pupae, days to adult emergence, and survivorship.

The second no-choice feeding test was conducted using artificial insect diet to confirm results of the first feeding experiment. Fresh tissue of each test entry was harvested and leaves and petioles were separated. A 3-g sample of each plant part was immediately homogenized in 10 ml of d H_2O (Polytron® tissue homogenizer) for 2.5 min. Each dietary treatment was prepared by vortexing 10 ml of the homogenate in 7 g of lima bean diet (Shorey & Hale, 1965) for 2.5 min. The mixtures were dispensed into 2.5-ml plastic cups (1 ml per cup, 16 cups per treatment) and allowed to cool at ambient temperature. One neonate *S. exigua* then was placed in each cup and cups were sealed with a plastic lid with pin-holes. Treatments were arranged as a split-plot design with nine replicates of 16 cups per replicate. Main plots were the three celery entries and sub-plots were the two plant parts. The first three replicates were conducted when celery was 4 mo old. Replicates 4 through 9 were conducted 3 weeks later. Larval weight and survival at 7 d were recorded.

Extraction of linear furanocoumarins. A rapid method for analysis of linear furanocoumarins was developed. Unless otherwise specified, all solvents used were Fisher Scientific Optima grade. Sample tubes (28 × 116 mm, round bottom) were spiked with 5 μg of a synthetic internal standard, 7-benzyloxycoumarin (synthesized from commercially available 7-hydroxycoumarin (Aldrich Chemical) (Trumble *et al.*, unpublished). Samples of leaf (2 g) or petiole (4 g) tissue were homogenized in 10 ml of d H_20 (Polytron® tissue homogenizer) for 2.5 min. Toluene (10 ml) was added to each tube, the tubes were capped with aluminum foil and vortexed for 1.5 min, and the resulting thick emulsions were centrifuged for 40 min at 330 g to separate the layers. The upper toluene layers were transferred to clean 13 × 100 mm culture tubes and concentrated to dryness with a Jouan RC 10.10 centrifugal evaporator (Jouan Inc., Winchester, Virg., USA) at 60 °C with a vacuum of approx. 100 mm Hg. A further 0.5 ml of toluene was added to the tubes, which were concentrated to dryness again to remove any traces of water by azeotropic distillation. The samples were reconstituted in 100 μl of toluene, and loaded onto Extract Clean® solid phase extraction tubes (500 mg silica, #209250,

Alltech Assoc., Inc., Deerfield Ill., USA) which had been preconditioned with 4 × 2 ml toluene. The sample was rinsed onto the cartridge with 2 × 0.1 ml toluene, discarding the eluate. The tube was then eluted by gravity flow with 5% acetone in chloroform (3 × 0.5 ml), discarding the first 0.5 ml of eluate. The eluate containing the furanocoumarin fraction was collected in 5 ml centrifuge tubes, and concentrated to dryness as before. The residue was vortexed 30 sec in HPLC mobile phase (vide infra), centrifuged briefly to pelletize any particulate matter, and a 20 µl aliquot was analyzed by HPLC. If not used immediately, the dried-down tubes were capped and stored at −20 °C.

HPLC analyses were carried out with a Hewlett-Packard 1040 HPLC pump and an H.-P. 1050A diode array detector with a Chemstation data system (Hewlett-Packard, Avondale, Penn., USA). Peaks were monitored and quantified at 290 nm. This wavelength was chosen because all three compounds and the internal standard had strong and similar absorbances at this wavelength, and interference from other compounds was minimized. Relative response factors at this wavelength were: ISTD, 1.00; psoralen, 1.23; 5-methoxypsoralen, 1.51; 8-methoxypsoralen, 1.34.

An Alltech Econosil silica column (25 cm × 4.6 mm, 5µ particle size) with a 10 mm × 4.6 mm guard column filled with the same packing material were used, eluted isocratically with hexane:tetrahydrofuran (81:19, mixed by HPLC pump). Tetrahydrofuran (HPLC grade) from Aldrich Chemical Co. gave markedly better resolution than THF from Fisher Scientific. Relative retention times were: ISTD, 1.00; psoralen, 1.15; 5-methoxypsoralen, 1.19; 8-methoxypsoralen, 1.38.

Extraction efficiencies were calculated at 1 and 20 µg/g, and were as follows: psoralen, 90.7 ± 5.7% and 95.6 ± 0.5%; 5-methoxypsoralen, 87.7 ± 5.4% and 96.9 ± 1.0%; 8-methoxypsoralen, 90.2 ± 6.6% and 95.2 ± 3.0%. Calibration curves for the three compounds were linear over the region of interest (0.005 to 10.0 µg/g plant material) with r^2 values of 1.00. Minimum detectability was conservatively estimated as 0.005 µg/g) for each compound.

Data analyses. A $\chi 2$ test ($\alpha = 0.05$) (Gomez & Gomez, 1984) was used to analyze the number of egg batches laid on the different celery genotypes. All other data sets were analyzed with ANOVA (Super ANOVA, 1989) and statistically different means were separated at the 5% significance level using Tukey's honestly significant difference (HSD) test (Keselman & Rogan, 1978).

Results and discussion

Oviposition substrate preference experiment. The number of egg batches/plant were 3.9, 3.1, and 3.5, respectively on 52-70R, *A. nodiflorum*, and *A. prostratum*; the total number of eggs/plant were 104.3, 48.7, and 58.5, respectively. However, no significant differences were found between the three test entries for the total number of eggs/plant ($P = 0.2242$; $F = 1.565$; df = 2,10). The reason for the lack of significant differences between treatments could be the high standard error (127.733) in the data collected on 52-70R (ANOVA). The $\chi 2$ test used to analyze the number of egg masses/plant also revealed no significant oviposition preference among the three *Apium* genotypes at the $\alpha = 0.05$ level (df = 2).

During this experiment, all the eggs were laid on leaves (or petioles in a few cases) of the upper half of the plant. No eggs were found on the lower plant parts. Zalom *et al.* (1983) also reported that *S. exigua* deposited the majority of its eggs on leaves of the upper half of the tomato, *Lycopersicon esculentum* Mill. 'Sunny', branches. These observations suggest that the sampling systems for the insect in celery could be improved. The methods currently used to monitor *S. exigua* larval population dynamics in the field are whole plant counts. Because larvae are usually hidden in the lower parts of the plant where they feed on the petiole and sometimes the plant heart (Jones & Granett, 1982), the celery plant is sometimes destructively sampled to assess the insect's damage or number. This latter scouting method, by itself,

can result in economic losses; therefore, growers are somewhat reluctant to use it and rather spray on a prophylactic basis, facing unnecessarily increased treatment costs. Since the moth only oviposits on easily accessible and detectable leaves and petioles, sampling for eggs instead of grown larvae should be desirable; this would allow an early detection of the insect's presence and more effective control programs since early instars tend to be more susceptible to biological control agents such as *Bacillus thuringiensis* var. *kurstaki* (Dulmage, 1973; Morris, 1986).

Free-choice feeding experiment. Though *S. exigua* showed no statistical differences in host acceptance for oviposition on the three celery lines, differences were observed for larval feeding preference. Both *A. prostratum* and *A. nodiflorum* were less preferred ($P = 0.0001$; $F = 87.4$; df = 2, 60) by first instars than the commercial line 52-70R (Fig. 1). Less than 10% of the first instars fed at all on *A. prostratum* while over 50% of the larvae were observed feeding on 52-70R. Equal numbers of fourth instar larvae fed on 52-70R and *A. nodiflorum*. However, no larvae fed on *A. prostratum*, which again was significantly ($P = 0.0040$; $F = 7.0$; df = 2, 40) less preferred than the commercial line 52-70R (Fig. 1). The reason for the strong nonpreference (antixenosis) for *A. prostratum* by *S. exigua* larvae has not been identified. However, the lack of feeding, especially by later instars, suggests that the resistance may be due to chemical repellency, lack of feeding stimulants, or leaf structural characteristics.

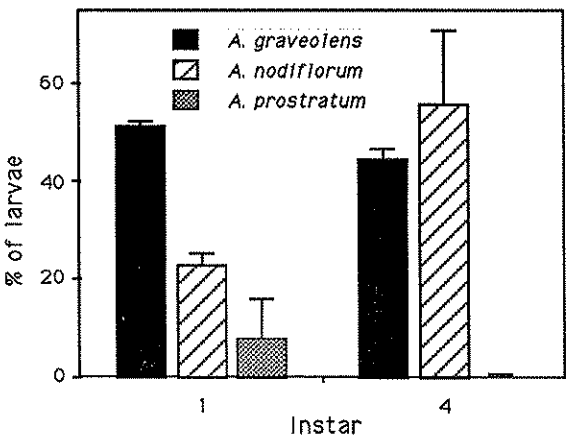

Fig. 1. Spodoptera exigua larval feeding preference for fresh tissue of *Apium* species. Leaves were used to test first instars, both leaves and petioles were used to test fourth instars. Extensions above bars denote standard errors.

No-choice feeding experiments. A. prostratum was highly resistant to *S. exigua* during the first feeding experiment where larvae were directly reared on fresh tissue from the three celery test entries. No larvae survived beyond the second instar on this plant accession; therefore, data on *A. prostratum* were not included in the ANOVA due to 0 variance. For the other two test entries (*A. nodiflorum* vs. 52-70R), plant part by entry interactions were significant ($P < 0.05$; $F > 10.00$; df = 1,6) for larval weight at 7, 8, and 9 d, and pupal weight. Therefore, comparison of these results were made within plant part and within celery entry. Results were compared across plant part and across celery entry where no significant interaction occurred. Overall, *S. exigua* fed more and produced the heaviest larvae and pupae on the plant accession *A. nodiflorum* compared with the commercial line 52-70R (Table 1). Feeding on *A. nodiflorum* also significantly reduced the generation time in number of days from egg to pupa and from egg to adult. *S. exigua* survival was, however, higher on 52-70R than on *A. nodiflorum*.

Larvae fed the petioles weighed significantly less, produced lighter pupae, took longer to pupate and emerge as adults, and had reduced survival as compared with larvae reared on the leaves (Table 1). Griswold & Trumble (1985) also observed that rearing *S. exigua* on celery leaves resulted in significantly greater insect growth rate and reproduction than rearing on petioles. The authors suggested that differences in these developmental variables occurred in response to higher nitrogen concentrations in the leaves.

The second no-choice feeding test was conducted by mixing ground fresh plant tissue in artificial insect diet, and results were similar to those obtained with direct feeding on fresh plant material. No larvae survived beyond the second instar on *A. prostratum* and data on this genotype were

Table 1. Developmental variables of *Spodoptera exigua* reared on fresh petioles (P) and leaves (L) of greenhouse grown *Apium* accessions at 27 ± 2°C, 75% RH, and 16:8 (L:D) photoperiod

Treatments	Wt[1] (mg)												Days to pupa	Days to adult	% survival to adult
	7 d larvae			8 d larvae			9 d larvae			Pupae					
	P		L	P		L	P		L	P		L			
52–70R	13.7a	*	34.7a	26.4a	*	62.4a	37.6a	*	91.2a	70.1a	*	84.7a	17.4a	24.1a	47.2a
Apium nodiflorum	12.9a	*	64.5b	40.4b	*	136.4b	51.1b	*	183.4b	66.0a	*	99.0a	15.4b	22.0b	41.5b
Apium prostratum	–		–	–		–	–		–	–		–	–	–	0.0[2]

Means within a column not followed by the same letter are statistically different at the 5% level (ANOVA). Also, petioles vs. leaves means separated by an asterisk * are statistically different (ANOVA).

[1] Interactions between treatments and plant parts were significant ($P < 0.001$; $F > 10.0$; df = 1, 1) for 7, 8, and 9 d wt and for pupal wt, but not for days to pupa, days to adult, and survival to adult.

[2] Mean comparison invalid because of 0 variance.

not included in the ANOVA due to 0 variance. *S. exigua* growth rate at 7 d was significantly greater ($P = 0001$; $F = 47.985$; df = 2, 16) on the diet supplemented with *A. nodiflorum* compared with growth rate on the diet containing the commercial celery 52-70R (Table 2). Weight gain at 7 d was greater on the diet supplemented with leaves than on the diet containing the petioles. No differences were found in insect survival to 7 d on diets containing the two celery entries. These observations confirmed results of the first feeding test. Although larvae were subjected to a no-choice condition, they did have the option to feed or starve as demonstrated by previous studies (Wiseman *et al.*, 1983). Therefore, the resistance in this wild species could be due to chemical non-preference as opposed to morphological non-preference (Diawara *et al.*, 1991a). The diet supplied the necessary nutrients so differences due to nitrogen contents of plant material should be minimized in this test. Thus, the differential development due to feeding on diet containing the two celery genotypes may be due to secondary plant chemistry: deterrents, repellents, toxins, or lack of stimulants.

Table 2. Developmental variables of *Spodoptera exigua* reared on artificial diet supplemented with homogenized fresh tissue of greenhouse grown *Abium* accessions at 27 ± 2°C, 75% RH, and 16:8 (L:D) photoperiod

Treatments	7 d[1] larval wt (mg)			% survival at 7 d[2]
	Petioles		Leaves	
52-70R	5.69a	*	13.52a	97.9
Apium nodiflorum	16.68b	*	52.58c	100.0
Apium prostratum	–		–	0.0
Control bean diet	40.17c		41.96b	100.0

Means within a column not followed by the same letter are statistically different at the 5% level as determined by Tukey's HSD test (Keselman & Rogan, 1978). Also, petioles vs. leaves means separated by an asterisk * are statistically different (ANOVA).

[1] Interactions between treatments and plant parts were significant for the 7 d larval wt variable ($P = 0.0001$; $F = 18.196$; df = 2, 16) (ANOVA).

[2] Mean comparison invalid because of 0 variance in data for all treatments except for 52-70R.

Linear furanocoumarin concentrations. The linear furanocoumarins analyzed were the three major phototoxic compounds isolated in *Apium* ssp., psoralen, bergapten (5-methoxypsoralen), and xanthotoxin (8-methoxypsoralen) (Trumble *et al.*, 1990). The concentrations of these compounds varied among the three celery genotypes. For each compound, significant ($P < 0.05$; $F > 7.00$; df 2, 6) celery entry by plant part interactions occurred; thus linear furanocoumarin concentrations also varied within entry and by location within plant. The levels of linear furanocoumarins in the commercial celery 52-70R (1.41 μg/g in the petioles; 5.85 μg/g in the leaves) and the plant accession

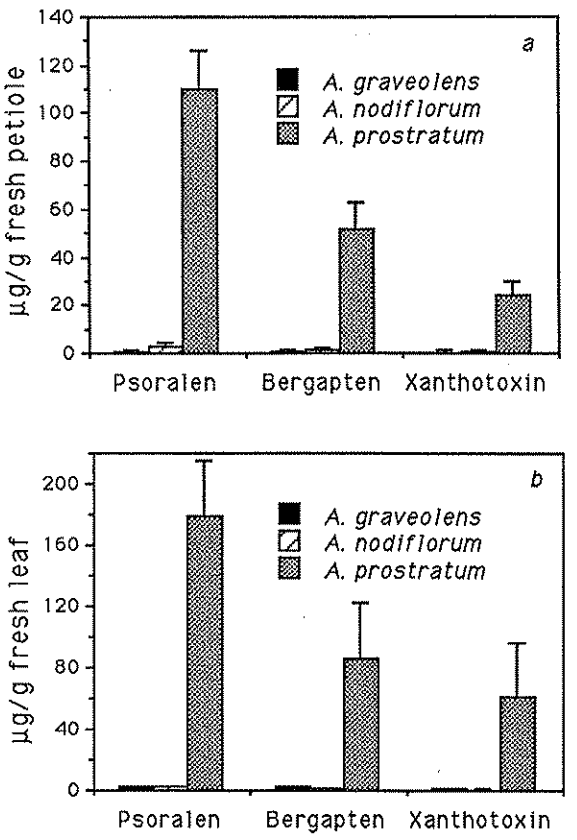

Fig. 2. Concentrations of linear furanocoumarins in petioles (a) and leaves (b) of *Apium* accessions. Extensions above bars denote standard errors.

A. nodiflorum (5.40 µg/g in the petioles; 2.99 µg/g in the leaves) (Fig. 2) were below the concentrations known to be hazardous to human and animal health (Austad & Kavli, 1983; Seligman *et al.*, 1987). The resistant line *A. prostratum*, however, had concentrations of linear furanocoumarins in the petioles (186.14 µg/g) and leaves (326.45 µg/g) 10 and 18 times higher, respectively, than the amount reported to cause acute contact dermatitis (18 µg/g) (Austad & Kavli, 1983). Though these concentrations are lower than the levels reported by Trumble *et al.* (1990), they are high enough to justify serious concerns, given that repeated exposure to celery with concentrations as low as 7 to 9 µg/g can result in photodermatitis (Seligman *et al.*, 1987).

With the exception of 52-70R, where more xanthotoxin and bergapten were detected in leaves than in petioles ($P < 0.05$; $F > 79.00$; df = 2, 4), no significant differences were found in the concentrations of the different compounds in leaves and petioles of the three plants (ANOVA). The general trend for furanocoumarin occurrence in 52-70R was similar to that observed by Trumble *et al.* (1990), xanthotoxin < psoralen < bergapten. In the two plant accessions, the trend was xanthotoxin < bergapten < psoralen.

Implications for breeding for *S. exigua* resistance in celery

A. nodiflorum showed some degree of non-preference resistance to *S. exigua* larvae and slightly reduced the insect's survival during the free-choice and no-choice feeding experiments, respectively. This accession also had a very low concentration of linear furanocoumarins. However, if larval feeding damage is expressed in terms of insect biomass, large larvae would cause more important economic damage than small larvae (Diawara *et al.*, 1991b). *S. exigua* larvae reared on *A. nodiflorum* weighed more than those reared on 52-70R during the no-choice feeding tests. In addition, hybridization of *A. nodiflorum* with other *Apium* ssp. is very difficult (personal observation, C. F. Quiros). Therefore, the low level of resistance observed for *A. nodiflorum* should be given minor consideration.

Resistance in *A. prostratum*, however, deserves particular attention despite the plant's high furanocoumarin content. The results of the chemical analyses suggest that resistance in *A. prostratum* may be furanocoumarin-based; however, these chemicals did not appear to be the basis of the resistance shown by this plant accession. As discussed above, *A. prostratum* showed a strong non-preference as a major mechanism of resistance to *S. exigua* during the two feeding experiments; larvae did not feed on *A. prostratum* when exposed to fresh plant material or when reared on diet containing tissue from the plant. However, the furanocoumarins isolated in this plant did not inhibit larval feeding when mixed in the insect's diet at concentrations two times higher than the

ones detected in the plant (Trumble *et al.*, 1991; Diawara *et al.*, unpublished). Therefore, other compounds may be acting as repellents or feeding deterrents. Attempts are currently being made to safely transfer the resistance to commercial celery by hybridizing *A. prostratum* (A230) with 'Tall Utah' 52-70R. The F1 hybrid, the progeny of its backcrosses to 52-70R, and the F2 hybrid will be evaluated for resistance to *S. exigua* and tested for furanocoumarin content. Studies also are underway to determine the chemical basis of the non-preference resistance in *A. prostratum*.

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References

Ashwood-Smith, M. J., G. A. Poulton, M. Baker & M. Mildenberger, 1980. 5-methoxypsoralen, an ingredient in several suntan preparations, has lethal, mutagenic and clastogenic properties. Nature 285: 407–409.

Austad, J. & G. Kavli, 1983. Phototoxic dermatitis caused by celery infected by *Schlerotinia sclerotiorum*. Contact Dermatitis 9: 448–451.

Dercks, W. J. T. Trumble & C. Winter, 1989. Impact of atmospheric pollution on linear furanocoumarin content in celery. J. Chem. Ecol. 16: 443–453.

Diawara, M. M., B. R. Wiseman & D. J. Isenhour, 1991a. Mechanism of whorl feeding resistance to fall armyworm among converted sorghum accessions. Entomol. Exp. Appl. 60: 225–231.

Diawara, M. M., N. S. Hill, B. R. Wiseman & D. J. Isenhour, 1991b. Panicle-stage resistance to *Spodoptera frugiperda* (Lepidoptera:Noctuidae) in converted sorghum accessions. J. Econ. Entomol. 84: 337–344.

Downs, R. J. & H. Hellmers, 1975. Environment and the experimental control of plant growth. Academic Press. London: 145 pp.

Dulmage, H. T., 1973. Assay and standardization of microbial insecticides. Ann. N.Y Acad. Sci. 217: 187–199.

Gomez, K. A. & A. A. Gomez, 1984. Statistical procedures for agricultural research, version 2 ed. Wiley & Sons. New York: 680 pp.

Griswold, M. J. & J. T. Trumble, 1985. Consumption and utilization of celery, *Apium graveolens*, by the beet armyworm *Spodoptera exigua*. Entomol. Exp. Appl. 38: 73–79.

Johnson, M. W., E. R. Oatman & J. A. Wyman, 1980. Effects of insecticides on populations of the vegetable leafminer and associated parasites on summer pole tomatoes. J. Econ. Entomol. 73: 61–66.

Jones, D. & J. Granett, 1982. Feeding site preferences of seven lepidopteran pests of celery. J. Econ. Entomol. 75: 449–453.

Kennedy, G. G., F. Gould, O. de Ponti & R. E. Stinner, 1987. Ecological, agricultural, genetic, and commercial consideration of deployment of insect-resistant germplasm. Envir. Entomol. 16: 327–338.

Keselman, H. J. & J. C. Rogan, 1978. A comparison of the modified-Tukey and Scheffé methods of multiple comparisons for pairwise contrasts. J. Amer. Stat. Assoc. 73: 47–51.

Matkin, O. A. & P. A. Chandler, 1957. The U.C.-type soil mixes, pp. 68-85, In K. Baker [ed.], The U.C. system for producing healthy container-grown plants through the use of clean soil, clean stock and sanitation. California Agricultural Experiment Station Manual 23. Berkeley: 331 pp.

Morris, O. N., 1986. Susceptibility of the bertha armyworm, *Mamestra configurata* (Lepidoptera:Noctuidae), to commercial formulations of *Bacillus thuringiensis* var. kurstaki. Can. Entomol. 118: 473–478.

Oatman, E. R. & G. G. Kennedy, 1976. Methomyl-induced outbreak of *Liriomyza sativae* on tomato. J. Econ. Entomol. 69: 667–668.

Scott, B. R., M. A. Pathak & G. R. Mohn, 1976. Molecular and genetic basis of furanocoumarin reactions. Mutat. Res. 39: 29–74.

Seligman, P. J., C. G. Mathias, M. A. O'Malley, R. C. Beier, L. J. Fehrs, W. S. Serril & W. E. Halperin, 1987. Photodermatitis from celery among grocery store workers. Arch. Dermatol. 123: 1478–1482.

Shorey, H. H. & R. L. Hale, 1965. Mass rearing of the larvae of nine noctuid species on a simple artificial diet medium. J. Econ. Entomol. 13: 497–501.

Smits, P. H., Van de Vrie & J. M. Viak, 1986. Oviposition of beet armyworm (Lepidoptera:Noctuidae) on greenhouse crops. Envir. Entomol. 15: 1189–1191.

Super ANOVA, 1989. Abacus Concepts Inc., Berkeley, CA.

Trumble, J. T., 1984. Integrated pest management of *Liriomyza trifolii*: influence of avermectin, cyromazine, and methomyl on leafminer ecology in celery. Agric. Ecosystems Environ. 12: 181–188.

Trumble, J. T., 1990. Vegetable insect control with minimal use of insecticides. HortSci. 25: 159–164.

Trumble, J. T. & C. F. Quiros, 1988. Antixenotic and antibiotic resistance in *Apium* species to *Liriomyza trifolii* (Diptera: Agromyzidae). J. Econ. Entomol. 81: 602–607.

Trumble, J. T. & M. P. Parrella, 1987. California law and the development of pesticide resistance. California Policy Seminar, Institute of Governmental Studies, Univ. of California. Berkeley: 23 pp.

Trumble, J. T. & N. C. Toscano, 1983. Impact of methamidophos and methomyl on populations of *Liriomyza* species (Diptera:Agromyzidae) and associated parasites in celery. Can. Entomol. 115: 1415–1420.

Trumble, J. T., W. Dercks, C. F. Quiros & R. C. Beier, 1990. Host plant resistance and linear furanocoumarin content of *Apium* accessions. J. Econ. Entomol. 83: 519–525.

Trumble, J. T., W. L. Moar, M. J. Brewer & W. G. Carson, 1991. Impact of UV radiation on activity of linear furanocoumarins and *Bacillus thuringiensis* var. *kurstaki* against *Spodoptera exigua*: implications for tritrophic interactions. J. Chem. Ecol. 17: 973–987.

Van Steenwyk, R. A. & N. C. Toscano, 1981. Relationship between lepidopterous larval density and damage in celery and celery plant growth analysis. J. Econ. Entomol. 74: 287–290.

Wiseman, B. R., F. M. Davis & W. P. Williams, 1983. Fall armyworm larval density and movement as an indication of non-preference in resistant corn. Prot. Ecol. 5: 135–141.

Zalom, F. G., L. T. Wilson & R. Smith, 1983. Oviposition patterns by several lepidopterous pests on processing tomatoes in California. Environ. Entomol. 12: 1133–1137.