Linear Furanocoumarins of Three Celery Breeding Lines: Implications for Integrated Pest Management†

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Bergapten and xanthotoxin were the major furanocoumarins isolated from the *Fusarium*-resistant celery breeding lines UC-08, UC-10, and UC-26 and the standard cultivar Tall Utah 52-70R. Petiole contents of bergapten and xanthotoxin in the new lines were similar to those in 52-70R. All petiole concentrations were below levels reported to cause either acute (18.0 μg/g fresh weight) or chronic dermatitis (7.0 μg/g). Leaf contents of furanocoumarins in the new lines also were statistically comparable to those in 52-70R but were high enough to cause chronic dermatitis, thus justifying use of safety measures by workers handling leaves. The new genotypes were equally (UC-26) or less susceptible (UC-08, UC-10) to beet armyworm feeding than 52-70R. No correlation existed between insect resistance and furanocoumarins. Because the new celery genotypes have resistance to the major celery disease, they have considerable potential as components of an integrated celery pest management program.

INTRODUCTION

Celery (*Apium graveolens* [L.]) is a vegetable crop that generates over $145 million per year in California alone (California Celery Research Advisory Board, 1986). The major pest problems facing celery growers in the United States include the disease-causing pathogen *Fusarium oxysporum* f. sp. *apii* (Hart and Endo, 1978; Elmer and Lacy, 1984; Awuah et al., 1986; Martyn, 1987; Toth and Lacy, 1991) and two insects, the beet armyworm *Spodoptera exigua* (Hübner) and the leaf miner *Liriomyza trifolii* (Burgess) (Van Steenwyk and Toscano, 1981; Trumble et al., 1990). *Fusarium* causes vascular discoloration and necrosis of the roots and crowns, resulting in chlorotic, stunted, and wilted plants. Beet armyworm feeding on leaves and especially on the plant heart prevents new petiole production, while damage to petioles results in reduced product marketability due to cosmetic injury.

Plant resistance is the only economically viable means for controlling *F. oxysporum* f. sp. *apii* in celery (Toth and Lacy, 1991), and breeding efforts have resulted in the development of resistant lines (Elmer and Lacy, 1984; Orton et al., 1984; Quiros et al., 1993; Toth and Lacy, 1991). However, bacterial toxicity and insect resistance have both been correlated with higher concentrations of linear furanocoumarins in celery and other furanocoumarin-containing plants (Trumble et al., 1990; McCloud et al., 1992; Afek et al., 1993). The furanocoumarins isolated from *Apium* species (psoralen, 5-methoxypsoralen or bergapten, and 8-methoxypsoralen or xanthotoxin) have been used since ancient times to cure human skin disorders such as skin depigmentation (vitiligo) and psoriasis (Musajo and Rodighiero, 1962; Scott et al., 1976; Van Scott, 1976). However, the use of these furanocoumarins in medicine was correlated with higher incidence of skin cancer in humans (Musajo and Rodighiero, 1962; Stern et al., 1979; Grekin and Epstein, 1981). The furanocoumarins have been reported to be carcinogenic, mutagenic (Roelandts, 1984; Koch, 1986; Young, 1990), and photodermatitic (Ljunggren, 1990; Berkley et al., 1986; Fleming, 1990). Consequently, it is of utmost importance to test new celery cultivars for linear furanocoumarin composition and concentration before they are released for large-scale commercial production. Therefore, a primary objective of our research was to investigate three new celery breeding lines, UC-08, UC-10, and UC-26, developed for resistance to *F. oxysporum* f. sp. *apii* (Quiros et al., 1993), for linear furanocoumarin composition and concentration with respect to the widely grown commercial celery cultivar Tall Utah 52-70R. A *Fusarium*-resistant celery genotype that is very susceptible to major insect damage would not be a viable component of an integrated celery pest management program; therefore, the second objective of this study was to examine the new plant accessions for susceptibility to *S. exigua*.

MATERIALS AND METHODS

The three new plant accessions (UC-08, UC-10, and UC-26) and the commercial celery Tall Utah 52-70R were obtained from germplasm resources held at the University of California, Davis, Department of Vegetable Crops. UC-08, UC-10, and UC-26 originated from UC1, a *Fusarium*-resistant line derived from celeriac and Tall Utah 52-70R (Orton et al., 1984; Quiros et al., 1993). Beet armyworm larvae were from a laboratory colony maintained on artificial diet (Shorey and Hale, 1965) at 27 ± 2 °C and 16:8 (L:D) photoperiod.

All four celery treatments were seeded on May 24, 1991, and transplanted in the greenhouse (July 25, 1991) and field (August 5, 1991). The greenhouse was equipped with charcoal filters to remove air pollutants, and plants were grown in 2-L pots in University of California soil mixture (Matkin and Chandler, 1957) and fertilized once a week with half-strength Hoagland's nutrient solution (Downs and Hellmers, 1975). Field plants were transplanted in single rows of 8 m × 76.2 cm on sandy loam soil at the University of California's Agricultural Operations field in Riverside, CA. Plots were furrow-irrigated to maintain adequate soil moisture, and local standard cultural practices were followed. Plants in the greenhouse and field were divided into two groups; the first group was tested at 8 weeks after transplanting (WAT) for linear furanocoumarin content and beet armyworm susceptibility. The second group was tested at 11 WAT. In the field, the first 4 m of row was used at 8 WAT and the second 4 m at 11 WAT. A total of 45 plants per celery test line (referred to as

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"treatment" in the rest of the text) per group (referred to as "stage" in the rest of the text) were tested in the greenhouse and in the field. The four treatments in each stage were randomly arranged in three replicates of 15 plants per treatment per replicate. Experiments were started 8 WAT because, after this time, all petiole production would be part of the harvested product (Van Steenwyk and Toscano, 1981).

Linear Furanocoumarin Analysis. All four celery entries were analyzed for the three major linear furanocoumarins isolated in *Apium* species—psoralen, 5-methoxypsoralen (bergapten), and 8-methoxypsoralen (xanthotoxin) (Trumble et al., 1990). Sample collections for determination of furanocoumarin composition and concentration were made in the greenhouse and field at 8 and 11 WAT. At each stage a young petiole with fully expanded leaves was collected from each plant and samples were pooled within treatment in each replicate. The petiole was cut just above the first pair of leaflets located at the base. Sample leaves and petioles were separated and stored at −65 °C until time of chemical analysis. Extraction of linear furanocoumarins for the different treatments was conducted as previously described (Diawara et al., 1992; Trumble et al., 1992). Sample tubes were spiked with 5 μg of a synthetic internal standard, 7-(benzyloxy)coumarin [synthesized from commercially available 7-hydroxycoumarin (Aldrich Chemical Co.) (Trumble et al., unpublished data)]. Plant samples were homogenized in d-H_2O, extracted with toluene, and eluted with acetone in chloroform. 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, PA). Peaks were monitored and quantified at 280 nm. An Alltech Econosil silica column (25 cm × 4.6 mm, 5-μm particle size) with a 10 mm × 4.6 mm guard column filled with the same packing material was used, eluted isocratically with hexane/tetrahydrofuran.

Beet Armyworm Feeding Bioassays. The relative susceptibility of the three newly bred celery lines to beet armyworm with respect to 52-70R was determined by rearing the insects on fresh tissue. Four bioassays, one for each group (8 WAT, 11 WAT) and location (greenhouse, field), were begun on the same days as linear furanocoumarin sample collections. Thirty-milliliter cups containing a solidified agar solution (Diawara et al., 1992) were filled with fresh plant parts (leaf plus petiole) of each treatment. One neonate beet armyworm was placed in each cup, which then was capped with a plastic lid with pinholes. The plant tissue was renewed every other day and the agar solution every week. For each bioassay, cups were arranged as a complete block with three replicates of 15 cups per replicate. All tests were maintained in environmental chambers at 27 ± 2 °C, 75% relative humidity, and 16:8 (L:D) photoperiod. Weight of larvae at 9 days, time to pupation, weight of pupae, time to adult emergence, and survivorship were recorded for each treatment.

Statistical Analyses. All data sets were analyzed as a split-plot using ANOVA (Statistical Analysis Sysytems, 1985). Stages (8 vs 11 WAT) were main plots, and the four treatments were subplots. Statistically different means were ranked using 5% level Tukey's honestly significant difference test (Keselman and Rogan, 1978). Correlations (Pearson's) between variables were analyzed using the GLM CORR procedure of SAS (Statistical Analysis Systems, 1985). Due to the absence of psoralen in detectable amounts in a large number of samples (only a few samples in two treatments had trace levels), data on this compound were not included in the ANOVA.

RESULTS

Linear Furanocoumarin Composition and Concentration in Greenhouse-Grown Celery. No psoralen was found in samples collected 8 WAT, and only traces were detected in a few samples at 11 WAT. Comparisons of the concentrations of bergapten in leaves were made within growth stage (8 and 11 WAT) and within treatment because of a significant stage by treatment interaction ($P = 0.0421$; $F = 3.44$; df = 3, 16). Results were compared across growth stages and across celery entries when no significant interaction occurred, suggesting that concentrations of the different furanocoumarins were then additive.

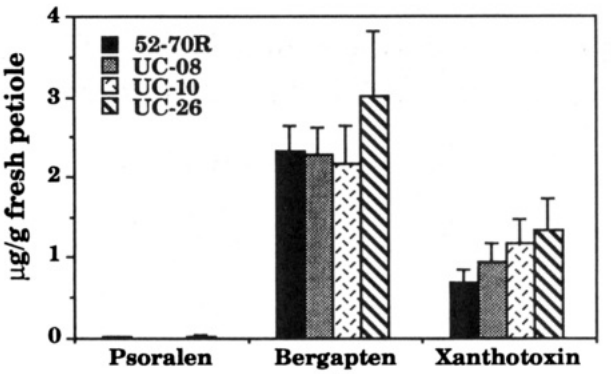

Figure 1. Concentrations of psoralen, bergapten, and xanthotoxin in petioles of greenhouse-grown celery lines. Extensions above bars denote standard errors. Means represent average across samples taken at 8 and 11 weeks after transplanting (no significant treatment by stage interaction occurred: bergapten $P = 0.5494$, $F = 0.73$, df = 3, 16; xanthotoxin $P = 0.3983$, $F = 1.05$, df = 3, 16). See text for 8 vs 11 weeks after transplanting mean comparisons.

In petioles, none of the new breeding lines had concentrations of bergapten or xanthotoxin significantly higher than levels found in the commercial cultivar 52-70R (bergapten $P = 0.6819$, $F = 0.51$, df = 3, 16; xanthotoxin $P = 0.4075$, $F = 1.03$, df = 3, 16) (Figure 1). No significant changes occurred in the concentrations of these compounds between 8 and 11 WAT in petioles (bergapten 2.278 vs 2.605 μg/g, $P = 0.5597$, $F = 0.35$, df = 1, 8; xanthotoxin 0.780 vs 1.294 μg/g, $P = 0.0732$, $F = 3.68$, df = 1, 8).

In leaves, no significant differences were found among treatments for concentrations of xanthotoxin ($P = 0.2022$, $F = 1.72$, df = 3, 16) (8 and 11 WAT pooled, no interactions: $P = 0.1746$, $F = 1.87$, df = 3, 16) (Figure 2a). For bergapten, differences among treatments were significant at 11 WAT ($P = 0.0361$, $F = 4.67$, df = 3, 8) (Figure 2b) but not at 8 WAT ($P = 0.2040$, $F = 1.93$, df = 3, 8) (Figure 2a). The breeding line UC-10 had significantly higher concentration of bergapten than UC-08 at 11 WAT, but none of the new breeding lines had higher concentrations than 52-70R. Production of xanthotoxin did not increase significantly from 8 to 11 WAT (3.466 vs 3.941 μg/g, $P = 0.6486$, $F = 0.22$, df = 1, 8). Bergapten levels varied; production of bergapten increased significantly between 8 and 11 WAT for UC-10 (3.424 vs 13.197 μg/g, $P = 0.0058$, $F = 28.75$, df = 1, 4) but did not change for UC-08 (4.320 vs 4.272 μg/g, $P = 0.9817$, $F = 0.0$, df = 1, 4), UC-26 (11.814 vs 8.130 μg/g, $P = 0.5470$, $F = 0.43$, df = 1, 4), and 52-70R (5.543 vs 8.373 μg/g, $P = 0.2970$, $F = 1.43$, df = 1, 4). A significant correlation was found between pooled leaf and petiole contents of bergapten ($P = 0.0162$, $r = 0.80$) but not for xanthotoxin ($P = 0.2089$, $r = 0.50$).

Beet Armyworm Survival on Greenhouse-Grown Celery. No treatment by stage interaction occurred for 7-day larval weight, 9-day larval weight, pupal weight, days to pupation, and days to adult emergence (Table I); stage effects were therefore averaged for these variables. None of the new celery accessions resulted in greater larval development than the commercial line 52-70R (Table I). Larvae reared on UC-08 weighed significantly less at 7 and 9 days than those reared on 52-70R. Younger plants (8 WAT) were more suitable for insect development than 11 WAT celery (7-day larval weight 33 vs 22 mg, $P = 0.0001$, $F = 63.85$, df = 1, 322; 9-day larval weight 73 vs 33 mg, $P = 0.0001$, $F = 105.05$, df = 1, 322; days to pupation 15 vs 21 days, $P = 0.0033$, $F = 9.22$, df = 1, 72; pupal weight 75 vs 38 mg, $P = 0.0014$, $F = 11.11$, df = 1, 73; days to adult emergence 21 vs 29 days, $P = 0.0017$, $F = 10.76$, df = 1, 63).

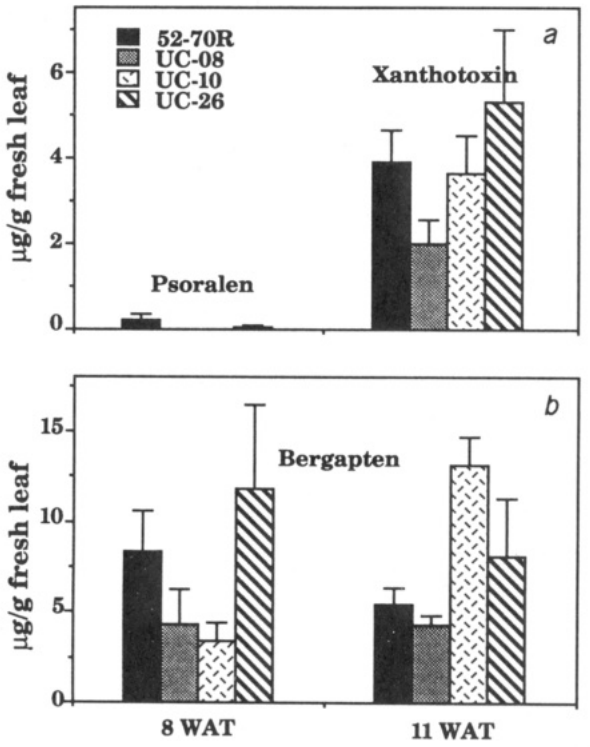

Figure 2. Concentrations of psoralen, xanthotoxin (a), and bergapten (b) in leaves of greenhouse-grown celery lines. Extensions above bars denote standard errors. Means for psoralen and xanthotoxin represent average across samples taken at 8 and 11 weeks after transplanting (WAT) (no significant treatment by stage interaction occurred: xanthotoxin $P = 0.1746$, $F = 1.87$, df 3, 16). Significant treatment by stage interactions occurred for the concentrations of bergapten ($P = 0.0421$, $F = 3.44$, df = 3, 16). See text for 8 WAT vs 11 WAT mean comparisons.

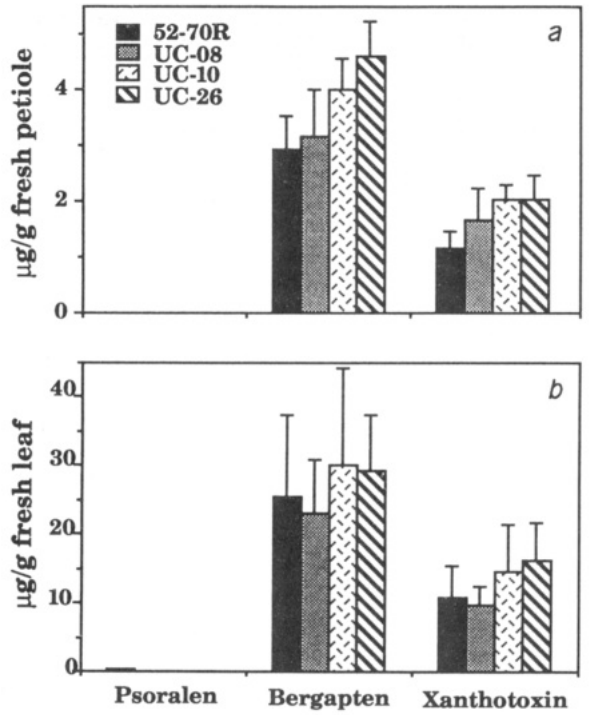

Figure 3. Concentrations of psoralen, bergapten, and xanthotoxin in petioles (a) and leaves (b) of field-grown celery lines. Extensions above bars denote standard errors. Means represent average across samples taken at 8 and 11 weeks after transplanting (no significant treatment by stage interaction occurred: for petioles bergapten $P = 0.5208$, $F = 0.78$, df = 3, 16; xanthotoxin $P = 0.1365$, $F = 2.13$, df = 3, 16; for leaves bergapten $P = 0.9753$, $F = 0.07$, df = 3, 16; xanthotoxin $P = 0.5389$, $F = 0.75$, df = 3, 16). See text for 8 vs 11 weeks after transplanting mean comparisons.

A significant treatment by stage interaction occurred for survivorship ($P = 0.0145$; $F = 4.78$; df = 3, 16), and differences were observed between the two stages (with more resistance in older tissue) for 52-70R (44 vs 2%, $P = 0.0031$, $F = 40.43$, df = 1, 4), UC-10 (40 vs 0%, $P = 0.0005$, $F = 106.93$, df = 1, 4), and UC-26 (60 vs 2%, $P = 0.0019$, $F = 0.52.18$, df = 1, 4) but not for UC-08 (20 vs 0%, $P = 0.0681$, $F = 6.16$, df = 1, 4).

Linear Furanocoumarin Composition and Concentration in Field-Grown Celery. The composition of linear furanocoumarins in field samples was similar to that of greenhouse samples; bergapten and xanthotoxin were the major compounds isolated. Except for traces in only one sample at 8 WAT, psoralen was not found in any other samples (detectable level = 0.005 μg/g of fresh tissue). No significant treatment by stage interactions occurred in the petiole data for bergapten ($P = 0.521$, $F = 0.78$, df = 3, 16) or xanthotoxin ($P = 0.136$, $F = 2.13$, df = 3, 16), suggesting that concentrations of these compounds were additive between 8 and 11 WAT. None of the new breeding genotypes had significantly higher concentrations of xanthotoxin in petioles than the commercial line 52-70R ($P = 0.0951$, $F = 2.52$, df = 3, 16), and only UC-26 had significantly more bergapten than 52-70R (4.59 vs 2.92 μg/g, $P = 0.0387$, $F = 3.54$, df = 3, 16) (Figure 3a). For both compounds, concentrations significantly increased between 8 and 11 WAT (bergapten 2.440 vs 4.900 μg/g, $P = 0.0001$, $F = 36.24$, df = 1, 16; xanthotoxin 0.970 vs 2.453 μg/g, $P = 0.0001$, $F = 33.32$, df = 1, 16).

In leaves, the concentrations of bergapten and xanthotoxin were of greater magnitude for all treatments. Stage effects were additive, as no treatment by stage interactions occurred with either compound (bergapten $P = 0.9750$, $F = 0.07$, df = 3, 16; xanthotoxin $P = 0.5390$, $F = 0.75$, df = 3, 16). The amounts of linear furanocoumarins in the new lines were not significantly different from those in 52-70R (bergapten $P = 0.942$, $F = 0.13$, df = 3, 16; xanthotoxin $P = 0.547$, $F = 0.73$, df = 3, 16) (Figure 3b). Levels of furanocoumarins increased in all genotypes between 8 and 11 WAT (bergapten 11.420 vs 42.370 μg/g, $P = 0.004$, $F = 10.97$, df = 1, 16; xanthotoxin 4.640 vs 21.249 μg/g, $P = 0.0003$, $F = 21.72$, df = 1, 16). As for the greenhouse study, pooled (across stages) leaf and petiole contents of bergapten and xanthotoxin were significantly correlated (bergapten $P = 0.0024$, $r = 0.90$; xanthotoxin $P = 0.0151$, $r = 0.81$).

Beet Armyworm Survival on Field-Grown Celery. Significant treatment by stage interactions occurred for 7-day larval weight, days to pupation, days to adult emergence, and survival to adult (Table II); results are therefore discussed within stage and within treatment for these variables. Larvae weighed significantly less at 7 and 9 days when fed UC-08 and UC-10 than when fed the commercial celery 52-70R (Table II). Feeding on UC-10 also significantly extended larval stage and reduced pupal weight compared with the commercial line. No significant differences in larval survival were found among the four treatments when bioassays were started 8 WAT; however, when bioassays were initiated at 11 WAT, survival was zero on UC-08 and UC-10 compared with 18% on 52-70R. All treatments were more suitable for insect development at 8 WAT than at 11 WAT on the basis of larval weight at 9 days (58 vs 40 mg, $P = 0.0001$, $F = 91.42$, df = 3, 334) and pupal weight (68 vs 58 mg, $P = 0.0006$, $F = 6.61$, df = 3, 64). Differences between 8 and 11 WAT in 7-day larval weight were significant for UC-08 (19 vs 12 mg, $P = 0.0001$, $F = 26.76$, df = 1, 85), UC-10 (17 vs 11 mg, $P =$

Table I. Developmental Variables of Beet Armyworm Reared on Fresh Tissue of Greenhouse-Grown Celery Breeding Lines at 27 ± 2 °C, 75% Relative Humidity, and 16:8 (L:D) Photoperiod[a]

	wt, mg					% survival to adult[g]	
treatment	7-day larvae[b]	9-day larvae[c]	pupae[d]	days to pupation[e]	days to adult emergence[f]	8 WAT[h]	11 WAT[i]
52-70R	31a	59a	68a	15.1a	21.6ab	46ab	2
UC-08	16b	28b	67a	16.6a	23.3a	21a	0
UC-10	30a	61a	78a	15.6a	19.9b	40ab	0
UC-26	31a	61a	76a	15.4a	21.9ab	60b	2

[a] Means within a column not followed by the same letter are statistically different at the 5% level (Keselman and Rogan, 1978). See text for 8 vs 11 weeks after transplanting mean comparisons. [b] $P = 0.0001$, $F = 27.99$, df = 3, 329. Data pooled across growth stages because of no interaction ($P = 0.2580$, $F = 1.35$, df = 1, 322). [c] $P = 0.0001$, $F = 19.28$, df = 3, 329. Data pooled across growth stages because of no interaction ($P = 0.1023$, $F = 2.08$, df = 3, 322). [d] $P = 0.2895$, $F = 1.27$, df = 3, 78. Data pooled across growth stages because of no interaction ($P = 0.4801$, $F = 0.50$, df = 1, 73). [e] $P = 0.4535$, $F = 0.88$, df = 3, 77. Data pooled across growth stages because of no interaction ($P = 0.8730$, $F = 0.88$, df = 1, 72). [f] $P = 0.0778$, $F = 2.38$, df = 3, 68. Data pooled across growth stages because of no interaction ($P = 0.8941$, $F = 0.02$, df = 1, 63). [g] Significant treatment by stage interaction ($P = 0.0145$, $F = 4.78$, df = 3, 16). 8 WAT = 8 weeks after transplanting; 11 WAT = 11 weeks after transplanting. [h] $P = 0.0218$, $F = 5.71$, df = 3, 8. [i] Mean comparison invalid because of zero variance.

Table II. Developmental Variables of Beet Armyworm Reared on Fresh Tissue of Field-Grown Celery Breeding Lines at 27 ± 2 °C, 75% Relative Humidity, and 16:8 (L:D) Photoperiod[a]

	wt, mg									
	7-day larvae[b]				days to pupation[b]		days to adult emergence[b]		% survival to adult	
treatment	8 WAT[e]	11 WAT[f]	9-day larvae[c]	pupae[d]	8 WAT[g]	11 WAT[h]	8 WAT[i]	11 WAT[j]	8 WAT[k]	11 WAT[l]
52-70R	41a	41a	86a	65a	14.9b	15.3b	21.6a	20.5b	31a	18
UC-08	19b	12c	28c	68a	16.1b		23.0a		21a	0
UC-10	17b	11c	26c	46b	19.2a		23.3a		7a	0
UC-26	35a	23b	53b	65a	14.7b	19.0a	21.3a	27.0a	7a	14

[a] Means within a column not followed by the same letter are statistically different at the 5% level (Keselman and Rogan, 1978). [b] Significant treatment by stage interactions (7-day larvae $P = 0.0064$, $F = 3.96$, df = 3, 341; days to pupation $P = 0.0064$, $F = 7.94$, df = 1, 64; days to adult emergence $P = 0.0002$, $F = 17.78$, df = 1, 37; % survival to adult $P = 0.0497$, $F = 3.25$, df = 3, 16). 8 WAT = 8 weeks after transplanting; 11 WAT = 11 weeks after transplanting. [c] $P = 0.0001$, $F = 91.42$, df = 3, 334. Data pooled across growth stages because of no interaction ($P = 0.6960$, $F = 0.48$, df = 3, 334). [d] $P = 0.0006$, $F = 6.61$, df = 3, 64. Data pooled across growth stages because of no interaction ($P = 0.1671$, $F = 1.95$, df = 1, 64). [e] $P = 0.0001$, $F = 42, 60$, df = 3, 167. [f] $P = 0.0001$, $F = 63.00$, df = 3, 174. [g] $P = 0.0001$, $F = 12.69$, df = 3, 36. [h] $P = 0.0044$, $F = 9.62$, df = 1, 28. [i] $P = 1619$, $F = 1.86$, df = 3, 25. [j] $P = 0.0002$, $F = 26.34$, df = 1, 12. [k] $P = 0.619$, $F = 3.69$, df = 3, 8. [l] Mean comparison invalid because of zero variance.

0.0001, $F = 18.73$, df = 1, 85), and UC-26 (35 vs 23 mg, $P = 0.0001$, $F = 22.49$, df = 1, 86) but not for 52-70R (41 vs 41 mg, $P = 0.9718$, $F = 0.0$, df = 1, 85). No larvae survived to pupation on UC-08 and UC-10. Feeding on older tissue (11 WAT) of UC-26 significantly extended the number of days to pupation (15 vs 19 days, $P = 0.0003$, $F = 20.89$, df = 1, 16) and to adult emergence (21 vs 27 days, $P = 0.0006$, $F = 35.49$, df = 1, 7). Growth stage did not affect days to pupation (15 vs 15 days, $P = 0.5840$, $F = 0.31$, df = 1, 35) or days to adult emergence (22 vs 21 days, $P = 0.1561$, $F = 2.17$, df = 1, 20). On the basis of percent larvae surviving to adult, increased resistance between 8 and 11 WAT was only observed for UC-08 (21 vs 0 %, $P = 0.0138$, $F = 17.57$, df = 1, 4).

No correlations were found between beet armyworm survival and the concentrations of linear furanocoumarins in the different celery lines (with leaf and petiole considered together). For the greenhouse studies the correlation coefficients were bergapten $P = 0.7921$, $r = 0.10$, and xanthotoxin $P = 0.5239$, $r = 0.26$. For the field studies the correlation coefficients were bergapten $P = 0.2806$, $r = 0.44$, and xanthotoxin $P = 0.3590$, $r = 0.37$.

DISCUSSION

The concentrations of psoralen, bergapten, and xanthotoxin detected in the petioles of the different celery lines grown in either the greenhouse or field were below the 18 μg/g level reported to cause acute contact dermatitis (Austad and Kavli, 1983) or the 7.0 μg/g level reported to cause chronic dermatitis (Seligman et al., 1987). These concentrations are conservative because the petioles analyzed here were the top parts directly connected with the fully expanded leaflets; these parts are more likely to have higher concentrations of furanocoumarins than the full-grown lower part of the petiole, which is usually the marketable product. Thus, unlike previous accessions selected for insect resistance (Trumble et al., 1990), these new breeding lines have petioles that are safe for handling and consumption.

Under field conditions, leaves of the different celery lines (including the commercial cultivar 52-70R) had levels of furanocoumarins higher than those reported to cause at least chronic dermatitis. Trumble et al. (1992) also found that concentrations of linear furanocoumarins occasionally reached a maximum of 15.853 μg/g in leaves of the commercial celery Tall Utah 52-70R. Higher concentrations of linear furanocoumarins in celery leaves than petioles have been previously reported (Berkley et al., 1986; Trumble et al., 1990; Diawara et al., 1992). The levels of linear furanocoumarins detected here represent no threat to the health of consumers, who usually only have contact with the petioles. However, with concentrations exceeding even 7 μg/g of fresh leaf, safety measures (e.g., protective clothing) should be used by pest control advisors and workers handling celery leaves in the field. Trumble et al. (1992) found no significant correlation between concentrations of linear furanocoumarins in leaves and petioles of Tall Utah 52-70R and suggested that both plant parts may need to be tested. The discrepancy between those results and the study reported herein, where leaf and petiole contents were generally correlated, is not clear and may require further investigation.

Both leaves and petioles had higher concentrations of furanocoumarins when grown in the field than in the greenhouse. This finding suggests that furanocoumarin production in these celery genotypes may be subject to environmental conditions such as variability in soil type, water and fertilization practices, temperature, light in-

tensity, or root confinement. Further studies are required to investigate the effects of growing conditions on furanocoumarin production of these new breeding lines. Increased linear furanocoumarin production due to UV light exposure has been documented (Zangerl and Berenbaum, 1989; Dercks and Trumble, 1990).

Of all three linear furanocoumarins, bergapten was produced in the highest amounts in leaves and petioles of all four celery genotypes in both the greenhouse and the field. Recent studies by Trumble et al. (1992) revealed a similar trend. Bergapten has been referred to as a "senescence compound" due to its increase relative to other furanocoumarins in older *Ruta graveolens* leaves (Zobel and Brown, 1991). McCloud et al. (1992) also reported higher ratios of bergapten to psoralen in older leaves of the rough lemon *Citrus jambhiri*. However, while increasing bergapten concentrations in a growing plant may be due to changes in plant physiology, the studies reported herein were based on one petiole (and associated leaves) per plant and did not compare different-aged parts of the same plant. The concentration of linear furanocoumarin in younger and older celery plant parts has yet to be determined.

No correlations were found between between resistance to beet armyworm feeding and the concentrations of linear furanocoumarins in the different celery lines. These findings support suggestions by Diawara et al. (1992) that the linear furanocoumarins may not be the only compounds involved in *Apium prostratum* ssp. *prostratum* var. Filiform (A230) resistance to beet armyworm.

The new breeding lines UC-08, UC-10, and UC-26 had concentrations of linear furanocoumarins in petioles and leaves comparable to levels found in the commercial cultivar Tall Utah 52-70R. These celery genotypes also were equally or less susceptible to beet armyworm larval feeding than 52-70R, and no correlation was found between insect resistance and plant contents of linear furanocoumarins. Since these celery breeding lines have been developed for resistance to the major celery disease, *F. oxysporum* f. sp. *apii*, they represent good potential components of an integrated celery pest management program. However, due to the discrepancy found between greenhouse and field concentrations, and the high levels of furanocoumarins sometimes observed in the leaves, it is advisable to test the new plant accessions for linear furanocoumarin production under various crop management systems before they are used for large-scale commercial consumption.

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