Plant Age and Seasonal Variations in Genotypic Resistance of Celery to Beet Armyworm (Lepidoptera: Noctuidae)

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ABSTRACT Plant physiological growth stage and growing environment significantly interacted with celery (*Apium graveolens* L.) genotypes to influence the expression of genetic resistance of celery to the beet armyworm, *Spodoptera exigua* (Hübner). Plant vegetative growth, as measured by plastochron index, was primarily linear with physiological time and showed no major season-related variations. Insect developmental times from egg to pupa and from egg to adult showed the largest variations during this study, with significant genotype-by-season, genotype-by-plant growth stage, and season-by-stage interactions. Overall, all four celery genotypes tested, 'Tall Utah 52-70R', 'UC-08', 'UC-10', and 'UC-26', were more resistant to beet armyworm during the warm season and as plants matured. Because both plant age and growing environment proved to interact significantly with plant genotype to magnify or suppress expression of genetic plant resistance to pests, it is important to study test plant genotypes under various growing conditions and at different stages of plant growth to determine the potential genotype-by-environment and genotype-by-stage interactions before characterization and utilization of the resistance in breeding for pest resistance and integrated pest management programs.

KEY WORDS *Spodoptera exigua*, host plant resistance, plant age variations

INSECT RESISTANCE IN HOST PLANT can be a vital component of integrated pest management in agricultural ecosystems. The development and use of plant cultivars resistant to pest insects requires continuous identification and characterization of sources of resistant germplasm. Stable expression of plant resistance to insects over time is desirable. However, level of resistance is often susceptible to a multitude of plant, insect, and environmental factors (Tingey & Singh 1980, Smith 1989, Kennedy & Barbour 1992). Several plant factors, including density and planting arrangement, plant height, plant age, disease incidence, and mechanical or herbivore injury have been shown to affect plant–insect relationships.

Influence of plant age on expression of insect resistance has been documented for a number of plants. Resistance to insect feeding was greater in older than in younger plants of tobacco (*Nicotiana tabacum* L.) (Abernathy & Thurston 1969); rice (*Oryza sativa* L.) 'IR36' (Rapusa & Heinrichs 1987); wild tomato, *Lycopersicon hirsutum* L. (Sinden et al. 1978); tomato accession 'PI134417' (Kennedy et al. 1985); and lettuce (*Lactuca sativa* L.) (Byrne & Draeger 1989). Resistance, however, decreased with age in sorghum (*Sorghum bicolor* L. [Moench]) (Fisk 1978) but did not significantly change for cabbage (*Brassica oleraceae* L.) (Eigenbrode & Shelton 1990). Diawara et al. (1993) reported that insect resistance increased in some sorghum genotypes but decreased in others as plants matured.

Variations in temperature, quality and quantity of light, and relative humidity also can influence the expression of insect resistance in host plant. Reduced temperatures resulted in loss of insect resistance in sorghum (Wood & Starks 1972) and in alfalfa (*Medicago sativa* L.) (Schalk et al. 1969, Karner & Manglitz 1985). Conversely, extreme high temperatures reduced expression of wheat (*Triticum aestivum* L.) resistance to insect damage (Sosa & Foster 1976, Sosa 1979). Kennedy et al. (1981) reported increased insect resistance in wild tomato plants grown under long day lengths. Reduced light also has been shown to decrease resistance to insects in sugar beet (*Beta vulgaris* L.) (Lowe 1967), sorghum (Woodhead 1981), maize (*Zea mays* L.) (Manuwoto & Scriber 1985), and soybean (*Glycine max* L.) (Khan et al. 1986).

Because environmental factors are difficult to control, bioassay techniques and experimental designs are important in obtaining consistent re-

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sults in the determination of differential genetic resistance among plant cultivars. These studies need to be designed carefully to assess resistance appropriately, especially with plant genotypes in which expression of insect resistance is conditioned by specific plant and environmental factors. In their discussion on plant age-related variations in host resistance to insects, Tingey & Singh (1980) reported that "no general inferences as to influence on expression of genetic resistance can be made, however, owing to the absence of varietal comparisons or significant age–cultivar interaction." Experimental studies designed to determine differential insect resistance both among plant varieties and among plants of the same physiological age within a variety as results of genotype-by-environment interactions are lacking. It is not clearly understood whether differential plant age-related resistance to insects is caused by physiological changes during successive plant growth stages or to changes in the plant characteristics that are induced when plants are grown under different conditions.

We report here differential age-related resistance in selected celery (*Apium graveolens* L.) genotypes to the beet armyworm, *Spodoptera exigua* (Hübner), an important celery pest insect, and the interactions between genetic resistance and the growing environment.

Materials and Methods

Plant and Insect Sources. The celery genotypes tested, three new breeding lines ('UC-08', 'UC-10', and 'UC-26') and the commercial celery 'Tall Utah 52-70R', were obtained from the celery breeding program 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 (*Apium rapaceum*) and 'Tall Utah 52-70R' (Orton et al. 1984, Quiros et al. 1992). Beet armyworms were from a laboratory colony maintained on artificial diet (Shorey & Hale 1965) at 27 ± 2°C and a photoperiod of 16:8 (L:D) h.

Experimental Design. Two separate experiments were designed so that feeding bioassays were initiated at 4, 8, and 12 wk after celery transplanting. These intervals were chosen because plants were too small before 4 wk to provide enough tissue for bioassay and celery is usually harvested around 16 wk after transplanting. Because of preference for leaves by early instars (Griswold & Trumble 1985), beet armyworm infestations occurring after 15 wk after transplanting would not be a threat to commercial celery production. For the bioassay initiated at 12 wk after transplanting, plant tissue produced just before harvest was tested because the bioassay feeding period usually lasts 3 wk. The following two experiments distinguished between the intrinsic effects of crop age and the extrinsic effects of environment on resistance in the four celery genotypes.

Experiment 1 (Bulk Planting Design). All plants were seeded the same day, and the three stages of plant growth (4, 8, and 12 wk after transplanting) were tested at different times. Seeds of all four celery genotypes were bulk planted on 3 January 1992. Seedlings of all genotypes were transplanted on 12 March 1992 in single-row plots of 18 m by 76.2 cm on a sandy loam soil at the University of California's Agricultural Operations fields in Riverside. Plots were furrow irrigated to maintain adequate soil moisture, and standard cultural practices were followed. A randomized complete block, multiple factorial type with three replicates was used; plot size was 60 plants per genotype per replicate. In each replicate and for each genotype, the 20 plants in the first 6 m of row were used in the bioassays initiated at 4 wk after transplanting. Plants in the second 6 m of row were used at 8 wk after transplanting and plants in the remaining 6 m were used at 12 wk after transplanting. Bioassays were started 9 April for 4 wk after transplanting plants, 11 May for 8 wk after transplanting plants, and 8 June for 12 wk after transplanting plants. For each bioassay, 30-ml transparent plastic cups containing moisturizing agar gel (Diawara et al. 1992) were filled with fresh plant parts (leaf + petiole) of each celery genotype. 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 gel every week. For each bioassay, cups were arranged as a complete block as in field with three replicates of 20 cups per replicate (i.e., a total of 60 cups per genotype per stage was tested). All tests were maintained in environmental chambers at 27 ± 2°C, 75% RH, and 16:8 (L:D) h photoperiod. Chambers were illuminated by cool-white and warm-white 40-W fluorescent lamps (North American Philips Lighting Corporation, Bloomfield, NJ). Time to pupation, weight of pupae, time to adult emergence, and survivorship were recorded for each treatment.

Experiment 2 (Staggered Planting Design). All four celery test entries were planted and transplanted in a staggered manner to produce bioassay plants that were at 4, 8, and 12 wk after transplanting on 8 June 1992. Seeds of the four celery genotypes were planted in a staggered fashion on 3 and 31 January and 28 February 1992. Seedlings were transplanted in adjacent plots of 18 m by 76.2 cm in the same field as experiment 1. Transplanting dates were 12 March for the 3 January seeding, 9 April for the 31 January seeding, and 11 May for the 28 February seeding. Bioassays for all four genotypes and all three stages of plant growth were started on 8 June. Treatment cups were arranged as a

Table 1. Average daily weather data from celery transplanted 3 wk after the beginning of feeding bioassays for cool- and warm-season plantings, Riverside, CA, 1992

Season	Stage	Celery transplant date	Start of bioassay	Total no. of days	Avg solar radiation, W/m²	Air temp, °C			Relative humidity, %		
						Max	Min.	Avg.	Max	Min.	Avg.
Cool season	Stage 1	12 March	9 April	50	210	23.0	11.5	17.3	80.6	39.3	60.0
	Stage 2	12 March	11 May	81	225	24.3	12.6	18.5	82.8	42.6	61.7
	Stage 3	12 March	8 June	110	243	25.5	13.1	19.3	82.8	41.5	62.2
Warm season	Stage 1	11 May	8 June	50	274	27.9	14.5	21.2	84.3	42.0	63.2
	Stage 2	9 April	8 June	81	265	27.5	14.1	20.8	83.3	40.2	61.8
	Stage 3	12 March	8 June	110	243	25.5	13.1	19.3	82.8	41.5	62.2

Feeding bioassays were initiated at 4, 8, and 12 wk aafter transplanting, respectively, for stage 1, stage 2, and stage 3 plants.

randomized complete block, multiple factorial type with three replicates of 10 cups per replicate. All other experimental procedures were the same as in experiment 1.

To provide an estimate of plant vegetative and physiological stage at the time of each bioassay, the plastochron index (Erickson 1976) of three to four plants per genotype per replicate (a total of 10 plants) per stage and per season was measured. The plastochron-index value increases as plants mature. For the purpose of this study, the number of leaves per plant was used to determine the plastochron index. Though the two experiments were initiated at the same time, bioassays were begun under warmer growing conditions for experiment 2 than for experiment 1 (Table 1), except for stage-3 plants. For this reason, experiment 1 is referred to in the rest of the text as cool-season planting, and experiment 2 as warm-season planting.

Statistical Analyses. Results of the two experiments were combined, and data for the variables measured (plastochron index, insect pupal weight, days to pupation, days to adult emergence, and survival to adult) were analyzed separately using the PROC GLM procedure of SAS (SAS Institute 1985). Variations in resistance related to the interaction of season (cool versus warm) and plant growth stage (4 versus 8 versus 12 wk after transplanting) were examined using nested contrasts. Seasonal effects were calculated at stages 1, 2, and 3, and linear and quadratic components of stage influence were determined for each season. The three-way interaction terms were not significant for the different variables measured. Celery genotype effects were determined within season and within stage for days to pupation and days to adult emergence, because of significant genotype-by-season and genotype-by-stage interactions (Table 2), using modified Tukey's w procedure (Keselman & Rogan 1978).

Results

The results of the analyses of variance for the different variables measured are reported in Ta-

Table 2. Analyses of variance for plant growth index and beet armyworm developmental variables on celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting during the cool and warm seasons

Source	Plastochron index			Pupal wt			Days of pupation			Days to adult emergence			% adult survival		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Genotype	3, 239	4.44	0.005	3, 442	2.13	0.096	3, 442	8.45	0.000	3, 348	1.19	0.313	3, 68	7.11	0.001
Season	1, 239	17.80	0.000	1, 442	137.00	0.000	1, 442	96.40	0.000	1, 348	59.46	0.000	1, 68	165.98	0.000
Genotype * season	3, 239	0.57	0.635	3 442	0.81	0.489	3, 442	4.58	0.004	3, 348	3.59	0.014	3, 68	2.13	0.109
Stage	2, 239	681.54	0.000	2, 442	98.16	0.000	2, 442	54.02	0.000	2, 348	25.33	0.000	2, 68	77.69	0.000
Genotype * stage	6, 239	2.82	0.012	6, 442	1.08	0.374	6, 442	2.28	0.035	6, 348	2.15	0.047	6, 68	1.50	0.199
Season * stage	2, 239	27.52	0.000	2, 442	16.22	0.000	2, 442	55.18	0.000	2, 348	15.73	0.000	2, 68	60.76	0.000
Genotype * season * stage	6, 239	1.44	0.199	6, 442	0.23	0.922	6, 442	1.83	0.122	6, 348	1.54	0.191	6, 68	1.01	0.431
Nested contrasts															
Season at stage 1	1, 239	0.24	0.622	1, 442	93.67	0.000	1, 442	189.35	0.000	1, 348	130.32	0.000	1, 68	69.84	0.000
Season at stage 2	1, 239	71.62	0.000	—	—	—	—	—	—	—	—	—	1, 68	213.39	0.000
Season at stage 3	1, 239	0.44	0.509	1, 442	1.12	0.103	1, 442	0.08	0.772	1, 348	1.99	0.159	1, 68	0.54	0.467
Stage linear for cool season	1, 239	640.29	0.000	1, 442	113.13	0.000	1, 442	456.59	0.000	1, 348	189.58	0.000	1, 68	199.89	0.000
Stage linear for warm season	1, 239	648.81	0.000	1, 442	0.43	0.512	1, 442	0.00	0.936	1, 348	0.72	0.397	1, 68	11.18	0.002
Stage quadratic for cool season	1, 239	0.75	0.389	1, 442	16.55	0.000	1, 442	3.60	0.058	1, 348	0.91	0.341	1, 68	5.34	0.025
Stage quadratic for warm season	1, 239	127.73	0.000	—	—	—	—	—	—	—	—	—	1, 68	80.92	0.000

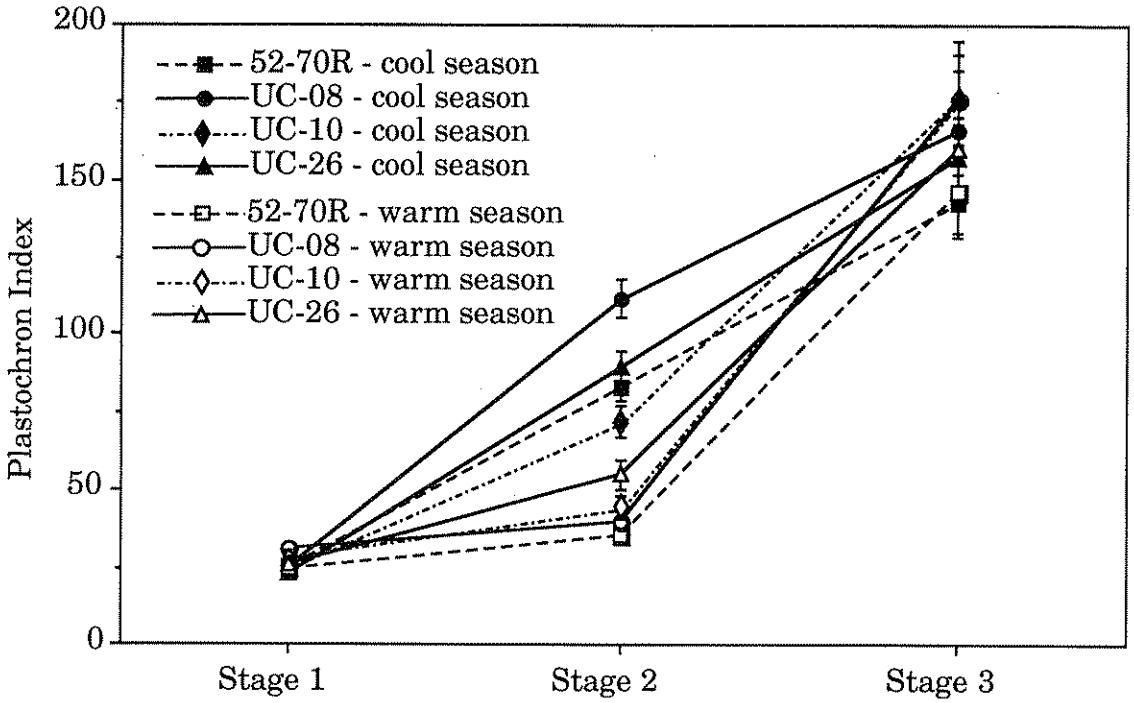

Fig. 1. Differential plastochron index measurements of celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting in the field during the cool and warm seasons. Extensions above data points denote standard errors.

ble 2. Overall, cool-season plants seemed to have greater vegetative growth than warm-season plants (plastochron index 91.7 versus 78.6) (Fig. 1). However, this differential growth occurred only at stage 2, during which young plants were stressed because of hot weather (Table 1); no seasonal effects were observed between plants at stages 1 and 3. Because stage-3 test entries were transplanted at the same time (12 March) during both experiments, no variations were expected or observed between the two seasons at this stage. Plants were probably too small during stage 1 to show differential growth. The breeding lines 'UC-08' and 'UC-10' had the greatest vegetative growth across the two seasons. 'UC-08' plants were significantly bigger than the commercial celery '52-70R' plants (overall plastochron index 91.7 for 'UC-08', 87.4 for 'UC-10', 85.3 for 'UC-26', and 76.2 for '52-70R'). Plant growth was primarily linear in physiological time (as indicated by a greater F value for the linear component than the quadratic) in both seasons. However, vegetative growth between stages 1 and 2 was different from that between stages 2 and 3 for warm season because both stage-linear and stage-quadratic components were significant.

Beet armyworm developmental parameters followed different trends than the plant growth index. Pupal weights varied significantly between seasons and growth stages (Table 2; Fig. 2). As measured by this variable, plants were significantly more resistant during the warm season than the cool season (52.9 versus 81.1 mg) and as they matured (90.4, 70.1, and 59.6 mg, respectively, for stages 1, 2, and 3). However, a significant season-by-stage interaction occurred, and variations due to season were observed only during stage 1 but not stage 3. Variations within stage 2 could not be determined because of zero larval survival to pupation for 'UC-08' and 'UC-10' during stage 2 of the warm season (zero variance violates the assumptions of ANOVA). Similarly, stage quadratic could not be calculated for this season. Pupal weight significantly decreased in a linear manner as plants matured in the cool season (greater linear component F value). However, the changes between stages 1 and 2 were not of the same magnitude as changes between stages 2 and 3 (both linear and quadratic components were significant); greater variations were observed between stages 1 and 2 than between stages 2 and 3 (Fig. 2). Stages were not significantly different in pupal weight when plants were evaluated during the warm season. There were no significant differences in pupal weight among celery genotypes when averaged across seasons and stages (no genotype-by-season or genotype-by-stage interaction occurred).

Insect generation times from egg to pupa and from egg to adult showed the largest variations during this study, with significant genotype-by-season, genotype-by-stage, and season-by-stage

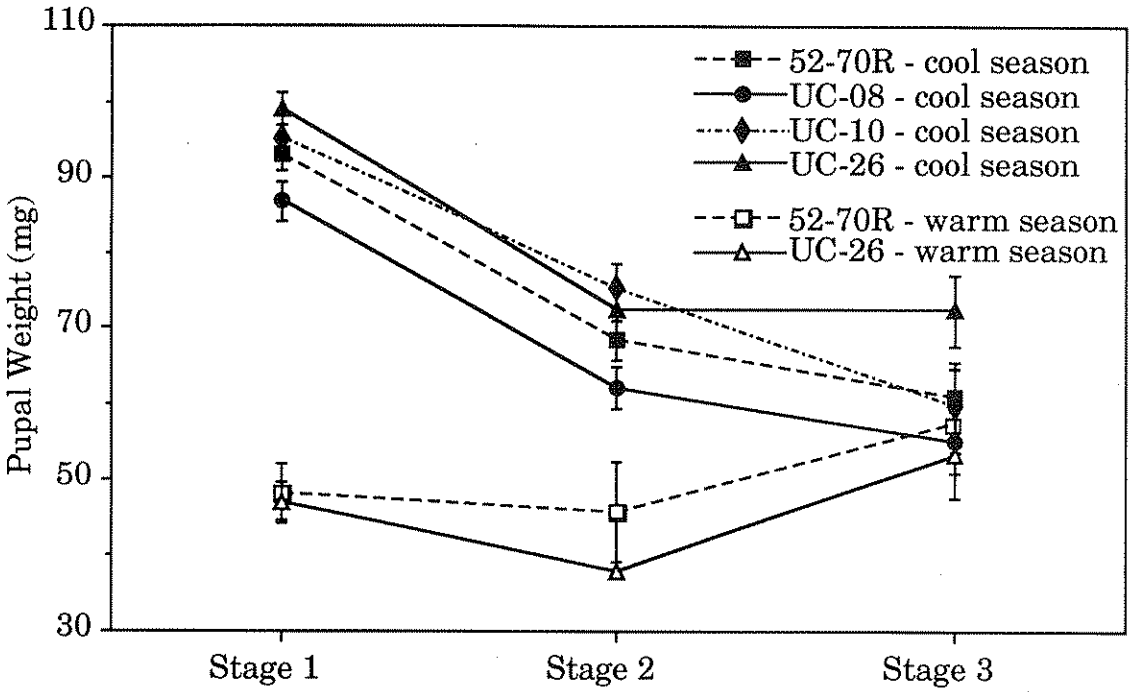

Fig. 2. Differential pupal weight of beet armyworm reared on celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting in the field during the cool and warm seasons. Data on 'UC-08' and 'UC-10' were not plotted for season 2 because of missing cells. Extensions above data points denote standard errors.

interactions (Table 2). As for pupal weight, seasonal variations during stage 2 and stage quadratic for the warm season could not be determined for days to pupation and days to adult emergence because of missing cells (Figs. 3 and 4). Larvae reared on celery transplanted during the warm season required significantly longer times to pupate (21.98 versus 17.18 d), but this was primarily a result of development on stage 1 plants because no seasonal effects were observed during stage 3 (Table 2; Figs. 3 and 4). The differences observed among the three growth stages also were associated only with the cool season, during which larval developmental time to pupa and adult had a significant linear increase between younger and older plant growth stages. The three stages did not differ significantly in insect developmental time when plants were tested during the warm season.

The four celery genotypes varied in their resistance to beet armyworm based on insect developmental time. No significant differences were found among genotypes during the cool season, but feeding on 'UC-08' significantly extended the number of days to pupation and to adult emergence compared with feeding on the commercial line '52-70R' and 'UC-10' during the warm season (Table 3). Genetic resistance also varied within plant growth stage. Feeding on the commercial line resulted in the fastest larval development during stage 1, but not during stage 2 (Table 4). 'UC-08' induced fast insect growth during stage 2, but not during stages 1 and 3.

Significant differences were found among seasons and plant physiological growth stages in insect survival (Table 2; Fig. 5). Resistance, as expressed in overall insect survival, was significantly influenced by the growing season. Insect survival was significantly less during the warm season (13.65 versus 44.15%) and as plants matured (51.78, 26.36, and 13.32%, respectively, for stages 1, 2, and 3). Seasonal variations were greatest during stage 2 (higher F value) and nonsignificant at stage 3. Stage-related variations were more linear during the cool season (F value 199.89 for linear versus 5.34 for quadratic) but were quadratic (F value 80.92 for quadratic versus 11.18 for linear) during the warm season. Therefore, the differences observed between stages 2 and 3 were caused only by variations induced during the cool season because there was a shift during the warm season and stage 2 was more resistant (Fig. 5). Genotype-by-season and genotype-by stage interactions were not significant, and 'UC-08' was significantly more resistant than the commercial line '52-70R' and 'UC-26' when averaged across seasons and stages (21.92, 30.04, 31.96, and 34.44% survival for 'UC-08', 'UC-10', 'UC-26', and '52-70R', respectively).

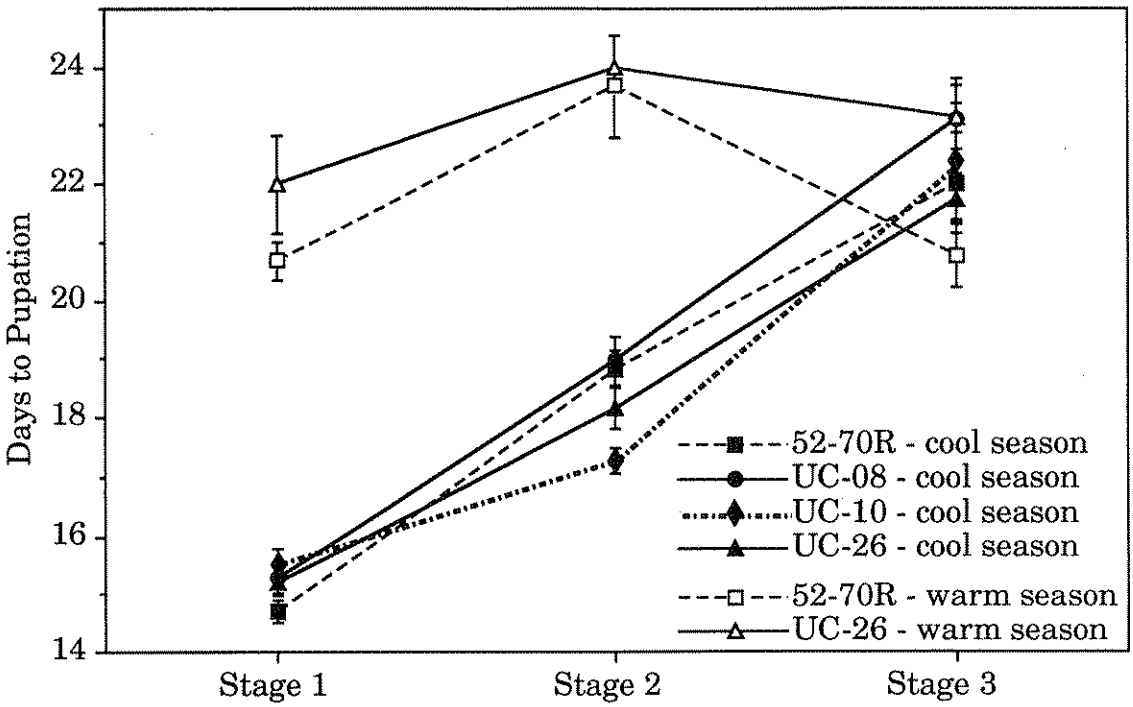

Fig. 3. Differential number of days to pupation of beet armyworm reared on celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting in the field during the cool and warm seasons. Data on 'UC-08' and 'UC-10' were not plotted for season 2 because of missing cells. Extensions above data points denote standard errors.

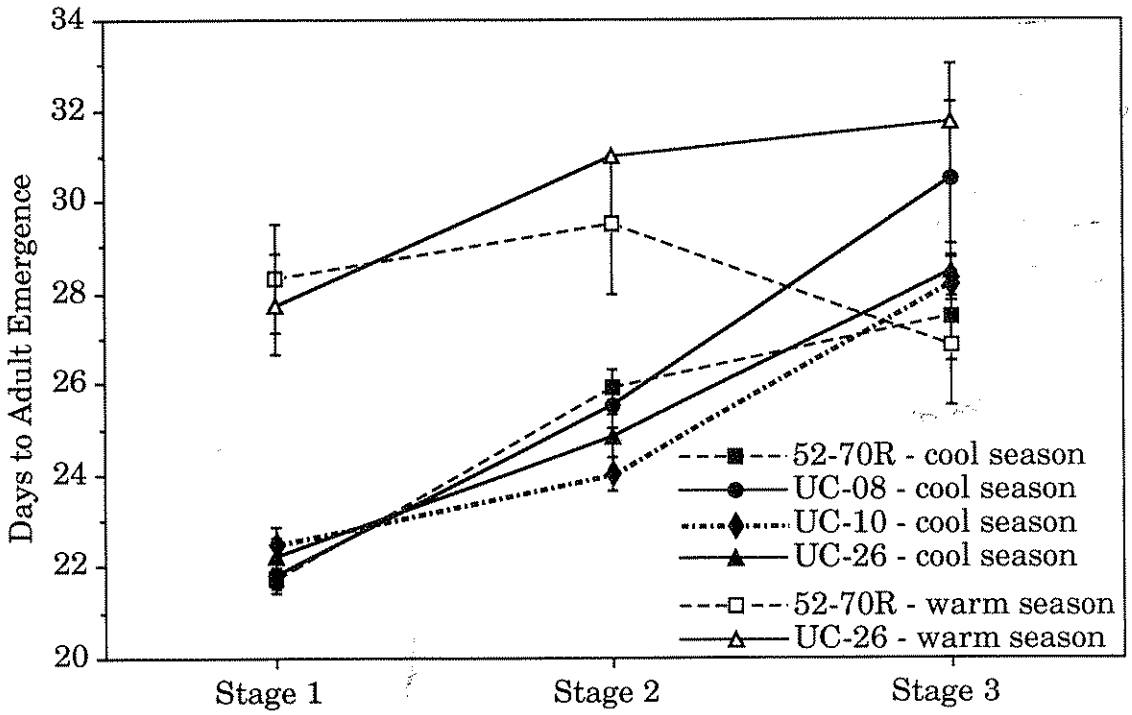

Fig. 4. Differential number of days to adult emergence of beet armyworm reared on celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting in the field during the cool and warm seasons. Data on 'UC-08' and 'UC-10' were not plotted for season 2 because of missing cells. Extensions above data points denote standard errors.

Table 3. Beet armyworm developmental time on celery genotypes grown during cool and warm seasons (average across growth stages)

Genotype	Days to pupation		Days to adult emergence	
	Cool[a]	Warm[b]	Cool[c]	Warm[d]
'52-70R'	16.8a	21.2b	23.7a	27.7b
'UC-08'	17.6a	24.3a	23.5a	33.3a
'UC-10'	17.1a	21.0b	23.7a	27.4b
'UC-26'	17.3a	22.8ab	24.1a	29.9ab

Means within a column followed by the same letter are not significantly different at the 5% level using modified Tukey's w procedure (Keselman & Rogan 1978).
[a] $F = 2.16$; df = 3, 389; $P = 0.0924$.
[b] $F = 5.40$, df = 3, 52; $P = 0.0030$.
[c] $F = 1.30$, df = 3, 315; $P = 0.2738$.
[d] $F = 4.12$, df = 3, 32; $P = 0.0177$.

Table 4. Beet armyworm developmental time on celery genotypes at various stages of plant growth (average across growing seasons)

Genotype	Days to pupation			Days to adult emergence		
	Stage 1[a]	Stage 2[b]	Stage 3[c]	Stage 1[d]	Stage 2[e]	Stage 3[f]
'52-70R'	15.0b	19.1a	21.2a	22.1a	26.1a	27.2b
'UC-08'	16.0a	19.0a	23.1a	22.7a	25.5ab	31.0a
'UC-10'	16.0a	17.3b	22.0a	23.0a	24.0b	28.2ab
'UC-26'	15.8a	18.3ab	22.2a	22.7a	25.0ab	29.3ab

Means within a column followed by the same letter are not significantly different at the 5% level using modified Tukey's w procedure (Keselman & Rogan 1978).
[a] $F = 7.20$; df = 3, 204; $P = 0.0001$.
[b] $F = 5.33$; df = 3, 161; $P = 0.0016$.
[c] $F = 1.50$; df = 3, 75; $P = 0.2232$.
[d] $F = 1.54$; df = 3, 178; $P = 0.2053$.
[e] $F = 3.10$; df =3, 125; $P = 0.0292$.
[f] $F = 4.56$; df = 3, 43; $P = 0.0083$.

Discussion

To allow an accurate assessment of seasonal variations in resistance, the experiment was designed so that stage-3 plants were tested only once, in June, during the study, not at different times of the year like stages 1 and 2. The growth stage-related differences observed during the warm season, when considered alone, demonstrate that results obtained during the study were not caused by shifts in the susceptibility of the insect colony used. The lack of significant differences between cool-season and warm-season stage-3 plants shows that no soil heterogeneity was involved because all warm-season plantings were on plots adjacent to cool-season plantings. Unlike the plastochron index measurements, in which no differences existed among cool-season and warm-season stage-1 and stage-3 plants (Fig. 1), significant differences were found between the two seasons in insect developmental variables when these plants were used in bioassays (Figs. 2–5). As shown by these insect growth figures, variation was reduced as plants matured because, as suggested by earlier studies (M.M.D., J.T.T., & C.F.Q., unpublished data),

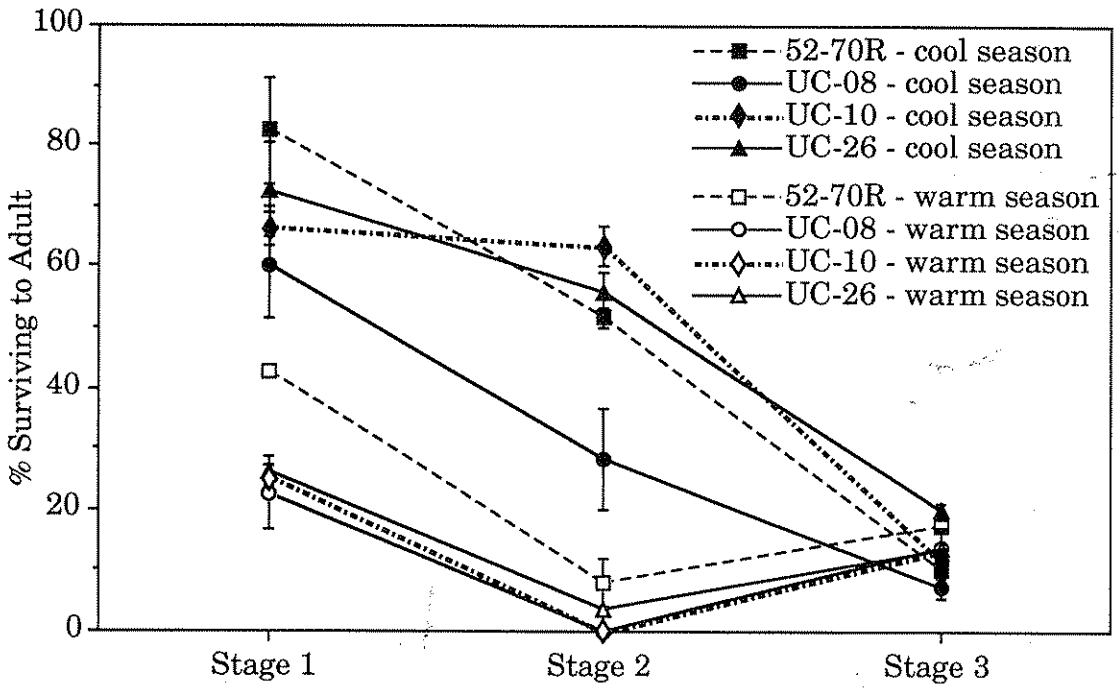

Fig. 5. Differential beet armyworm survival on celery genotypes at 4 (stage 1), 8 (stage 2), and 12 (stage 3) wk after transplanting in the field during the cool and warm seasons. Extensions above data points denote standard errors.

older celery plants were more resistant to insect feeding. The differences between the two seasons were large during plant growth stage 1, small during stage 2, and almost none by stage 3. Stage effects were significant for all insect parameters measured during the cool season, but not during the warm season (Table 2; Figs. 2–5). This suggests that resistance to beet armyworm is much more affected by growing conditions than by plant age.

Cool-season stage-1 plants and warm-season stage-1 plants were at the same physiological age of plant growth (4 wk after transplanting) when tested. One difference between these two groups is their exposure to different weather conditions. Similarly, weather conditions changed for stage-2 plants, but not for stage-3 plants. These variations in environmental conditions may have contributed to the differential insect development recorded between the two seasons. Both temperature and solar radiation of the experimental area increased during the study and were highest during the warm season (Table 1). No consistent variations were recorded in relative humidity. Cool- and warm-season stage-1, stage-2, and stage-3 plants were exposed to weather conditions for the same length of time (50, 81, and 110 d, respectively), but at different times of the year. Because bioassays were conducted under similar conditions, higher temperatures and levels of solar radiation could be partially responsible for the increased beet armyworm feeding resistance in the different celery genotypes during the warm season. Both of these factors have been shown to influence expression of insect resistance in other plants (Wood & Starks 1972, Tingey & Singh 1980, Kennedy et al. 1981, Karner & Manglitz 1985, Manuwoto & Scriber 1985, Khan et al. 1986, Smith 1989).

Why plants of the same age expressed differential resistance to beet armyworm when grown on the same soil under different weather conditions is not clear. In our study, plants were grown in the field from March to June and were exposed to cumulative and varying temperatures, levels of solar radiation, relative humidity, and other environmental factors. Feeding bioassays, however, were conducted in environmental chambers maintained at a constant temperature (27 ± 2°C), photoperiod (16:8 [L:D] h), light intensity (250–300 μI/m^2/s), and relative humidity (75%). Therefore, the seasonal effects observed in the study acted indirectly on insect development by affecting plant suitability as a result of change in plant physiological (Tingey & Singh 1980), physical, or chemical characteristics.

Our study demonstrates that both plant age and growing environment can interact significantly with plant genotype to magnify or suppress expression of genetic resistance to pests. Assessment of these interactions requires use of appropriate experimental designs and statistical analyses for partitioning of genetic versus environmental and plant age-related variations in host plant resistance to insects. The techniques used to evaluate plant cultivars for pest resistance determine the success of the plant resistance program. It is important to study test plant genotypes under various growing conditions and at different stages of plant growth to determine the potential genotype-by-environment and genotype-by-stage interactions before characterization and utilization of the resistance in breeding for pest resistance and integrated pest management programs.

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