RESISTANCE IN GERMPLASM OF *CUCURBITA PEPO* TO SILVERLEAF, A DISORDER ASSOCIATED WITH *BEMISIA ARGENTIFOLII* (HOMOPTERA: ALEYRODIDAE)

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ABSTRACT

Elite breeding lines and susceptible varieties of *Cucurbita pepo* L. (zucchini and yellow crookneck squash) and accessions of two wild species, *Cucurbita ecuadorensis* Cutler and Whitaker and *Cucurbita martinezii* Bailey, were evaluated in spring and fall 1995 for resistance to silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring, and to squash silverleaf, a physiological disorder associated with feeding by *B. argentifolii*. Populations of whitefly and severity of silvering were greater in the spring season than in the fall. In general, the yellow squash variety, 'Supersett', and the two yellow squash breeding lines (A24-10 and K26-4) supported larger populations of whitefly than the zucchini variety, 'Elite', and A21-7 and Sunseeds 3, the zucchini breeding lines. However, whitefly populations within the yellow squash cultigens or within the zucchini cultigens did not differ significantly. In contrast, 'Elite' was severely silvered in the spring (average rating of 4.8 at the end of the season) while Sunseeds 3 never exhibited silverleaf and only one plant of A21-7 exhibited slight silvering (rating of 1). 'Supersett' was usually significantly more silvered than the yellow squash breeding lines, but the lines nevertheless exhibited significant levels of silvering (average rating of 3.2 compared to 3.9 for 'Supersett' at the end of the spring season). Four accessions of the two wild species, *C. ecuadorensis* and *C. martinezii*, all supported moderate populations of whiteflies and developed silverleaf. In the case of the zucchini breeding lines, silverleaf severity was not related to numbers of immature whiteflies. Resistance to silverleaf in the zucchini breeding lines may be due to some form of tolerance to the effects of whitefly feeding.

Key Words: Plant resistance, silverleaf disorder, squash, tolerance, zucchini.

RESUMEN

La resistencia a la mosca blanca, *Bemisia argentifolii* Bellows y Perring, y al plateado de la calabaza, un desorden fisiológico asociado con el ataque de *B. argentifolii* fueron evaluados en líneas promisorias y variedades susceptibles de *Cucurbita pepo* L. (zucchini y calabaza amarilla) y en accesiones de dos especies salvajes, *Cucurbita ecuadorensis* Cutler y Whitaker y *Cucurbita martinezii* Bailey, durante la primavera y el otoño de 1995. Las poblaciones de moscas blancas y la severidad del plateado fueron mayores en la primavera que en el otoño. En general, la variedad de calabazas amarillas 'Supersett' y las dos líneas de calabazas amarillas A24-10 y K26-4 soportaron mayores poblaciones de moscas blancas que la variedad 'Elite' y las lineas A21-7 y Sunseeds 3 de zucchini. Sin embargo, las poblaciones de moscas blancas en los cultigenes de calabazas amarillas o de zucchini no difirieron signifiacativamente. En contraste, 'Elite' fue severamente plateada en la primavera (grado promedio de 4.8 al final de la estación) mientras Sunseeds 3 nunca mostró síntomas de plateado y sólo una planta de A21-7 mostró plateado ligero (grado 1). 'Supersett' fue significativamente más plateada que las líneas de calabazas amarillas, pero las líneas sin embargo exhibieron niveles significativos de plateado (grado promedio de 3.2 comparado con 3.9 para 'Supersett' al final de la primavera). Cuatro accesiones de las dos especies salvajes, *C. ecuadorensis* y *C. martinezii*, resistieron poblaciones moderadas de moscas blancas y desarrollaron el plateado. En el caso de las líneas seleccionadas de zucchini, la severidad del plateado no estuvo relacionada con el número de moscas blancas inmaduras. La resistencia al plateado en las líneas de zucchini podría deberse a alguna forma de tolerancia a los efectos del daño de las moscas blancas.

In recent years, the silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (= *Bemisia tabaci*, 'B' strain), has become an increasingly severe pest of vegetables, agronomic crops, and ornamental plants. Silverleaf whitefly can induce physiological disorders in several species of plants, including *Cucurbita* species (Costa & Brown 1990, Schuster et al. 1991, Yokomi et al. 1990), tomato (Maynard & Cantliffe 1989, Schuster et al. 1990), crossandra (Hoelmer et al. 1991), and *Brassica* species (Brown et al. 1992). In addition, the silverleaf whitefly vectors geminiviruses, contaminates plant products with honeydew and sooty mold, and reduces plant vigor. Squash silverleaf is one such physiological disorder that first became apparent in the New World in the fall of 1987 (Maynard & Cantliffe 1989), causing severe economic loss for growers of *Cucurbita* species in southwest Florida (Simons et al. 1988). Silverleaf disorder subsequently was recorded on pumpkin, *Cucurbita moschata* (Duchesne) Poir, in Puerto Rico in 1987 (Segarra-Carmona et al. 1990), on zucchini, *Cucurbita pepo* L., in Arizona in 1989 (Brown et al. 1992), and on *C. pepo* in California in the fall of 1990 (Cohen et al. 1992).

Silverleaf disorder is characterized, in mild cases, by silvering parallel to leaf veins on the upper surface of leaves, but may progress to silvering of the entire leaf surface and bleaching of fruit, stems and flowers in severe cases (Paris et al. 1987). The silvered appearance is due to air spaces formed between the epidermis and palisade cells (Burger et al. 1988, Jimenez et al. 1995). Photosynthesis is reduced (Burger et al. 1988), and silvered squash may yield less (Costa et al. 1994). Silverleaf was originally thought to be caused by dsRNA associated with whiteflies (Bharathan et al. 1990, 1992). However, the general consensus now is that silverleaf is a plant response to feeding by whiteflies, and its severity varies directly with numbers of immature whiteflies (Yokomi et al. 1990, Schuster et al. 1991, Costa et al. 1993, Jimenez et al. 1993).

Most of the *Cucurbita* species grown commercially in Florida are susceptible to *B. argentifolii* and to silverleaf disorder (Simons et al. 1988, Maynard & Cantliffe 1989, G.W.E. unpublished data). Some variation in susceptibility to silverleaf was observed among the six cultivar groups of *C. pepo*, with several members of the cocozelle group appearing less susceptible to silverleaf (Paris et al. 1993a,b). Whitefly populations on these cultivars were not recorded, however. Varieties and breeding lines of *C. pepo* have been evaluated in the field since the fall of 1991 at the Central Florida Research and Education Center, Leesburg, for resistance to silverleaf (Elmstrom 1993). Some breeding lines were found to have substantially less silvering than control varieties, but again, populations of whiteflies were not evaluated. The primary objective of the following experiment was to determine the relationship between whitefly populations and silverleaf symptoms on four elite breeding lines showing little silverleaf in previous trials and on susceptible control varieties of *C. pepo*. In addition, we examined the susceptibility to leaf silvering of two wild species, *Cucurbita ecuadorensis* Cutler and Whitaker and *Cucurbita martinezii* Bailey.

MATERIALS AND METHODS

Plant Material

Cucurbita pepo varieties 'Elite' (zucchini) and 'Supersett' (yellow crookneck squash) are commonly grown in Central Florida. Previous studies (G. W. E., unpublished data) have shown them to be highly susceptible to silverleaf whitefly and to squash silverleaf. The cucurbit breeding program at the University of Florida has developed elite breeding lines of *C. pepo* that exhibit little leaf silvering (G. W. E., unpublished data). We evaluated both zucchini (A21-7 and Sunseeds 3) and yellow squash (A24-10 and K26-4) breeding lines and the two susceptible varieties ('Elite' and 'Supersett') for resistance to leaf silvering and to silverleaf whitefly. In addition, we looked at two accessions of two wild species, *C. ecuadorensis* (PIs 540895 and 432443) and *C. martinezii* (PIs 512099 and 438698), obtained from the USDA/ARS Southern Regional Plant Introduction Station, Griffin, GA.

Spring Field Season, 1995

Research was conducted at the Central Florida Research and Education Center farm in Leesburg, Lake Co., FL. Fertilization followed standard practices [bed (preplant), 900 kg per ha 16-8-8; emergence, 112.5 kg per ha 15-0-14; sidedress, 225 kg per ha 15-0-14; layby, 394 kg per ha 15-0-14]. The experiment was designed as a randomized complete block with four replicates. Plots consisted of single rows with nine hills. Two seeds were sown per hill on 13 April, hills were 76 cm apart and rows per 3.05 m apart. Seedlings were thinned to one per hill on 4 May. Chlorothalonil [Bravo 720, ISK Biotech Corp., Mentor, OH, (1.7 kg AI per ha)] and mancozeb [Manzate, Du Pont Agricultural Products, Wilmington, DE (1.7 kg AI per ha)] were applied at weekly intervals from 12 May to 16 June for control of gummy stem blight, *Didymella bryoniae* (Auersw.) Rehm, and powdery and downy mildew, *Erysiphe cichoracearum* DC and *Pseudoperonospora cubensis* (Berk. & M. A. Curtis) Rostovzev, respectively. *Bacillus thuringiensis* Berliner var. *kurstaki* [Dipel 2X, Abbott Laboratories, North Chicago, IL (1.1 kg AI per ha)] was applied 9 and 16 June for control of pickleworm, *Diaphania nitidalis* (Stoll) and melonworm, *Diaphania hyalinata* (L.). Plots were irrigated with overhead sprinklers up to twice a week, as necessary.

Leaves were sampled at weekly intervals from 22 May until 13 June. Two leaves from the crown region were taken from five randomly chosen plants in each plot. Leaves were taken to the laboratory in an ice chest. Two disks were cut randomly from one half of each leaf using a cork borer (area = 3.14 cm^2). We counted on the abaxial and adaxial surfaces of the disk the number of eggs, young nymphs (sum of first to third nymphal instars), parasitized fourth nymphal instars, unparasitized fourth nymphal instars and red-eyed nymphs. Leaf disks were placed in 473-ml cardboard cans (Gainesville Paper, Gainesville, FL) to allow for emergence of parasitoids. After 4 weeks, emerged parasitoids were sorted by sex and species. Density of trichomes on the abaxial surfaces of five leaves from each plot (20 per plant accession) was assessed on 13 June.

Plants were evaluated for leaf silvering at weekly intervals from 11 May to 20 June. Each plant in the plot was rated on a scale of 0 to 5 (0, no silvering to 5, 95-100% silvering) (Paris et al. 1987).

Fall Field Season, 1995

The field plots were prepared as for the spring field season. Seeds of wild species were sown on 15 August, and missing hills were replanted on 23 August. Breeding lines and varieties were planted on 28 August. Fungicides and *B. thuringiensis* were applied weekly from 22 September to 13 October. Plants were sampled and silverleaf ratings were made weekly from 18 September to 16 October. Density of trichomes on the abaxial surfaces of five leaves from each plot was assessed on 9 October.

Statistical Analyses

Counts of whitefly stages were transformed via $\sqrt{(x+0.1)}$ and three-way analysis of variance was performed (Proc GLM, SAS Institute 1987) using date, replicate and cultigen/accession as the main effects. When F tests indicated a significant effect of cultigen/accession, means were separated using least significant difference (LSD) tests at a significance level of 0.05. Counts of whiteflies on the *C. pepo* cultigens were analyzed separately from counts on the four wild *Cucurbita* accessions because of uncertainty in relating within-plant sample location on the vining wild species to location within the bushy *C. pepo* cultigens.

Silverleaf ratings of individual plants within a replicate were averaged for each cultigen/accession on each date. Ratings were analyzed via Proc GLM using the design described for whitefly counts. Ratings were regressed on density of immature whiteflies (average density of eggs and nymphs in each replicate) separately for 'Elite', 'Supersett', and the two yellow squash breeding lines in spring and fall field seasons.

RESULTS

Spring Field Season, 1995

Counts of eggs on the abaxial and adaxial surfaces of the disks were combined, as were counts of young nymphs (sum of first, second and third nymphal instars). Counts on both disk surfaces of unparasitized and parasitized fourth nymphal instars and red-eyed nymphs were combined (old nymphs). All life stages were rare on the adaxial leaf surface: 0 to 0.7% of eggs, 0.4 to 2.4% of young nymphs, and 0 to 4.9% of old nymphs were located on the adaxial surface.

Analysis of variance indicated a significant interaction of date with *C. pepo* cultigens (elite breeding lines and varieties) for all whitefly stages (Table 1) (eggs: $F = 2.16$; df = 15, 1862; $P = 0.0060$, young nymphs: $F = 7.55$; df = 15, 1862; $P < 0.0001$, and old nymphs: $F = 11.54$; df = 15, 1862; $P < 0.0001$). Interactions of date with wild *Cucurbita* accessions were significant for eggs ($F = 4.70$; df = 7, 1035; $P < 0.0001$), and young nymphs ($F = 6.56$: df = 7, 1035; $P < 0.0001$), but not for old nymphs. Further analysis was performed by date.

Counts of eggs on the *C. pepo* cultigens did not differ significantly on any date (Fig. 1,A). On 13 June, the yellow squash cultigens supported significantly more young nymphs than the zucchini cultigens ($F = 2.92$; df = 5, 15; $P = 0.0492$) (Fig. 1,B). Also on 13 June, 'Supersett' supported significantly more old nymphs than any other cultigen ($F = 3.01$; df = 5, 15; $P = 0.0446$) (Fig. 1,C).

Counts of eggs on the wild *Cucurbita* accessions differed significantly on 6 June ($F = 4.73$; df = 3, 9; $P = 0.0301$) (Fig. 2,A) with *C. ecuadorensis* PI 540895 supporting significantly more than the other accessions. The two *C. ecuadorensis* accessions also

TABLE 1. REPRESENTATIVE ANOVA TABLE FOR COUNTS OF WHITEFLIES ON LEAF DISKS (DATA ARE NUMBER OF YOUNG NYMPHS ON *C. PEPO* CULTIGENS IN SPRING 1995).

Source	df	MS	*F*	*P*
Replicate	3	952.94	2.41	0.1077
Cultigen/accession	5	1398.19	3.53	0.0291
Replicate × cultigen/accession	15	395.74		
Date	3	20299.52	234.95	0.0001
Date × cultigen/accession	15	694.39	8.04	0.0001
Residual	1862	86.40		

supported significantly more young nymphs than the *C. martinezii* accessions on 6 June ($F = 5.15$; df = 5, 15; $P = 0.0241$) and 13 June ($F = 7.47$; df = 5, 15; $P = 0.0082$) (Fig. 2,B). Numbers of old nymphs did not differ significantly on any date (Fig. 2,C).

Trichome density of the abaxial leaf surface varied significantly ($F = 198.2$; df = 9, 181; $P < 0.0001$), with the two accessions of *C. ecuadorensis* being the hairiest (Table 2). *C. pepo* cultigens were significantly less hairy than *C. ecuadorensis* but not *C. martinezii*, and in general, yellow squash cultigens were hairier than the zucchini cultigens.

Silverleaf rating was significantly influenced by a date by cultigen/accession interaction ($F = 32.65$; df = 52, 1782; $P < 0.0001$). Therefore, further analysis was done separately for each date. Silvering was first detected on 11 May on 'Supersett' (Table 3), and by 5 June, all accessions and cultigens, except Sunseeds 3, showed some level of silvering. From 5 June onwards, the commercial varieties suffered the greatest severity of silvering, averaging 4.81 for 'Elite' and 3.86 for 'Supersett' on 20 June. 'Elite' exhibited significantly worse silvering than the two breeding lines. In fact, neither of the zucchini breeding lines showed silvering except for one A21-7 plant with a rating of 1 (less than 25% of leaf surface silvered) on 5 June. 'Supersett' was significantly more silvered than the two yellow squash breeding lines on 5 June and 20 June, however, both A24-10 and K26-4 were significantly silvered by 20 June, with average ratings of 3.21. All accessions of the wild *Cucurbita* species showed silvering (Table 3), with levels somewhat lower than the *C. pepo* cultigens.

Regressions of silverleaf rating on density of immature whiteflies yielded significant linear relationships for 'Elite' [silverleaf rating = 0.046 + 0.298(density of immatures), $r^2 = 0.62$, SE slope = 0.062, df = 1, 14] and 'Supersett' [silverleaf rating = 0.226 + 0.064(density of immatures), $r^2 = 0.52$, SE slope = 0.016, df = 1, 14]. Significant linear relationships also existed for the squash breeding lines, A24-10 [silverleaf rating = -0.14 + 0.097(density of immatures), $r^2 = 0.55$, SE slope = 0.023, df = 1, 14] and K26-4 [silverleaf rating = -0.29 + 0.086(density of immatures), $r^2 = 0.76$, SE slope = 0.013, df = 1, 14]. Intercepts did not differ significantly from 0 for any cultigen.

Relative levels of parasitism, as indicated by the number of adult parasitoids emerging from leaf disks, was very low. A total of 1,394 whiteflies and 37 parasitoids emerged from the zucchini cultigens. *Encarsia pergandiella* Howard was the most common species (24 females, 0 males), followed by *Encarsia nigricephala* Dozier (11 females, 0 males), and *Eretmocerus* sp. (0 females, 2 males). A total of 2,149 whiteflies and 36 parasitoids emerged from yellow squash cultigens (19 female *E. pergandiella,* 1 female *E. nigricephala*, and 6 female and 10 male *Eretmocerus* sp.) and 369 whiteflies and 7 parasitoids (5 female *E. pergandiella*, 1 female *Eretmocerus* sp., and 1 female *E. nigricephala*) emerged from the wild accessions.

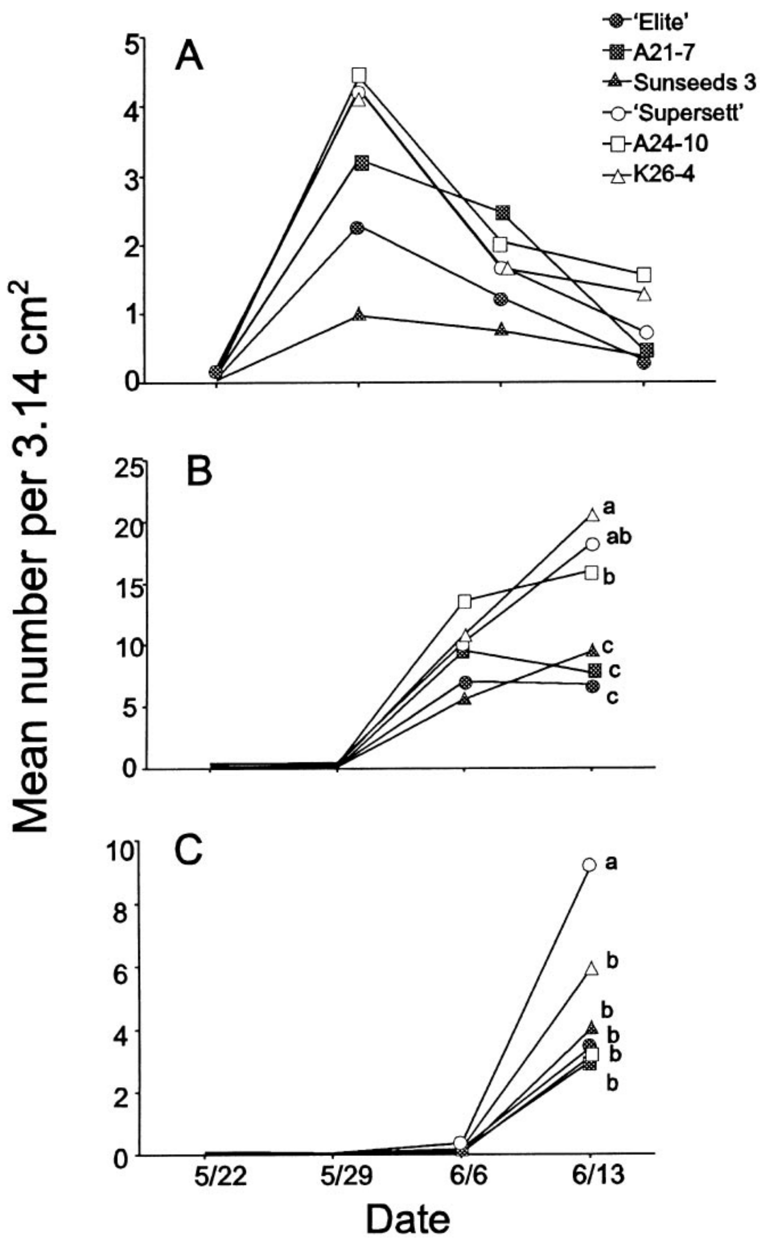

Figure 1. Mean numbers of silverleaf whitefly (A) eggs, (B) young nymphs, and (C) old nymphs on *C. pepo* yellow squash (open symbols) and zucchini cultigens (patterned symbols) during Spring 1995 in Leesburg, FL. Data points within a date followed by different letters differ significantly ($P = 0.05$; LSD test).

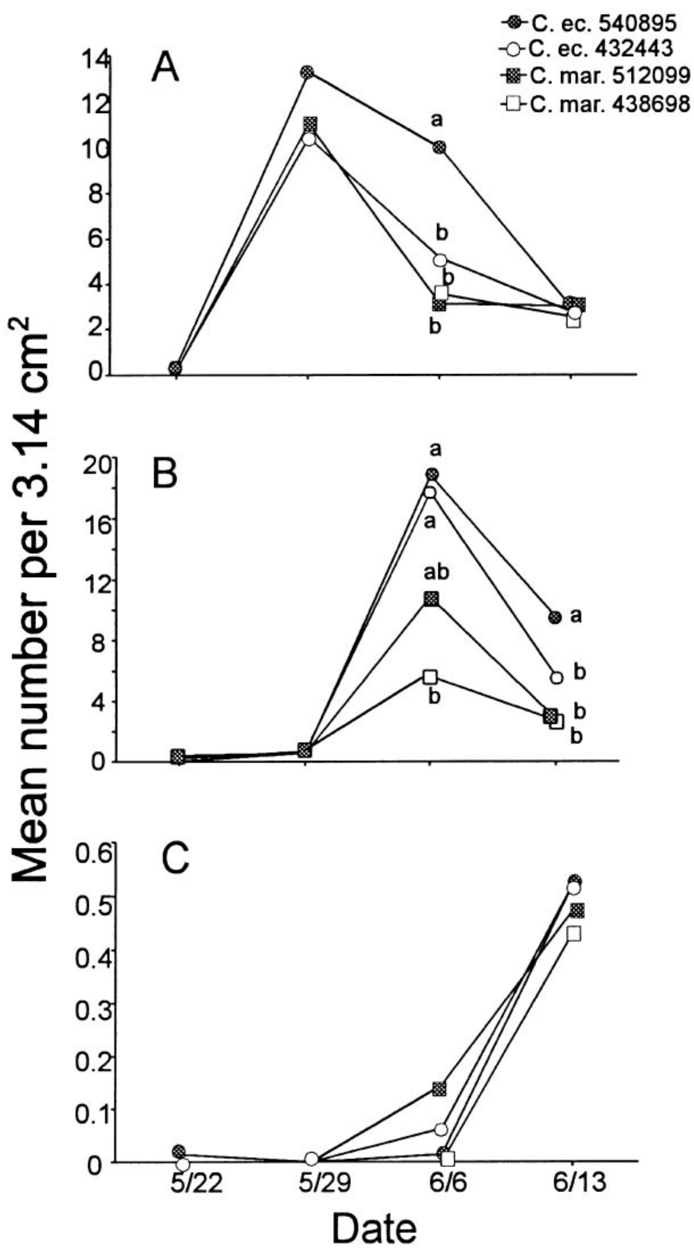

Figure 2. Mean numbers of silverleaf whitefly (A) eggs, (B) young nymphs, and (C) old nymphs on *C. ecuadorensis* (circles) and *C. martinezii* accessions (squares) during Spring 1995 in Leesburg, FL. Data points within a date followed by different letters differ significantly (P = 0.05; LSD test).

TABLE 2. AVERAGE NUMBER OF TRICHOMES PER 8.1MM² (±SEM) ON THE ABAXIAL LEAF SURFACE OF *C. PEPO* CULTIGENS AND ACCESSIONS OF WILD *CURCURBITA* SPECIES.

Type	Field Season	
Cultigen/Accession	Spring	Fall
Zucchini		
'Elite'	81.4 ± 4.0h[1]	56.7 ± 2.6g
A21-7	99.9 ± 4.9gh	136.1 ± 25.8def
Sunseeds 3	90.5 ± 4.9gh	64.8 ± 3.1fg
Yellow squash		
'Supersett'	131.8 ± 7.1ef	86.8 ± 6.8efg
A24-10	169.4 ± 7.1cd	206.6 ± 31.2cd
K26-4	180.2 ± 9.1c	149.1 ± 11.7cde
Wild species		
C. ecuadorensis PI 540895	489.7 ± 20.3a	465.7 ± 33.4b
C. martinezii PI 512099	112.4 ± 6.3fg	88.9 ± 7.8efg
C. martinezii PI 438698	141.2 ± 6.6de	225.1 ± 41.7c
C. ecuadorensis PI 432443	437.4 ± 19.4b	596.4 ± 63.0a

[1]Numbers within a column followed by different letter differ significantly ($P = 0.05$; LSD).

Fall Field Season, 1995

Analysis of variance indicated a significant interaction of date with *C. pepo* cultigen for eggs ($F = 5.06$; df = 20, 2292; $P < 0.0001$), young nymphs ($F = 10.15$; df = 20, 2292; $P < 0.0001$), and old nymphs ($F = 2.02$; df = 20, 2292; P 0.0046). Interactions of date with wild *Cucurbita* accession were also significant for eggs ($F = 8.19$; df = 12, 1157; $P < 0.0001$), young nymphs ($F = 2.33$; df = 12, 1157; $P = 0.0059$), and old nymphs ($F = 1.97$; df = 12, 1157; $P = 0.0238$). All further analysis was done separately for each date.

C. pepo cultigens supported significantly different numbers of eggs only on 18 September ($F = 7.04$; df = 5, 15; $P = 0.0014$) when yellow squash breeding line K26-4 was more heavily infested than any of the other cultigens (Fig. 3,A). Numbers of young nymphs on the cultigens differed significantly on the first four dates (18 September: $F = 7.90$; df = 5,15; $P = 0.0008$; 25 September: $F = 9.27$; $P = 0.0003$; 3 October: $F = 13.83$; $P < 0.0001$; 9 October: $F = 8.53$; $P = 0.0005$). In general, yellow squash cultigens were more heavily infested than zucchini cultigens (Fig. 3,B). The yellow squash cultigens supported significantly more old nymphs than the zucchini cultigens on 9 October ($F = 4.05$; df = 5, 15; $P = 0.0159$) (Fig. 3,C).

Numbers of eggs, young nymphs, and old nymphs did not differ significantly among the four wild *Cucurbita* accessions except on 25 September ($F = 8.66$; df = 3, 7; $P = 0.0051$) when *C. ecuadorensis* PI 540895 had more eggs than the other accessions (Fig. 4).

Silverleaf rating was significantly influenced by a date by cultigen/accession interaction ($F = 15.30$; df = 36, 1214; $P < 0.0001$). Silverleaf was less severe than in the

TABLE 3. SILVERLEAF RATING FOR CULTIGENS OF *C. PEPO* AND ACCESSIONS OF TWO WILD *COCURBITA* SPECIES GROWN IN SPRING 1995 IN LEESBURG, FL.

Type	Silverleaf Rating (Mean ± SEM)[1]						
Cultigen/Accessioin	May 11	May 18	May 25	May 31	June 5	June 13	June 20
Zucchini							
'Elite'	0.0 ± 0.0	0.0 ± 0.0b[2]	0.29 ± 0.10b	0.0 ± 0.0	2.04 ± 0.15ab	4.38 ± 0.18a	4.81 ± 0.10a
A21-7	0.0 ± 0.0	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0	0.03 ± 0.03e	0.0 ± 0.0e	0.0 ± 0.0d
Sunseeds 3	0.0 ± 0.0	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0d
Yellow squash							
'Supersett'	0.15 ± 0.08	0.0 ± 0.0b	0.22 ± 0.09bc	0.06 ± 0.06	1.33 ± 0.17bc	2.61 ± 0.35b	3.86 ± 0.29ab
A24-10	0.0 ± 0.0	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0	0.40 ± 0.11de	2.75 ± 0.44b	3.21 ± 0.29b
K26-4	0.0 ± 0.0	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0	0.45 ± 0.09de	2.39 ± 0.33bc	3.21 ± 0.32b
Wild species							
C. ecuadorensis PI 540895	0.0 ± 0.0	0.23 ± 0.13ab	0.64 ± 0.16a	0.07 ± 0.05	1.30 ± 0.16c	1.93 ± 0.24bcd	0.97 ± 0.21cd
C. martinezii PI 512099	0.0 ± 0.0	0.0 ± 0.0b	0.0 ± 0.0c	0.0 ± 0.0	1.17 ± 0.10cd	0.79 ± 0.10de	0.52 ± 0.14cd
C. martinezii PI 438698	nd[3]	nd	0.0 ± 0.0c	0.0 ± 0.0	2.21 ± 0.25a	1.27 ± 0.26 cde	0.89 ± 0.20cd
C. ecuadorensis PI 432443	0.0 ± 0.0	0.34 ± 0.17a	0.44 ± 0.13ab	0.09 ± 0.05	1.41 ± 0.18bc	2.31 ± 0.25bc	1.45 ± 0.22c

[1]Silverleaf rating scale—grade 0, green; grade 1, <25%; grade 2, 25-50%; grade 3, 50-75%; grade 4, 75-95%; grade 5, 95-100% silvering.
[2]Means within a column followed by different letters differ significantly ($P = 0.05$; LSD).
[3]Nd, no data taken because plants were too small.

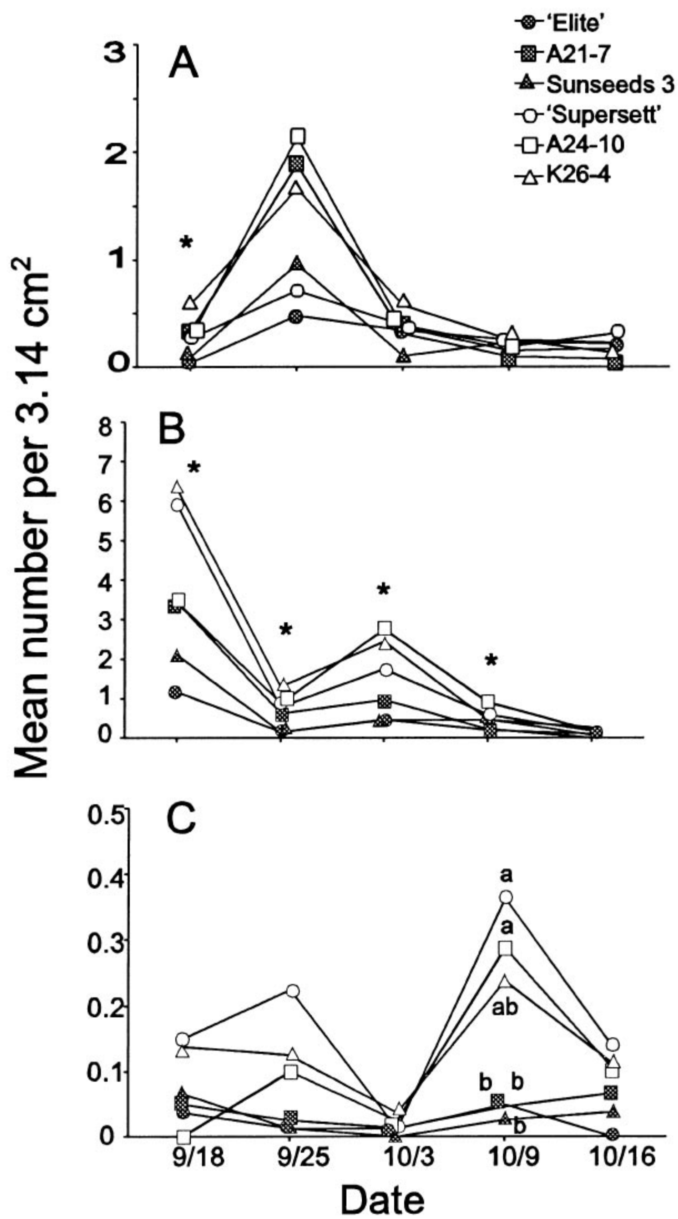

Figure 3. Mean numbers of silverleaf whitefly (A) eggs, (B) young nymphs, and (C) old nymphs on *C. pepo* yellow squash (open symbols) and zucchini cultigens (patterned symbols) during Fall 1995 in Leesburg, FL. Data points within a date followed by different letters differ significantly ($P = 0.05$; LSD test). Asterisks on (A) and (B) indicate dates on which cultigens differed significantly.

spring field season and declined over the rating period (Table 4). Ratings differed significantly among the *C. pepo* cultigens and the wild species on each date. 'Supersett' was the *C. pepo* cultigen most silvered, and was always more silvered than the two yellow squash breeding lines. 'Elite', despite supporting fewer whiteflies than 'Supersett' throughout the sampling period was as silvered as 'Supersett' by the 9 and 16 October sample dates. The zucchini breeding lines, A21-7 and Sunseeds 3, never exhibited any silvering despite supporting whitefly populations greater than or equal to populations on 'Elite'. The wild *Cucurbita* accessions were more heavily silvered than the *C. pepo* cultigens at the beginning of the sampling period. The two *C. ecuadorensis* accessions were significantly more heavily silvered than the *C. martinezii* accessions.

Relationships between silverleaf rating and density of immature whiteflies were significantly linear for 'Elite' [silverleaf rating = 0.47 + 0.40(density of immatures), $r^2 = 0.21$, SE slope = 0.194, df = 1, 18] and 'Supersett' [silverleaf rating = 1.04 + 0.25(density of immatures), $r^2 = 0.51$, SE slope = 0.059, df = 1, 18]. Silverleaf rating was significantly related to immature density for K26-4 [silverleaf rating = 0.134 + 0.15(density of immatures), $r^2 = 0.49$, SE slope = 0.036, df = 1, 18] but not for A24-10. Intercepts did not differ significantly from 0.

Trichome density of the abaxial leaf surface varied significantly with cultigen/accession ($F = 46.72$; df = 9, 160; $P < 0.0001$). Accessions of *C. ecuadorensis* were hairier than the cultigens (Table 2).

Very few whiteflies and parasitoids emerged from leaf disks, making difficult any assessment of levels of parasitism. Twelve whiteflies and 1 female *E. pergandiella* emerged from zucchini cultigens, 8 whiteflies and 1 female *Encarsia transvena* (Timberlake) emerged from yellow squash cultigens, and 3 whiteflies and 1 female *E. nigricephala* emerged from wild accessions.

Discussion

Squash silverleaf has been observed in all *Cucurbita* species grown commercially in Florida and the Caribbean region [*i.e., C. pepo*, *C. moschata*, and *Cucurbita maxima* Duch. ex Lam. (Simons et al. 1988, Maynard & Cantliffe 1989)]. Results of our field experiments indicate that the wild species, *C. ecuadorensis* and *C. martinezii*, are also susceptible to squash silverleaf. Silverleaf has not been observed, however, in watermelon (*Citrullus*), cucumber or melon (*Cucumis*), despite the fact that these plants are good hosts for *B. argentifolii*. The reason for the susceptibility of *Cucurbita* species to silverleaf disorder is not known.

Silverleaf disorder is thought to be a species-specific plant response to feeding by immature, but not adult, silverleaf whitefly (Yokomi et al. 1990, Costa et al. 1993). Silverleaf severity was linearly related to density of immature whiteflies feeding on *C. pepo* zucchini variety 'Ambassador' (Costa et al. 1993) and on acorn squash variety 'Table Ace' (Schuster et al. 1991). In our experiments, two zucchini breeding lines, A21-7 and Sunseeds 3, supported population levels of immature *B. argentifolii* similar to those on 'Elite' (Figs. 1, 3), yet never showed silverleaf symptoms (except for one A21-7 plant with a rating of 1) (Tables 3, 4). In these two breeding lines, density of immature whiteflies is obviously not related to silverleaf severity. Silverleaf rating was positively correlated with numbers of immature whiteflies on 'Elite' in the spring and fall. Two yellow squash breeding lines (A24-10 and K26-4) were often significantly less silvered than the susceptible variety 'Supersett', yet still suffered significant silvering in the spring (Table 3). In this case, linear relationships existed between silverleaf rating and density of immature whiteflies for 'Supersett' and the yellow squash breeding lines.

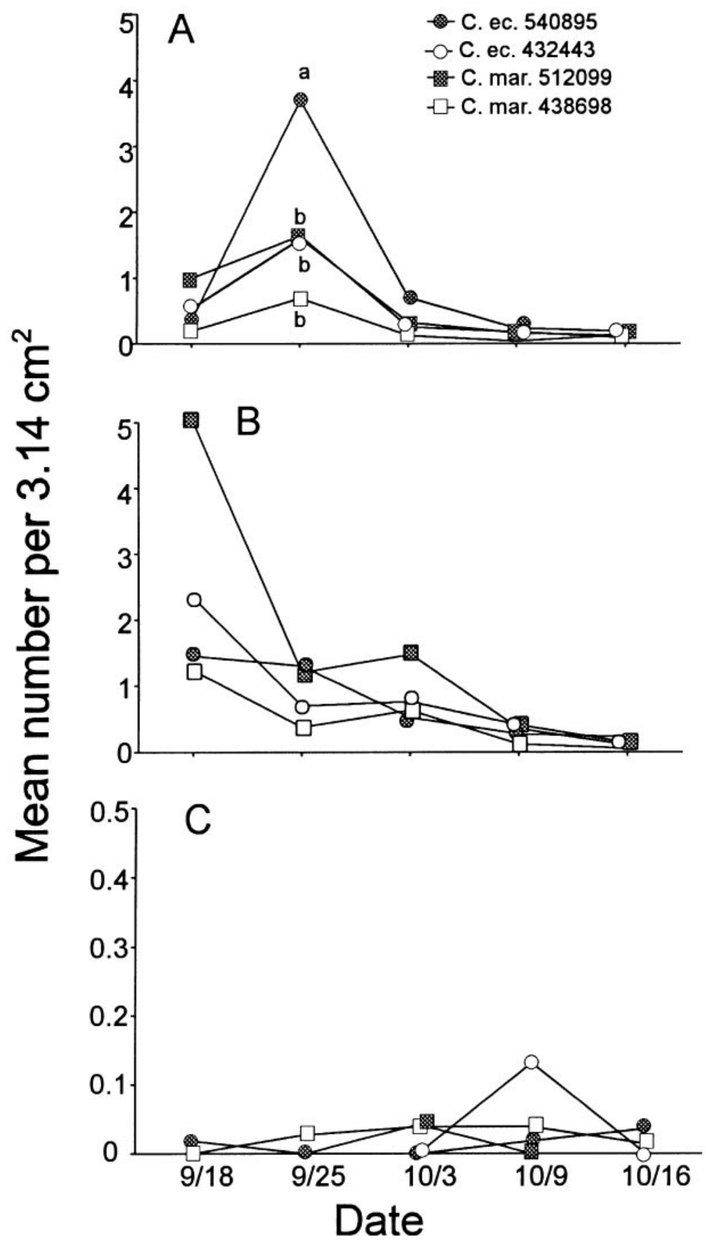

Figure 4. Mean numbers of silverleaf whitefly (A) eggs, (B) young nymphs, and (C) old nymphs on *C. ecuadorensis* (circles) and *C. martinezii* accessions (squares) during Fall 1995 in Leesburg, FL. Data points within a date followed by different letters differ significantly ($P = 0.05$; LSD test).

TABLE 4. SILVERLEAF RATING FOR CULTIGENS OF *C. PEPO* AND ACCESSIONS OF TWO WILD *CUCURBITA* SPECIES GROWN IN FALL 1995 IN LEESBURG, FL.

Type	Silverleaf Rating (Mean ± SEM)[1,2]				
Cultigen/Accession	Sept. 18	Sept. 25	Oct. 3	Oct. 9	Oct. 16
Zucchini					
'Elite'	0.81 ± 0.24cd	0.58 ± 0.14cde	0.19 ± 0.10cde	1.56 ± 0.15a	0.71 ± 0.13a
A21-7	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0b	0.0 ± 0.0b
Sunseeds 3	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0b	0.0 ± 0.0b
Yellow squash					
'Supersett'	2.58 ± 0.29b	2.40 ± 0.21a	1.11 ± 0.11b	1.29 ± 0.14a	0.82 ± 0.13a
A24-10	0.25 ± 0.09cd	0.79 ± 0.10bcd	0.06 ± 0.04de	0.38 ± 0.10b	0.04 ± 0.04b
K26-4	0.97 ± 0.20c	1.20 ± 0.11bc	0.20 ± 0.07cde	0.46 ± 0.11b	0.0 ± 0.0b
Wild species					
C. ecuadorensis PI540895	3.50 ± 0.39a	1.36 ± 0.25b	0.64 ± 0.17bc	1.36 ± 0.17a	0.07 ± 0.07b
C. martinezii PI512099	0.17 ± 0.17cd	0.67 ± 0.26cd	0.50 ± 0.20cd	0.25 ± 0.13b	0.0 ± 0.0b
C. martinezii PI438698	0.83 ± 0.28cd	0.39 ± 0.20de	0.17 ± 0.10cde	0.17 ± 0.08b	0.0 ± 0.0b
C. ecuadorensis PI432443	3.74 ± 0.33a	2.84 ± 0.24a	1.84 ± 0.16a	1.21 ± 0.18a	0.10 ± 0.07b

[1]Silverleaf rating scale—grade 0, green; grade 1, <25%; grade 2, 25-50%; grade 3, 50-75%; grade 4, 75-95%; grade 5, 95-100% silvering.
[2]Means within a column followed by different letters differ significantly ($P = 0.05$; LSD).

Leaf pubescence has been shown to influence whitefly oviposition on cotton (Butler et al. 1986, Wilson et al. 1993), soybean (McAuslane et al. 1996, in press), and wild cucurbitaceous species (McCreight & Kishaba 1991, Kishaba et al. 1992). In general, hairy varieties are preferred up to a certain level when hairiness begins to interfere with feeding and attachment of eggs to the leaf epidermis. Also, arrangement of hairs can influence resistance. The white-flowered gourd, *Lagenaria siceraria* (Molina) PI 432342, was resistant to *B. tabaci* even though the abaxial leaf surface averaged only 48.7 hairs per mm^2 compared to the susceptible *C. ecuadorensis* PI 540895 with 51.0 to 85.6 hairs per mm^2 (Kishaba et al. 1992). Among our wild accessions tested, *C. ecuadorensis* PIs 540895 and 432443 were significantly hairier (Table 2) and supported significantly larger populations of whiteflies (Figs. 2, 4) than the two *C. martinezii* accessions (PIs 512099 and 438698). Among the cultigens of *C. pepo* that we examined, the hairier yellow squash cultigens supported larger populations of whiteflies than the less hairy zucchini cultigens (Table 2, Figs. 1, 3). It is not known, however, whether these observations are due to cause-and-effect or are simply coincidental.

Parasitism was extremely low in both spring and fall field seasons. Parasitism of whiteflies in the fall in soybean (McAuslane et al. 1995), and in peanut (McAuslane et al. 1993) is regularly very high in northcentral Florida. Low levels of parasitism have been noted previously in melons and squash in Texas and California (summarized in Henneberry et al. 1995). Parasitism of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), by *Encarsia formosa* Gahan on hairy cucumber (382 hairs per cm^2) was less than on a less hairy cucumber variety (156 hairs per cm^2) (Hua et al. 1987). All of our varieties were hairier than the cucumber varieties which may explain the low levels of parasitism.

The exact mechanism of silverleaf induction is unknown. Manifestation of the symptoms was first associated with environmental stresses, such as drought and high light intensity (Burger et al. 1983, Paris et al. 1987, Simons et al. 1988). Later, it was realized that *B. argentifolii* was the causal agent but that water deficit could still exacerbate the condition (Paris et al. 1993c). Resistance to silvering in the zucchini breeding lines studied in these experiments may be due to drought tolerance. Silverleaf-like symptoms can be induced in cucurbit plants treated with plant growth bioregulators, and it is hypothesized that whitefly feeding may induce some form of hormonal imbalance, explaining the many color disturbances noticed with whitefly feeding (Yokomi et al. 1995). In addition to providing potentially useful silverleaf resistance to squash breeder, the zucchini breeding lines will make useful model systems with which to examine the effects of whitefly feeding on silverleaf induction.

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