Comparison of Silverleaf Whitefly–Induced and Chlormequat Chloride–Induced Leaf Silvering in *Cucurbita pepo*

R. K. Yokomi, Research Entomologist, **D. R. Jiménez,** Research Associate, USDA, ARS, U.S. Horticultural Research Laboratory, 2120 Camden Rd., Orlando, Fla. 32803-1419; **L. S. Osborne,** Associate Professor of Entomology, University of Florida, IFAS, Central Florida Research and Education Center, 2807 Binion Rd., Apopka 32703; and **J. P. Shapiro,** Research Entomologist, USDA, ARS, U.S. Horticultural Research Laboratory, 2120 Camden Rd., Orlando, Fla. 32803-1419

ABSTRACT

Yokomi, R. K., Jiménez, D. R., Osborne, L. S., and Shapiro, J. P. 1995. Comparison of silverleaf whitefly–induced and chlormequat chloride–induced leaf silvering in *Cucurbita pepo*. Plant Dis. 79:950-955.

Whitefly-mediated squash silverleaf is induced by the feeding of nymphs of the silverleaf whitefly, *Bemisia argentifolii,* but the mechanism involved in symptom expression is unknown. Several plant biochemical regulators were tested to determine whether they could mitigate expression of squash silverleaf in *Cucurbita pepo*. Application of chlormequat chloride, a gibberellic acid biosynthesis inhibitor, induced leaf silvering symptoms similar to those induced by the silverleaf whitefly in squash plants, cvs. Senator and Dixie, but not in cv. Small Sugar Pumpkin. Chlormequat chloride–induced silvering never extended over more than 80% of the upper leaf surface, compared with 100% for whitefly-induced silverleaf. Paclobutrazol, but not Alar, also produced leaf silvering symptoms. Chlormequat chloride treatment also resulted in internodal stem shortening, increased chlorophyll levels, and increased root and stem weight in Small Sugar Pumpkin and Senator but not in Dixie. Chlormequat chloride did not produce detectable double-stranded RNAs (dsRNAs) or changes in intercellular fluid proteins in any of the *C. pepo* cultivars tested. Silvered leaves from whitefly-infested plants, in contrast, had 15 to 40% lower chlorophyll levels, two induced intercellular leaf proteins, and some reductions in foliar and root biomass. No dsRNAs were detected in whitefly-silvered tissues or plants. Gibberellic acid applied after chlormequat chloride or paclobutrazol treatment resulted in less internodal shortening and decreased both chemical- and whitefly-induced leaf silvering. Chlormequat chloride–treated plants attracted greater whitefly oviposition and had more nymphs than untreated controls in greenhouse tests. These data suggest that leaf silvering induced by gibberellic acid biosynthesis inhibitors and by the silverleaf whitefly results from hormonally mediated alterations in the plant's physiology. Because the silverleaf whitefly also induces discoloration disorders in plants other than squash, hormonal inhibition may be a general component of whitefly phytotoxicity.

Additional keywords: Alar, *Bemisia tabaci*, disorder, sweetpotato whitefly

Leaf silvering of cucurbits, first described in Israel in 1987 (22), differs from silver-leaf mottling, which is controlled by a single dominant gene and occurs as patches of silver in the axils of veins (10, 24). Leaf silvering is developmentally reversible (new growth can be normal when silvering stimulus is absent) and can occur regardless of whether the affected cultivar possesses the silver-mottle gene. Burger et al. (5) described the physiological and cytological features of leaf silvering and concluded that it was a physiological disorder. Whitefly-induced squash silverleaf was first described in Florida in 1989 (19). The purported finding of double-stranded RNAs (dsRNAs) and increased RNA-dependent RNA polymerase activity in whitefly-mediated silvered tissue led Bharathan et al. (2,3) to suggest that the causal agent was a virus or viruslike agent either carried by or in the whitefly. Similar sized dsRNA bands were found in the sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), which induced leaf silvering but were not detected in silvered tissue (15,29). Yokomi (29) correlated the induction of leaf silvering with feeding by nymphs of sweetpotato whitefly and suggested that a toxicogenic factor was involved. This whitefly, which causes leaf silvering, is known as *B. tabaci*, Biotype B, and has now spread across the U.S., parts of the Caribbean, Israel, and Japan (16). Recently, Bellows et al. (1) suggested that this whitefly is a new species and proposed the name, silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring. The common name reflects one of its principal characteristics, the ability to induce leaf silvering in susceptible cucurbits.

Plant biochemical regulators have a variety of effects on growth and development of plants (6,17), such as modifying coloration and maturation time of foliage and fruit (30), as well as reducing infestation of some insects (6). The gibberellic acid biosynthesis inhibitor, chlormequat chloride (13), has been reported to inhibit whitefly growth and development (12). We observed that chlormequat chloride induced leaf silvering symptoms similar to those induced by silverleaf whitefly on *Cucurbita pepo* L. The ability to compare leaf silvering caused by a chemical with that caused by a whitefly offered an opportunity to characterize the mechanism involved in expression of leaf silvering. In this report, we present a comparison of leaf silvering induced by the silverleaf whitefly and by plant bioregulators.

MATERIALS AND METHODS

Insect colony. Silverleaf whitefly was collected from local populations that were causing serious problems in commercial greenhouses in central Florida (29). The colony was maintained at the U.S. Horticultural Research Laboratory, Orlando, Fla,. in a greenhouse on *C. pepo* cvs. Senator, Dixie (Asgrow Seed Co., Kalamazoo, Mich.), and Small Sugar Pumpkin (W. Atlee Burpee & Co., Warminster, Pa.). These cucurbits are susceptible to leaf silvering and served a dual purpose as host plant and indicator for the whitefly. Periodically, 10 to 20 individual whiteflies were homogenized and esterase allozyme patterns examined (8,18) to confirm that a homogeneous colony of the whitefly was maintained.

Plant bioregulator tests. Squash seeds were planted in 3.78-liter pots and 2- to 3-week-old seedlings with two expanded leaves were transferred to 0.46 m (wide) × 0.46 m (deep) × 0.76 m (tall) isolation

Present address of second author: Novo Nordisk Entotech Inc., Entomology Department, Plant Protection Division, 1497 Drew Ave., Davis, Calif. 95616-4880.

Mention of a trademark, warranty, propriety product, or vendor does not constitute a guarantee by the U.S. Department of Agriculture and does not imply its approval to the exclusion of the other products or vendors that may be suitable.

Corresponding author: Raymond K. Yokomi
E-mail: ryokomi@asrr.arsusda.gov

Accepted for publication 14 June 1995.

cages constructed of splined aluminum frames covered with monofilament nylon screen (300 mesh, Nitex, Aquatic Eco-Systems Inc., Apopka, Fla.). Chlormequat chloride (Cycocel, American Cyanamid, Wayne, N.J.) was sprayed on seedlings of Small Sugar Pumpkin, Senator, and Dixie to runoff at two treatment rates, 460 ppm and 920 ppm in water. Another treatment was continuous exposure to 50 adult whiteflies per unsprayed plant. Unsprayed and whitefly-free plants served as controls. Chlormequat chloride was applied twice at a 7-day interval by spray bottle. Treatments were replicated from three to 13 times. All experiments were maintained in a greenhouse with ambient sunlight and an average temperature of 25 to 27°C (maximum = 32°C; minimum = 20°C) and monitored daily.

Plants were harvested from 21 to 41 days after treatment exposure, separated into roots, stem, and leaves, and weighed. Leaf silvering (silver index) was graded visually on a 0 to 5 scale as follows: 0 = healthy, no symptoms; 1 = slight acropetal silvering of the veins and areoles; 2 = slight to moderate; 3 = moderate; 4 = moderate to severe; 5 = complete leaf blade silvering (16). Total number of silverleaf whitefly nymphs from infested plants were counted under magnification. Chlorophyll concentration was determined on 6-mm-diameter leaf disk samples (10 to 20 mg total) collected from four locations per leaf, extracted with N,N-dimethylformamide (1/100 wt/vol) as described by Moran (20) and Jiménez et al. (16). Leaves from all treatments were pulverized in liquid nitrogen with a mortar and pestle, extracted, purified, and electrophoresed for dsRNAs as described by Jiménez et al. (15). Leaf intercellular fluids were extracted and analyzed by electrophoresis as described in Jiménez et al. (16).

Gibberellic acid (ProGibb 4%, Abbott Laboratories Chemical and Agricultural Products Division, North Chicago, Ill.) at 10 ppm and 50 ppm Silwet Surfactant L-77 (Union Carbide Chemicals and Plastics Inc., Danbury, Conn.) in water was applied 24 h after application of plant bioregulators to determine the effect on leaf silvering. These tests also included paclobutrazol (Bonzi, Uniroyal Chemical, Middlebury, Conn.) at 31.7 ppm (0.78 ml per 100 ml), and daminozide (butanedioic acid mono [2,2-dimethylhydrazide]) (Alar) (B-Nine SP, Uniroyal Chemical) at 2,125 ppm (0.25 g per 100 ml). These plant bioregulators were sprayed onto 3-week-old plants to runoff.

Oviposition tests. The influence of chlormequat chloride treatment on whitefly oviposition was determined in two experiments. Test 1 was conducted in isolation cages with plants treated with chlormequat chloride at 920 ppm versus an unsprayed control. The cultivars tested included Small Sugar Pumpkin, Dixie, and Senator. Each cage contained four plants that were simultaneously exposed to 200 whitefly adults for the duration of the experiment. Test 2 was conducted in a small greenhouse infested with the whitefly and three chlormequat chloride treatments of the same cultivars not isolated in cages were compared. Chlormequat chloride was applied twice, 7 days apart: (i) at 920 ppm and 460 ppm for the first and second application, respectively; (ii) 920 and 920 ppm for the first and second application, respectively; and (iii) drench treatment at 460 ppm. Each treatment had 4 plants and oviposition was determined from the number of whitefly eggs and nymphs observed on 4 to 12 leaves per plant.

Statistical analysis. Statistical analyses were performed by general linear model procedures and by orthogonal contrasts

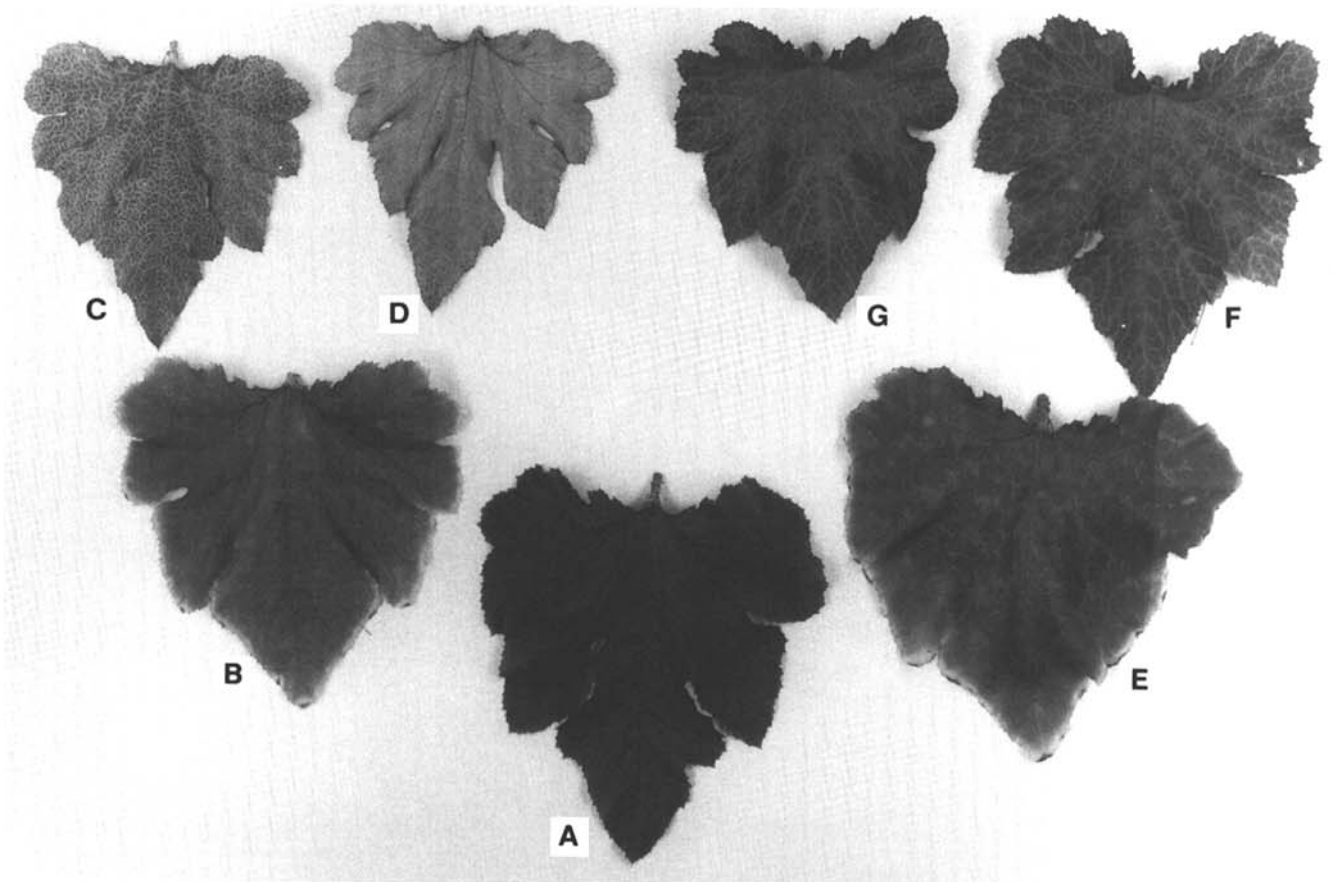

Fig. 1. Leaf silvering symptoms in *Cucurbita pepo* cv. Senator. **(A)** Control. **(B–D)** Silverleaf whitefly–induced squash silverleaf. **(B)** Leaf from whitefly-infested plant showing whitefly-induced chlorosis at leaf margin and at feeding site of the sessile nymph. **(C)** Network of venal chlorosis (grade 3 leaf silvering). **(D)** Complete silvering of the upper leaf surface. **(E–G)** Chlormequat chloride-induced leaf silvering. **(E)** Silvering starts in the main veins. **(F–G)** Silvering spreads across the interaxils of the main veins. Chlormequat chloride silvering resembled genetic silvering of cucurbits more than that associated with the whitefly.

with SAS software (SAS Institute, Cary, N.C.). Whitefly egg and nymph counts were normalized by transformation to log $(x + 0.5)$ values and subjected to analysis of variance.

RESULTS

Foliar and drench application of chlormequat chloride resulted in leaf silvering similar in appearance to whitefly-induced leaf silvering in Senator and Dixie squash (Fig. 1; Table 1). Foliar application of chlormequat chloride caused a chlorosis of leaf margins of treated leaves (Fig. 1E). This symptom was similar in appearance to the chlorosis at the feeding site induced by whitefly nymphs (Fig. 1B). New growth of treated plants had shorter internodes and leaf silvering appeared in leaves that emerged 3 days after application, paralleling the temporal development of whitefly-induced leaf silvering. Chlormequat chloride-induced leaf silvering symptoms first appeared along major veins and extended laterally from there, never extending over more than 80% of the leaf surface (Fig. 1 F,G). Although shortening of stem internodes persisted, silvering of the new leaves ceased as treated plants aged unless additional applications were made. Senator squash exhibited a mean silver index of 2.0 with the 920 ppm rate of chlormequat chloride, Dixie had a low silver index of 0.3, whereas Small Sugar Pumpkin had no leaf silvering (Table 1). The whitefly induced a silver index of 5 in all three cultivars tested (Table 1; Fig. 1D). In contrast to the plant regulator, whitefly leaf silvering began along small tertiary veins (yellowish vein netting) (Fig. 1C) and intensified to white to fill in between the major veins; silvering continued as long as the plant was infested with whiteflies.

Chlorophyll levels of chlormequat chloride–treated plants increased over the controls in Small Sugar Pumpkin ($P = 0.0057$) and Dixie ($P = 0.019$) but not in Senator ($P = 0.386$) (Table 1). Whitefly-induced leaf silvering was accompanied by loss of chlorophyll compared with the control in Senator (10.7 vs. 17.7 µg per 10 mg fresh tissue, whitefly vs. control, respectively; $P = 0.009$), but not significantly in Small Sugar Pumpkin (10.5 vs. 13.6 µg per 10 mg; $P = 0.11$), or Dixie (16.3 vs. 19.1 µg per 10 mg; $P = 0.291$) (Table 1). The effects of chlormequat chloride and whitefly infestation on vegetative weight varied. For Small Sugar Pumpkin, whiteflies significantly reduced root weights (4.4 vs. 6.0 g for the control), whereas chlormequat chloride increased leaf weights (8.8 and 7.7 vs. 6.0 g for chlormequat chloride at 460 ppm, chlormequat chloride at 920 ppm, and control, respectively) (Table 1). Whitefly infestation significantly reduced stem weight (61.1 g) vs. control (68.5 g), whereas chlormequat chloride significantly increased stem weight 80.3 and 82.5 vs. 68.5 g for chlormequat chloride at 460 ppm and 920 ppm vs. control, respectively. Few differences in weights were noted with Senator or Dixie squash. Some variation in cultivar response may have been due to cultivar-specific susceptibility and uneven density of developing whitefly populations.

Table 1. Comparison of chlormequat chloride-induced and silverleaf whitefly-induced leaf silvering in three cultivars of *Cucurbita pepo* ± SEM.

Treatment	Plants (no.)	Leaves (no.)	Whitefly nymphs (no.)	Silver index[w]	Avg. chlor. plant^{-1} (µg per 10 mg)	Weight (g) per plant			
						Root	Stem	Leaves	Total
Cucurbita pepo cv. Small Sugar Pumpkin[x]									
Control	8	172	0	0	13.6 ± 1.3	6.0 ± 1.0	68.5 ± 9.0	0.9 ± 0.09	75.9
Whitefly	7	174	9,283	1.2	10.5 ± 1.8	4.4 ± 0.7	61.1 ± 8.2	1.1 ± 0.2	66.6
Chlormequat chloride 460 ppm	8	143	0	0	16.1 ± 0.8	8.8 ± 1.6	80.3 ± 14.8	1.6 ± 0.2	90.1
Chlormequat chloride 920 ppm	8	136	0	0	19.1 ± 1.3	7.7 ± 1.5	82.5 ± 13.1	1.8 ± 0.09	91.1
Control vs whitefly[y]					NS	NS	**	NS	NS
Whitefly vs. chemical[y]					**	*	**	NS	NS
Chemical linear regression[y]					**	NS	**	NS	NS
Cucurbita pepo cv. Senator[x]									
Control	13	47	0	0	17.7 ± 2.0	4.5 ± 0.6	49.6 ± 8.0	1.5 ± 0.2	56.2
Whitefly	3	42	1,454	3.6	10.7 ± 1.1	5.0 ± 0.7	51.3 ± 11.3	2.0 ± 0.1	59.4
Chlormequat chloride 460 ppm	13	52	0	1.3	16.8 ± 1.0	7.4 ± 0.7	30.8 ± 4.8	1.8 ± 0.2	39.9
Chlormequat chloride 920 ppm	13	53	0	2.0	19.1 ± 1.3	8.5 ± 2.0	37.1 ± 9.2	2.1 ± 0.4	55.9
Control vs. whitefly[y]					**	NS	NS	NS	NS
Whitefly vs. chemical[y]					**	NS	NS	NS	NS
Chemical linear regression[y]					NS	*	NS	NS	NS
Cucurbita pepo cv. Dixie[z]									
Control	3	57	0	0	19.1 ± 1.1	12.6 ± 3.4	143.0 ± 45.2	2.2 ± 0.5	157.3
Whitefly	3	40	746	3.7	16.3 ± 2.4	7.7 ± 1.8	70.8 ± 27.1	2.2 ± 0.6	81.0
Chlormequat chloride 460 ppm	3	51	0	0	27.4 ± 2.2	8.2 ± 2.5	95.7 ± 46.8	1.9 ± 0.6	107.1
Chlormequat chloride 920 ppm	3	55	0	0.3	26.4 ± 0.7	6.5 ± 1.0	100.6 ± 34.0	1.9 ± 0.4	109.6
Control vs. whitefly[y]					NS	NS	NS	NS	NS
Whitefly vs. chemical[y]					**	NS	NS	NS	NS
Chemical linear regression[y]					*	NS	NS	NS	NS

[w] Silver index = leaf silvering symptoms where 0 = no silvering and 5 = 100% silvering.
[x] Plants harvested after 41 days.
[y] NS = not significant; * = $P \leq 0.05$; ** = $P \leq 0.01$ in each column.
[z] Plants harvested after 21 days.

Paclobutrazol also induced leaf silvering but without the initial phytotoxicity caused by chlormequat chloride (Fig. 2B), whereas Alar did not induce leaf silvering (Fig. 2A). Foliar application of gibberellic acid immediately following chlormequat chloride treatment attenuated stem internode shortening and reduced plant bioregulator–induced leaf silvering from 1.3 to 0.4 and 2.0 to 1.4 for chlormequat chloride at 460 ppm and 920 ppm, respectively (Table 2; Fig. 2C). Gibberellic acid also reduced whitefly-induced leaf silvering somewhat from a rating of 3.6 to 2.9 (Table 2).

No dsRNAs were found in plant bioregulator–induced silvered plants. Leaf intercellular fluids of bioregulator-silvered plant tissue exhibited the same protein profile as the controls and did not express the two proteins (M_r 31,000 and 70,000) found in leaf intercellular fluids of whitefly-infested leaves expressing leaf silvering (16).

All three *C. pepo* cultivars treated with chlormequat chloride attracted slightly greater oviposition from the silverleaf whitefly in test 1 ($P = 0.073$ and 0.079, for eggs and eggs + nymphs, respectively) compared with controls (Table 3). No interactions between treatments and cultivars were found, thus means between cultivars were combined. These observations were confirmed in test 2. Chlormequat chloride applied as a drench showed the greatest affect ($P = 0.05$) (Table 3). In addition, the whitefly preferred to oviposit on Small Sugar Pumpkin over Dixie or Senator regardless of treatment.

DISCUSSION

Although leaf silvering is of unknown etiology, it appears to be a physiological plant response induced specifically by the silverleaf whitefly but not by other whiteflies (15,16,29) including the sweetpotato whitefly. Paris et al. (23) indicated the leaf silvering in Florida and Israel were identical and that silvering was more severe when plants exposed to sweetpotato whitefly (B biotype) are further subjected to low soil moisture. Bharathan et al. (2,3) claimed to find distinctive dsRNAs in whitefly-induced silvered tissue. We have not detected these dsRNAs from leaf silvered plants or tissue free of nymphs or adults of the silverleaf whitefly but find them in the whitefly and find other dsRNAs from saprophytic fungi associated with whitefly honeydew (15,29). Our findings that chlormequat chloride and paclobutrazol could induce leaf silvering without dsRNAs is further evidence that leaf silvering can occur as a physiological disorder and is not necessarily a direct result of a virus or viruslike agent.

Although phenotypically similar, plant bioregulator–induced and whitefly-induced leaf silvering were accompanied by different physiological responses. Foliar and root weight decline and altered leaf intercellular fluid proteins, components of whitefly-induced leaf silvering (16), were absent in plant bioregulator–induced silvering. Gibberellic acid reduced chlormequat chloride–induced and paclobutrazol-induced leaf silvering and also reduced expression of leaf silvering in plants infested with silverleaf whiteflies. Chlormequat chloride and paclobutrazol are gibberellic acid biosynthesis inhibitors that affect two different enzyme systems (4,13), whereas Alar does not inhibit gibberellin biosynthesis. Plant growth retardants can affect other processes such as sterol biosynthesis (11). Our results suggest that plant bioregulator silvering and whitefly-induced leaf silvering result from similar hormone-mediated alterations in growth and development. Other stress factors, such as low soil moisture (5,22,23) or high light intensity (7), may also influence leaf silvering expression. Because the silverleaf whitefly also induces discoloration disorders in other plants such as carrot light root disease

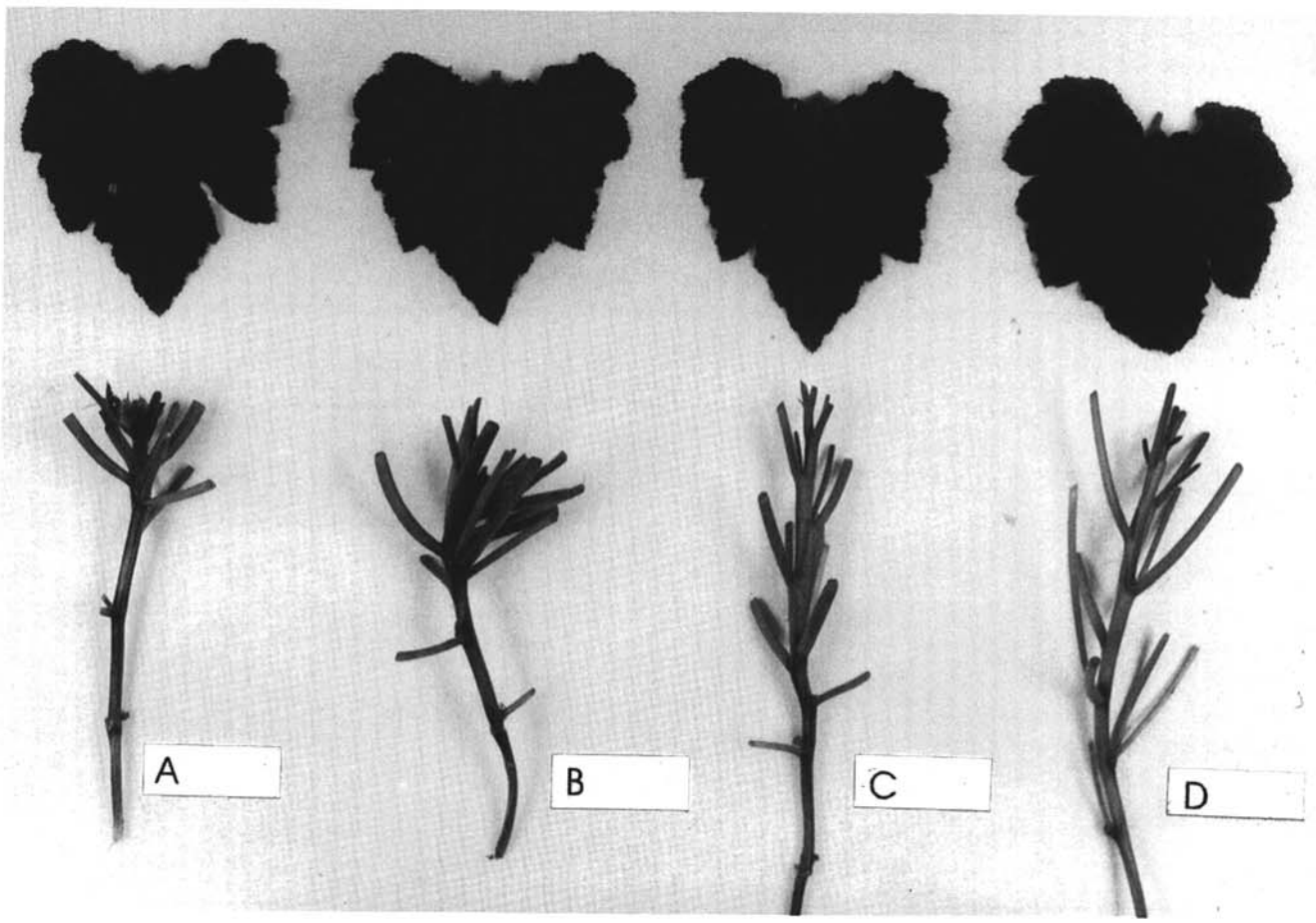

Fig. 2. Effects of plant biochemical regulator application to *Cucurbita pepo* cv. Senator. **(A)** Alar caused shortening of the internodes but did not induce silvering. **(B)** Paclobutrazol-induced leaf silvering and internode shortening. **(C)** Application of gibberellic acid eliminated silvering in paclobutrazol-treated plants and attenuated the internodal stunting. **(D)** Control plant.

and cole crop white-streaking (9), *Crossandra* (14), and tomato irregular ripening (26), hormonal inhibition may be a non-host-specific component of whitefly phytotoxicity. Whether this effect is mediated by a translocatable component of whitefly saliva or by an elicitor released by damaged plant cells is unknown.

In most cases when chlormequat chloride is applied to crop plants, populations of sap-sucking arthropods are reduced (12, 21,27,28). In contrast, Scheurer (25) observed an increase in aphids after chlormequat chloride treatment. In general, chlormequat chloride treatment has reduced insect pests on plants, possibly due to altered plant chemistry. In our study, oviposition of silverleaf whitefly increased approximately 1 week following chlormequat chloride treatment. However, chlormequat chloride may deter actual whitefly feeding as has been demonstrated for the greenhouse whitefly, *Trialeurodes vaporariorum* Westw. (12). The variation in insect population levels in response to plant regulator treatment suggests that there is a close interaction between the insect and host plant. Any changes in the biochemistry or physiology of the plant will likely affect the insect.

ACKNOWLEDGMENTS

The authors thank Ana Maria Rodriguez and George Q. Perrin (USDA, ARS, U.S. Horticultural Research Laboratory, Orlando, Fla. 32803) and Margarite Wettstein and Kathryn Houben (Univ. Florida, IFAS, Central Florida Research and Education Center, Apopka 32703) for technical assistance; Victor Chew (USDA, ARS, South Atlantic Area, Dept. of Statistics, University of Florida, Gainesville 32611) for assistance in the statistical analysis of the data. We are indebted to B. C. Campbell, D. L. Hendrix, C. A. Powell, P. J. Stoffella, and P. A. Stansly for critically reviewing earlier drafts of this manuscript.

LITERATURE CITED

1. Bellows, T. S., Jr., Perring, T. M., Gill, R. J., and Headrick, D. H. 1994. Description of a species of *Bemisia* (Homoptera: Aleyrodidae). Ann. Entomol. Soc. Am. 87:195-206.
2. Bharathan, N., Graves, W. R., Narayanan, K. R., Schuster, D. J., Bryan, H. H., and McMillan, R. T., Jr. 1990. Association of double-stranded RNA with whitefly-mediated silvering in squash. Plant Pathol. 39:530-538.
3. Bharathan, N., Narayanan, K. R., and McMillan, R. T., Jr. 1992. Characteristics of sweetpotato whitefly-mediated silverleaf syndrome and associated double-stranded RNA in squash. Phytopathology 82:136-141.
4. Britz, S. J., and Saftner, R. A. 1987. Inhibition of growth by ancymidol andtetcyclacis in the gibberellin-deficient *dwarf-5* mutant of *Zea mays* L. and its prevention by exogenous gibberellin. J. Plant Growth Regul. 6:215-219.
5. Burger, Y., Schwartz, A., and Paris, H. S. 1988. Physiological and anatomical features of the silvering disorder of cucurbits. J. Hortic. Sci.. 63:635-640.
6. Campbell, B. C. 1988. The effects of plant growth regulators and herbicides on host plant quality to insects. Pages 205-247 in: Plant Stress-Insects Interaction. E. A. Heinrichs, ed. John Wiley & Sons, New York.
7. Cohen, S., Duffus, J. E., and Liu, H. Y. 1992. A new *Bemisia tabaci* biotype in the southwestern United States and its role in silverleaf of squash and transmission of lettuce infectious yellows virus. Phytopathology 82:86-90.
8. Costa, H. S., and Brown, J. K. 1991. Variation in biological characteristics and esterase patterns among populations of *Bemisia tabaci*, and the association of one population with silverleaf symptom expression. Entomol. Exp. Appl. 61:211-219.
9. Costa, H. S., Ullman, D. E., Johnson, M. W., and Tabashnik, B. E. 1993. Association between *Bemisia tabaci* density and reduced growth, yellowing and stem blanching of lettuce and kai choy. Plant Dis. 77:969-972.
10. Coyne, D. P. 1970. Inheritance of mottled-leaf in *Cucurbita moschata* Poir. HortScience 5: 226-227.
11. Douglass, T. J., and Paleg, L. G. 1972. Inhibition of sterol biosynthesis by 2-isopropyl-4-dimethylamino-5-methylphenyl-1-piperidine carboxylate methyl chloride in tobacco and rat liver preparations. Plant Physiol. 49:417-420.
12. Fischer, S. J., and Shanks, J. B. 1979. Whitefly infestation on chrysanthemum and poinsettia treated with plant and insect growth regulators. J. Am. Soc. Hort. Sci. 104:829-830.
13. Hedden, P., and Graebe, J. E. 1985. Inhibition of gibberellin biosynthesis by paclobutrazol in cell-free homogenates of *Cucurbita maxi-*

Table 2. Effect of gibberellic acid spray on expression of silverleaf whitefly-induced and chlormequat chloride–induced leaf silvering on *Cucurbita pepo* cv. Senator

	No gibberellic acid[w]		Gibberellic acid[x]	
Treatment	**No. of plants observed**	**Leaf silvering index[y]**	**No. of plants observed**	**Leaf silvering index[y]**
Control	13	0	8	0
Whitefly	3	3.6	7	2.9
Chlormequat chloride 460 ppm	13	1.3	11	0.4[z]
Chlormequat chloride 920 ppm	13	2	8	1.4

[w] Data collected from two separate experiments.
[x] Plants harvested after 23 days.
[y] Silver index = leaf silvering symptoms where 0 = no silvering and 5 = severe silvering.
[z] Plants harvested after 35 days.

Table 3. Evaluation of chlormequat chloride treatment on three *Cucurbita pepo* cultivars on oviposition and nymph counts of the silverleaf whitefly, *Bemisia argentifolii*, ± SEM

		Cucurbita pepo cultivar[x]							
		Avg. no. eggs per leaf				Avg. no. eggs + nymphs per leaf			
Treatment	**No. observed**	**Small Sugar Pumpkin**	**Dixie**	**Senator**	**Total**	**Small Sugar Pumpkin**	**Dixie**	**Senator**	**Total**
Test 1[y]									
Control	10	104.7 ± 58.8	32.9 ± 13.9	69.7 ± 38.1	70.3 ± 24.4	187.2 ± 78.4	94.6 ± 64.3	101.4 ± 58.7	129.6 ± 39.0
Chlormequat chloride (920 ppm)	12	207.4 ± 97.4	237.9 ± 122.4	108.2 ± 70.8	186.7 ± 57.1 $P = .073$	315.3 ± 137.5	343.6 ± 154.0	155.3 ± 96.6	274.7 ± 76.1 $P = .079$
Test 2[z]									
Control	4	48.0 ± 26.1	131.0 ± 94.9	20.8 ± 9.3	66.6 ± 33.0 b	313.5 ± 193.0	244.8 ± 110.7	53.3 ± 20.8	203.8 ± 75.1 b
Chlormequat chloride (920/460 ppm)	4	598.8 ± 444.1	30.3 ± 14.1	56.5 ± 43.2	228.5 ± 156.1 ab	813.5 ± 525.5	121.0 ± 22.6	107.3 ± 53.3	347.3 ± 187.9 ab
Chlormequat chloride (920/920 ppm)	4	148.3 ± 69.2	276.3 ± 70.3	46.3 ± 10.2	156.9 ± 41.2 a	334.0 ± 42.9	410.0 ± 67.7	112.3 ± 29.4	285.4 ± 46.0 a
Chlormequat chloride drench (460 ppm)	4	285.0 ± 105.6	76.5 ± 30.1	100.5 ± 38.8	154.0 ± 45.0 a	584.8 ± 206.8	241.8 ± 73.9	245.8 ± 44.4	357.4 ± 83.0 a
	All	270.0 ± 116.5 a	128.5 ± 36.4 ab	56.0 ± 15.3 b		511.4 ± 143.8 a	254.4 ± 43.0 a	129.6 ± 25.3 b	

[x] Actual counts are given but P values are from analysis of variance using $\log(x + 0.5)$.
[y] Test 1 was conducted in cages in a greenhouse and harvested after 21 days.
[z] Test 2 was conducted on uncaged test plants maintained in a greenhouse infested with silverleaf whiteflies and harvested after 21 days. No treatment x cultivar interactions were found. Means associated with the same letter within a column are not significantly different ($P \leq 0.05$) by Duncan's test.

ma endosperm and *Malus pumila* embryos. J. Plant Growth Regul. 4:111-122.
14. Hoelmer, K. A., Osborne, L. S., and Yokomi, R. K. 1991. Foliage disorders in Florida associated with feeding by sweetpotato whitefly. Fla. Entomol. 74:162-166.
15. Jiménez, D. R., Shapiro, J. P., and Yokomi, R. K. 1994. Biotype-specific expression of dsRNA in the sweetpotato whitefly. Entomol. Exp. Appl. 70:143-152.
16. Jiménez, D. R., Yokomi, R. K., Mayer, R. T., and Shapiro, J. P. 1995. Cytology and physiology of silverleaf whitefly-induced squash silverleaf. Physiol. Mol. Plant Pathol. 46:227-242.
17. Jung, J. 1985. Plant bioregulators: overview, use, and development. Pages 95-107 in: Bioregulators for Pest Control. P. A. Hedden, ed. Am. Chem. Soc. Symp. Ser. 276. Washington, D.C.
18. Liu, H. Y., Cohen, S., and Duffus, J. E. 1992. The use of isozyme patterns to distinguish sweetpotato whitefly (*Bemisia tabaci*) biotypes. Phytoparasitica 20:187-194.
19. Maynard, D. N., and Cantliffe, D. J. 1989. Squash silverleaf and tomato irregular ripening: New vegetable disorders in Florida. Fla. Coop. Ext. Ser., IFAS, VC-37.
20. Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with N,N-dimethylformamide. Plant Physiol. 69: 1376-1381.
21. Osborne, L. S., and Chase, A. R. 1990. Chlormequat chloride growth retardant reduces spider mite infestations of *Hibiscus rosa-sinensis*. HortScience 26:648-650.
22. Paris, H. S., Nerson, H., and Burger, Y. 1987. Leaf silvering in *Cucurbita*. Can. J. Plant Sci. 67:593-598.
23. Paris, H. S., Stoffella, P. J., and Powell, C. A. 1993. Sweetpotato whitefly, drought stress, and leaf silvering of squash. HortScience 28: 157-158.
24. Scarchuk, J. 1954. Fruit and leaf characters in summer squash. J. Heredity 45:295-297.
25. Scheurer, S. 1976. The influence of phytohormones and growth regulating substances on insect development processes. Symp. Biol. Hung. 16: 255-259.
26. Schuster, D. J., Mueller, T. F., Kring, J. B., and Price, J. F. 1990. Relationship of the sweetpotato whitefly to a new tomato fruit disorder in Florida. HortScience 12:1618-1620.
27. Singer, M. C., and Smith, B. D. 1976. Use of the growth regulator chlormequat chloride to control the aphid *Hyperomyzus lactucae* on black currants. Ann. Appl. Biol. 82:407-414.
28. van Emden, H. F. 1969. Plant resistance to *Myzus persicae* induced by a plant regulator and measured by aphid relative growth rate. Entomol. Exp. Appl. 12:125-131.
29. Yokomi, R. K., Hoelmer, K. A., and Osborne, L. S. 1990. Relationships between sweetpotato whitefly and the squash silverleaf disorder. Phytopathology 80:895-900.
30. Yokoyama, H., and Keithly, J. H. 1989. Chemistry of bioregulatory agents: Impact on food color. Pages 65-70. in: Quality Factors of Fruits and Vegetables: Chemistry and Technology. J. J. Jen, ed. ACS Symposium Series No. 405.