Archives of Insect Biochemistry and Physiology 51:151–169 (2002)

Multitrophic Interactions of the Silverleaf Whitefly, Host Plants, Competing Herbivores, and Phytopathogens

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Our laboratory found that silverleaf whitefly (SLW; *Bemisia argentifolii* Bellows & Perring) feeding alters host plant physiology and chemistry. The SLW induces a number of host plant defenses, including pathogenesis-related (PR) protein accumulation (e.g., chitinases, β-1,3-glucanases, peroxidases, chitosanases, etc.). Induction of the PR proteins by SLW feeding occurs in various plant species and varieties. The extent and type of induction is dependent on a number of factors that include host plant growing conditions, the length of time the host plant is exposed to SLW feeding, the plant variety, and SLW population densities. The appearance of PR proteins correlates well with reduced infestations of conspecific insect herbivore competitors. Greenhouse and field experiments in which herbivore competitors (cabbage looper, *Trichoplusia ni*; leaf miner, *Liromyza trifolii*) were placed on plants previously exposed to SLW feeding demonstrated behavioral differences (oviposition, feeding preferences) and reduced survival rates and development times of these insects. The interaction was asymmetrical, i.e., SLW infestations of plants previously exposed to leaf miners had little or no effect on SLW behavior (oviposition). Induction of plant-defensive proteins by SLW feeding was both local (at the feeding site) and systemic (uninfested leaves distant to the feeding site). There are interactions between diseases such as tomato mottle virus (ToMoV; a geminivirus) and the host plant and SLW. PR proteins were induced in tomato plants infected with ToMoV much as they were via non-viruliferous SLW feeding. The presence of ToMoV in tomato plants significantly increased the number of eggs produced by SLW females. Experiments using tomato plants, powdery mildew (PM), and tobacco mosaic virus (TMV) show that whitefly infestations can affect plant pathogen relationships but the effects vary among pathogen types. Enzyme analyses prior to pathogen inoculation showed that whitefly treatment significantly increased the activities of foliar chitinase and peroxidase. Evaluation of pathogen growth 3 weeks after inoculation showed that whitefly feeding significantly reduced the incidence of PM. However, TMV levels evaluated by ELISA were not significantly affected by whitefly feeding. Six weeks after inoculation with pathogens, the chitinase and peroxidase activities were still elevated in plants initially fed on by whiteflies but continuing pathogen infection had no effect on these enzymes. The possibility that geminivirus infection and/or SLW infestations isolate the host plant for the selected reproduction of the virus and the insect is discussed. Multitrophic cascade effects may contribute to the successful eruptive appearance of SLW on various crops, ranking them as a major pest. They may explain the general observation that when SLW infest a host plant there are few if any competing insect herbivores and pathogens found in the host. However, the results indicate that certain SLW-virus relationships could be mutualistic. Arch. Insect Biochem. Physiol. 51:151–169, 2002.

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Received 2 May 2002; Accepted 10 September 2002

Published 2002 Wiley-Liss, Inc.
DOI: 10.1002/arch.10065
Published online in Wiley InterScience (www.interscience.wiley.com)

INTRODUCTION

Since its introduction into the United States in 1986, the silverleaf whitefly (*Bemisia argentifolii* Bellows & Perring; SLW) has been of widespread concern to growers of many different crops throughout the United States (Faust, 1992; Henneberry et al., 1993; Perring, 1996; Gerling and Mayer, 1996). The pest causes crop damage by vectoring a number of plant pathogens (more than 60 different viruses; Moffat, 1999; Polston and Anderson, 1997). Phytotoxicity and several plant disorder–related problems resulting from feeding include squash silverleaf (Maynard and Cantliffe, 1989), chlorosis (Osborne, 1988; Osborne et al., 1990), and tomato irregular ripening (Schuster et al., 1996; Shapiro, 1996).

The exotic SLW displaced *B. tabaci* when it was introduced in the United States (Bellows et al., 1994; Reitz and Trumble, 2002). Displacement may have been caused by a greater reproductive capacity of SLW on a broad host plant range and more aggressive courting behaviors of SLW males (Reitz and Trumble, 2002). Competitive displacement by SLW of other sucking insects (e.g., leafhoppers and aphids) may be greatly influenced by insecticide applications (Patil, 1996). Because of the broad host plant range of SLW (more than 500 host plants known), there are numerous possibilities for host plant–mediated interactions with other herbivores. Interspecies competition and displacement may be mediated by various factors that shift the balance of resources in favor of SLW (Reitz and Trumble, 2002). In this study, we focus our attention on plant-insect interactions and the correlation of these effects caused by whitefly feeding on other competing insect herbivores. Compared to the body of knowledge available for aphid-host plant interactions and interspecies competition (Walling, 2000), little is known about whiteflies.

Like many other homopterans, whiteflies use interlocking mouthparts (maxillary stylets) to penetrate sieve elements of the phloem of the host plant (Rosell et al., 1995). Exchange of fluids between the insect and the host plant occurs through a salivary canal that transports two types of saliva (viscous saliva forming a salivary sheath around the inserted stylets, and watery saliva that is thought to lubricate the stylet penetration; Cohen et al., 1998) into the plant and a food canal that transports the host plant phloem sap into the insect. It is this exchange of fluids that allows transmission of viruses from the SLW vector into the plant and also SLW-derived substances that cause plant disorders.

The exchange of fluids and associated processes during feeding may activate and/or deactivate plant resistance systems. A number of reviews have been written regarding the effects of plant-insect interactions as they pertain to herbivory (Bernays and Chapman, 1994; Constabel, 1999; Felton and Eichenseer, 1999; Rhoades, 1979; Stout and Bostock, 1999; Walling, 2000). Karban and Baldwin (1997) define induced responses as being any change in the host plant that results from damage. Induced resistance (negative effect on the herbivore *sensu* Karban and Baldwin, 1997) can result from increased levels of putative defensive primary and secondary plant metabolites. For example, pathogenesis-related (PR) proteins are produced in response to a number of stresses (including pathogen infection, herbivory, nematodes, wounding, etc.) to the plant and are thought to play a role in plant defense and systemic acquired resistance (SAR) to pathogens (Van Loon et al., 1994; Kombrink and Somssich, 1997). However, it should be noted that there is some evidence suggesting that PR proteins are not always causal of or associated with SAR (Glazebrook, 1999). Manipulation of induced resistance (a term used to describe resistance to insect herbivores) and SAR can be achieved through the use of elicitors (Farmer and Ryan, 1990; Baldwin et al., 1998; Inbar et al., 1997; Lyon and Newton, 1999; Ciba-Geigy, 1995). Plants may develop either specific or broad responses to stresses and in the latter case the responses may have overlapping effects and exhibit "crosstalk" (Stout and Bostock, 1999; Walling, 2000). Likewise, application of chemical elicitors may also result in broad overlapping effects on pathogens and insect herbivores (Inbar et al., 1997). Underwood (1999) discussed the possibilities that induced resistance can affect insect herbivore population dynamics.

Our approach was to investigate SLW-plant interactions in a multitrophic ecological framework. Specifically, we asked if insect herbivores manipulate plant resistance to their advantage to reduce interspecies competition and whether or not induced resistance resulting from herbivory has overlapping effects on the incidence of diseases. Here we investigate the effects of SLW feeding on other possible competing herbivores and pathogen infection. We also examine the effect of a geminivirus (tomato mottle virus; ToMoV) on the host plant and on the SLW vector.

MATERIALS AND METHODS

Insects

Colonies of *B. argentifolii* were maintained in greenhouses on collards (*Brassica* sp.) and tomatoes (*Lycopersicon esculentum*). The whiteflies were determined to be free of pathogenic viruses by extended plant monitoring for disease symptoms. Viruliferous whiteflies were needed for experiments involving ToMoV; confirmation of SLW infection with ToMoV prior to infestation of healthy host plants was by PCR analysis (Sinisterra et al., 1999). Leafminers (*Liromyza trifolii*, Burgess) were obtained from a colony maintained on cowpea (*Vigna sinensis*, Stickm.) since 1983 at the CFREC, Sanford, Florida (Inbar et al., 1999a). Corn earworm (*Helicoverpa zea*, Boddie) and cabbage looper (*Trichoplusia ni*, Hübner) larvae were obtained from the USDA, ARS, CMAVE, Gainesville, FL, where they had been maintained on artificial diets.

Plants

Collards used in experiments were *Brassica* sp. and tomato cultivars were either Lanai or Agriset (Mayer et al., 1996; Inbar et al., 1999a,b). Generally the plants were 4–6 weeks old and grown in 5.7–10.1-cm pots with Metro Mix 500 growing medium (Grace-Sierra, California) and received varying amounts of fertilizer depending on the experiments conducted. Collard plants were initially treated with fungicide (0.4 g/L Bayleton, Bayer Corp., Kansas City, MO). Details of specific treatments are listed in the cited references. Numbering of leaves on tomato plants started with the oldest leaf (lowest on the plant) being number 1 to the youngest leaf (highest leaf on the plant) for the data reported here.

Experiments With SLW, Cabbage Loopers, Leafminers, Corn Earworms, and ToMoV

Specific information on the experimental design involving whiteflies and cabbage loopers, leafminers, corn earworm, ToMoV, and host plant-insect-pathogen interactions are given in Mayer et al. (1996), Inbar et al. (1997, 1999a,b, 2001a,b), and McKenzie et al. (2002) and include both laboratory and field experiments.

Experiments on Effects of SLW Infestations on Disease Incidence

Experiments were also conducted to determine if SLW infestations had any effects on the incidence of phytopathogen infection. Florida Lanai tomatoes were grown from seed in 10-cm-diameter pots containing steamed Metro Mix 500 growing medium. Plants were grown in four fabric cages on a greenhouse bench in ambient light, fertilized two times a week with a 50% solution of Peters Professional™ fertilizer for tomatoes (9-45-15 N-P-K), and watered regularly. Just prior to whitefly treatment, when most plants were producing the third true leaf, half of the plants in each cage were randomly selected for transfer to a second cage paired with the first.

One cage in each of the four pairs was randomly assigned to receive whiteflies. Due to low population sizes of the whitefly colonies, small numbers of whitefly adults were added repeatedly to assigned cages starting on day 19 post-germination. A final 360 adults were added to the assigned cages 32 d post-germination, giving a total of 720 adults per cage, or 60 adults per plant. By this time the plants had four true leaves.

Admire™ 2F (Imidacloprid; 1-[(6-chloro-3-pyridinyl)methyl]-N-nitro-2-imidazolidnimine; Bayer

Corporation, Kansas City, MO) was applied according to the manufacturer's instructions to all plants to kill insects on day 54, i.e., 5 weeks after whiteflies were first introduced to cages when the plants were 19 days old. The next day, the largest leaflet proximal to the terminal leaflet on the second, third, and fourth leaves below the lowest reproductive structures (flowers) on 8 of the 12 plants was removed and rinsed with water for analyses.

Following sampling for enzyme and protein measurements, the plants were transferred to another greenhouse for inoculation with pathogens. SLW-treated and control plants from paired cages were intermixed as a group on the greenhouse bench, giving four groups of uncaged plants. The treatments (water; powdery mildew, *Erysiphe cichoracearum*, PM; tobacco mosaic virus, TMV) were randomly assigned to the plants in each group (8 plants per group were used). To inoculate plants, a cotton swab was saturated with sap from TMV-infected tobacco, a spore suspension of mildew in water from a field tomato, or water and rubbed on three young leaves of each plant.

Plants were evaluated three times at weekly intervals for disease progression and statistical analysis of the data is reported for the last evaluation (plants were 77 days old). PM was evaluated using a disease rating system with 0 = no detectable disease, 1 = detectable disease, 2 = >50% leaves infected, 3 = 100% of leaves infected. TMV (for control and inoculated plants) was evaluated by ELISA (Clark and Adams, 1977) using a polyclonal antibody to TMV that was prepared in rabbits. Values for disease incidence from the two plants within groups receiving the same whitefly-pathogen combination were averaged, giving a total of four replicates per treatment. Three weeks later, the plants were harvested as above and were again assayed for protein and enzymes, and dry mass was recorded for the vegetative shoot and fruit.

Statistical Analyses

Specifics of statistical analyses of data involving whiteflies and cabbage loopers, leafminers, corn earworm, ToMoV, and host plant-insect-pathogen interactions are given in Inbar et al. (1997, 1999a,b, 2001a,b) and McKenzie et al. (2002). For experiments determining the effects of SLW infestations on phytopathogen infections, total protein, chitinase, β-1,3-glucanase, and peroxidase levels were determined before and after inoculation with pathogens and were analyzed in separate MANOVAs. Paired cages were treated as a random block effect with whitefly, pathogen, and their interaction as fixed experimental factors. Although plants had not yet been challenged with pathogens at the first sampling, pathogen was included as an effect to confirm that protein induction was neutral with respect to this factor prior to inoculation. Significant MANOVA tests were followed by univariate tests and differences among least squares means were examined using Tukey adjustment for multiple comparisons. Dry vegetative shoot mass and fruit mass were similarly analyzed by MANOVA.

Disease rating was analyzed by two-way ANOVA with SLW (no, yes), pathogen (PM, TMV), and their interaction as fixed effects. A significant interaction was tested with the Tukey adjustment for multiple comparisons. Due to the small sample size (n = 16) and nature of the rating system for PM, the data set did not meet all assumptions for ANOVA. Consequently, interpretation of effects of SLW infestation on pathogen disease rating must be viewed with caution.

Biochemical Analyses

Methods used for preparation of leaf samples for protein/enzyme analyses have been reported in Mayer et al. (1995, 1996) and Inbar et al. (1999b). Chitinase assays followed the colorimetric method of Sawborowski et al. (1993) using a dye-labeled chitin. Lysozyme measurements were via turbidimetry using suspensions of *Micrococcus lysodeikticus* (Sigma, St. Louis, MO) according to the Sigma technical bulletin. Chitosanase activities were determined according to Osswald et al. (1992, 1993) using solubilized shrimp chitosan and are reported as nmol GlcN (glucosamine). β-1,3-Glucanase was after the method of Abeles and Forrence (1970) and reported in moles Glc (glucose). Peroxidase activity was analyzed according to the method

given in the Worthington Enzyme Manual (Worthington, 1978). All values are presented as the means ± SE. Enzyme values for control (no SLW) and SLW-infested plants are reported for every experimental setting and used as a measure of infestation effects.

RESULTS

SLW Induction of PR Proteins

Tomato plants infested with SLW had elevated levels of PR-proteins after 2 weeks of feeding (Table 1; Mayer et al., 1996). β-1,3-Glucanase, chitinase, and peroxidase activities were significantly increased when calculated either on a per mg protein or total activity basis. Foliar protein decreased in this experiment and lysozyme activity was not detected. The effects on activity of chitosanases were not significant. These results were confirmed via Western blots using antisera for tomato chitinase and β-1,3-glucanase (data not shown). The tomato PR proteins P2 and P4 were also induced as evidenced by Western blotting (Mayer et al., 1996); these proteins have no known enzymatic activity.

The effects of SLW feeding on chitinase, β-1,3-glucanase, and foliar protein over time can be seen in Figure 1. Induction of chitinase and β-1,3-glucanase was observed within 3 days post-infestation. Induction appeared to peak at about 21 days. At day 26 of SLW exposure, the plants were washed with Safer's insecticidal soap to remove the whiteflies. The activity levels of chitinase and β-1,3-glucanase fell to control levels within 2 weeks after the whiteflies were removed. Foliar protein levels were varied throughout the experiment; SLW feeding had no clear effect on foliar protein.

Interactions of SLW With Competing Herbivores

SLW vs. Leafminer. Experiments were conducted to determine the effects of early SLW infestations on leafminer (*L. trifolii*) performance on tomatoes. In these experiments, plants (4–5 weeks old) were exposed to adult SLW for 3 days and then the adults were removed and the immature SLW were allowed to develop on the plants for 14 days (Inbar et al., 1999a). At this point, control plants had 0.92 ± 0.03 mg protein/g leaf, 35.1 ± 1.2 ΔA_{510}/min/g leaf peroxidase activity, 3.37 ± 0.08 ΔA_{510}/min/g leaf chitinase activity, and 0.68 ± 0.07 mmol Glc/min/g leaf β-1,3-glucanase activity while SLW preinfested plants had 0.94 ± 0.07 mg protein/g leaf, 41.06 ± 3.2 ΔA_{510}/min/g leaf peroxidase activity, 3.92 ± 0.03 ΔA_{510}/min/g leaf chitinase activity, and 0.81 ± 0.07 mmol Glc/min/g leaf β-1,3-glucanase activity. Only peroxidase and chitinase increased significantly ($P < 0.05$, $n = 24$).

SLW preinfested and control plants were then exposed to newly emerged adult leafminers (5 each females and males) for 24 h and then removed. Host preference was measured by counting leaf and

TABLE 1. Enzyme Activity Measurements of Lanai Tomato Leaf Samples From Silverleaf Whitefly Infested and Non-Infested Plants (Adapted from Mayer et al., 1996)†

		β-1,3 Glucanase		Chitinase	
Sample	Protein (mg/g leaf)	Specific activity (mg Glc/min/mg ptn)	Total activity (mg Glc/min)	Specific activity (ΔA_{550}/min/mg ptn)	Total activity (ΔA_{550}/min/mg ptn)
Uninfested	1.3 ± 0.2	0.1 ± 0	0.2 ± 0	0.5 ± 0.1	0.7 ± 0.3
Infested	0.4 ± 0*	0.6 ± 0.1*	0.3 ± 0.1***	2.9 ± 0.4*	1.2 ± 0.1**

	Chitosanase		Peroxidase		Lysozyme
	Specific activity (nmol GlcN/min/mg ptn)	Total activity (nmol GlcN/min)	Specific activity (ΔA_{550}/min/mg ptn)	Total activity (ΔA_{550}/min)	Specific activity (ΔA_{510}/min/mg ptn)
Uninfested	69.3 ± 61.4	90.2 ± 79.8	5.7 ± 0.9	7.6 ± 2.3	ND
Infested	96.8 ± 25.9	38.9 ± 4.2	24.9 ± 4.1*	10.8 ± 2.4***	ND

†Total Act, total activity calculated on a per g leaf basis; ND = not detectable. Values are the means ± SE. Glc = glucose; GlcN = glucosamine; ptn = protein.
*$P \leq 0.01$; **$P \leq 0.05$; ***$P \leq 0.2$. Significance between infested and uninfested determined by Student's *t*-test.

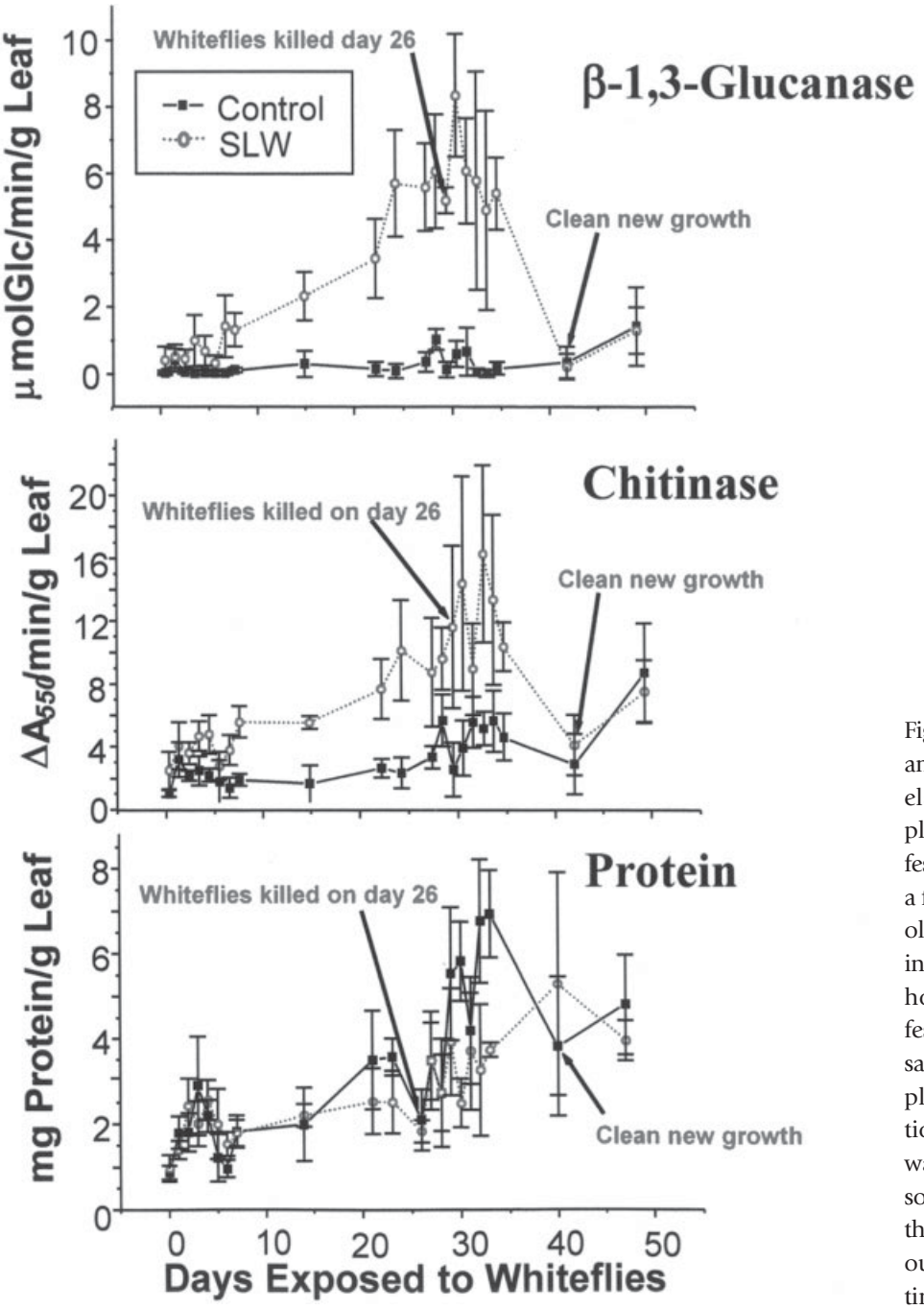

Fig. 1. Comparison of β-1,3-glucanase, chitinase, and protein levels in leaves of Agriset tomato plants either infested or non-infested with silverleaf whiteflies as a function of time. Plants (5 weeks old) were infested by placing them in SLW colonies housed in a greenhouse. Control plants (non-infested) were in cages within the same greenhouse as SLW infested plants. On day 26 post-infestation, all plants were removed and washed with Safer's insecticidal soap to kill SLW. The plants were then moved to a greenhouse without whiteflies. Three plants per time point were used.

oviposition punctures and larval survival was determined by dividing the number of pupae collected by the number of oviposition punctures (Inbar et al., 1999a). Significant reductions in oviposition punctures and feeding events by adult leafminers on SLW preinfested plants indicated a distinct preference for uninfested plants (Table 2). Leafminer larval survival was significantly higher on uninfested plants suggesting that feeding on SLW-infested plants had deleterious effects on leafminer development.

Preferences were also observed with regard to where leafminer feeding occurred on control and SLW-preinfested plants (Fig. 2). Few immature SLW were found on young (not fully expanded) leaves regardless of treatment. Leafminer feeding shifted

TABLE 2. Effect of SLW Preinfestations on Adult Leafminer Preferences and Larval Performance (from Inbar et al., 1999a)†

Variable	Control plants	SLW-infested	Paired *t*
Eggs/plant	18.6 ± 2.7	12.9 ± 4.4	2.32*
Eggs/cm^2	0.52 ± 0.07	0.36 ± 0.09	2.01*
Feedings/plant	58.8 ± 14.4	30.7 ± 14.1	2.34*
Leaves with eggs	2.9 ± 0.3	2.3 ± 0.4	1.7 ns
Leaflets with eggs	7.0 ± 0.9	4.4 ± 1.2	2.6*
No. leaves used for feeding	3.04 ± 0.32	2.0 ± 0.25	3.2**
No. leaflets used for feeding	8.1 ± 1.2	3.9 ± 0.6	3.8**
% Larval survival	33.9 ± 4	24.9 ± 4.1	2.41*

†Values are the means ± SE. ns = not significant.
*$P < 0.05$, **$P < 0.01$.

from older leaves (no. 4) on control plants to younger leaves (no. 6) on SLW-infested plants. Unlike feeding, leafminer oviposition did not differ among old and young leaves on SLW-infested and uninfested plants (Inbar et al., 1999a). Nonetheless, in a subsequent experiment where SLW preinfested and control (no insect infestations) plants were transplanted to the field, leafminer populations were significantly lower on SLW preinfested plants for 3 weeks ($F_{1,96} = 23.62$, $P < 0.01$); at 4 weeks no preinfestation effects were observed (Fig. 3; Inbar et al., 1999a).

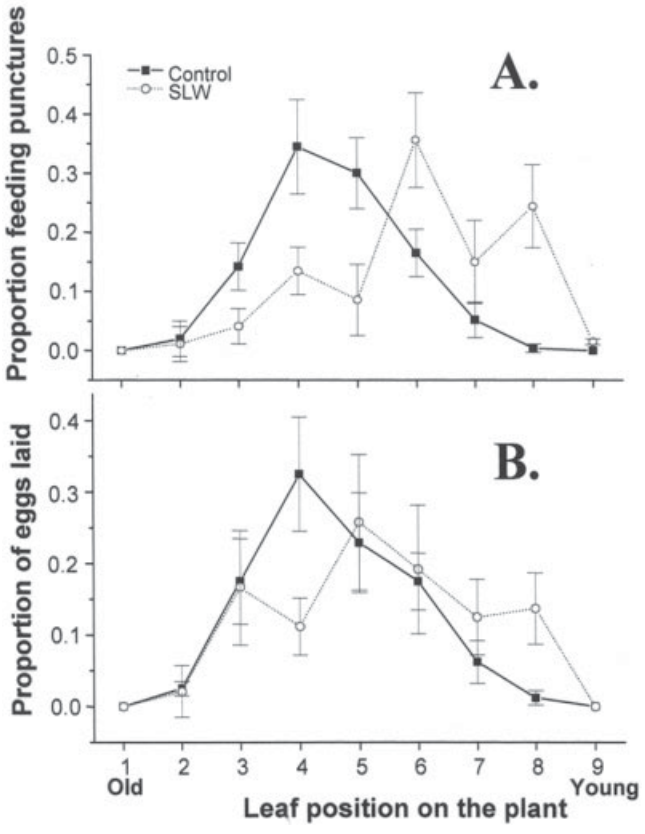

Fig. 2. Distribution of leafminers among leaves of SLW-preinfested and control (uninfested) plants in the whole plant experiment. **A:** Proportion of leafminer feeding. **B:** Oviposition punctures. LM preference values are given in Table 2. Values are means ± SE (Adapted from Inbar et al., 1999a).

In another experiment, tomato plants were exposed to leafminer adults for 3 days and then the adults were removed and the immature leafminers allowed to develop for 14 days (leafminers reach pupal stage in 14 days) to determine if leafminer preinfestations affected SLW performance (Inbar et al., 1999a). After 14 days, control and leafminer preinfested plants were exposed to SLW. No significant effects on SLW oviposition by leafminer preinfestations were evident ($F_{1,342} = 0.45$, $P = 0.53$). SLW females oviposited preferentially on young leaves (6–8) regardless of leafminer preinfestations indicating that SLW host selection was apparently unaffected by leafminer preinfestations. Enzyme and protein assays were conducted to confirm induction of defensive proteins in local leaf no. 4 and systemic leaf no. 7 of SLW and leafminer preinfested plants (Tables 3 and 4). SLW feeding significantly induced lysozyme, chitinase, and β-1,3-glucanase both locally and systemically, while peroxidase was induced systemically and not locally (Table 3). Leafminer preinfestations significantly raised levels of peroxidase and lysozyme locally in leaf no. 4 and induced chitinase and β-1,3-glucanase systemically in leaf no. 7. Leaf protein content was unaffected by SLW in the local leaf but was significantly reduced in the systemic leaf (Table 3). The opposite result was observed for leafminer preinfestations (Table 4).

SLW vs. Cabbage Looper. Interspecific competition between SLW and cabbage looper larvae was examined on collards (Inbar et al., 1999b). Four-week-old plants were exposed to SLW adults in a greenhouse for 17–21 days resulting in 9.25 ± 2.95 SLW nymphs per cm^2 leaf area. Control plants were maintained in cages in the greenhouse to prevent SLW infestations. Individual 1st instar cabbage looper larvae were fed detached SLW-in-

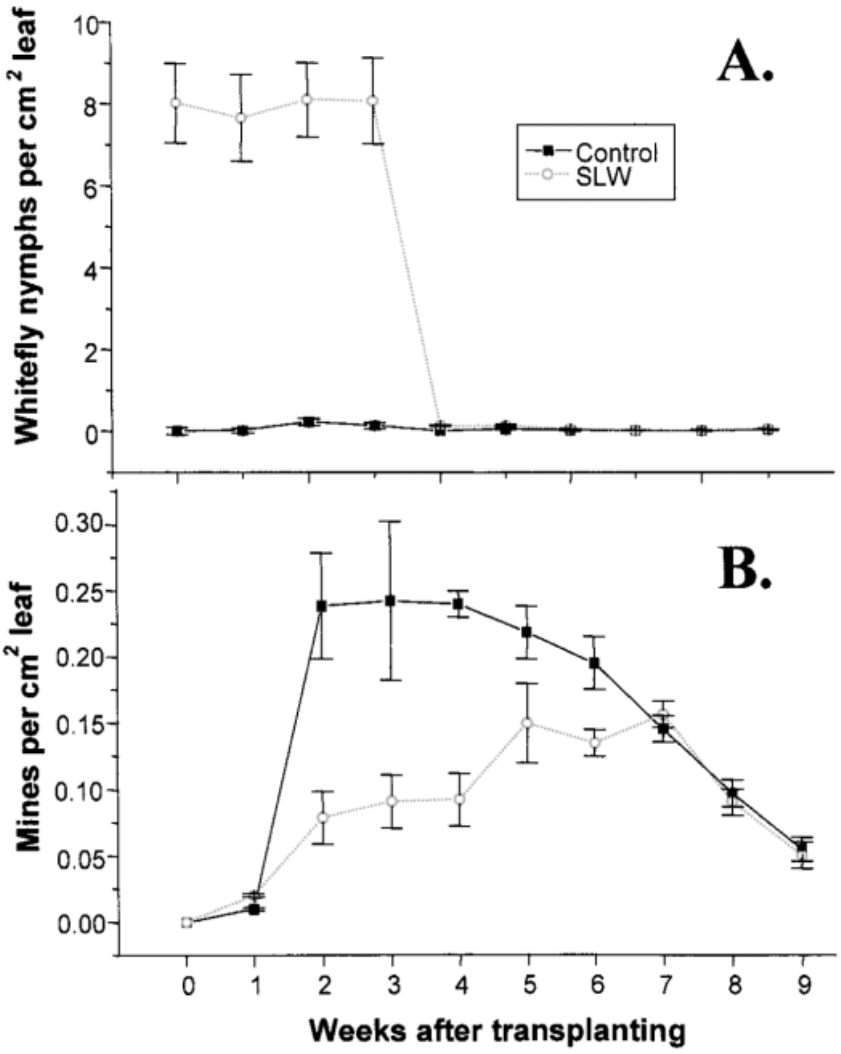

Fig. 3. Field populations of SLW nymphs on SLW-preinfested and control (uninfested) plants (**A**) and effects of SLW preinfestation on leafminer population dynamics in field conditions (**B**). Data points are the means ± SE (from Inbar et al., 1999a).

TABLE 3. Local and Systemic Induction Resulting From Silverleaf Whitefly Preinfestation of Agriset Tomatoes (from Inbar et al., 1999a)[†]

Treatment	Total protein (mg/g leaf)	Peroxidase	Lysozyme	Chitinase	β-1,3-glucanase (mmol Glc/min/g leaf)
			(ΔA_{510}/min/g leaf)		
Local (leaf no. 4)					
Control	0.90 ± 0.06a	21.27 ± 1.49a	328.83 ± 34.41a	3.89 ± 0.19a	0.95 ± 0.17a
SLW	1.11 ± 0.14a	22.92 ± 1.98a	425.36 ± 46.78b	4.31 ± 0.16b	2.22 ± 0.16b
Systemic (leaf no. 7)					
Control	1.54 ± 0.13a	9.87 ± 1.96a	81.80 ± 26.62a	1.94 ± 0.25a	0.21 ± 0.03a
SLW	1.27 ± 0.11b	19.92 ± 1.39b	295.92 ± 24.12b	4.19 ± 0.22b	0.81 ± 0.11a
Split plot ANOVA			F value		
Source of variation					
Treatment (SLW)	0.18 ns	14.81*	32.94*	31.21*	57.51*
Leaf position	28.41*	25.21*	45.42*	39.46*	91.44*
Treatment X position	66.75*	26.30*	18.58*	43.29*	0.71 ns

[†]Leaf position no. 4 (in the treated plants) was preinfested with SLW and thus represents local induction. Leaf no. 7 was not exposed to SLW at any time thus reflects systemic induction. Values are the means ± SE (n = 15). The results of the split-plot ANOVA test (F values) for each enzyme are given at the bottom. Similar letters within pairs indicate non-significant mean separation (LSD). ns = not significant.
*$P < 0.001$.

TABLE 4. Local and Systemic Induction Resulting From Leafminer Preinfestation of Agriset Tomatoes (from Inbar et al., 1999a)†

Treatment	Protein (mg/g tissue)	Peroxidase (ΔA_{510}/min/g leaf)	Lysozyme (ΔA_{510}/min/g leaf)	Chitinase (ΔA_{510}/min/g leaf)	β-1,3-Glucanase (mmol Glc/min/g leaf)
Local (leaf no. 4)					
Control	3.01 ± 0.31a	33.93 ± 9.69a	107.2 ± 108.5a	3.69 ± 1.33a	0.21 ± 0.21a
Leafminer	1.98 ± 0.68b	67.25 ± 2.77b	422.3 ± 633.4b	4.62 ± 1.83a	0.41 ± 0.48a
Systemic (leaf no. 7)					
Control	0.45 ± 0.12a	9.78 ± 3.16a	87.8 ± 43.38a	1.49 ± 0.39a	0.56 ± 0.16a
Leafminer	0.58 ± 0.27a	8.51 ± 8.36a	65.6 ± 42.83a	2.70 ± 1.03b	1.06 ± 0.47b
Split plot ANOVA (F value)					
Source of variation					
Treatment (leafminer)	12.01***	2.31 ns	4.75*	6.56*	10.77**
Leaf position	174.15***	68.27***	6.85*	26.08***	37.93***
Treatment X position	13.34***	11.51***	8.8**	ns	0.51 ns

†Leaf position no. 4 (in the treated plants) was preinfested with leafminers and thus represent local induction. Leaf no. 7 was not exposed to leafminers at any time thus reflects systemic induction. Values are the means ± SE (n = 15). The results of the split-plot ANOVA test (F values) for each enzyme are given at the bottom. Similar letters within pairs indicate non-significant mean separation (LSD). ns = not significant.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

fested (immature SLW stages were present) and control leaves (leaf no. 2–4 counting down from the top) that were placed in Petri dishes (15 × 1.5 cm) were kept in a controlled atmosphere room at 28°C and 50% relative humidity. Leaves were replaced every day and larval survival, weight, and relative growth rates (RGR) were recorded daily. In laboratory experiments, SLW-infestations did not significantly affect cabbage looper survival (χ^2 = 0.007, df = 1), final larval, and pupal weights (Table 5). Larval development times (time to reach the pupal stage) for insects feeding on SLW-infested leaves were extended 2.5 days and larvae were heavier compared to those feeding on control leaves. This is reflected in higher RGR values (35% higher) for control larvae. The effect on RGR was evident in the early development stages, i.e., the first three days, but indistinguishable from controls during later development (Fig. 4). Cabbage loopers feeding on SLW-infested leaves generally were found most often on the adaxial side of the leaf as opposed to cabbage loopers feeding on control leaves that were located on the abaxial side of the leaves (Inbar et al., 1999b).

Similar to the results with tomatoes, collard plants that were exposed to SLW had significantly elevated foliar levels of chitinase, β-1,3-glucanase, and peroxidase (Table 6; Inbar et al., 1999b). Lysozyme activity was elevated and total protein was lower in SLW-infested leaves, but these differences were not statistically significant.

Field experiments were conducted using control (no SLW) and SLW-preinfested collard plants (n = 50 each group) that were randomly placed (in pots) into the field. Three days after transplanting two 1st-instar cabbage looper larvae were placed on leaf no. 3 (from the top) of each plant and larval survival and position were recorded ev-

TABLE 5. Effect of SLW-infested Collard Leaves on Cabbage Looper Development in the Laboratory (from Inbar et al., 1999b)†

Cabbage looper parameter	Control (n = 23)	SLW-infested (n = 24)	t-test (df = 45)
Survival (n = 30)	76%	80%	—
Final larval weight (fresh mg)	275 ± 80	294 ± 80	1.57 ns
Pupa weight (dry g)	21 ± 6	22 ± 6	0.72 ns
RGR (mg/mg/day)	0.28 ± 0.009	0.23 ± 0.004	20.9**
RGR first 3 d (mg/mg/day)	0.302 ± 0.04	0.19 ± 0.05	14.8**
RGR last 3 d (mg/mg/day)	0.20 ± 0.01	0.217 ± 0.01	0.6 ns
Developmental duration (days)	12 ± 0.11	14.5 ± 0.49	5.03*
Developmental duration range (days)	11–13	12–23	

†Controls are SLW-free leaves. Relative growth rate (RGR) is the amount of cabbage looper larval weight gained per body weight unit per day (i.e., mg body weight gained/mg body weight/d). Figures represent full larval RGR; calculations were based on larval fresh weight. Values are means ± 1 SEM (except for developmental duration range).
*$P < 0.01$.
**$P < 0.001$.

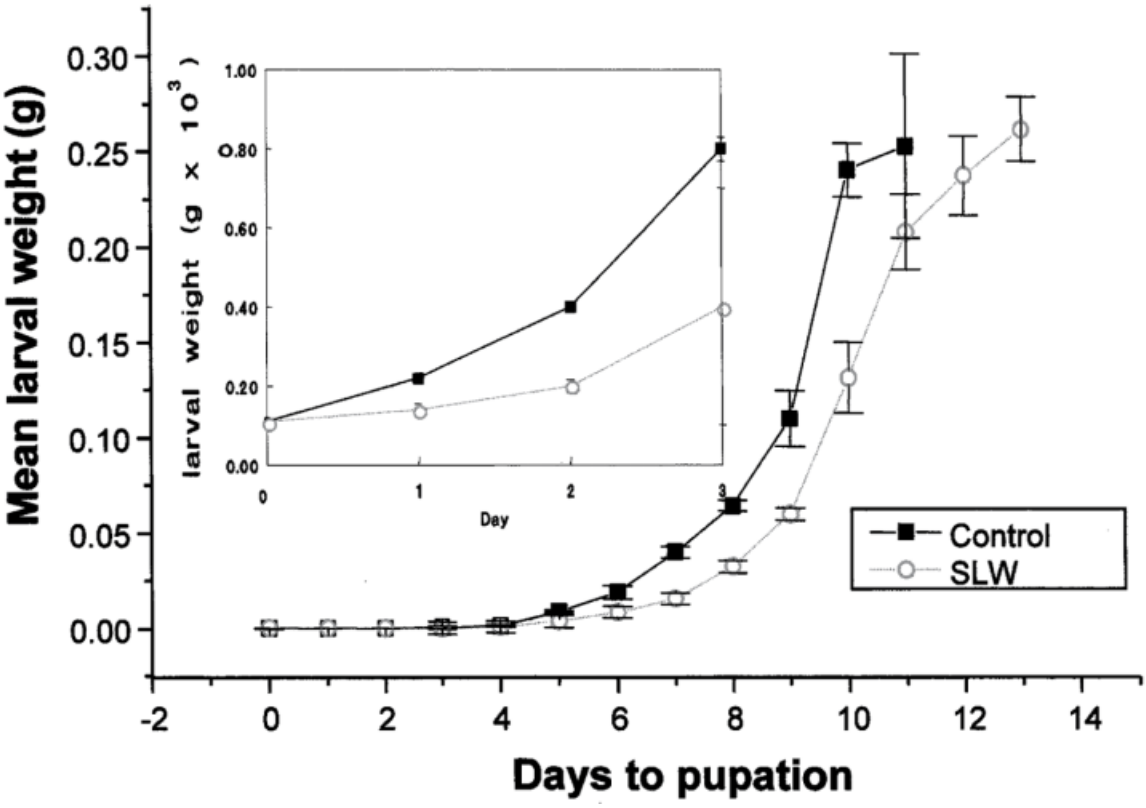

Fig. 4. Effects of feeding on SLW-infested collard leaves on cabbage looper larval weight during development. **Inset:** The differences in larval weight during the first 3 days using an expanded scale. Values are the means ± SE (From Inbar et al., 1999b).

ery two days. Survival of cabbage looper larvae in both control and SLW-preinfested plant groups was low (18 and 4%, respectively; χ^2 = 6.8, df = 1, $P << 0.01$; Fig. 5). Greater mortality occurred in the early larval instars for the larvae feeding on SLW-preinfested plants (day 5, Fig. 5). There was no difference in larval survival rates beyond the early larval stages for the control and SLW-preinfested groups (χ^2 = 0.705, df = 1, not significant; day 10, Fig. 5). No larvae were observed feeding on the adaxial side of leaves as was found in the laboratory experiments.

Systemic Effects

Gauze sleeves were used to isolate the top two leaves of tomato plants (leaves 7, 8, and the unfolded 9) in experiments to determine if SLW feeding effects were systemic (distant from the feeding site); plants with isolated leaves were then exposed

TABLE 6. Protein and Enzyme Characteristics of Control and Whitefly-Infested Collard Leaves (n = 15) (From Inbar et al., 1999b)[†]

Parameter	Total protein (mg protein/g leaf)	Chitinase (ΔA_{550}/min/g leaf)	β-1,3-glucanase (μmol Glc/min/g leaf)	Peroxidase (ΔA_{510}/min/g leaf)	Lysozyme (ΔA_{510}/min/g leaf)
Control	0.57 ± 0.144	0.46 ± 0.048	0.42 ± 0.049	1.69 ± 0.175	49.09 ± 21.59
Whitefly	0.52 ± 0.035	0.67 ± 0.087	0.79 ± 0.085	2.62 ± 0.373	71.54 ± 26.94
t-test (df = 28)	t = 0.79 ns	t = 2.13*	t = 3.79**	t = 2.24*	t = 0.62 ns

[†]Data was subjected to square root transformation before analyses.
*$P < 0.05$.
**$P < 0.01$.

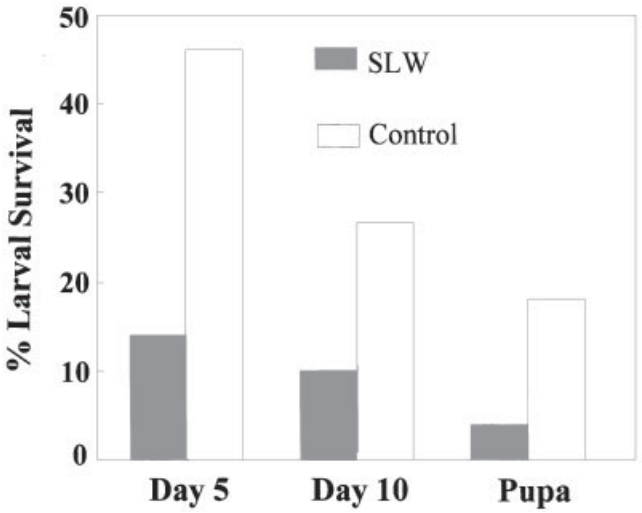

Fig. 5. The effect of SLW preinfestation on cabbage looper larval survival in field experiments (pooled data, n = 100 larvae for each treatment). It was estimated (by size) that 5 days after the beginning of the experiment, larvae were in the 1st to 3rd stages. After 10 days, it was estimated the larvae were at >3rd larval stage. Note that the greatest effect was found during early instars (Inbar et al., 1999b). Pooled data, n = 100 larvae for each treatment.

to adult whiteflies (Inbar et al., 1999a). After removal of SLW adults, the sleeves were removed and the infested plants were put into a greenhouse with uninfested plants for 20 days. On the 21st day the six lower leaves of all plants were removed using a razor blade. The control and preinfested plants were randomly divided into 24 pairs and challenged with leafminer adults as described earlier. SLW preinfestation effects were limited to the immediate leaf above the preinfested leaves, i.e., leaf no. 7. Leafminer oviposition and feeding punctures were reduced 24 and 27% by SLW preinfestation, respectively, on leaf no. 7; no significant effects were observed for larval survival (Inbar et al., 1999a). No differences were observed for leaves nos. 8 and 9 of control and preinfested plants.

Host Plant-ToMoV-SLW Interactions

Very little information is available on how geminivirus infection affects the behavior and physiology of SLW. A series of experiments were initiated to determine if there was any effect of tomato mottle virus on the host plant (Lanai dwarf cherry tomato) and the SLW vector (McKenzie et al., 2002). Tomato plants with 5 to 6 fully expanded leaves were exposed to viruliferous and non-viruliferous SLW; in addition, there was an uninfested control. ToMoV titers were determined via ELISA (Pathoscreen 3F7 ELISA Kit, Agdia Incorporated, Elkhart, IN) and ToMoV was detected at 42 days post-infestation with viruliferous SLW (McKenzie et al., 2002). The appearance of ToMoV in the host plant correlated with the induction of chitinase, β-1,3-glucanase, and peroxidase (Table 7) and was not surprising as other viral phytopathogens have been reported to induce these enzymes in plants (Kombrink and Somssich, 1997). SLW performance was measured by the number of immature SLW on the plants (Table 8). No whiteflies were found on the uninfested control plants. The number of immature SLW differed significantly between plants infested with non-viruliferous and viruliferous whiteflies; all stages, i.e., eggs, nymphs,

TABLE 7. Correlation Between Enzyme Activity and Geminivirus Titer as Determined by ELISA in Tomato Plants Over Time (McKenzie et al., 2002)[†]

Enzyme	Expression of enzyme activity	Days after infestation 0	14	28	42	56	Overall
Chitinase	per mg protein	–0.28 ns	0.30 ns	0.49*	0.55**	0.29 ns	0.11 ns
	per g leaf	–0.09 ns	0.21 ns	0.24 ns	0.41 ns	0.08 ns	0.23*
Glucanase	per mg protein	–0.07 ns	0.57**	0.39 ns	0.64**	0.33 ns	0.38***
	per g leaf	0.01 ns	0.24 ns	0.16 ns	0.51*	0.16 ns	0.40***
Peroxidase	per mg protein	–0.06 ns	0.27 ns	0.36 ns	0.73***	0.51*	0.36***
	per g leaf	0.03 ns	0.04 ns	0.17 ns	0.47*	0.53*	0.36***

[†]The numbers in the table are the actual correlation coefficients. ns = not significant.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

TABLE 8. Comparison of the Mean Number of Immature SLW Forms on Tomato 56 Days Post-SLW Infestation (McKenzie et al., 2000)*

	Mean number (±SE) immature whitefly		
Whitefly treatment	Eggs	Nymphs	Red-eyes
Untreated control	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a
non-viruliferous	18.6 ± 2.9b	2.4 ± 0.3a	0.8 ± 0.2b
viruliferous	46.8 ± 4.2c	10.8 ±1.7b	1.2 ± 0.3b

*Column means followed by the same letter are not significantly different ($P < 0.05$, HSD); $n = 35$ samples per treatment.

and red-eyed nymphs, were more numerous on plants infested with viruliferous whiteflies. These data corroborate the observation that ToMoV viruliferous SLW oviposited significantly more eggs than non-viruliferous SLW (McKenzie, 2002). There is an apparent benefit of increased fecundity in SLW vectors of ToMoV.

Effects of SLW Infestations on Disease Incidence in Host Plants

It is evident that SLW feeding induces many of the same enzymes/defensive systems that are believed to provide pathogen resistance in plants (Van Loon et al., 1994; Kombrink and Somssich, 1997). What is not clear is whether or not induction of these defensive systems via SLW feeding will reduce the incidence of plant diseases. Plants (uninfested controls and SLW-preinfested for 5 weeks) were infected by two known tomato pathogens: powdery mildew and tobacco mosaic virus. Enzyme analyses prior to pathogen inoculation showed that whitefly treatment had significantly increased the activities of foliar chitinase, β-1,3-glucanase, and peroxidase without increasing total proteins (Table 9; Fig. 6). The most notable effect was the plant chitinase response to SLW. Six weeks after inoculation with pathogens, a significant effect of whiteflies on the pattern of PR protein activity persisted (Table 9). Glucanase contributed the most to this significant whitefly effect but now previously infested plants exhibited suppressed β-1,3-glucanase activities (Fig. 6). Chitinase and peroxidase activities were still elevated in whitefly-treated plants. Pathogens did not significantly affect the foliar proteins/enzymes sampled 6 weeks after challenge and did not alter the effects of whitefly infestation (Table 9).

Evaluation of pathogens 3 weeks after inoculation revealed that SLW infestations significantly reduced disease rating ($F_{1,12}$ = 6.04, P = 0.0302). However, the effect depended upon the pathogen ($F_{1,12}$ = 5.16, P = 0.0422). SLW reduced disease rating for PM (P = 0.0260) but did not significantly affect TMV (P = 0.9992; Fig. 7). This study suggests that SLW herbivory can affect plant-pathogen relationships and that the effect may vary among pathogen types.

SLW treatments significantly affected partitioning of mass (Pillai's trace = 0.0001) and the effect

TABLE 9. MANOVA Results of Protein and Enzyme Assays of Plants Treated With SLW and Later With Pathogens*

		Pillai's trace	Standardized canonical coefficients			
Source	df	*P*	Protein	Peroxidase	Chitinase	Glucanase
Before challenge with pathogens						
Block	3	0.0014	1.5686	–0.4369	–0.9529	1.1820
SLW	1	0.0001	–0.2970	0.0176	0.9765	0.6203
Block × SLW	3	0.3478	1.4488	–0.7425	–0.4324	1.0609
Pathogen	2	0.2525	1.2790	0.2374	–2.0966	1.2506
Path × SLW	2	0.8803	0.5620	–1.1528	0.3045	1.6809
Error	35					
After challenge with pathogens						
Block	3	0.0001	–0.1771	0.1638	–0.6245	1.5373
SLW	1	0.0001	0.0437	0.7069	0.7350	–1.2054
Block × SLW	3	0.2107	0.9894	0.9523	–0.0367	–0.5120
Pathogen	2	0.1760	–1.0590	0.4907	–0.2143	0.7479
Path × SLW	2	0.2766	0.6770	0.7975	0.4082	–1.1274
Error	35					

*In the first analysis, plants were evaluated before challenge with pathogens, hence we expect no pathogen effect. Data were log transformed.

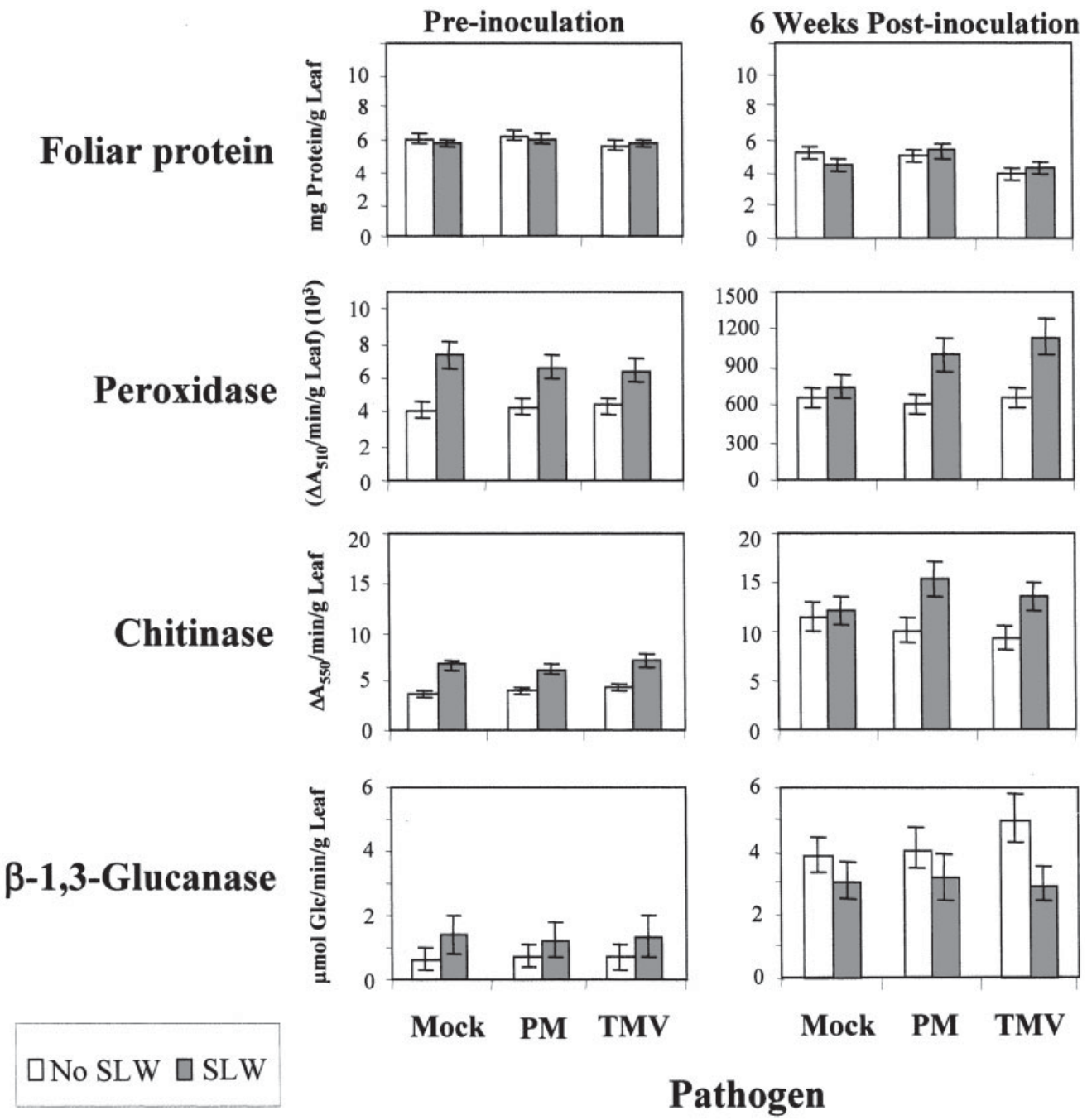

Fig. 6. Effects of SLW preinfestation on Lanai tomato plants prior to powdery mildew (PM) and tobacco mosaic virus (TMV) inoculation and 6 weeks post-inoculation. Results are back-transformed least square means (± SE) for total proteins, peroxidase, chitinase, and β-1,3-glucanase in leaves.

was mostly due to reduced fruit mass from infested plants (standardized canonical coefficients: shoot = 0.8034, fruit = 2.3135). Pathogens did not affect partitioning of mass (Pillai's trace = 0.1180).

DISCUSSION

Silverleaf whitefly feeding can have broad effects on the host plant, competing herbivores, and

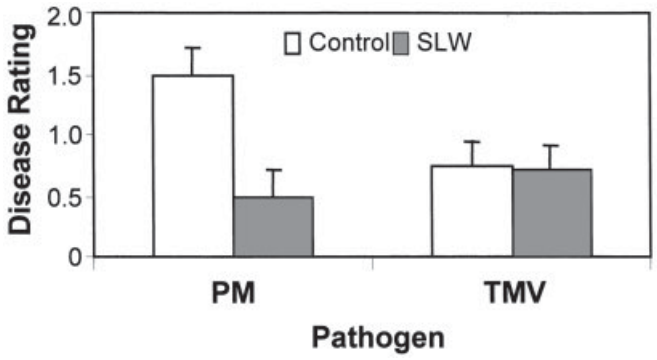

Fig. 7. Least square means (±1 SE) for pathogen disease rating in the presence and absence of SWF. Disease rating was taken 3 weeks after challenge with pathogens.

pathogens (Mayer et al., 1996; Inbar et al., 1999a,b; Walling, 2000). These effects can be direct, e.g., phytotoxic effects such as leaf silvering in cucurbits (Maynard and Cantliffe, 1989; Jiménez et al., 1995), chlorosis (Osborne et al., 1990), and irregular ripening in tomatoes (Schuster et al., 1996; Shapiro, 1996). Direct effects are also observed in regard to interference and/or exploitation interactions with leafminers and cabbage loopers (Inbar et al., 1999a,b).

SLW effects can also be indirect as in the case of induction of host plant defensive responses, e.g., chitinases, β-1,3-glucanases, peroxidases, and secondary plant metabolites, that may influence the incidence of disease and/or provide an advantage with regard to interspecies competition. These indirect effects correlate with induced resistance against herbivores and pathogens. It is our opinion that the decrease in competing herbivore populations is a combination of both direct and indirect effects of SLW infestations. Probably indirect effects play a larger role with insects that normally dwell on the adaxial side of leaves, e.g., the leafminer field experiments with SLW preinfested plants (Inbar et al., 1999a). The reasoning for this is that SLW (all stages) reside largely on the abaxial side of the leaves and leafminers infest the adaxial side. Direct effects of SLW presence on the abaxial sides of leaves probably explain the behavioral change of cabbage loopers from feeding on the abaxial to feeding on the adaxial side of leaves in SLW-infested plants (Inbar et al., 1999b). Thus far, the most convincing evidence that the presence/appearance of these proteins raises resistance comes from work with phytopathogens (Kombrink and Somssich, 1997; Stout and Bostock, 1999). There is circumstantial evidence that the appearance of PR proteins, e.g., chitinases, affects insects. For example, Broadway et al. (1998) report that inclusion of bacterial chitinases in artificial diets raised mortality of SLW and aphids and Smirnoff (1971) reported that the presence of bacterial chitinases in *Bacillus thuringiensis* applications against the spruce budworm increased the efficacy of the biological control agent. The action of the bacterial chitinases may be on the peritrophic membrane that lines the guts of many insects. Mayer et al. (1995) reported that plant chitinases digest the larval peritrophic membranes of the *Diaprepes* root weevil (*Diaprepes abbreviatus*). A chitinase from seeds of Job's tears (*Coix lachryma-jobi)* reportedly acts as an inhibitor for insect α-amylase (Ary et al., 1989). Another plant defensive protein, polygalacturonase inhibitor protein, is effective against fungal and insect polygalacturonases (Doostdar et al., 1997). Cotton plants fed upon by *Helicoverpa zea* larvae had increased peroxidase, ascorbate oxidase, and diamine oxidase activities in both damaged foliage and squares; *H. zea* larvae fed previously damaged plant parts had decreased growth (Bi et al., 1997).

The mechanism(s) of induction of plant defenses by SLW are not known. SLW-related phytoxicities could result from toxins that are released during feeding (Jiménez et al., 1995). However, no such toxins have been identified. If SLW toxins exist they may play a role(s) in the activation of plant defenses. A more likely source of activation substances would be salivary components released by phloem-feeding insects that aid in the lubrication of the stylets, formation of the stylet sheaths, or assist in the digestion of plant components (Cohen et al., 1998; Felton and Eichenseer, 1999; Miles, 1999; Rosell et al., 1999; Funk, 2001). Salivary components can contain proteins (alkaline phosphatase, pectinesterase, polygalacturonase, peroxidase, sucrase, etc.), carbohydrates, and lipids. The

components can act individually or in concert with each other to either directly or indirectly stimulate host plant defenses (Kombrink and Somssich, 1997; Felton and Eichenseer, 1999; Stout and Bostock, 1999; Walling, 2000; Yamaguchi et al., 2000).

In addition to the possibility that significant induction of plant defenses can result from the action of salivary components, it is also possible that the honeydew produced by SLW can act as an elicitor. Oligosaccharides have long been known to elicit defense responses in plants (Yamaguchi et al., 2000). The major components of whitefly honeydew are monosaccharides and the disaccharide trehalulose (α-D-glucose-1-1-α-D-fructose) (Byrne and Miller, 1991; Hendrix et al., 1992). Oligosaccharides with a degree of polymerization of three or more are also excreted (Hendrix et al., 1996; Salvucci, 2000). These larger oligosaccharides may act as potent elicitors of phytoalexins and defensive proteins (Roby et al., 1987; Côté and Hahn, 1994; Yamaguchi et al., 2000). Moreover, large amounts of honeydew can collect on plants heavily infested by whiteflies resulting in mold growth (Hendrix et al., 1996). Possibly any molds growing on plants will result in the induction of plant defenses. To our knowledge, no reports exist on the abilities of either honeydew or honeydew-supported mold colonies to induce plant defense systems.

SLW and apparently other phloem-feeding insects are not significantly affected by the induction of plant defenses caused by their feeding or by the feeding of other herbivores. Plants preinfested with leafminers and corn earworms exhibited elevated levels of PR proteins, but these biochemical changes had no obvious effects on SLW survival and development (Inbar et al., 1999a).

In experiments in which tomato plants were grown at optimal conditions (vigorous), or were resource limited (water and nutritional stress), or mechanically injured (hole punched) there were no effects on SLW oviposition in vigorous or injured plants, but oviposition was reduced on nutritionally- and water-stressed plants (Inbar et al., 2001a). Leafminer and corn earworm performance was greater on vigorously growing plants and lower on damaged, water-deficient, and nutritionally stressed plants (Inbar et al., 2001a). Secondary plant metabolites (phenolics) and peroxidase levels were elevated in the water and nutritionally stressed plants (similar results were reported by English-Loeb et al., 1997). Bi et al. (2001) reported increasing numbers of immature SLW on cotton with increasing concentrations of nitrogen fertilization. The plant vigor hypothesis proposed by Price (1991) suggests that insect herbivores will perform better on vigorously growing plants while the plant stress hypothesis (White, 1984; Mattson and Haack, 1987) proposes that when plants are subjected to a variety of stresses, they become more nutritious for and/or less well defended against arthropod herbivores. Our results reject the plant stress hypothesis. If one considers that plants with heavy SLW infestations are under great stress and that, generally, stressed plants have elevated levels of plant defensive chemicals and proteins, it is a logical assumption that such plants would retard insect herbivore performance. Reduced insect performance, e.g., reduced RGR of cabbage looper fed SLW-infested collards, can affect survival by increasing the length of time for development and, consequently, increasing exposure to predators, parasitoids, entomopathogens, environmental stresses, and so on.

The use of chemical elicitors such as Actigard (BTH; BION; benzo(1,2,3)thiadiazole-7-carbothioic acid(S)-methyl ester) to raise plant resistance offers a new prospect to controlling plant diseases and possibly insect populations. In experiments in which Actigard was applied to tomatoes, there was no significant effect on SLW populations but there were significant effects on leafminers (Inbar et al., 1997). Similarly, Actigard applications to cotton elevated foliar levels of chitinase, peroxidase, and β-1,3-glucanase but there were no obvious effects on either SLW or cotton bollworms (*Helicoverpa armigera*, Hübner) populations (Inbar et al., 2001b).

The SLW does not appear to be affected by elevated plant defenses (that we have measured) and plant stresses to the same extent as other herbivores. A possible explanation for this is that SLW is a phloem-feeding insect. Feeding occurs directly in the phloem and a sheath protects the feeding stylet even

though the stylet passes through intercellular spaces where PR proteins are known to reside. Defensive chemicals, whether they are secondary metabolites or proteins, are usually not expressed or available in the phloem. Consequently, phloem-feeding insects may be protected from many plant defenses to which chewing insects are sensitive. The SLW uses this protection in conjunction with the ability to induce defensive responses in host plants to the fullest advantage in competing with other herbivores. The effects of ToMoV on plant defensive responses, the increased fecundity of SLW feeding on ToMoV-infected plants, and the reduced competition with other herbivores and diseases observed in SLW-infested plants maximally ensures reproduction of the species. We hypothesize that SLW and viruses vectored by SLW have co-evolved to develop a mutually beneficial association. Such an association could explain the eruptive population explosions of the SLW and their vectored viruses while simultaneously displacing competitors.

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