

Recognition of *Brassica oleracea* L. Resistance against the Silverleaf Whitefly

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Additional index words. cole crops, *Bemisia argentifolii*, *Bemisia tabaci*, collard, kale, cauliflower, glossy leaves, sweetpotato whitefly

Abstract. Resistance of a *Brassica oleracea* germplasm collection (broccoli, Italica Group; cauliflower, Botrytis Group; and collard and kale, Acephala Group) to silverleaf whitefly (SLW; *Bemisia argentifolii* Bellows and Perring) infestation was evaluated using several measures of insect infestation (including adult vs. nymph counts) taken at plant growth stages ranging from seedling to mature plant. An initial study was conducted in an outdoor screen cage artificially infested with the SLW adults; subsequent field trials relied on natural infestations. The glossy-leaved lines ('Broc3' broccoli, 'Green Glaze' collard, and 'SC Glaze' collard) had low SLW infestations in cage and field tests. SLW adult counts were less variable than similar comparisons using nymphal counts, although adult and nymph counts were positively and significantly correlated at late plant stages. Based on this study, comparing relative SLW adult populations would be a preferred criterion for identifying *B. oleracea* resistance to this insect.

In recent years, infestations and damage of vegetable crops by the silverleaf whitefly (SLW; *Bemisia argentifolii*) (Perring et al., 1993), previously recognized as *Bemisia tabaci* (Gennadius) strain B, has become an increasing problem across the southern United States. The magnitude of this problem probably is linked to the wide host range of the SLW and the increased resistance of this pest to insecticides (Stockwin, 1992). *Brassica oleracea* crops, such as broccoli, cauliflower, and cabbage, are among the vegetable crops severely damaged by SLW, and these crops also serve as an overwintering reservoir for infestations of spring and summer crops, such as melon (Coudriet et al., 1985).

In a previous study, the responses of six *B. oleracea* types and three cultivars within a type to SLW infestations were compared in several environments (Elsey and Farnham, 1994). In field tests, brussels sprouts (Gemifera group), collard, and kale were preferred hosts over broccoli and cabbage. The only differences among cultivars within a crop were that red brussels sprout and cabbage cultivars were less infested than green cultivars. In subsequent laboratory studies, we determined that preference factors were re-

sponsible for the observed differences among and within crops.

As SLW becomes increasingly resistant to insecticides, SLW resistance in cole crops presents an alternative strategy for limiting infestations. In our study, the objectives were 1) to evaluate a collection of *B. oleracea* germplasm (broccoli, cauliflower, collard, and kale) infested with SLW for identifying potentially resistant plant materials and 2) to determine what host criteria (e.g., plant age) and insect stage (e.g., adult vs. nymph) would be useful in identifying resistance.

Materials and Methods

Screen cage test. This and all subsequent tests were conducted at the U.S. Vegetable Laboratory, Charleston, S.C. In Spring 1993, an outdoor screen-cage study was conducted to evaluate broccoli, cauliflower, collard, and kale entries for resistance. Fifty broccoli entries included 17 commercial cultivars; 16 accessions from Horticulture Research International (Wellesbourne, U.K.); nine accessions from the Institut für Genetik und Kulturpflanzenforschung (Gatersleben, Germany); six U.S. plant introductions; one experimental glossy line ('Broc3') from K.A. Stoner, Connecticut Agricultural Experiment Station, New Haven, Conn.; and one experimental hairy line ('B8744') from S. Sinden, U.S. Dept. of Agriculture, Agricultural Research Service, Beltsville, Md. Seven commercial cauliflower entries were evaluated. The five collard entries included three commercial cultivars and two glossy lines ('Green Glaze' and 'SC Glaze'). Two kale entries ('Vates' and glossy 'Red Green Glaze' from E.A. Borchers, Hampton Road Agricultural Experiment Station, Virginia Beach, Va.) also were included in this study.

In this and all subsequent tests, seedlings for transplanting were produced in the same greenhouse in Charleston with no supplemental lighting. In spring, greenhouses were maintained at 25C day/20C night, and in the summer, they ranged from 25 to 32C depending on outside conditions. On 10 Mar. 1993, seeds were planted into a commercial peat mix (Metromix 360; Grace Sierra, Milpitas, Calif.) in the greenhouse. During the week of 12 Apr., seedlings were transplanted into a 40 × 20 × 3.4-m, outdoor, screen cage. The plot area consisted of single rows on raised beds 1 m apart with 0.7-m spacing between plants within a row. This area was fumigated with monobromomethane (methyl bromide) and fertilized by broadcast incorporation at 1135 10.0N–4.3P–8.3K kg/ha before transplanting. All plots were sidedressed with NH₄NO₃, as recommended for broccoli (Cook and Ezell, 1983), and the plots were irrigated using overhead sprinklers as needed.

The design for this study and all subsequent field trials was a randomized complete block with four replications. Each complete replication (a particular section of the screen cage) contained all 64 *B. oleracea* entries randomized throughout. In each replication, an entry was represented by two adjacent plants in the same row. On each of four dates, (21 and 28 Apr. and 12 and 18 May), ≈30,000 SLW adults were released at random throughout the screen-cage area.

The number of SLW adults per plant was counted on 23 and 30 Apr. and 7 May. On 9 June, the number of adults on four similar-sized, fully expanded leaves on the upper third of each plant was determined. After counts were made, leaf length and width were measured, and a nondestructive estimate of leaf area was made using the following formula: leaf area = 4 × (length × width). The number of adults per unit area of the leaf surface then was computed for each entry. On 26 May and 16 June, the oldest intact leaf on each plant was removed. A quarter section of each leaf was cut from distal to proximal, immediately to the right of the midrib (facing the abaxial side), and the number of SLW third-instar nymphs was counted using a dissecting microscope. After nymphs were counted, leaf area of each section was determined using a leaf area meter (LI3000; LI-COR, Lincoln, Neb.), and the number of nymphs per square centimeter was computed. For all measures of whitefly infestation, numbers from the two separate plants per entry in a replication were averaged, and that value was used as a plot mean in statistical analysis. Analysis of variance (ANOVA) and linear correlation of entry means for the different criteria (e.g., nymph vs. adult counts) measured in this trial were conducted using SAS procedures (SAS, 1985). A protected least significant difference (LSD) was used to separate all entry means when ANOVA indicated a significant ($P \leq 0.05$) entry effect.

Collard field test. In Spring 1993, 12 collard entries were compared under standard production practices in an open-field test. These entries included the two glossy cultivars ('Green Glaze' and 'SC Glaze'); the commer-

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cial cultivars Vates, Morris Heading, Champion, Georgia, Heavycrop, Top Bunch, and Blue Max; and three landraces of collard collected by M.W.F. Seeds were planted in a greenhouse on 15 Feb., and seedlings were transplanted to the field on 30 Mar. In each replication, an entry was grown in a plot that was a single row of 25 plants. Row spacing was 1.0 m and within-row plant spacing was 0.3 m. All cultural practices were as described for the screen cage, but the field was not fumigated. Subsequent field trials were conducted in the same manner. Artificial SLW infestation was not implemented, and a relatively heavy natural infestation occurred over the spring. On 8 June, the number of SLW adults per plant was counted on five random plants per plot. On 23 June, one leaf from each of five random plants per plot was sampled as described in the screen-cage study, and the number of nymphs per leaf area was determined. Using the five samples, a plot average was computed for adult and nymph density and was used in statistical analyses. On 24 June, each plot was visually rated for level of sooty mold present on adaxial leaf surfaces of the bottom (oldest) half of plants. A rating scale from 0 to 10 (0 = no sooty mold present, 5 = about 50% of leaf surfaces covered with mold, and 10 = 100% of leaf surface covered) was used.

Broccoli field test. During Fall 1993, a total of 32 commercial cultivars (17 of which were grown in the screen-cage study), 'B8744', 'Broc3', and an additional glossy broccoli line ('Broc5', obtained from K.A. Stoner) were compared in the field under natural infestation. Seeds were planted in a greenhouse on 6 Aug., and seedlings were transplanted to the field on 23 Sept. In each replication, an entry was grown in a single-row plot of 12 plants. On 18 Oct., the number of SLW adults per plant was counted on five random plants per plot, and on 22 Nov., nymphs were counted as described in previous trials.

Mixed-planting collard field test. In the field during Fall 1993, SLW counts on solid plantings of glossy or nonglossy collard were compared to mixed plantings of the two foliage types. Seeds were planted in a greenhouse in mid-July, and seedlings were transplanted to the field 19 Aug. The three plot arrangements in each replication were as follows: 1) solid planting of glossy 'SC Glaze', 2) solid planting of nonglossy 'Vates', and 3) mixed planting (alternating glossy and nonglossy plants within and across rows) of 'SC Glaze' and 'Vates'. Each plot consisted of 24 plants (4 rows x 6 plants), and each plot was 10 m away from any other plot in each direction. From 9 Sept. to 12 Oct., SLW adults were counted weekly on the central four plants of each plot, and the average number per plant was determined. Using those weekly adult counts, cumulative insect days (Ruppel, 1983) per plant were calculated. This statistic combines the number of insects present and the duration in which they persisted and provides a better measure of overall presence than individual weekly density records. However, computation requires regularly scheduled sam-

Table 1. Number of adult and nymph silverleaf whiteflies on leaves of 64 *Brassica oleracea* (broccoli, cauliflower, collard, and kale) entries grown in a Spring 1993 screen-cage study in Charleston, S.C.

Crop	Entry	Adults		Nymphs (no./100 cm ²)	
		7 May ^z (no./plant)	9 June ^y (no./100 cm ²)	26 May ^x	16 June ^y
Broccoli	B8744	76.1	19.8	412	262
	Baccus	56.5	11.8	533	115
	BRA109	41.4	19.0	402	184
	BRA114	29.1	11.3	85	138
	BRA1186	30.5	12.0	109	183
	BRA1193	24.0	7.7	55	45
	BRA1194	31.6	7.7	296	66
	BRA160	40.3	9.9	317	317
	BRA222	42.9	14.8	143	158
	Brigadier	27.9	10.3	147	105
	Citation	32.6	20.9	599	434
	Cruiser	52.8	6.8	428	45
	Emerald City	46.1	12.1	395	96
	Florette	42.3	7.7	200	189
	Futura	33.9	2.3	123	68
	Galleon	44.1	17.4	413	102
	BROC3	4.8	0.8	1	3
	Green Comet	26.0	7.7	25	71
	Green Duke	58.9	12.4	81	192
	HiCaliber	39.3	15.0	241	165
	K2723	43.0	12.3	219	178
	K6886	22.0	2.9	166	157
	Lancelot	30.6	8.1	308	146
	Packman	37.3	7.9	230	105
	PI 115881	39.3	10.0	220	80
	PI 249556	38.5	16.6	256	118
	PI 267721	43.9	10.0	270	147
	PI 462206	44.4	9.8	121	88
	PI 462207	26.5	6.7	141	83
	PI 462208	38.9	16.8	429	265
	Pinnacle	35.8	12.1	70	83
	Pirate	35.6	3.6	19	44
Premium Crop	50.9	13.8	174	144	
Symphony	41.3	6.7	149	166	
WE 3197	36.1	9.3	429	87	
WE 4700	49.9	15.5	147	53	
WE 4703	43.1	6.8	200	144	
WE 4705	31.5	9.4	85	133	
WE 4708	31.8	9.8	77	233	
WE 4710	51.0	19.7	328	347	
WE 4717	42.3	26.3	434	327	
WE 4885	54.1	12.9	627	310	
WE 5281	34.1	11.8	159	329	
WE 5282	22.1	15.5	149	117	
WE 5297	20.3	5.8	333	69	
WE 5406	20.7	4.2	412	115	
WE 5415	28.8	7.8	313	174	
WE 5419	32.5	7.7	269	47	
WE 5429	28.4	6.8	234	107	
WE 6318	29.4	18.4	184	171	
Cauliflower	Cashmere	26.4	4.1	151	151
	Early White	28.3	11.9	256	205
	Majestic	21.3	8.1	282	203
	Snowball 123	31.9	18.4	503	500
	Snowcone	19.3	15.4	738	271
	Snow Crown	26.3	13.7	722	302
	Yukon	24.5	11.3	288	107
Collard	Blue Max	60.9	13.4	132	84
	Green Glaze	8.8	4.0	6	24
	HiCrop	58.0	12.3	53	92
	SC Glaze	7.5	1.9	3	1
	Vates	54.5	19.3	323	147
Kale	Red Green Glaze	57.4	10.1	234	31
	Vates	67.5	48.3	742	413
LSD _{0.05}		23.8	13.0	380	180

^zOn this date, plants evaluated were in early vegetative stage (six to seven leaves).

^yBroccoli and cauliflower plants evaluated on these dates were undergoing heading; collard and kale were in late vegetative stage.

^xOn this date, broccoli and cauliflower plants were in late vegetative or early heading stages; collard and kale were vegetative.

pling over time, which was not done in the previously described trials. Insect days were determined using the following formula: insect days = $(X_{i+1} - X_i) [(Y_i + Y_{i+1}) - 2]$, where X_i and X_{i+1} are adjacent points of time and Y_i and Y_{i+1} are the corresponding points of insect counts. Cumulative insect days are computed by sequentially summing the individual insect days. On 15 Oct., lower leaves were removed from four plants per plot, and nymphal counts were taken and analyzed as in other tests.

Results

Screen-cage test. There were significant differences among entries for all measures of whitefly infestation (Table 1). On 23 and 30 Apr. and 7 May, all lines were vegetative and at 3- to 4-, 4- to 5-, and 6- to 7-leaf stages, respectively. During these early vegetative stages, all entries were of similar size. Because results of the three early samplings were similar, SLW adult counts per plant are presented for 7 May only (Table 1). At the early vegetative stages, glossy 'Broc3' broccoli, 'SC Glaze' collard, and 'Green Glaze' collard had significantly lower adult counts than most of all other lines; 'B8744' (the hairy broccoli) and 'Vates' kale exhibited the highest counts of adults at this time.

SLW adult counts also were made on 9 June when plants were at late growth stages (Table 1). Evaluating adults per sampling unit (four leaves) or per leaf area to compare entries gave similar results. At this sampling, 'Broc3', 'SC Glaze', and 'Green Glaze' had the lowest SLW adult counts, and many evaluated entries harbored significantly more adults than the three glossy entries. 'Vates' kale had the highest SWL adult count at this sampling.

Brassica oleracea entries in this study had nymphal counts that were highly variable among replications. Consequently, even though entry means ranged from <1 to >600 nymphs per 100 cm² of leaf surface on 26 May (mid to late vegetative stage sampling, Table 1), the LSD at $P \leq 0.05$ was large and identified few entry means that were significantly different. Similarly, when nymph counts were taken 16 June, the LSD was large. Although nymphal counts were less effective in differentiating entries, trends were similar as for SLW adults. 'Broc3', 'SC Glaze', and 'Green Glaze' always had the lowest numerical nymph counts. 'Vates' kale had the highest nymph count on 26 May and the third highest count on 16 June. Several other lines had consistently low counts at the late stages of evaluation (26 May to 16 June). Most notable were one German accession (BRA1193) and the two broccoli cultivars Futura and Pirate. Conversely, there were other lines in this study that exhibited consistently high counts for all criteria measured. In addition to 'Vates' kale, these included 'B8744', 'Citation', PI462208, WE4710, WE4717, and WE4885 broccoli and 'Snowball 123' and 'Snowcrown' cauliflower.

Linear correlation of screen-cage entry means showed that, regardless of sampling date, several SLW adult counts were always positively and significantly ($P \leq 0.01$) corre-

lated with each other (Table 2). Similarly, correlation of two nymph counts and correlations between nymph counts and adult counts on 9 June were also positive and significant ($P \leq 0.01$). However, early evaluations of adults usually were not correlated with evaluations of nymphs at late plant stages.

Collard field test. When adult and nymph counts were taken at late vegetative stages on field-grown collard, entries differed, and adult and nymph means were positively correlated (Fig. 1). As in the screen cage, 'SC Glaze' and 'Green Glaze' had the lowest SLW counts. In addition, 'Blue Max' supported relatively low whitefly counts. Mean sooty mold ratings of individual collard entries were positively correlated with mean SLW adult ($r = 0.64$) and nymph ($r = 0.77$) counts of those entries. 'SC Glaze', 'Green Glaze', and 'Blue Max' exhibited the lowest sooty mold levels on foliage,

but lines heavily infested with SLW had high sooty mold ratings. Sooty mold levels differed in the screen-cage study, with the lowest levels on entries harboring the least SLW. However, plants with the highest whitefly counts in that study deteriorated so rapidly in late June, it became impossible to make formal comparisons.

Broccoli field test. In Fall 1993, SLW counts differed among broccoli entries under a natural infestation (Fig. 2). When adult counts were taken during an early vegetative stage (analogous to 7 May in the screen cage, Table 1), 'Broc3' and 'Broc5' supported lower counts than most other entries. Counts were significantly higher on 'B8744' than on most others, but all others exhibited intermediate levels. Although, in the fall, plants had relatively low nymph counts, on entries evaluated at a late vegetative stage (analogous to 26 May in screen

Table 2. Linear correlation coefficients between entry means for different criteria used in evaluation of *Brassica oleracea* entries for silverleaf whitefly resistance in a Spring 1993 screen-cage study in Charleston, S.C.

Measure of infestation	Sample date ^z	Correlation coefficient (r)						
		Measure of infestation						
		Plant		100 cm ²		Nymphs/100 cm ²		
		30 Apr.	7 May	9 June	9 June ^z	26 May	16 June	
Adults/plant	23 Apr.		0.58**	0.27*	0.32**	0.22	0.09	0.27*
	30 Apr.		---	0.68**	0.30**	0.31**	0.13	0.09
	7 May		---	---	0.54**	0.59**	0.26*	0.20
Adults/100 cm ²	9 June		---	---	---	0.83**	0.53**	0.62**
	9 June		---	---	---	---	0.34**	0.43**
Nymphs/100 cm ²	26 May		---	---	---	---	---	0.60**

^zSample unit of each plant was four similar-sized, fully expanded leaves on upper one-third of plant.

*, **Significant at $P \leq 0.05$ or 0.01, respectively.

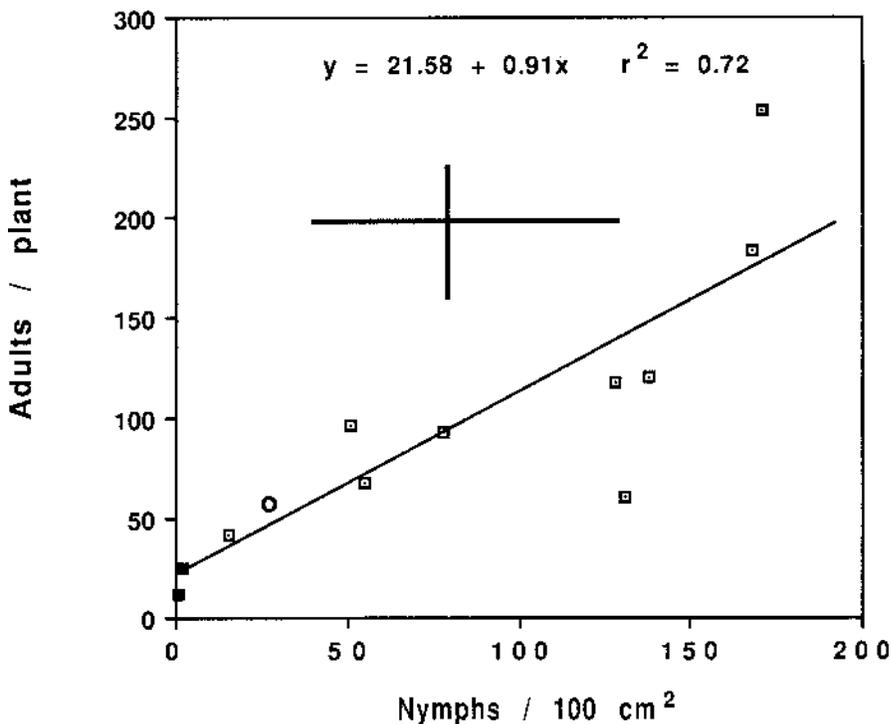


Fig. 1. Mean number of adult and nymph silverleaf whiteflies on leaves of 12 collard entries grown in a Spring 1993 field test in Charleston, S.C. (■) = glossy line, (○) = 'Blue Max', and (□) = nonglossy cultivar. Vertical bar indicates least significant difference (LSD) at $P \leq 0.05$ for comparing adult counts and horizontal bar the $LSD_{0.05}$ for nymphs. Regression line represents best fit for the data.

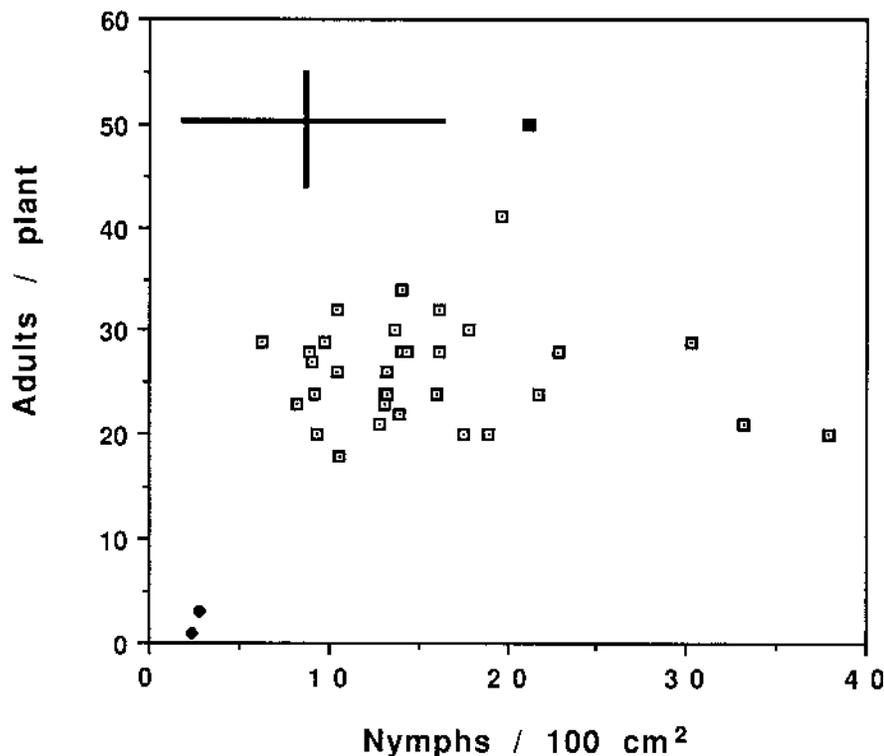


Fig. 2. Mean number of adult and nymph silverleaf whiteflies on leaves of 35 broccoli entries grown in a Fall 1993 field test in Charleston, S.C. (◆) = glossy line, (■) = B8744, and (□) = nonglossy cultivar. Vertical bar indicates least significant difference (LSD) at $P \leq 0.05$ for comparing adult counts and the horizontal bar the $LSD_{0.05}$ for nymphs.

cage) nymph counts were parallel with adult counts, except that 'B8744' did not exhibit the highest numerical nymph count. Adult and nymph counts were not correlated in this test.

Mixed-planting collard field test. In all weekly examinations of this study, SLW adult counts (on a per plant basis) differed among the 'Vates', 'SC Glaze', and mixed cultivar plot types. 'Vates' plots were always highest, mixed plots intermediate, and 'SC Glaze' low. Over all samplings, counts range from 54 to 266 adults per plant for the solid 'Vates', 33 to 177 for mixed plots, and 4 to 44 for solid 'SC Glaze'. Mean cumulative insect days per plant were 5811, 3977, and 1014 ($LSD_{0.05} = 1713$) for 'Vates', Mixed, and 'SC Glaze' plots, respectively. The three plot types also differed in nymph counts at a single sampling, and plot ranking was the same as for adult counts.

Discussion

This comparison of *B. oleracea* genotypes focused on the SLW infestation level that occurred on an individual plant. Differences in resistance reflected by yield or quality characteristics were not evaluated. 'Broc3', 'SC Glaze', and 'Green Glaze' exhibited resistance to SLW compared to other entries in studies where the insect had a choice between numerous genotypes. This SLW nonpreference for these entries occurred in the screen cage and then was verified in subsequent field trials. An additional line ('Broc5') was found to be similar to 'Broc3' in the fall broccoli trial. Elsey and Farnham (1994) did not find 'Green

Glaze' to be consistently less infested than other genotypes. However, the commercial seed lot used in that work produced a 'Green Glaze' population that segregated for glossy and nonglossy foliage, confounding evaluation of the true glossy line. In our studies, all 'Green Glaze' plants were glossy. Thus, our results suggest that glossy foliage might be associated with SLW resistance. Thompson (1963) made similar, although limited, observations in field research comparing the relative resistance to cabbage whitefly of a glossy and nonglossy kale (*Alueroide brassicae* Walk.). It is well documented that cole crops with glossy foliage exhibit resistance to feeding by lepidopterous caterpillars, such as the diamondback moth (*Plutella xylostella* L.) (Eigenbrode et al., 1990) and the imported cabbageworm (*Artogeia rapae* L.) (Stoner, 1992). Eigenbrode et al. (1991) showed that reduced wax content of leaf surfaces, which results in a glossy appearance, is correlated with lepidoptera resistance in *B. oleracea*. This resistance is believed to be an example of nonpreference, wherein larvae prefer not to feed on glossy leaves. In field trials, red cabbage and brussels sprout cultivars were infested less by SLW than were green cultivars (Elsey and Farnham, 1994). This resistance is also nonpreference, as demonstrated in no-choice laboratory tests where red cultivars were equal to green cultivars in sustaining growth and development stages of whitefly. We have conducted a limited number of no-choice laboratory tests with 'Broc3', 'Broc5', 'Green Glaze', 'SC Glaze', and other broccoli

and collard entries, and it seems that any SLW resistance associated with the glossy trait also occurs due to nonpreference factors (unpublished data).

Adult and nymph counts showed 'Broc3', 'SC Glaze', and 'Green Glaze' to be relatively SLW free. Additionally, low counts always prevailed on the glossy entries, regardless of plant age. Conversely, numerous other entries (e.g., 'Vates' kale and 'B8744') always had high counts. Glossy *B. oleracea* genotypes have been described for several decades but are used little commercially. However, they are likely to receive more attention in the future as cole crop growers seek new ways to control insect pests like SLW. In the meantime, 'Broc3' or 'SC Glaze' should prove particularly useful as noninfested controls in resistance screening nurseries, allowing plant breeders to identify potential SLW resistances among a large collection of cole crop germplasm. Clearly, unlike crops where trichomes are associated with resistance to sweetpotato whitefly (Berlinger, 1986; Kishaba et al., 1992), the presence of trichomes on 'B8744' actually may have increased SLW preference. This result is consistent with those observed in cotton (*Gossypium hirsutum* L.), where increasing hairiness is correlated with increased whitefly infestation (Niles, 1980). Using 'B8744' in combination with a nonpreferred line such as 'Broc3' likely will provide a practical differential for resistance screening. In the cage study, certain nonglossy lines (e.g., BRA1193) evaluated at late development stages had low SLW infestations. Eigenbrode et al. (1990) described two types of resistance (one associated with glossiness and the other not) to diamondback moth in cabbage. Several types of SLW resistance also might exist.

SLW adult counts were always less variable among experimental units than nymph counts and were more effective for differentiating entry means. High nymph variability may result from inherent error in sampling older leaves. Plants may differ in the rate at which lower leaves die and fall. Indeed, heavily infested leaves may tend to fall from the plant more readily than less infested ones. This problem may limit the value of nymph counts for differentiating genotypes. We are inclined to use adult counts for evaluating resistance and nymph counts for confirming response of potential resistant plants.

The glossy 'Red Green Glaze' kale did not seem as SLW resistant in the screen cage as did other glossy entries. However, it may be noteworthy that the glossy kale did have lower adult counts on 9 June and lower nymph counts on 26 May and 16 June than nonglossy 'Vates' kale. Stoner (1990) determined that glossiness in 'Broc3', 'SC Glaze', and 'Green Glaze' are conferred by dominant genes, but glossiness in 'Red Green Glaze' kale is recessive. The background (e.g., kale) in which glossiness is expressed may affect the SLW response to the character. Also, glossiness conferred by different genes may result in phenotypes that differ in ways that influence insect preference.

Results of the collard field test indicate that

sooty mold rating can be positively correlated with SLW counts and may be used as an indirect measure of SLW infestation and cole crop resistance. This fungal proliferation derived from SLW excrement, or "honey dew," was used as a substrate for growth.

The mixed-planting study with collard showed that a nonpreferred line might be grown in a mixed stand with a susceptible line and effectively lower the whitefly population in that stand. These results are similar to those of Altieri and Schmidt (1987) who reported lower counts of cabbage aphids (*Brevicoryne brassicae* L.) in mixed stands of broccoli cultivars. As SLW gains resistance to existing insecticides and infestations become an increasing problem, using a nonpreferred resistant line in mixed plantings might be explored as an alternative means of control.

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