Influence of Variety on Abundance and Within-Plant Distribution of Onion Thrips (Thysanoptera: Thripidae) on Cabbage

KIMBERLEY A. STONER[1] AND A. M. SHELTON[2]

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ABSTRACT Numbers of onion thrips, *Thrips tabaci* Lindeman, were significantly lower in August and early September in the heads of two resistant cabbage varieties ('Titanic 90' and 'Falcon') than in two susceptible varieties ('Market Prize' and 'Supergreen'). Numbers of onion thrips on the frame or outer leaves were significantly higher on resistant than susceptible varieties in September. These differences remained when thrips numbers were adjusted using the head and frame dry weight as covariates to remove any effect of differences in head or frame size among varieties. After adjustment, the populations on susceptible heads ranged from 2.8 to 11.5 times as high as populations on resistant heads from 17 August to 14 September in 1983 and 1984. The resistant varieties 'Falcon' and 'Titanic 90' had as many thrips per plant as suceptible varieties, but fewer thrips infested the head of resistant varieties and caused less cosmetic damage to the marketable product.

KEY WORDS Insecta, *Brassica oleracea* var. *capitata, Thrips tabaci,* plant resistance

ONION THRIPS, *Thrips tabaci* Lindeman, has been a serious problem on cabbage in New York for the last 6 yr (Andaloro et al. 1983a). Thrips do direct cosmetic damage to the head, causing rough brown blisters (Fox & Delbridge 1977). Although thrips can be found as deep as 11 layers (22 leaves) into the head (North & Shelton 1986), insecticides currently used do not reliably control thrips more than three layers (six leaves) deep (Shelton et al. 1981). Thus, alternative methods of control are needed.

Varietal differences in *T. tabaci* damage at harvest have been documented among commercial varieties used for sauerkraut production (Shelton et al. 1983), but no adequate resistance has been reported for fresh market and storage varieties used in New York. To transfer resistance to varieties suitable for fresh market and storage, information on the inheritance and mechanisms of resistance is needed. In this study, we address three basic questions about thrips resistance. Is the reduced visible damage on resistant varieties associated with reduced numbers of onion thrips? If so, where on the plant, and when during the season, are thrips numbers reduced? Can differences in thrips numbers among varieties be explained by differences in plant size for that particular date? The answer to the first question should reveal whether the plant expresses resistance by reducing thrips numbers through antibiosis or nonpreference, or by not responding to thrips injury; i.e., not producing the obvious brown blisters that are the economically important form of thrips damage. Knowing when and where resistance acts most strongly should help focus further mechanistic studies. Removing the effect of head or frame size on thrips numbers by comparing predicted numbers at a common head or frame weight is a first step toward separating differences in growth rate from other factors determining thrips resistance.

We studied four varieties, two that had high levels of thrips damage to the head in previous studies and were classified as susceptible, and two with very low levels of damage classified as resistant. From detailed study of these two groups, hypotheses about the general nature of thrips resistance can be developed for testing on a wider range of varieties. However, thrips resistance or susceptibility may not be caused by the same factors or may not operate in the same way across even such a small group of varieties; therefore, we also compared thrips abundance on the two varieties within the groups.

Materials and Methods

Based on previous work (Shelton et al. 1983, Shelton et al. 1988), four varieties were chosen to represent the range of observed susceptibility to thrips—'Market Prize' (Harris Moran Seed, Rochester, N.Y.) and 'Supergreen' (Reed's Seeds, Cortland, N.Y.) were severely damaged in previous tests (susceptible group), whereas 'Titanic 90' (Ferry-Morse Seed, San Juan Bautista, Calif.) and 'Falcon' (Royal Sluis, Salinas, Calif.) were only slightly damaged (resistant group). These varieties were planted in a randomized complete block design at the New York State Agricultural Experiment Station Vegetable Research Farm near Geneva, N.Y., in 1983

[1] Department of Entomology, Cornell University, New York State Agricultural Experiment Station, Geneva, N.Y. 14456 and Department of Entomology, Connecticut Agricultural Experiment Station, New Haven, Conn. 06504.

[2] Department of Entomology, Cornell University, New York State Agricultural Experiment Station, Geneva, N.Y. 14456.

and 1984. On 30 June 1983, six lines were planted in three blocks; each plot included 11 rows 0.9 m apart, with five plants 45 cm apart in each row. On 14 June 1984, four varieties were planted in four blocks, and each plot had four rows of 10 plants with the same spacing. Soil was a silt-loam with pH of 6.5 and was fertilized on a per-ha basis with 184 kg of 15-15-15 on 23 May and sidedressed with 32 kg N on 10 July. Commercial preparations of *Bacillus thuringiensis* (Berliner) were used to control caterpillars. No other insecticides were used.

We began sampling two plants per plot on a weekly basis but switched to one plant per plot on 26 July 1983 and to sampling every 2 wk after 3 August 1983. Each plant sampled was divided into two parts: the tightly folded central leaves, labelled "head" throughout (but in early samples included young heart leaves that ultimately unfold to become outer leaves; see Andaloro et al. [1983b] for a description of cabbage growth), and the open outer leaves ("frame leaves"). These were carefully separated in the field and then immediately plunged into containers of 70% ethanol. Samples were stored in the ethanol at 1–2°C. In the laboratory, all leaves were separated and washed individually in water, and all the water and alcohol were filtered through a Nytex screen (85 μm, Tetko, Elmsford, N.Y.). Adults, larvae, and pupae were counted on the screen at 18–20× magnification. Virtually all adults were female *T. tabaci*.

Plant measurements were also taken beginning on 3 August 1983 to monitor difference in growth among varieties. The frame and head (after removing the core) were weighed after drying in an oven for at least 48 h at 65–80°C in 1983, and at 100–110°C in 1984.

Damage to the heads was evaluated on three heads per plot on 12 October and 19 October 1983 with heads chosen from among the most mature plants, and on 23 September 1984 with heads chosen randomly. The first 10 layers (20 leaves) were peeled off and each was evaluated for presence or absence of thrips damage, and the head as a whole was qualitatively rated on a scale of 0 (no injury) to 4 (severe injury) as described in Shelton et al. (1983).

Damage ratings were analyzed using rank transformation and analysis of variance (ANOVA) of the ranks, an appropriate nonparametric analysis for an ordinal variable (Conover & Iman 1981). Head and frame dry weights were also analyzed with ANOVA, and "protected" least significant differences were used to separate means for those dates with a significant ($P < 0.05$) F test (Snedecor & Cochran 1980). Thrips numbers were transformed to natural logarithms (of thrips numbers + 1) to stabilize the error variance. A separate ANOVA was performed for each sample date to analyze the differences among all four varieties. In addition, a contrast between the susceptible group and resistant group (using $P < 0.05$ as the critical significance level) was made for each sample date. Because of the large number of dates on which separate analyses were significant at $P = 0.05$, 5% of the tests made would be expected to be significant by chance alone. One sample of frame leaves from 17 August 1983 and three samples (counted by the same person on the same day) from 17 August 1984 had less than one-tenth the number of thrips in other samples from the same date. Errors in handling these samples were strongly suspected, so they were treated as missing values in the analysis. Plant dry weights were also analyzed with analysis of variance.

Because we found differences among varieties in head and frame dry weight, we wanted to determine whether differences in thrips numbers could be explained by differences in head or frame size among varieties, and to compare susceptible and resistant groups with the effect of differences in size removed. We did this by fitting a series of candidate models for each sample date (Allen & Cady 1982). The first model was a simple regression of thrips numbers on dry weight of the head or frame leaves. In the notation of Snedecor & Cochran (1980, 365–367), the model was

$$Y_{ij} = \alpha + \beta(X_{ij} - X_{..}) + \epsilon_{ij},$$

in which i is 1–4 (representing the four varieties), j represents the number of observations per variety (equal to the number of blocks in most cases), Y_{ij} is the number of thrips (log transformed) on the head or frame in the jth observation in the ith class, α is the overall mean number of thrips (transformed) in all treatments, β is the regression coefficient of Y on X for all observations, X_{ij} is the dry weight of the head or frame in the jth observation in the ith class, $X_{..}$ is the observed mean dry weight in all treatments, and ϵ_{ij} is a normally distributed random variable. The second model assumed a common slope for the regression, with different means (and thus different intercepts) for the four varieties:

$$Y_{ij} = \alpha_i + \beta(X_{ij} - X_{..}) + \epsilon_{ij},$$

where all variables were defined as above except that α_i is the varietal mean for each of the four varieties. The third model assumed different slopes and intercepts for the four varieties:

$$Y_{ij} = \alpha_i + \beta_i(X_{ij} - X_{..}) + \epsilon_{ij},$$

where all variables were defined as above except that β_i is the varietal regression coefficient for each of the four varieties.

Each model in the series was tested to see if it explained significantly more variation (F test, $P < 0.05$) than the preceding model. For those dates where different slopes did not add significantly to the model, the susceptible and resistant groups of varieties were compared by using head or frame dry weight as a covariate and adjusting group means to allow us to compare predicted group means at a common head or frame size, as measured by the dry weight (Snedecor & Cochran 1980). For dates

Table 1. No. of cabbage heads of each variety with each rating[a] for thrips damage, Geneva, N.Y., 1983–84

Variety	Rating							
	0	0.5	1.0	1.5	2.0	2.5	3.0	3.5
			1983[b]					
Market Prize				2	10	4	1	1
Supergreen	1	3	6	3	4	1		
Titanic 90	5	7	6					
Falcon	12	6						
			1984					
Market Prize					4	4	4	
Supergreen					6	4	2	
Titanic 90		1	9	2				
Falcon	5	5	2					

[a] Scale is from 0 (none) to 4 (severe). (See text.)
[b] Table for 1983 combines ratings from 12 and 19 October.

where susceptible and resistant groups had significantly different numbers of thrips at a common head or frame weight, an estimate of the difference was calculated. When this difference in logarithmic data is converted to antilogarithms, it gives an estimate of the ratio of thrips on susceptible varieties to thrips on resistant varieties (after adjustments for head or frame size). By adding and subtracting the standard error (SE) to the estimated logarithmic difference, then taking antilogarithms, we calculated the range of ratios within one SE unit of the mean to give an estimate of the range of variability. For dates where the four varieties had significantly different slopes, we chose subsets of the four varieties that had the same slope, and these varieties were compared at a common head or frame weight.

Results

As expected, damage ratings differed significantly among varieties (Table 1: ANOVA on rank transformed data. 1983: $F = 59.8$; df = 3, 68; 1984: $F = 78.4$; df = 3, 44; $P < 0.0001$ for both years). The susceptible group of varieties, 'Market Prize' and 'Supergreen,' also differed significantly from the resistant group, 'Titanic 90' and 'Falcon' (1983: $t = 12.1$, df = 68; 1984: $t = 14.7$, df = 44; $P < 0.0001$ for both years).

The differences in dry weight of the head and frame leaves over the season on the four varieties is illustrated by the 1984 data in Table 2. Of the four varieties, 'Market Prize' is the first to produce a sizeable head, followed by 'Titanic 90,' then 'Supergreen,' and then 'Falcon.' 'Falcon' had a greater dry weight of frame leaves than 'Market Prize' on 31 August 1984, and 'Falcon' and 'Titanic 90' had significantly greater dry weight of frame leaves than both of the susceptible varieties on 14 September 1984. Data for 1983 showed similar trends for dry weight of both head and frame leaves, but the differences were generally not significant. The only exception was 14 September, when the dry weights for 'Market Prize' (53.1 g) and 'Titanic 90' (54.2 g) heads were significantly greater than those for 'Supergreen' (30.7 g) and 'Falcon' (25.0 g) (LSD = 14.3 g; $F = 13.36$; $P < 0.01$).

Trends in differences of thrips numbers between susceptible and resistant groups were present only when thrips were counted separately on the frame and head. When thrips numbers were analyzed on a whole-plant basis (Fig. 1), only two sample dates, 17 August 1983 and 31 August 1984, had significant differences between susceptible and resistant groups; on the former, susceptible varieties had more thrips per plant, and on the latter, the resistant varieties had more thrips. On frame leaves (Fig. 2), the resistant group had significantly more thrips at the end of both years. Additional significant differences occurred on 17 August 1983 (with the susceptible group having more thrips) and 12 July 1983 (with the resistant group having more).

In the heads (Fig. 3) for all dates with significant differences, the susceptible varieties had more

Table 2. Dry weight of heads and frame leaves of four cabbage varieties, Geneva, N.Y., 1984

Date	Variety[a]				SEM	LSD[b]	F test[c]
	M	S	T	F			
			Heads				
6 July	0.05	0.02	0.03	0.04	0.008	—	NS
20 July	0.62	0.20	0.18	0.17	0.107	—	NS
3 Aug.	4.33	0.97	1.48	0.74	0.782	—	NS
17 Aug.	28.00	11.60	11.50	6.10	2.910	9.31	**
31 Aug.	56.40	31.60	62.00	17.40	7.860	25.14	*
14 Sept.	67.30	40.40	80.70	33.90	8.330	26.65	*
			Frame leaves				
6 July	3.43	3.06	3.33	2.6	0.578	—	NS
20 July	21.30	15.50	17.70	14.9	3.330	—	NS
3 Aug.	30.70	27.90	33.70	32.0	5.260	—	NS
17 Aug.	38.00	45.90	49.70	66.4	8.780	—	NS
31 Aug.	40.30	57.00	56.50	75.7	6.330	20.2	*
14 Sept.	41.90	49.90	74.40	77.0	7.230	23.1	*

[a] M, Market Prize; S, Supergreen; T, Titanic 90; F, Falcon.
[b] LSD (least significant difference) given only for dates with a significant F test; i.e., a "protected LSD" (Snedecor & Cochran 1980).
[c] NS, F test is not significant at the 5% level. *, $P < 0.05$; **, $P < 0.01$.

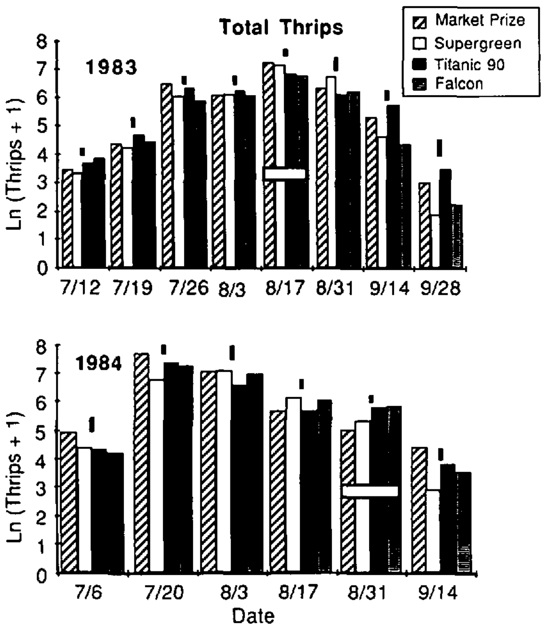

Fig. 1. Total thrips per plant for four cabbage varieties. Black rectangles at the top of the columns for each date indicate standard error of the variety means derived from mean square error in analysis of variance. Horizontal white rectangles mark the dates for which the susceptible ('Market Prize' and 'Supergreen') and resistant ('Titanic 90' and 'Falcon') varieties had significantly different ($P < 0.05$) numbers of thrips.

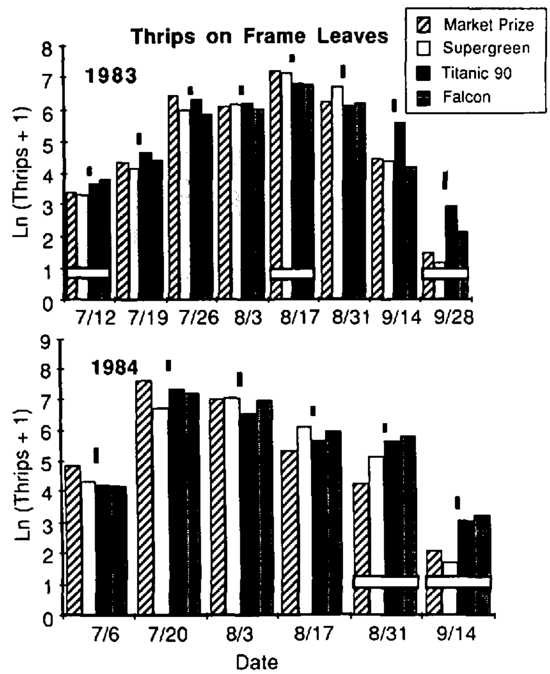

Fig. 2. Thrips on the frame leaves of four cabbage varieties. Black rectangles at the top of the columns for each date indicate standard error of the variety means derived from mean square error in analysis of variance. Horizontal white rectangles mark the dates for which the susceptible ('Market Prize' and 'Supergreen') and resistant ('Titanic 90' and 'Falcon') varieties had significantly different ($P < 0.05$) numbers of thrips.

thrips. In both years, one midsummer and a group of three late-summer samples had the significant differences. The shift in time of differences between the two years may be caused by earlier planting and earlier development and maturation in 1984.

From visual inspection of Fig. 3, five (26 July 1983, 14 September 1983, 6 July 1984, 3 August 1984, 31 August 1984) of eight dates with significant differences between susceptible and resistant groups are primarily caused by a large difference between 'Market Prize' and 'Falcon,' with 'Supergreen' and 'Titanic 90' approximately equal in thrips numbers. Because 'Market Prize' generally had the largest heads and 'Falcon' the smallest (Table 2), we wanted to assure that the differences between groups in thrips numbers were not simply a reflection of differences in head size between these two varieties. Likewise, for thrips on frame leaves at the end of both seasons, the two resistant varieties have both the largest biomass of frame leaves (Table 2, same trend, but difference not significant in 1983) and the largest numbers of thrips on those leaves (Fig. 2). Thus, we compared predicted group means at a common head or frame dry weight to see if the differences between susceptible and resistant groups remained after adjustment to compensate for differences in weight.

Comparison of the predicted means for susceptible and resistant groups at a common frame weight (Table 3) gave results only slightly different from the unadjusted data for thrips on frame leaves in Fig. 2. After adjusting for frame weight, the susceptible varieties still had significantly more thrips on the frame leaves for only one date, 31 August 1983. The other tests of significance had the same results as with unadjusted means. For 14 September 1984, the slopes of the regression lines were significantly different among the four varieties ($P < 0.05$), so the size of the differences among varieties depended on the common frame weight chosen for comparison. We analyzed the data for this date by excluding 'Supergreen,' the only variety with a slope significantly different from the other varieties, from the analysis. When 'Market Prize,' 'Titanic 90,' and 'Falcon' were used to estimate the difference between the (one) susceptible and (two) resistant varieties, the contrast was significant ($t = -4.66$; df = 8; $P < 0.01$), and a mean ratio of thrips on susceptible varieties to thrips on resistant varieties was 0.30 (range within one SE unit, 0.39 to 0.23). Together with the data for 28 September 1983 and 31 August 1984, this result confirms that the numbers of thrips on the frame leaves of susceptible varieties are much lower than on resistant varieties at the end of the season after adjustment for differences in frame biomass. In 1983, the numbers on susceptible varieties were greatly reduced for

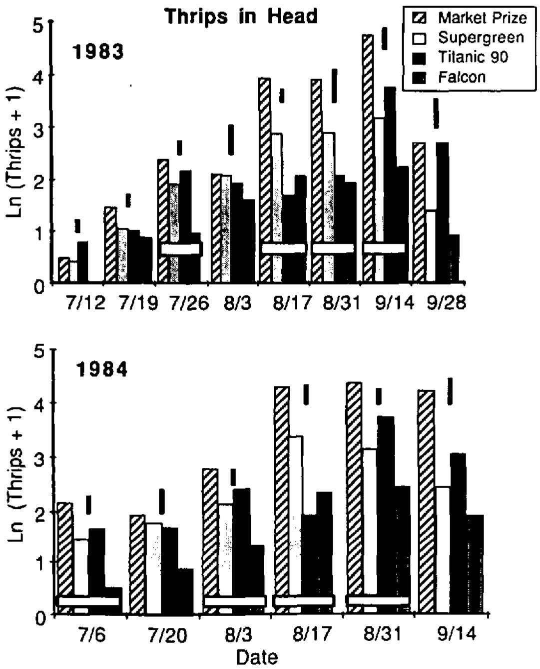

Fig. 3. Thrips inside the folded central leaves of four cabbage varieties. Black rectangles at the top of the columns for each date indicate standard error of the variety means derived from mean square error in analysis of variance. Horizontal white rectangles mark the dates for which the susceptible ('Market Prize' and 'Supergreen') and resistant ('Titanic 90' and 'Falcon') varieties had significantly different ($P < 0.05$) numbers of thrips.

one sample date (ca. 1/25 the numbers on resistant varieties, with range ± SE of 1/7 to 1/83) while in 1984, the numbers were not as low (1/2 to 1/6, including the range ± SE for both samples) but were reduced over a longer period.

For thrips in the heads, only the significance of 6 July 1984 changed from the unadjusted data in Fig. 3 when comparisons were made at a common head weight. For 3 August 1984, the slopes of the regression lines were once again significantly ($P < 0.05$) different among the four varieties. Two pairs of varieties could be separated (each including one susceptible and one resistant variety) that did not have significant differences in slope within the pair, so that comparisons at a common head weight could be performed within each pair. 'Market Prize' and 'Titanic 90,' when compared this way, did not have significant differences in populations at the same head weight (t = 0.70; df = 5; P = 0.51), but 'Supergreen' and 'Falcon' did (t = 2.81; df = 5; $P < 0.05$). The estimate of the contrast between these two varieties transformed back to a susceptible/resistant ratio of 1:90 (range ± SE, 2.39 to 1.51).

Thus, after adjustment for differences in head dry weight, there was still a pattern of significant differences in thrips numbers in the head between the susceptible and resistant groups from mid-August to mid-September.

Table 3. Ratios of thrips numbers on susceptible varieties to thrips numbers on resistant varieties, as adjusted for head or frame dry weight; see text for explanation of transformations and the process of adjusting for dry weight as a covariate

	Date										
	1983[a]					1984					
	3 Aug.	17 Aug.	31 Aug.	14 Sept.	28 Sept.	6 July	20 July	3 Aug.	17 Aug.	31 Aug.	14 Sept.
Thrips on frame	NS	NS	$P < 0.05$	NS	$P < 0.05$	NS	NS	NS	NS	$P < 0.01$	Diff.[b] slopes
Mean ratio (susc./resist.)			3.3		0.039					0.23	
Antilog (mean + SE)			5.0		0.129					0.33	
Antilog (mean − SE)			2.2		0.012					0.17	
Thrips in head	NS	$P < 0.05$	$P < 0.05$	$P < 0.05$	NS	NS	NS	Diff.[b] slopes	$P < 0.01$	$P < 0.05$	$P = 0.052$
Mean ratio (susc./resist.)		2.8	11.5	6.7					10.7	3.4	6.2
Antilog (mean + SE)		4.2	23.2	13.0					20.2	5.7	14.2
Antilog (mean − SE)		2.0	5.7	3.4					5.7	2.1	2.7

NS, contrast between susceptible and resistant varieties not significant at $P < 0.05$. If P is less than or approximately equal to 0.05, level of significance is given.
[a] Dry weights not taken before 3 August 1983.
[b] Diff. slopes, significant ($P < 0.05$) differences in slope among varieties. Contrast not made because the size of susceptible vs resistant contrast depends on the head or frame weight chosen for comparison. See text for further information.

Discussion

This study indicated that reduced damage previously observed on these cabbage varieties is associated with reduced thrips numbers in the head, particularly during the late summer (mid-August to mid-September). Differences in thrips numbers were greatest for those varieties with the largest differences in observed thrips damage, 'Market Prize' and 'Falcon.' These differences in thrips numbers per head remained after adjustment for head dry weight as a covariate to remove any effect of differences in head size among varieties. After this adjustment, thrips numbers on susceptible heads were approximately 10 times (range ± SE, 5.7 to 23.2) as high as on resistant varieties for one date each year (31 August 1983 and 17 August 1984). Thrips numbers on the frame leaves of resistant varieties were not lower, and at the end of the season were actually higher, relative to susceptible varieties.

Results of this study suggest that the observed reduction in thrips damage to cabbage is, at least in part, the result of reduced thrips numbers in the head rather than a difference in the cosmetically important response (production of bronzed and blistered areas) to thrips feeding or oviposition. These results also suggest that further studies on the mechanisms and inheritance of resistance should concentrate on studying the properties of the cabbage head influencing thrips behavior and population growth and the distribution of thrips on the plant between head and frame leaves. Finally, our data indicate that, while there are differences among varieties in rates of growth and senescence, and thus size of the head and frame leaves, the observed differences in thrips numbers cannot be entirely explained by these size differences and must be determined by other chemical or morphological differences in these cabbage varieties.

Sinçe the time of Painter, mechanisms of resistance have been classified by the categories of nonpreference, antibiosis, or tolerance. Painter (1951) defined tolerance as "a basis of resistance in which the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host." Painter worked mostly with grain or other seed crops, thus his definition of tolerance emphasizes the ability of the plant to reproduce. For the case of thrips resistance in cabbage, where we are concerned with cosmetic damage to a vegetative product, a more appropriate definition of tolerance would be the ability to produce a high quality and quantity of marketable yield in spite of supporting an insect population equal to that on a susceptible host. By this definition, resistance to thrips in cabbage could be considered a case of tolerance. The three categories are not mutually exclusive; nonpreference or antibiosis may also be involved in reducing thrips numbers in the heads of resistant varieties. The resistant varieties 'Falcon' and 'Titanic 90' had as many thrips per plant as susceptible varieties, but there were fewer thrips infesting the head of resistant varieties and thus less cosmetic damage to the marketable product. Because the numbers of thrips per plant are equal on susceptible and resistant plants (and because *T. tabaci* has a wide host range), the selection pressure on thrips to overcome resistance should be low.

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