

Inheritance of resistance to damage by *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) in Cabbage

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Summary

The inheritance of resistance in cabbage (*Brassica oleracea* var. *capitata*) to damage caused by *Thrips tabaci* Lindeman was studied in progeny from four crosses between resistant and susceptible inbred lines. In two families sharing the same susceptible parent, the narrow-sense heritability was calculated to be high (>90%), using the Warner method of calculation (Warner, 1952). The other two families, also sharing a susceptible parent, had very low narrow-sense heritability (0–11%). In three of the four families, however, the validity of the Warner calculations were called into question due to significant epistatic interactions. In all four families, the F₁ populations approached or exceeded the susceptibility of the susceptible parent, indicating that susceptibility is generally dominant. The importance of epistasis and dominance suggests that tests of hybrid combinations to determine combining ability for thrips resistance may be required, rather than selecting only on the basis of thrips damage to the inbred lines. The technique of planting wheat upwind from the cabbage test plot did generate adequate levels of thrips pressure, but the infestation was uneven in two of the four blocks, so that reasonable replication of tests is required.

Introduction

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

Host plant resistance to thrips appears to be a promising alternative to chemical control. A survey of varietal resistance to thrips in processing cabbage (Shelton et al., 1983) found that, although no variety went entirely undamaged, there were considerable differences in severity and depth of damage, including some varieties with impressive resistance. Varieties for fresh market and storage in New York State, however, are all either highly or moderately susceptible (Gardner et al., 1986). This indicates that there is a need to transfer thrips resistance from lines used for processing cabbage into cabbage varieties suitable for fresh market and

storage. This study of the inheritance of thrips resistance in cabbage should provide information useful in achieving that goal.

Material and methods

The inheritance of resistance to *T. tabaci* was examined in four families (Code numbers of families and parents are given in Table 1). Two additional populations were produced, but did not develop sufficient thrips populations and damage to show differences in resistance, probably because they were planted later than the four populations discussed here. The parental lines used were chosen from a replicated test of four resistant and four susceptible lines and their hybrids conducted at the same location in 1984. The lines used as susceptible parents are the parents of a fresh market hybrid variety previously demonstrated to be highly susceptible to thrips. The resistant lines had been inbred and selected for thrips resistance for six generations by one of the authors (M.H.D.) from material originally bred for high dry matter content.

Testing was conducted in 1985 at the New York State Agricultural Experiment Station Vegetable Research Farm near Geneva, NY. To ensure adequate populations of *T. tabaci*, a strip of wheat 1 m wide was planted in the fall of 1984 along the upwind side of the field. Previous work (North & Shelton, 1986b, c) had shown that *T. tabaci* overwinters in winter wheat (and, to a lesser degree, alfalfa) and that populations build up in wheat fields in early spring, then move to cabbage as the

wheat matures and begins to dry out.

Each family was planted in a single block, 6 rows, 1 m apart by 30 m long, except for 825, which was in a block of 7 rows by 26 m. For each family, six populations were produced: P₁, P₂, F₁ (also the reciprocal F₁ for three of the families), F₂, B₁, and B₂. The parental and F₁ populations were planted in rows of ten plants of the same genotype, and F₂ and backcross populations were in rows of twenty plants. These short rows were distributed at random within the family block. Also in each family block were four standard varieties known to represent a wide range of thrips susceptibility: 'Falcon' (Royal Sluis, highly resistant), 'Titanic 90' (Ferry-Morse, moderately resistant), 'Supergreen' (Reed's Seeds, moderately to highly susceptible), and 'Market Prize' (Harris Moran, highly susceptible).

Damage ratings were given to each cabbage head (excluding those plants whose heads did not properly develop, and those whose heads had split open or rotted). First, ratings of O (no damage), Very Light (0–1% of leaf area damaged), Light (1–10%), Moderate (10–25%), or Heavy (25–100%) were assigned, based on visual estimates, to leaves as they were peeled off the head. The wrapper and first ten leaves were rated for families 835 and 836, reduced to the first seven leaves for 825 and 826, unless heavy damage continued beyond the seventh leaf. Then, overall damage ratings (0–4.5, using 0.5 intervals) were assigned to each head, using the individual leaf ratings to ensure that overall ratings remained consistent over time. For example, a head with six leaves heavily damaged and several other leaves with moderate damage, would rate a 4.0.

Narrow-sense heritability estimates were calculated using the Warner method (Warner, 1952). The joint scaling test of the additive-dominance model, as described by Mather & Jinks (1977), was used to detect epistatic interactions which would invalidate the additive-dominance model, and hence, the calculations of heritability (Warner, 1952). This test was performed on the raw data and on data transformed by using the logarithms, square roots, and the squares.

Generation means were analyzed using weighted

Table 1. Parents used in each of the four families studied in detail

Family	Susceptible parent (P ₂)	Resistant parent ^a (P ₁)
835	708	705 (female)
836	708	706 (female)
825	707	705 (female)
826	707	706 (male)

^a Whether this parent was used as a male or female in the original cross is also indicated.

regression to fit the model:

$$Y = M + a_1A + a_2D + a_3AA + a_4AD + a_5DD$$

where Y is the mean of a given generation, M is the intercept, A is the additive genetic effect, D is the dominance effect, AA is the additive x additive epistatic effect, AD is the additive x dominance epistatic effect, and DD is the dominance x dominance epistatic effect. The coefficients (a_1 – a_5) for each of these effects for each generation (Gamble, 1962) are listed in Table 2.

As suggested in Mather & Jinks (1977), any genetic effect not significantly different from zero (t test, $p > 0.05$) was eliminated from the model, and the regression was run again with this reduced model. The sequential sums of squares from this model were used to calculate the percentage of the variability which could be explained by additive and dominance effects and the minimum percentage of the sums of squares which must be attributed to epistatic effects: as discussed in Hayman (1960), when epistasis is present, genetic variation cannot be partitioned uniquely into additive, dominance, and epistatic components. By using sequential sums of squares, we are attributing the maximum amount of variation possible to the additive effect, then to the dominance effect and, finally, to the epistatic effects. A chi-square test was also performed on this reduced model (when enough de-

grees of freedom were available) to test whether first order (two-loci) epistatic effects adequately accounted for the differences among generation means (Mather & Jinks, 1977). T-tests were performed to compare the susceptibility of lines and of standard varieties.

Results and discussion

Frequency distributions of damage ratings in the six generations of four families are given in Table 3. The F_1 mean susceptibility exceeds that of the susceptible parent (707) in families 825 and 826, and approaches that of the susceptible parent (708) in 835 and 836. This indicates that susceptibility tends to be dominant in relation to resistance. The greater susceptibility of F_1 's than of the susceptible parents together with the transgressive segregation for susceptibility in F_2 's could indicate either overdominance or that the resistant lines carry some genes for susceptibility. Both resistant inbreds used in this study were significantly more susceptible than the highly resistant standard variety 'Falcon' (706 compared to 'Falcon': $t = 11.14$, $df = 55$, $p < 0.001$; 705 compared to 'Falcon': $t = 8.96$, $df = 42$, $p < 0.001$. For actual damage ratings of standards, see Table 4), and 706 was also more susceptible than 'Titanic 90' ($t = 4.29$, $df = 55$, $p < 0.001$).

Changing the direction of the cross had no significant effect on the F_1 means (Table 3), but in all three reciprocal crosses, when the susceptible line was used as the female the variance was less than half that when the cross was reversed. (See Table 1 for the direction of the F_1 cross). Only in the case of the single F_1 in the 835 family, rated a full unit less damaged than any of the other F_1 's, was there an indication from the data of having mistakenly included a parental self in the F_1 's.

The Warner method of calculating narrow-sense heritability indicated very high heritability for 835 and 836 (98% and 92%, respectively) and very low heritability in 825 and 826 (11% and 0%, respectively). The low narrow-sense heritability in these two families may be related in part to the high environmental component of variability (35% and 54%, respectively).

Table 2. Matrix of coefficients used to estimate genetic effects from generation means

Generation	Genetic effect ^a					
	M	A	D	AA	AD	DD
B_1	1.0	0.5	0.0	0.25	0.0	0.0
B_2	1.0	-0.5	0.0	0.25	0.0	0.0
F_1	1.0	0.0	0.5	0.0	0.0	0.25
F_2	1.0	0.0	0.0	0.0	0.0	0.0
P_1	1.0	1.0	-0.5	1.0	-1.0	0.25
P_2	1.0	-1.0	-0.5	1.0	1.0	0.25

^a M = mean, A = additive genetic effect, D = dominance genetic effect, AA = additive x additive effect, AD = additive x dominance effect, DD = dominance x dominance effect (Gamble, 1962).

Along with generally high within-block variation (see variance column in Table 3), family 825 also had a specific notable trend toward higher damage in the seventh row (the row furthest from the wheat) than for the same genotypes elsewhere in the block or in other blocks. For example, P₁ had a mean damage rating in row 7 of 2.0, (SEM = 0.22), compared to the same line in row 6 with mean rating = 1.4, (SEM = 0.16). This difference is statistically significant ($t = 2.18$, $df = 15$, $p < 0.05$). Another example, not statistically significant, but showing the same trend: for P₂ in the same family, the mean damage rating in row 7 is 3.4, (SEM = 0.32), compared to the same line in row 1, the mean

damage rating of which is 2.6, (SEM = 0.30). Also, the two susceptible standards ('Market Prize' and 'Supergreen', see table 4) for 825 happened to be in row 7 of the plot. Although they can not be used to measure the within-block variance, because they were in only one location per block, these two varieties did have higher thrips damage in this location than elsewhere in the field (Table 4).

The data from block 826 for these same susceptible standards indicates that thrips pressure was lower and more variable in this block than in other blocks, with the exception of the high variation for 'Market Prize' in the 825 block. Inbred 707 (P₂ for both 825 and 826) similarly had lower thrips dam-

Table 3. Ratings of *T. tabaci* damage to cabbage heads in five generations of four families

Family	Generation	Damage rating ^a										No.	Mean	Var.
		0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5			
835	P ₁ (R)	2	11	5								18	1.08	0.096
	P ₂ (S)						5	11	3			19	3.45	0.11
	F ₁			1			7	11	1			20	2.78	0.17
	F ₁ (recip)						1	3	16			20	2.88	0.076
	F ₂	4	8	11	8	18	23	11	16	15		114	2.86	1.28
	B ₁	4	20	21	7	6	6	6	1			71	1.77	0.79
	B ₂		3	2	6	12	21	20	7			70	2.96	0.51
836	P ₁ (R)		7	12			1					20	1.38	0.13
	P ₂ (S)						1	7	12			20	3.28	0.091
	F ₁						3	9	6	2		20	3.17	0.19
	F ₁ (recip)						2	15	3			20	3.02	0.065
	F ₂			6	9	14	24	21	19	22		115	3.33	0.77
	B ₁		1	7	11	15	13	13	3	1		64	2.69	0.58
	B ₂			1	4	8	26	14	2			55	2.99	0.25
825	P ₁ (R)	1	2	9	2	2	1					17	1.65	0.37
	P ₂ (S)			4	1	1	4	4	3	1		18	2.94	0.97
	F ₁						3	3	1	2		9	3.61	0.36
	F ₁ (recip)						2	5	11	1		19	3.29	0.15
	F ₂		11	18	5	8	17	21	5	14		99	2.78	1.31
	B ₁	1	5	22	1	6	6	7	8	8		64	2.59	1.51
	B ₂			8	7	3	7	13	10	5		53	3.06	0.96
826	P ₁ (R)		5	8	4							17	1.47	0.14
	P ₂ (S)		2	8	4	1	3					18	1.86	0.41
	F ₁			2	1	4	3	5	2	2		19	3.08	0.79
	F ₂		3	11	22	20	14	33	16	7		126	2.91	0.82
	B ₁		3	18	10	6	11	12	2	2		64	2.45	0.86
	B ₂			6	7	6	3	13	4	1		40	2.82	0.78

^a 0.0 = no damage, 4.5 = severe damage. For further information, see text.

age in the 826 block than in 825 (even when the data from row 7 is omitted). In fact, this supposedly susceptible parent was barely more susceptible in the 826 block than the resistant parent, although the F_1 , F_2 , and backcrosses in this family were reasonably susceptible. In another strange result, the variance data from Table 3 indicate high variance in the P_2 and F_1 generations, relative to other families, but not in the F_2 or backcross generations. There is no obvious explanation from the pattern of planting why variance should be so high among the P_2 and F_1 generations, which should be genetically uniform, without being correspondingly higher in the F_2 and backcross generations, which should have more genetic diversity.

A problem with using the Warner calculations to measure narrow-sense heritability is that the joint scaling test for epistatic interactions (Mather & Jinks, 1977) showed significant deviation in three of the four families (835, 836, and 826) from the additive-dominance model assumed in making Warner calculations (835: $\chi^2 = 15.7$, 3 df, $p < 0.005$; 836: $\chi^2 = 72.9$, 3 df, $p < 0.005$; 826: $\chi^2 = 10.1$, df = 3, $0.025 < p < 0.01$). When the data were transformed to other scales: logarithms, square roots and squares, the deviations generally remained significant. The only exception was that when using the x^2 -transformation for 826, the deviations were barely nonsignificant ($\chi^2 = 6.64$, 3 df, $0.10 > p > 0.05$). Thus, the problem appears

to be one of epistatic interaction, not one of finding a proper scale of measurement.

Generation means analysis (Table 5) can be used to determine how the pattern of means deviates from the additive-dominance model and to give some indication of the importance of epistatic effects, by measuring the additional percentage of the sums of squares accounted for beyond those of the additive and dominance effects. In 825, no epistatic effects are significantly different from zero. In 835, the additive X additive and dominance X dominance effects are statistically significant, but account for only a tiny fraction (2.5%) of the total sum of squares in the model. The importance of the additive effect in this family is also confirmed. In 836, all three epistatic effects are statistically significant, and their combined sum of squares is a substantial fraction (16.2%) of the total. In 826, the additive X additive effect accounts for most (70.7%) of the total sum of squares, with a small additive effect, and dominance effect so small that it is not statistically significant. If the overall P_2 mean for the 825 and 826 plots is substituted for the low 826 P_2 mean, we find that the same genetic effects are significant. Thus, this unusual pattern is not an artifact of the low P_2 mean in this block.

For both 835 and 826, the two-loci epistatic model adequately accounted for the generation means (for 835 $\chi^2 = 0.170$, df = 1, $0.75 > p > 0.50$; for 826,

Table 4. Ratings of thrips damage for the four cabbage varieties grown as standards in each of the four family blocks

Block		Variety			
		Market prize	Supergreen	Titanic 90	Falcon
835	Mean rating	3.10	2.20	0.85	0.39
	SE	0.067	0.15	0.11	0.073
836	Mean rating	3.17	2.95	1.20	0.45
	SE	0.14	0.19	0.082	0.05
825	Mean rating	3.80 ^a	3.70 ^a	1.22	0.45
	SE	0.24	0.11	0.12	0.05
826	Mean rating	2.44	2.06	0.90	0.50
	SE	0.27	0.28	0.10	0.00

^a These checks were in the 7th row of this plot, suspected of having an unusually high infestation of thrips. For details, see text.

$\chi^2 = 0.920$, $df = 3$, $0.90 > p > 0.75$). Because all the parameters in the model for 836 were significant, the model is a perfect fit estimate, and no degrees of freedom are available to test the adequacy of the model.

Conclusions

Of the four families studied, there appears to be a substantial additive component in the inheritance

of resistance in 835 and, with less certainty because of epistasis, in 836. While the two inbred lines used as sources of resistance behaved similarly in 835 and 836, they had quite different patterns of inheritance when crossed to a different susceptible parent in 825 and 826. Because of these different patterns and the importance of dominance and epistasis in some crosses, it would be advisable to test inbreds for their combining ability for thrips resistance in hybrid combinations, rather than selecting only on the basis of thrips damage to the inbred

Table 5. Analyses of generation means for thrips damage rating in four families. Means were weighted according to the reciprocal of the variance of the mean

Family	Gen. effect ^a	Six parameter model			Reduced model		
		Estimate	Prob. ^b	Std. error	Estimate ^c	Sequential SS ^d	% SS ^e
835	M	2.86	***	0.106	2.86	6474.99	
	A	-1.20	***	0.136	-1.18	588.45	89.4
	D	-1.43	**	0.509	-1.43	53.75	8.2
	AA	-1.99	***	0.503	-1.99	1.09	0.2
	AD	-0.015	-	0.147	-	-	-
	DD	2.71	***	0.706	2.70	14.96	2.3
836	M	3.33	***	0.082	3.33	9523.98	
	A	-0.303	*	0.117	-0.303	267.34	61.0
	D	-1.17	**	0.410	-1.17	99.62	22.7
	AA	-1.95	***	0.402	-1.95	31.70	7.2
	AD	0.65	***	0.128	0.65	33.88	7.7
	DD	1.44	*	0.592	1.44	5.92	1.3
825	M	2.78	***	0.036	2.82	2973.19	
	A	-0.47	*	0.204	-0.59	54.54	50.2
	D	1.28	**	0.464	1.13	53.44	49.2
	AA	0.19	-	0.434	-	-	-
	AD	0.18	-	0.246	-	-	-
	DD	-0.13	-	0.894	-	-	-
826	M	2.91	***	0.081	2.93	2622.48	
	A	-0.37	*	0.181	-0.23	49.98	28.0
	D	0.33	-	0.534	-	-	-
	AA	-1.08	*	0.486	-1.25	126.39	70.7
	AD	-0.18	-	0.220	-	-	-
	DD	0.012	-	0.909	-	-	-

^a Coefficients used in estimating the genetic effects given in Table 2.

^b * indicates that the parameter is statistically different from zero at the 95% level of probability, ** indicates the 99% level, and *** indicates the 99.9% level. Standard errors and degrees of freedom for the t tests are calculated as described in Mather & Jinks (1977).

^c All six genetic effects were significant for 836, so the estimates are the same as in the full six parameter model.

^d Sequential (Type 1) sums of squares for the reduced model including only those effects significantly different from zero at the 95% level or greater.

^e Percentage of (Total Uncorrected Sum of Squares - Sum of Squares for M) accounted for by each of the other statistically significant effects.

lines themselves. This would help avoid potential problems like the family 826 in which both parents appear moderately resistant, but the F_1 is strongly susceptible. It would also avoid problems with inbreds appearing resistant because they lack vigor and produce only small, loose, or late heads.

The resistant lines used in this study are only moderately resistant to thrips damage. Even in the inbred resistant parents, the level of damage was much higher than in the commercially available variety 'Falcon' and slightly higher than in 'Titanic 90'. Thus, the best use of these lines would probably be in combination with other sources of thrips resistance. Moderately resistant inbreds such as these might also be useful as tester lines to determine the resistance or susceptibility of other lines in hybrid combinations; susceptible lines would not be appropriate if susceptibility is generally dominant, as we found here.

The technique of planting wheat upwind provided a sufficient level of thrips infestation for differences in resistance to be evaluated, as long as the cabbage is planted early enough, so that heads are formed by the time the wheat has matured. By using this technique, the labor and cost of rearing large numbers of insects and inoculating plants can be avoided. Every single plant, except for some of the highly resistant 'Falcon' standards, showed some thrips damage, so there were no plants entirely skipped. There was, however, high within-plot variability in some family blocks. This was unexpected, based on data from onion fields, showing thrips' distribution within fields to be random or overdispersed, rather than clumped, and without noticeable differences of distribution in interior vs. exterior regions of a field (Shelton et al., 1987; Edelson et al., 1986). To avoid this problem, reasonable levels of replication should be used, perhaps by setting out alternating cabbage test plots and strips of maturing wheat.

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