Role of Nonpreference in the Resistance of Cabbage Varieties to the Onion Thrips (Thysanoptera: Thripidae)

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ABSTRACT Preference of *Thrips tabaci* Lindeman adults for four varieties of cabbage was tested in the field by putting uninfested potted plants next to plots of wheat, oats, or alfalfa as thrips were moving out of these crops, and in the laboratory by placing thrips adults in circular plastic boxes and allowing them to choose among leaf disks from the heads of the same four varieties. In the field tests, more *T. tabaci* adults accumulated on heads of varieties previously identified as susceptible ('Market Prize' and 'Supergreen,' means of 28.4 and 16.2 thrips per head, respectively, over five tests) compared with those identified as resistant ('Titanic 90' and 'Falcon,' means of 5.5 and 2.9, respectively). This difference was consistent for all three crops used as source plots and for all stages of cabbage development once the developing heads reached a fresh weight of 10 g. For the frame (outer) leaves of the cabbage plant, 'Falcon' was generally preferred over the other varieties, although the numbers of thrips colonizing frame leaves of all varieties decreased to nearly zero late in the season. In the laboratory tests, no differences in preference among leaf disks from the heads of the four varieties were observed.

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

BEFORE ANY detailed studies of mechanisms of host plant resistance to insects can be made, it must be determined whether resistance is caused by nonpreference, antibiosis, tolerance, or some combination of these (Painter 1951). The type of resistance may be important in determining its long-term durability. For example, the combination of nonpreference with antibiosis generally reduces selection pressure on the insect population to overcome the resistance compared with antibiosis alone, as long as alternative preferred food sources are available (Gould 1984). Information on the type of resistance is also useful for designing good assays for purposes of selection in breeding new varieties.

Nonpreference is most commonly measured by setting up an array of different plant varieties; releasing the insects into this array, taking care not to bias their choice by the particulars of the arrangement; then assessing preference by counting eggs, measuring damage, or counting numbers of individuals on the different varieties (e.g., Overman & MacCarter 1972, Teetes 1980, Elsey 1985, Heinrichs et al. 1985). Some important concerns about this kind of test are as follows. The appropriate dispersing stage of the insect and the appropriate plant stage or plant parts attacked by the dispersing insect should be used (Painter 1951). Any differences in preference found in this "choice test" should also be tested when the varieties are isolated from each other in uniform plantings (Cantelo & Sanford 1984). The environmental conditions of the test should be as close to field conditions as possible, to prevent anomalous results due to artificial lighting, uniform temperature, moisture stress, etc. (Tingey & Singh 1980).

In previous studies, the resistance of cabbage varieties to *Thrips tabaci* Lindeman, as measured by visible thrips damage to the head at harvest, has been demonstrated (Shelton et al. 1983, Stoner 1987). We have shown that this reduced damage in resistant varieties is associated with reduced numbers of *T. tabaci* in the head during approximately 1 mo as the cabbage heads are maturing (Stoner 1987). In this study, we investigated whether nonpreference by adult *T. tabaci* contributes to the reduction in numbers of *T. tabaci* on heads of resistant varieties. Specifically, we tested whether *T. tabaci* adults showed a preference for leaf disks from heads of susceptible varieties in the laboratory; whether varieties of cabbage susceptible to *T. tabaci* accumulate greater numbers of adult colonizers in the field than resistant varieties, either on a whole-plant basis, or only in the heads; whether the maturity of the cabbage plants or using different crops as sources of thrips affects varietal preference; and whether there is any relationship between preference for frame (outer) leaves and heads for different varieties.

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Materials and Methods

Two kinds of preference tests were used—a laboratory test involving a choice of leaf disks from the heads of four varieties of cabbage, and a field test approximating what we believe to be the circumstances of thrips colonization in the field.

The laboratory test used leaf disks from mature heads of field-grown plants of the four cabbage varieties used in previous work—'Market Prize' and 'Supergreen' (susceptible varieties) and 'Titanic 90' and 'Falcon' (resistant varieties). These heads had been sprayed only with *Bacillus thuringiensis* Berliner to reduce damage by Lepidoptera. The leaf disks were 5.2 cm in diameter and taken from the fourth to sixth leaves of the head (counting inward) on the day of the test. They included areas adjacent to, but not including, the main vein (areas which often have thrips damage on susceptible plants) and were selected to minimize pre-existing thrips damage on the disk itself. Four leaf disks, one from each of the four varieties, were arranged at equally spaced intervals around the edge of a clear circular plastic box 21.0 cm in diameter and 7.7 cm tall. Adult *T. tabaci* were collected from a laboratory culture started with thrips from cabbage but maintained on onions because of the much greater ease of rearing and recovering insects on onion plants. Forty thrips were collected into a vial using an aspirator. To move thrips into the test boxes, carbon dioxide was briefly released into the vial through the fine-mesh screen covering the lid, the vial was tapped on a flat surface to knock the thrips from the sides and lid to the bottom, then the thrips were released into the center of the test box. The test boxes were held at 24°C in a growth chamber with 10 34-W fluorescent bulbs spanning the length of the ceiling. At the end of 2 h, the boxes were opened, and each leaf disk was immediately placed in a container of 70% ethanol. The thrips on each leaf disk were counted. This experiment was replicated four times; these data were analyzed with a chi-square test.

For our field preference tests, we used a technique suggested by data from North & Shelton (1986) showing that *T. tabaci* adults move out of wheat, oats, and alfalfa, especially as these crops senesce or are cut, and colonize cabbage. Thus, putting uninfested cabbage plants of different varieties adjacent to maturing wheat, oats, and alfalfa plots and recording the number and distribution of adult *T. tabaci* on the plants provides a test under circumstances similar to the real conditions of colonization of cabbage fields.

Plants of the four varieties mentioned previously were grown in Cornell mix in 25-cm pots in the greenhouse. Metal halide lamps were used for supplemental lighting (initial photoperiod 16:8 [L:D] for young plants, decreasing as the plants matured to induce heading). In 1985, 30-10-10 (N-P-K) fertilizer was given in the watering solution on alternate weeks at 200 ppm N. In 1986, 20-20-20 (N-P-K) fertilizer was provided continuously in the watering solution at 100 ppm N. The greenhouse was fumigated weekly with nicotine to reduce thrips invasions, and any plant with visible thrips or thrips damage was immediately destroyed. All plants were checked for signs of thrips before they were used in the field.

The wheat, oats, and alfalfa plots used in 1985 at the Vegetable Crops Farm near Geneva, N.Y. were 6.1 by 6.1 m, with 4.6-m alleyways between plots; the alleyways were kept free of weeds. There were 27 plots of the three crops, arranged in one 3 × 3 and one 3 × 6 array. Three plots for each testing period were chosen on the basis of a visual assessment of maturity as likely sources of *T. tabaci*. A row of four potted cabbage plants, one of each of the four varieties, was set 1 m from the downwind edge of the three chosen plots, with 60 cm between pots. Thus, there were three replicates, each allowing the thrips a choice among four plants (one of each variety), for each testing period. The pots were placed in holes with 5 cm of pot above the soil surface to prevent the pots from tipping over and to put the cabbages at about their natural height in the field. One week was chosen as a period long enough to allow reasonable numbers of thrips to colonize the cabbage plants, but short enough to preclude production of a new generation of adults and to reduce the possible effects of antibiosis on thrips numbers.

The dates, source crops, and stage of cabbage plants used (see Andaloro et al. [1983] for a description of cabbage growth stages) for each of the tests in 1985 were as follows: test 1, 10–17 July, next to wheat, cabbage precupping; test 2, 23–30 July, next to oats, cabbage cupping, except for 'Market Prize,' which was in the early head stage; test 3, 1–8 August, next to late-planted oats, cabbage in early head stage, except for 'Falcon,' which was still cupping; test 4, 14–21 August, next to alfalfa, cabbage in early head stage but 'Falcon' much smaller than other varieties (46 g fresh weight head compared with 171–218 g for other varieties, SE of the means 31 g); and test 5, 5–16 September (extended beyond 1 wk because of cold, wet weather unsuitable for thrips movement), next to alfalfa, cabbage in head-fill stage, 'Falcon' (343 g fresh weight head) and 'Supergreen' (416 g fresh weight) smaller than 'Titanic 90' (503 g) and 'Market Prize' (558 g, SE of the means 31 g).

In 1986, a single test was run from 30 June to 8 July next to one wheat field (60 by 23 m). A row of 14 cabbages (three sets of the four varieties, with two additional 'Supergreen' plants used as borders) was put next to the wheat field as in 1985. In this test, all plants had mature heads, with the 'Falcon' heads the largest (mean fresh weight 1,293 g, SE = 92 g) and 'Market Prize' the smallest (636 g, SE = 92 g).

After the testing period, the head and frame leaves were cut, sealed separately in plastic bags, weighed, and washed thoroughly in 70% ethanol. The ethanol and the water used to rinse the bags was filtered through fine-mesh plastic screens, and *T. tabaci* were counted at 18–20× magnification. Any plants with pupae were considered to have

Table 1. Mean numbers[a] of *T. tabaci* adults on whole plants, in heads, and on frame leaves of potted cabbage plants of four varieties set adjacent to plots of wheat, oats, and alfalfa, Geneva, N.Y., 1985

Variety[b]	Adults on whole plant		Adults in head		Adults on frame leaves	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
Market Prize	45.7	37.6–54.6	28.4	23.0–34.4	14.1	11.0–17.8
Supergreen	38.9	31.7–46.6	16.2	12.0–21.1	18.8	15.3–22.7
Titanic 90	21.9	17.0–27.4	5.5	3.4–8.1	15.2	12.1–18.7
Falcon	31.6	25.6–38.2	2.9	1.4–4.8	27.6	23.3–32.2
F statistics	$F = 9.0$ $P < 0.0003$		$F = 41.5$ $P < 0.0001$		$F = 10.8$ $P < 0.0001$	

[a] Transformed back to actual numbers from square root transformations used for analysis of variance. Least-squares means (SAS Institute 1985) used when there are missing values.
[b] 'Market Prize' and 'Supergreen' are susceptible varieties; 'Titanic 90' and 'Falcon' are resistant.

been infested in the greenhouse before the test began, and any nonzero data from these plants were treated as missing. Dry weights were taken after the plant material had dried for at least 2 d at 100–110°C.

The numbers of adults in heads, on frame leaves, and total adults on whole plants were analyzed using a general analysis of variance over all tests for 1985, using as the independent variables date (a variable indicating the different tests), block nested within date (the row next to each plot was treated as a block), variety, and variety by date interactions. For all three of the dependent variables (thrips adults in heads, on frame leaves, and total on whole plants), a square-root transformation was used to stabilize the variance. Because there were a substantial number of zero values for adults on frame leaves (mainly for the last two tests), the square root of (thrips + 1) was used. The variation explained by variety was also analyzed using a preplanned, orthogonal set of single degree of freedom contrasts. The pair of susceptible varieties ('Market Prize' and 'Supergeen') was contrasted with the pair of resistant varieties ('Titanic 90' and 'Falcon'), and the other two contrasts compared the two varieties within each of these pairs. Each test in 1985 was also analyzed separately with an analysis of variance and the same orthogonal contrasts. Where any missing values occurred, least-squares means (SAS Institute 1985) were used. For the single 1986 test, blocking was not important and was not used in the analysis. Otherwise the analysis was the same as for the individual tests in 1985.

Results

Laboratory Test. There was no indication of any preference among leaf disks from the heads of the four varieties in this experiment ($\chi^2 = 2.232$; df = 3; $P > 0.50$). For each of the four tests, between 5 and 25% of the thrips adults died in handling or were not on any of the four leaf disks at the end of the test.

Overall Analyses of Variance for 1985 Tests. Variety was highly significant for all three dependent variables (for adults in the head, $F = 41.5$; df = 3, 27; $P < 0.0001$; for adults on the frame, $F = 10.8$; df = 3, 29; $P < 0.0001$; for total adults, $F = 9.0$; df = 3, 27; $P = 0.0003$), and the contrast between susceptible and resistant varieties was also significant for all three (in head, $F = 109.4$; df = 1, 27; $P < 0.0001$; on frame leaves, $F = 141.8$; df = 1, 29; $P = 0.018$; total adults, $F = 22.7$; df = 1, 27; $P < 0.001$). The means over the 1985 season (Table 1) show that the pair of susceptible varieties had more adults on whole plants and on the head than the pair of resistant varieties. For adults on frame leaves, the significant difference between susceptible and resistant varieties is apparently because of the high numbers of thrips on 'Falcon' frame leaves, causing the average of the resistant varieties to be high, even though 'Titanic 90' has the same numbers as the susceptible varieties (95% confidence intervals overlap).

Analyses of Individual Tests—1985 and 1986. The variety × date interaction (date indicates the five different tests in 1985, with their different source plots and stages of cabbage maturity) was important enough (in head, $F = 3.56$; df = 12, 27; $P = 0.0030$; on frame leaves, $F = 3.38$; df = 12, 29; $P = 0.0036$; total thrips, $F = 2.04$, df = 12, 27; $P = 0.06$) to indicate that the effect of variety changed over the different tests, thus each test should be analyzed separately. These results, plus the analysis of the single test run in 1986, are shown in Fig. 1.

The heads had a consistent pattern of numbers of adults among varieties in all the tests. This also includes the 1986 test, when all the heads were mature and the 'Falcon' heads were largest and 'Market Prize' smallest (unlike the 1985 tests, when 'Market Prize' had larger and more mature heads throughout), indicating that differences in thrips numbers were caused by varietal characteristics other than head size. In all but test 1 in 1985, the differences among varieties are significant (*F* test, $P \leq 0.05$); the differences between susceptible and resistant pairs of varieties are significant ($P \leq 0.01$ for all five dates); and for the tests 2, 5, and 6 the difference between 'Market Prize' and 'Supergreen' is also significant ($P < 0.01$ for all three dates).

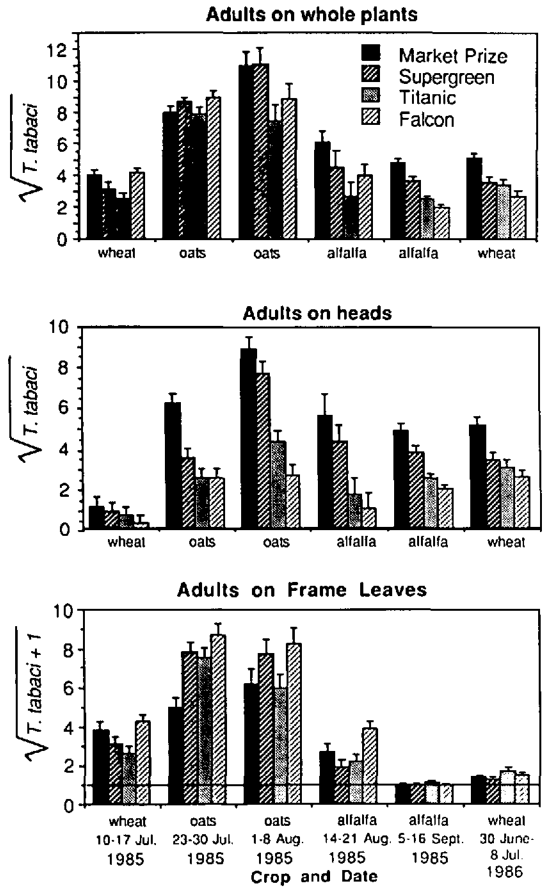

Fig. 1. Mean numbers of *T. tabaci* adults on whole plants, in heads, and on frame leaves of potted cabbage plants of four varieties set next to plots of wheat, oats, or alfalfa for the dates listed. Error bars represent the standard error of the means for each date, analyzed separately with analysis of variance.

For adults on frame leaves, the only consistent pattern visible among varieties is that 'Falcon' had the largest number of colonizers for all of the first four tests, the ones with substantial numbers of thrips. (Note that because these data were analyzed as $\sqrt{(\text{thrips} + 1)}$, only columns rising above the line at 1 had any adults present.) The significant contrasts were between 'Falcon' and 'Titanic 90' (tests 1 and 4, $P < 0.05$) and, for test 2, between resistant and susceptible pairs of varieties and between 'Supergreen' and 'Market Prize' ($P < 0.05$).

Differences among dates in the numbers of adults on frame leaves, without regard to variety, are also apparent. Because the cabbages were growing more mature with each successive test while different crops were also maturing, it is not entirely clear whether these differences are caused by low attractiveness of frame leaves in more mature cabbage plants, or whether thrips emigrating from oats tend to settle on frame leaves more often than thrips from alfalfa or wheat. However, comparison of the two tests with wheat, the first with young cabbage plants with no real head and the last with mature cabbage plants, shows that, over all four varieties, the number of adults was lower on frame leaves on the mature plants (mean of $\sqrt{(\text{thrips} + 1)} =$ 1.46 for the 1986 test, compared with 3.50 for test 1 in 1985), although the adults on the whole plants were equal (mean of $\sqrt{\text{thrips}}$ = 3.65 and 3.50, respectively). This suggests that frame leaves decline in relative attractiveness to colonizers as the heads mature.

When adults were counted on a whole-plant basis, 'Market Prize' (and, to a much smaller extent, 'Supergreen') had more thrips than the resistant varieties beginning with test 3. There are statistical differences ($P < 0.05$) between susceptible and resistant pairs of varieties in tests 3, 5, and 6, between 'Market Prize' and 'Supergreen' in tests 5 and 6, and between 'Falcon' and 'Titanic 90' in test 1. Thus, when the attractiveness of frame leaves was low in the later samples, or the numbers of thrips in the head were high and the preference for susceptible varieties was very distinct (as in test 3), the whole-plant counts followed the usual pattern for thrips on the head. When the attractiveness of the head was low (and the size of the head was very small; i.e., <3 g fresh weight for all varieties) in the first test, 'Falcon' had the largest number of thrips.

Discussion

Although no differences in preference were seen in the laboratory experiment, in the field tests, adult *T. tabaci* colonizing cabbage did accumulate on heads of susceptible varieties in greater numbers than on heads of resistant varieties. This was true for thrips coming out of all three crops and for all stages of cabbage head development except precupping (when the "head" was actually a small group of unexpanded leaves weighing <3 g for all the varieties). There are many possible reasons for the different results in these two tests. Cutting leaf disks can cause radical changes in the nutritional characteristics of the leaf, as illustrated by changes in the concentrations of nearly all the amino acids in leaf disks from brussels sprouts (Van Emden & Bashford 1976), and presumably can cause changes in other leaf characteristics (such as secondary compounds) as well. Two hours may be too short a time for thrips to exercise a choice, or the artificial conditions of the test may have altered thrips behavior. Rearing the thrips for many generations on onions may have altered host preferences from those of natural populations, specifically those moving out of wheat, oats, and alfalfa. Alternatively, thrips may prefer susceptible heads on the basis of some characteristic not present in leaf disks; for example, the amount of tightly enclosed, protected leaf area, which is believed to be important in *T. tabaci* preference in onions (Jones et al. 1934). It is also possible that antibiosis contributed somewhat to differences in colonization. Development of a laboratory biosassay for thrips nonpreference would require further study to resolve these questions.

The preference data from the field correspond well with field data on resident thrips populations on these varieties, which also showed significant differences in numbers of thrips in the head once the head began to develop (Stoner 1987). In both experiments, differences in thrips numbers appeared when the dry weight of the developing head reached 1 g or more or the fresh weight reached 10 g. The results for new colonizers on the frame leaves and on whole plants are different from those for resident populations in previous work (Stoner 1987). In that study, there were no consistent significant differences among varieties in numbers of thrips on whole plants, and no differences for frame leaves until the end of the season when resistant varieties had more thrips. The differences in results between these two studies are presumably caused by differences in the patterns of colonization compared with those of survival and reproduction on the frame leaves (where >90% of the resident thrips population was located through most of the season).

In this study, dramatic changes in the overall numbers of colonizing adults on the frame leaves do not have any noticeable effect on the overall numbers of adults in the heads or on the relative number among varieties. Thus, the probability of a colonizing thrips remaining in the head of a plant is independent of the attractiveness of the frame leaves of the same plant. This is unexpected if the thrips are perceiving whole plants and choosing among cabbage plants for colonization. This raises questions about the nature of the choices made in these preference tests: Is the thrips adult choosing among plants in the row? Among heads? Or does it choose whether to remain after alighting on a particular spot on the plant? And, if it leaves, does it walk or fly to another part of the plant, or simply take off and leave the experiment?

Lewis (1973) suggests that the ability of thrips in flight to orient toward and land on a surface is limited, except in still air or very light winds, because of their low air speed. The literature on field spread of a virus transmitted by *T. tabaci* indicates that there is very little local movement of adult thrips among host plants within an area of 9–14 m (Bald 1937, Carter 1939). Given the limited ability of thrips to direct their flight and the evidence that thrips adults do not move readily among plants in a plot, the differences in preference among heads of different varieties may be the result of more rapid take-off after landing on the head of a resistant variety, rather than choosing among the heads of the plants available. Thus, although this experiment is similar in design to many "choice tests" (e.g., Cantelo & Sanford 1984), the roles of long-distance orientation and short-range movement between neighboring plants and their effects on preference are not well understood for this little-studied group of insects, so it is difficult to determine to what extent they are choosing among plants in an array.

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