Direct Feeding Damage on Cucumber by Mixed-Species Infestations of *Thrips palmi* and *Frankliniella occidentalis* (Thysanoptera: Thripidae)

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ABSTRACT Distributions of *Thrips palmi* Karny and *Frankliniella occidentalis* (Pergande) within plants and relative contributions of each species to fruit scarring were investigated in field plantings of cucumber, *Cucumis sativus* (L.). Densities of *T. palmi* (number per unit area plant substrate) were greatest on foliage, whereas *F. occidentalis* densities were greatest on flowers. Densities of both species were lowest on fruits. Both species had secondary sex ratios that were biased towards females. The proportion of male *F. occidentalis* increased substantially in flower samples. Temporal variation in the incidence of fruit scarring, within and between field plantings, was related to variation in densities of *F. occidentalis* (but not *T. palmi*). Within-field spatial variation in fruit scarring on a given harvest was also associated primarily with variation in *F. occidentalis* densities. Because small, developing fruits physically support the female flowers, the high densities of *F. occidentalis* in flowers may create opportunities for them to incidentally feed upon and scar young fruit.

KEY WORDS Insecta, Thrips palmi, Frankliniella occidentalis, integrated pest management

MELON THRIPS Thrips palmi Karny has recently expanded its range from its native Malaysian-Indonesian region to include an area from Pakistan in the east to Hawaii in the west. The species has become established also in Puerto Rico and the Dominican Republic (Hamasaki 1987). T. palmi has become a severe pest of many commercially cultivated plants, including snap and kidney bean (Phaseolus vulgaris L.), mungbean (Vigna radiata (L.)), soybean (Glycine max (L.)), cowpea (Vigna unguiculata L.), bell pepper (Capsicum annuum L.), cucumber (Cucumis sativus (L.)), cantaloupe (Cucumis melo L.), watermelon (Citrullus vulgaris Schrad), eggplant (Solanum melongena L.), potato (Solanum tuberosum L.), chrysanthemum (Chrysanthemum morifolium Ram.), and cotton (Gossypium hirsutum L.). The complete host range is extremely broad (Hamasaki 1987, Waterhouse 1987, Hirose 1989). Effects of T. palmi on vegetable production in Hawaii (Johnson 1986, Johnson et al. 1989) and potential effects on agriculture in the continental United States if T. palmi is introduced have highlighted the need to improve our understanding of the basic biology of T. palmi and to develop an effective integrated pest management (IPM) program for this thrips.

Thrips palmi commonly occurs with a second thrips species, the western flower thrips, Frankliniella occidentalis (Pergande), in cucumber plantings on Oahu, Hawaii (J.A.R., unpublished data). Two types of damage were associated with these mixed-species infestations: indirect damage caused by feeding on foliage and stems and direct damage caused by feeding on developing fruit. Thrips feeding on immature fruit generate silvery, web or streaklike scarring, which may be accompanied by fruit malformation. Either scarring or fruit malformation may result in the downgrading of fruit at harvest. Here we analyze the distributions of T. palmi and F. occidentalis within plants and the relative contribution of each species to cucumber fruit scarring.

Materials and Methods

Two field experiments were done at the University of Hawaii Poamoho Agricultural Experiment Station on Oahu. Experimental protocols described below were the same for both experiments unless otherwise noted.

Experimental Design. Cucumber ('Sweet Slice') was planted on 21 January 1988 (day 0, Experiment I) and 22 August 1988 (day 0, Experiment II). Twenty-four plots were planted and treatments assigned in a randomized block design. Each of the six blocks included a control plot (lowest thrips density) and a low-, medium-, and high-density thrips treatment. Each plot consisted of three 8-m

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rows. Rows were separated by 2 m, and plots were separated by 3 m. $\,$

Plants were thinned to one plant per 30 cm and trellised on day 35 (Experiment I) and day 23 (Experiment II). Each plot received 2.0 kg of 10-30-10 fertilizer at planting and at trellising. Applications of foliar urea fertilizer (0.05 kg per plot) were made weekly beginning day 56 (Experiment I) and day 38 (Experiment II). Plots were furrow irrigated as needed.

Natural colonization of medium- and high-density plots by thrips was supplemented by releases of T. palmi and F. occidentalis on days 37 and 44 of Experiment I. No releases were made during Experiment II. Thrips densities were manipulated by combined weekly applications of avermectin (Avid 0.15 EC [emulsifiable concentrate], 0.024 g [AI]/liter); MSD AGVET, Rahway, N.J.), oxamyl (Vydate 2 L [liquid], 1.20 g [AI]/liter; E. I. Du Pont de Nemours & Company, Wilmington, Del.), and methomyl (Lannate 1.8 L, 1.08 g [AI]/liter; E. I. Du Pont de Nemours & Company) (Experiment I), or avermectin alone (Experiment II). In Experiment I, applications began on days 28, 61, and 71 for the control, low-, and medium-density treatments and continued until the final harvest; corresponding dates for Experiment II were days 25, 46, and 66. High-density plots were not sprayed for thrips control.

Other insect pests and plant pathogens were controlled as required with whole-field applications of pesticides that had no effect on either thrips species. Permethrin (Ambush 2 EC, 0.25 g [AI]/liter; ICI Americas, Wilmington, Del.) was applied weekly for control of the greenhouse whitefly, Trialeurodes vaporariorum (Westwood); oxythioquinox (Morestan 4 flowable, 0.15 g [AI]/liter; Mobay Corporation, Kansas City, Mo.) was applied for control of the carmine spider mite, Tetranychus cinnabarinus (Boisduval); cyromazine (Trigard 75 P [wettable powder], 0.16 g [AI]/liter; CIBA-GEIGY Company, Greensboro, N.C.) was applied for control of leafminers, Liriomyza spp.; metalaxyl (Subdue 2 EC, 0.024 g [AI]/liter; CIBA-GEIGY Company) was applied to control the fungal pathogen Pythium aphanidermatum (Edson); benomyl (Benlate 50 WP [wettable powder], 0.20 g [AI]/ liter; E. I. Du Pont de Nemours & Company) was applied to control the fungal pathogen anthracnose, Colletotrichum orbiculare (Berkeley and Montagne). During Experiment I, plants were infected by the angular leafspot pathogen, Pseudomonas syringae pv. lachrymans (E. F. Smith and Bryan), which was only partly suppressed by weekly applications of streptomycin sulfate (Agristrep type D 200 ppm; MSD AGVET) and maneb (Kocide 77 WP, 1.39 g [AI]/liter; Kocide Chemical Corporation, Houston). All pesticide applications except metalaxyl, benomyl, and maneb were made with a sprayer mounted to an all-terrain vehicle. One to four nozzles were used to apply 1.6-5.2 liters of formulated pesticide per plot; the volume was increased to maintain thorough coverage as plants grew. Metalaxyl (16 liters/plot), benomyl (12 liters/plot), and maneb (16 liters/plot) were applied with a tractor-mounted sprayer equipped with a hand held orchard gun.

Sampling. Thrips densities in each plot were assessed weekly by sampling foliage. The fifth leaf from the vine tip (the first leaf defined as one with a width >2.5 cm) was removed from the plant, cut along the midrib, and the half with the midrib was retained. Ten half-leaves were sampled per plot and washed with 70% ethanol. The ethanol and water rinses were passed through a sieve (79 meshes per cm) to isolate thrips for counting. Determination of species and sex were made for adults only. The area of all sampled leaves was measured with a LI-COR portable area meter (model LI-3000; LI-COR, Lincoln, Nebr.) to correct each foliar thrips count for variation in leaf size. Thrips densities are reported as numbers per 200 cm² of leaf surface (200 cm² is equal to the upper and lower surface area of an average-sized bisected cucumber leaf).

On days 60 and 95 (Experiment I) and days 35, 56, and 77 (Experiment II), samples of maturing fruit (length 5-8 cm; ten sampled per plot), male flowers (ten sampled per plot), and female flowers (two sampled per plot) were taken also. The surface areas of female and male flowers (n = 56 and 58)respectively) sampled on day 86 of Experiment II were measured for an estimate of the total surface area of flower samples. The length and width of developing cucumber fruit (n = 108; 5–8 cm long) sampled on day 77 of Experiment II were measured also. Fruit measurements were used to estimate the area of fruit samples by modeling the cucumber fruit as a cylinder (area equal approximately to $2\pi \cdot \text{width} \cdot \text{length}$). These single-sample estimates of flower and fruit surface areas were used to provide approximate measures of thrips densities per unit area of flower and fruit substrate.

Fruit were harvested twice a week. In Experiment I, only the fruit from the center row of each plot was scored; in Experiment II, all harvested fruit was scored for the presence of thrips scarring. Fruits were considered to be scarred if scar tissue covered an area $>1 \text{ cm}^2$ as estimated by visual inspection. Wind damage and other forms of damage not induced by thrips were generally readily distinguished from thrips scarring. However, in Experiment II, the final three harvests could not be scored for fruit scarring because a severe storm caused excessive wind damage.

Statistical Analysis. All analyses were performed with the BMDP computer statistics package (Dixon 1985). Means are presented throughout \pm one standard error. Pairwise comparisons were done using separate-variance t tests (Welch model) with overall α maintained at 0.05 using Bonferroni's inequality. Analyses of thrips distribution within plants and sex ratio included data from all experimental plots only if no significant difference was detected between plots being sprayed for thrips control and those not sprayed (separate-variance August 1990 ROSENHEIM ET AL.: DIRECT FEEDING DAMAGE ON CUCUMBER BY TWO THRIPS 1521

two-way analysis of variance; Brown-Forsythe model). Sprayed plots were excluded from the analysis when the difference between unsprayed and sprayed plots was significant.

Stepwise multiple regression was used to investigate the relative contributions of T. palmi and F. occidentalis densities (independent variables) to patterns of fruit scarring (dependent variable). Because only the youngest fruits appeared to be susceptible to scarring by thrips, percentage of fruit scarred at harvest was regressed on thrips densities measured 7-10 d earlier when the immature fruits had been bearing open flowers. Because only the center row of each 3-row plot was scored for fruit scarring during Experiment I, data from three successive harvests were grouped before analysis to increase the reliability of estimates of fruit scarring. Mean thrips densities, weighted by the number of fruits harvested in the corresponding harvest, were used in these analyses.

Results

Thrips Distributions Within Plants. The distributions of *T. palmi* and *F. occidentalis* within plants were markedly different (Fig. 1). *T. palmi* constituted a consistently greater proportion of all thrips present on foliage than on male or female flowers, where *F. occidentalis* was relatively more common. *T. palmi* was also the most common species sampled from developing fruits on four of the five sample dates.

The data presented in Fig. 1 provide an estimate of thrips species composition on different plant substrates. For each species we can compare also the densities per cm² of different plant substrates. Only data from the high-density treatments (unsprayed plots) were used. We calculated for each sample date the ratio of the densities of thrips on flowers and fruits to the density on foliage. The figures presented are the means of these ratios, averaged over all five sample dates (Experiments I and II combined). Figures for T. palmi on developing fruits, male flowers, and female flowers were 0.19 \pm 0.09 (range 0.00–0.51), 0.55 \pm 0.40 (range 0.00– 2.16), and 0.57 \pm 0.38 (range 0.00-2.08), respectively. Corresponding figures for F. occidentalis are 0.17 \pm 0.06 (range 0.00–0.34), 29.2 \pm 11.8 (range 2.91-69.9), and 50.1 \pm 36.2 (range 2.99-193.1) on fruit, male flowers, and female flowers, respectively. Thus, T. palmi densities were greatest on leaves, whereas F. occidentalis densities were greatest on flowers. Densities of both species were lowest on developing fruits.

Sex Ratio. The sex ratio of *F. occidentalis* varied with the plant substrate sampled (Fig. 2), suggesting that observed variation in densities across different plant substrates may in part reflect this species' mating behavior. A trend toward significantly increased proportions of males on cucumber flowers (mean = $38.2 \pm 2.4\%$, range 27.0-45.2%) compared with leaves and fruits (mean = $11.3 \pm$ 2.4%, range 0.00-24.3%) was observed in all samples. In contrast, the sex ratio of *T. palmi* was



Fig. 1. Thrips species composition on different cucumber plant parts. L, leaves; Fr, fruits; M, male flowers; F, female flowers. Within each sample date, bars with different letters are significantly different (P < 0.05). (A) Experiment I, (B) Experiment II.

consistently independent of plant substrate (Fig. 2; mean proportion males = $19.3 \pm 1.9\%$, range 5.7– 35.0%). Biases toward females in the sex ratios of both species were highly significant (*T. palmi*, *t* = 16.16, *P* \ll 0.001; *F. occidentalis* on leaves and fruits, *t* = 16.13, df = 8, *P* \ll 0.001; *F. occidentalis* on flowers, *t* = 4.92, df = 9, *P* < 0.001).

Fruit Scarring. The incidence of fruit scarring varied temporally, within and between the two field plantings, and spatially, across the 24 plots within a single harvest. Fig. 3 presents the trends of percentage of fruits scarred and foliar thrips densities in the high-density treatments (unsprayed plots) during Experiments I and II. In both plantings, T. palmi densities increased rapidly, whereas F. occidentalis densities either increased gradually (Experiment I) or increased and then stabilized as the plants matured (Experiment II) (Fig. 3B, D). Fruit scarring exhibited also only modest increases over time (Fig. 3A, C). Stepwise multiple regression identified F. occidentalis densities as the only significant contributor to fruit scarring (Experiment I, F. occidentalis, $B = 0.0049 \pm 0.0015$, r = 0.68, $P = 0.01; T. palmi, B = -0.00004 \pm 0.00075, P$ = 0.96; Experiment II, F. occidentalis, B = 0.0130 ± 0.0041 , r = 0.73, P = 0.01; T. palmi, B = 0.0003 \pm 0.0002, P = 0.16).

The different densities of *T. palmi* and *F. oc-cidentalis* in the field planting in Experiment I compared with Experiment II permitted testing the relative importance of each thrips in generating



Fig. 2. Thrips sex ratio on different cucumber plant parts. L, leaves; Fr, fruits; M, male flowers; F, female flowers; N, no data. Within each sample date, bars with different letters are significantly different (P < 0.05). (A) and (C) Experiment I, (B) and (D) Experiment II.

fruit scarring. Using data from the high-density treatments only, the mean density of T. palmi during harvest increased across plantings (Experiment I, mean = 38.40 ± 21.40 ; Experiment II, mean = 62.62 ± 39.25), whereas the mean density of F. occidentalis decreased (Experiment I, mean = 21.98 \pm 6.11; Experiment II, mean = 4.00 \pm 1.74). These changes resulted in a significant decrease in percentage of fruit scarred from $45.5 \pm 3.0\%$ in Experiment I to $17.3 \pm 2.2\%$ in Experiment II (t = 7.58, df = 23, $P \ll 0.001$). In agreement with the observed dependence of fruit scarring within plantings upon F. occidentalis densities, fruit scarring between plantings followed the decreasing trend of F. occidentalis densities rather than the increasing trend of T. palmi densities.

Spatial variation in the incidence of fruit scarring across the 24 experimental plots also appeared primarily to reflect spatial variation in *F. occiden*-

talis density (Table 1). For two of the five harvest series analyzed in Experiment I, percentage of fruit scarring was positively related to F. occidentalis density; T. palmi did not contribute to fruit scarring. F. occidentalis was again the sole contributor to fruit scarring in 6 of 11 harvests during Experiment II. In one additional harvest, F. occidentalis and T. palmi appeared to influence fruit scarring positively, and in two harvests, only T. palmi densities were significantly associated with fruit scarring. Because spatial variation in the density of both thrips species was strongly influenced by insecticides applied for their control, densities of T. palmi and F. occidentalis were correlated (mean r for all 11 harvests = 0.41 ± 0.10 , range 0.08-0.83 [Experiment II]). The apparent influence of T. palmi on fruit scarring may therefore be genuine or may simply reflect the correlated densities of the two thrips species.



Fig. 3. Time course of percentage of fruit scarred and thrips densities in field plantings of cucumber. (A) and (B) Experiment I, (C) and (D) Experiment II.

Discussion

Frankliniella occidentalis aggregated strongly in male and female flowers, whereas T. palmi densities were greatest on foliage. Compared with the sex ratio of F. occidentalis collected on foliage, the sex ratio of F. occidentalis collected in flowers was less biased towards females, suggesting that the distribution of this species within a plant may be related to its mating behavior. Because small, developing cucumber fruits are present before fertilization of flowers occurs and because these fruits physically support the female flowers, the presence of F. occidentalis in flowers may allow them to feed upon and scar the young fruit. Spatial and temporal variation in the incidence of fruit scarring within and between plantings were primarily, if not exclusively, caused by variation in F. occidentalis densities, despite absolute densities of T. palmi that were often substantially greater.

Thrips Distributions and Sex Ratios Within Plants. The attractiveness of flowers to *F. occidentalis* has been noted for various host plants (Bryan & Smith 1956, Yudin et al. 1986, Pickett et al. 1988, Yudin et al. 1988). Although a shift towards an increased proportion of males in floral structures has not previously been observed, Kirk (1985a) described male-dominated mating aggregations in

flowers for other thrips species. Besides the potential significance of thrips aggregation in flowers to fruit scarring, pollen feeding by thrips may sometimes deplete pollen stores and therefore depress fruit set (Kirk 1987). Pollen provides a critical source of dietary nutrients for many thrips species (Murai & Ishii 1982; Kirk 1984, 1985b). Thrips may, however, have the reverse effect in some systems, by enhancing pollination through pollen transport (Kirk 1984). Because of the importance of fruit scarring by F. occidentalis to overall IPM for cucumber, additional investigations of the role of cucumber flowers in the mating system and nutritional ecology of F. occidentalis, as well as the effect of F. occidentalis on cucumber pollination, fruit set, and fruit scarring, are needed.

The consistent bias of sex ratios toward females observed in field-collected *T. palmi* adults agrees with previous studies (Yoshihara & Kawai 1982; Kawai 1985, 1986a). Because our measurements (on adults) were made well after the primary allocation of sex at the time of oviposition, we were measuring secondary sex ratios. Deviation from a 1:1 sex ratio could, therefore, be due to either a biased primary sex ratio or to differential mortality between the sexes. The haplodiploid sex-determining mechanism of *T. palmi* (Yoshihara & Kawai 1982) and *F. occidentalis* (Bryan & Smith 1956)

Harvest days	Thrips	$B \pm SE$	Р	r
Experiment 1				
49-56	F. occidentalis T. palmi	$\begin{array}{r} 0.0915 \ \pm \ 0.0197 \\ -0.0551 \ \pm \ 0.0343 \end{array}$	<0.0001 0.12	0.70
60-67	F. occidentalis T. palmi	$\begin{array}{r} 0.0156 \pm 0.0039 \\ -0.0658 \pm 0.0201 \end{array}$	<0.001 <0.01	0.65
70–77	F. occidentalis T. palmi	$\begin{array}{r} 0.0045 \ \pm \ 0.0028 \\ 0.0126 \ \pm \ 0.0071 \end{array}$	0.13 0.09	
81-88	F. occidentalis T. palmi	$\begin{array}{r} 0.0025 \ \pm \ 0.0034 \\ 0.0009 \ \pm \ 0.0017 \end{array}$	0.47 0.61	_
91-95	F. occidentalis T. palmi	$\begin{array}{r} 0.0006 \ \pm \ 0.0016 \\ 0.0002 \ \pm \ 0.0004 \end{array}$	0.70 0.69	_
Experiment 2				
38	F. occidentalis T. palmi	$\begin{array}{r} 0.0722 \ \pm \ 0.1346 \\ 0.0106 \ \pm \ 0.0049 \end{array}$	0.60 0.04	0.42
42	F. occidentalis T. palmi	$\begin{array}{r} 0.1285 \ \pm \ 0.0549 \\ 0.0053 \ \pm \ 0.0104 \end{array}$	0.03 0.62	0.45
45	F. occidentalis T. palmi	$\begin{array}{r} 0.1406 \ \pm \ 0.0470 \\ 0.0114 \ \pm \ 0.0086 \end{array}$	<0.01 0.20	0.54
49	F. occidentalis T. palmi	$\begin{array}{r} 0.0740 \ \pm \ 0.0265 \\ 0.0071 \ \pm \ 0.0025 \end{array}$	<0.01 <0.01	0.62 ^a 0.63 ^a
52	F. occidentalis T. palmi	$\begin{array}{r} 0.1290 \ \pm \ 0.0411 \\ 0.0034 \ \pm \ 0.0042 \end{array}$	<0.01 0.42	0.56
56	F. occidentalis T. palmi	$\begin{array}{r} 0.0037 \ \pm \ 0.0021 \\ 0.0010 \ \pm \ 0.0012 \end{array}$	0.10 0.40	_
59	F. occidentalis T. palmi	$\begin{array}{r} 0.0046 \pm 0.0019 \\ -0.0008 \pm 0.0012 \end{array}$	0.03 0.50	0.45
63	F. occidentalis T. palmi	$\begin{array}{r} 0.0077 \ \pm \ 0.0037 \\ 0.0003 \ \pm \ 0.0008 \end{array}$	0.05 0.69	0.40
66	F. occidentalis T. palmi	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	0.65 0.63	_
70	F. occidentalis T. palmi	$\begin{array}{r} 0.0045 \ \pm \ 0.0027 \\ 0.0003 \ \pm \ 0.0001 \end{array}$	0.11 0.03	0.43
73	F. occidentalis T. palmi	$\begin{array}{r} 0.0100 \ \pm \ 0.0042 \\ 0.0001 \ \pm \ 0.0002 \end{array}$	0.03 0.50	0.45

Table 1. Multiple regression analysis of the influence of spatial variation in densities of *T. palmi* and *F. occidentalis* (independent variables) on the incidence of fruit scarring (dependent variable) within fields

^a Partial correlation coefficient.

provides a simple means for biasing primary sex ratios. Decreased longevity of adult males relative to females has been reported for *F. occidentalis* (Bryan & Smith 1956); however, Kawai (1985) found that adult male and female *T. palmi* were equally long lived.

Our finding that T. palmi did not contribute significantly to fruit scarring differs from those of Suzuki & Miyara (1983) and Kawai (1986b), who found linear relationships between density of T. *palmi* and the incidence of fruit damage in infestations of cucumber by T. palmi alone. The reasons for these divergent results are not known. Possibly, the effect of T. palmi may vary depending on the cultivar studied; the Japanese cultivars studied by Suzuki & Miyara (1983) and Kawai (1986b) are quite different in growth form from western cultivars. The tendency for T. palmi to induce fruit scarring is well known for some crop plants (e.g., bell pepper [D. H. Oi, University of Hawaii, Honolulu, personal communication], eggplant), and some cucumber cultivars may similarly be susceptible to scarring. In a similar system, varietal resistance in cabbage to feeding damage by T. tabaci was found to be related to different distributions of thrips within plants on different cabbage varieties (Stoner & Shelton 1988). In addition, T. palmi might induce some fruit scarring on all cucumber cultivars, but the effect may have been too small relative to the effect of F. occidentalis to be detected consistently in this study.

Our results have immediate implications for thrips management on cucumber. First, because effects of T. palmi and F. occidentalis are qualitatively different, accurate species identifications will be necessary for intelligent control decisions to be made. Second, the economic injury level for T. palmi will apparently be a function of its effect on foliage (i.e., indirect damage). Because cucumber appears to tolerate substantial foliar damage before a concomitant yield loss is observed (Welter et. al. in press), the economic injury level will be relatively high. Third, the economic injury level for F. occidentalis will be a function of its effect on fruit (i.e., direct damage). The observed relationships between F. occidentalis densities and percentage of fruit scarring (Fig. 3) suggest that thrips densities of approximately $20/200 \text{ cm}^2$ (Experiment I) and $8/200 \text{ cm}^2$ (Experiment II) are sufficient to increase fruit scarring by 10%. Eight thrips per 200 cm² is probably more suitable as an initial estimate of economic injury level because the incidence of fruit scarring during Experiment II was generally within an economically acceptable range (i.e., <30%), whereas in Experiment I it was not.

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