Effects of *Thrips palmi* and Western Flower Thrips (Thysanoptera: Thripidae) on the Yield, Growth, and Carbon Allocation Pattern in Cucumbers

STEPHEN C. WELTER, JAY A. ROSENHEIM,[1] MARSHALL W. JOHNSON,[1] R.F.L. MAU,[1] AND LAURA R. GUSUKUMA-MINUTO[1]

Department of Entomological Sciences, University of California, Berkeley, California 94720

J. Econ. Entomol. 83(5): 2092–2101 (1990)

ABSTRACT Mixed infestations of thrips, composed of ≈94% *Thrips palmi* Karny and 6% *Frankliniella occidentalis* (Pergande), resulted in significant reductions in total cucumber yield, mean fruit size, and total fruit. No significant reductions were observed at <9.4 thrips-days/cm^2 (0.48 thrips/cm^2 at peak densities). As the number of thrips-days increased to a maximum of 45.0 per cm^2, reductions of 54.2% in total fruit weight at final harvest were observed. Highly significant linear regressions between the total number of thrips-days per leaf and the various agronomic variables were obtained. Total yields for the season were reduced 10% by the highest level of thrips damage, possibly because 70% of all yield was harvested before significant build up of thrips populations. Moderate, yet significant, changes in growth patterns were associated with feeding damage by thrips. Less total leaf dry weight was associated with heavy feeding damage.

KEY WORDS Insecta, damage, thrips, cucumber

Thrips palmi Karny, known as melon thrips, is a relatively new and potentially severe pest of agriculture within the United States. The geographic distribution of *T. palmi* includes its native Malaysian–Indonesian region, as well as an area from Pakistan in the east to Puerto Rico and the Dominican Republic in the west. Management of *T. palmi* in Hawaii has proven difficult because of the lack of information about effective biological control agents and the lack of effective insecticides (Johnson 1986). Despite a wide host range, such as cotton, soybean, mungbean, cowpea, and a variety of fruit and vegetable crops (Waterhouse 1987, Hamasaki 1987), information on the effects of feeding damage by *T. palmi* on crop yields or growth is limited.

Two general classes of damage are associated with thrips damage on cucumber: general scarring of fruit and changes in yield, growth, or fruit shape. Rosenheim et al. (1990) demonstrated that infestations of the western flower thrips, *Frankliniella occidentalis* (Pergande), were responsible for observed scarring of fruit, whereas *T. palmi* is primarily a foliage feeder. Research by Suzuki & Miyara (1983) showed that infestations as low as one *T. palmi* per cucumber leaf resulted in reduced number of tendrils, fewer leaves, and increased plant mortality. Kawai (1986) and Suzuki & Miyara (1983) demonstrated significant linear relationships between mean densities of *T. palmi* and fruit scarring on cucumbers. Similarly, Kawai (1986) showed a negative correlation between the density of *T. palmi* before harvest and mean harvest yields with a proposed threshold of 10.6 thrips per leaf to avoid losses >10%. Other species of thrips adversely affect the growth or productivity of other crops. Temporary reductions in shoot growth were observed from mixed infestations of thrips on 'Chenin Blanc' grapes (McNally et al. 1985). Increased square losses that were later compensated for by the cotton plant were associated with infestations of *F. occidentalis* (Terry & Barstow 1988).

Because of the apparent severity of damage by *T. palmi* in Hawaiian agriculture and the relatively low thresholds previously proposed, we investigated the effects of *T. palmi* on cucumber cultivars commercially grown in Hawaii. The effects of *F. occidentalis* were studied concurrently because no control tactic exists to selectively manage only *T. palmi*.

Materials and Methods

Field studies were conducted at the University of Hawaii Branch Experiment Station at Poamoho, Oahu. Four levels of feeding damage by *T. palmi* on cucumber, *Cucumis sativus* (cv. Sweet Slice), were replicated six times within a randomized complete block design. Each replicate consisted of three rows of trellised cucumbers that were 8 m long with 2 m between rows. Three meters were cleared between the ends of each plot to serve as a buffer between plots. Cucumbers were planted on Julian date 235 (23 August) and furrow irrigated as needed. Plants were thinned so that 30 cm was

[1] Department of Entomology, 3010 Maile Way, University of Hawaii at Manoa, Honolulu, Hawaii 96822.

between plants on Julian date 268. Each plot received an application of 2.0 kg of 10-30-10 fertilizer at planting and trellising. Applications of foliar urea were made weekly starting on Julian date 273.

Pest management practices for the entire field included weekly pesticide applications that controlled specific pests whose effects might confound the experiment. Permethrin (Ambush 2.0 emulsifiable concentrate [EC]; ICI Americas, Wilmington, Del.) at 0.25 g (AI)/liter was applied for control of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). Oxythioquinox (Morestan 4 flowable [F]; Mobay Corporation, Kansas City, Mo.) was applied at 0.15 g (AI)/liter for control of the carmine spider mite, *Tetranychus cinnabarinus* (Boisduval), whereas cyromazine (Trigard 75 wettable powder [WP], CIBA-GEIGY Company, Greensboro, N.C.) was applied at 0.16 g (AI)/liter for control of leafminers, *Liriomyza* spp. Metalaxyl (Subdue 2.0 EC; CIBA-GEIGY Company) at 0.024 g (AI)/liter was applied to control the fungal pathogen, *Pythium aphanidermatum* (Edson), whereas maneb (Kocide 77 WP, Kocide Chemical Corporation, Houston, Tex.) at 1.39 g (AI)/liter was applied to minimize infection by angular leafspot, *Pseudomonas syringae* pv. *lachrymans* (E. F. Smith & Bryan). Infection by the fungal pathogen anthracnose, *Colletotrichum orbiculare* (Berk. & Mont.) was controlled with applications of benomyl (Benlate 50 WP, E. I. du Pont de Nemours & Company, Wilmington, Del.) at 0.20 g (AI)/liter. The volume of formulated spray was adjusted from 500 to 1,625 liters/ha to provide complete coverage as the plants grew.

Thrips Sampling and Damage Estimates. Four levels of feeding damage were established by the application of abamectin (Avid 0.15 EC; MSD AGVET, Rahway, N.J.) at 0.024 g (AI)/liter. Populations of thrips were allowed to develop unchecked until the desired level of damage was reached. After the desired level of damage was obtained, plots were treated weekly for the duration of the growing season. Initiation of thrips control for each treatment was determined by an overall visual examination of foliar damage. The four levels of damage (the undamaged control, low-, medium-, and high-damage treatments) spanned the range of damage normally observed in commercial plantings. Initial applications of abamectin to the control, low, and medium plots were made on Julian dates 247, 265, and 302, respectively. The visually estimated levels of damage were correlated with the number of thrips-days that had accumulated to date. Plots designated as high-damage plots did not receive any applications of abamectin for the entire season.

Ten leaves were selected weekly from each plot from Julian dates 263 to 318. The fifth leaf from the terminal end of the growing vine was selected for sampling. The first leaf with a width >2.5 cm was defined as the most terminal leaf. Leaves were removed from the plant and cut adjacent to the midrib with the half containing the midrib kept for counting. Sampled leaf halves were stored in 70% ethanol in the field and rinsed with water in the laboratory. Resulting ethanol and water rinses were screened through a sieve (79 meshes/cm) to collect larval and adult thrips.

Species determination was made for adult thrips collected. A maximum of 50 adult thrips was checked in any given sample. The size of each sampled leaf half was measured with a portable leaf area meter (LI-3000, LI-COR, Lincoln, Nebr.). Mean leaf size was estimated by doubling the leaf half area. Estimation of leaf size permitted the thrips counts to be corrected for leaf size as well as to determine the average leaf size for each treatment on each sample date. Mean thrips numbers were calculated for each week and multiplied by the number of days between samples, thus providing the number of thrips-days accumulated each week. The total number of accumulated thrips-days per leaf was divided by the mean leaf area including upper and lower leaf surface. The number of thrips-days per cm^2 accumulated to a particular date was used as an index of thrips damage.

Yield. All mature fruit were harvested from all rows within each plot twice a week from Julian dates 273 to 318. Fruit were separated into fruit quality categories based on fruit size and curvature. Fruit were divided into two main groups—jumbo (>400 g) and normal. Rapid growth is required for a fruit to attain 400 g between harvest periods. Thus, allocation to the jumbo class was used as an indirect measure of overall plant vigor within each plot. Each main group (jumbo and normal) was subdivided further into grades "A," "B," marketable, or cull fruit. Number of fruit and total fruit weight within each category were determined at each sample date for each plot. Fruit weights for categories "A" and "B" were pooled for analysis. Total marketable fruit per plot includes all fruit except culled fruit.

A single statistic was generated to summarize mean fruit quality for each plot on each harvest date. Mean fruit quality from each 1-wk harvest period was calculated by multiplying all fruit in the "A" category by 3, the "B" category by 2, and the combination of cull and marketable fruit by 1. Scores for each category were summed and divided by the total fruit number to determine an average fruit quality score. Thus, higher scores were indicative of higher overall fruit quality. For this study, fruit quality only refers to fruit shape and size, not fruit scarring. The number of plants within each plot was counted on Julian dates 273, 305, and 321.

Carbon Allocation Patterns. Dry weight accumulation per plant was determined on Julian dates 253, 272, 331, and 351. Three plants were removed at random from each plot and taken to the laboratory. Plants were subdivided into reproductive structures (flowers and fruit), leaves, root, or stem biomass. All samples were dried at 60°C until daily weight change ceased. In samples taken on Julian dates 272, 331, and 351, leaf blades were separated from the petiole and weighed separately. On each sample date, 15 subsamples of leaves were selected at random from the total leaf sample. To generate a regression that included the range of potential canopy sizes, subsamples were selected that ranged from a single leaf to a subsample containing approximately the total leaf area for an entire plant. The total leaf area per subsample was measured with the leaf area meter. The leaf samples were dried at 60°C and weighed. Total dry weight per sample was regressed against the total leaf area (total leaf area = constant + total leaf dry weight × slope coefficient). This regression allowed conversion of total leaf blade dry weight into an estimate of the total leaf canopy. Fifteen fruit that spanned the normal range of fruit sizes were picked and weighed immediately. Fruit were dried as described above and weighed. Fresh weight of fruit was regressed against the corresponding value for dry weight (fruit dry weight = constant + fruit fresh weight × slope coefficient).

On Julian dates 331 and 351, roots were rated on a range of 0–2 for visual symptoms of rootknot nematode, *Meloidogyne* spp. Roots with a score of 0 showed no signs of infestation, whereas a score of 2 indicated extensive nodulation and root thickening.

Statistical Analysis. Data were analyzed for each sample date as a randomized complete block design (Wilkinson 1986). Mean separations were determined by Duncan's multiple range test (Wilkinson 1986). Seasonal totals of all agronomic variables were compared as a repeated measure analysis of variance with harvest dates as repeated measures. Relationships between leaf dry weight and total leaf area were determined using simple linear regression (described above), whereas relationships between the various estimates of productivity and the independent variables (thrips-days and block number) were analyzed as multiple regressions (e.g., total yield = constant + coefficient × thrips-days + coefficient × block number).

Results

Thrips Population Levels. Applications of abamectin effectively changed the densities of the various thrips species. The seasonal phenologies of the thrips within the four treatments are presented in Fig. 1. There was a 10-fold difference in the number of thrips at peak densities between the control and high damage treatments, 0.38 and 3.8 thrips/cm^2, respectively. The relative proportion of *F. occidentalis* averaged only 0.06 (range, 0.01–0.11) for the nine sampling periods. Because the effect of each species on the photosynthetic rates of cucumber leaves appeared comparable (unpublished data), the species density data were combined to develop an average number of thrips per cm^2. Large increases in thrips densities were not evident until Julian date 298. The general shapes of the thrips

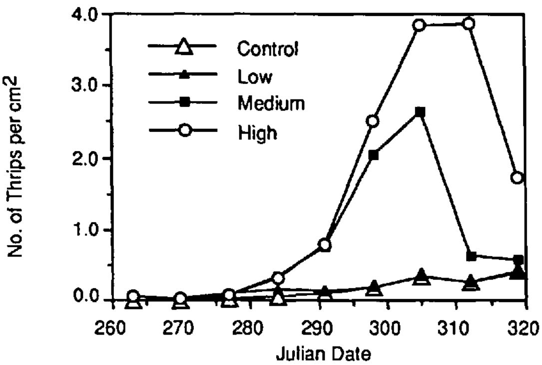

Fig. 1. Seasonal phenology of thrips within the four damage treatment levels.

population growth curves for the medium and high damage treatments appear similar until Julian date 305. The decline in number of thrips in the medium-damage treatment resulted from the applications of abamectin started on Julian date 302. Because the low-damage plots were treated prematurely, the total number of accumulated thrips-days per cm^2 did not differ for the season between the control and low-damage treatments (Table 1). The medium- and high-damage levels had significantly higher levels of damage at 25.0 and 45.0 thrips-days/cm^2 at the end of the season, respectively ($F = 82.04$; df = 3, 15; $P < 0.001$).

The relationship between the peak seasonal thrips densities and the total number of accumulated thrips-days per cm^2 was significantly linear across the 24 experimental plots (Fig. 2). Given the reluctance of some growers to adopt the concept of pest-days, thresholds for the Hawaiian islands could be presented in terms of number of thrips per cm^2. Similarly, the results could be presented as the number of thrips per leaf by multiplying our results by the average leaf size, which is approximately 200 cm^2 (single surface only). The relationship between peak number of thrips per cm^2 and total number of thrips-days per cm^2 is not expected to be the same for areas with different climatic conditions. Presentation of our data in terms of thrips-days per cm^2 should permit comparisons of our results with data from other geographic regions or crops. The relationships between peak number of thrips per cm^2 and the total number of accumulated thrips-days per cm^2 would have to be developed for a particular region.

Total number of accumulated thrips-days per cm^2 is presented relative to the vegetative dry weight accumulation in the cucumber plant in the undamaged control plots (Fig. 3). Total dry weight of the vegetative portion of the cucumber reached a peak on Julian date 300. The reduced accumulation in total dry weight reflects the reduced vegetative growth rate by the cucumber plants as they shifted to fruit production. The rapid growth by cucumber plants early in the season may have pre-

Table 1. Effects of various levels of thrips damage on the productivity of cucumbers ($\bar{x} \pm SD$) for harvests five, six, and seven

Treat-ment	Thrips-days/ cm^2 leaf	Total fruit weight per plot, g			Mean fruit weight, g	Total no. fruit/ plot	Mean fruit quality
		Total	Jumbo fruit	Marketable			
Harvest five							
Control	2.2 ± 0.8a	19,313 ± 2,239a	8,488 ± 1,812a	19,148 ± 2,195a	344.4 ± 96.8a	58.7 ± 13.2a	2.16 ± 0.07a
Low	3.0 ± 1.2a	18,433 ± 3,821a	8,431 ± 2,312a	18,296 ± 3,758a	357.4 ± 28.8a	51.5 ± 9.4a	2.14 ± 0.12a
Medium	17.0 ± 3.6b	15,873 ± 3,733a	5,428 ± 2,602b	15,618 ± 3,558a	309.2 ± 60.7a	51.2 ± 9.7a	2.09 ± 0.05a
High	21.0 ± 8.4b	17,173 ± 3,902a	5,066 ± 2,397b	16,910 ± 3,765a	286.4 ± 81.9a	61.2 ± 9.7a	2.07 ± 0.15a
Harvest six							
Control	3.4 ± 1.2a	13,938 ± 3,577a	1,745 ± 1,472ab	13,576 ± 3,676a	255.1 ± 15.2a	54.5 ± 12.6a	1.95 ± 0.04a
Low	4.0 ± 1.4a	12,391 ± 5,006ab	2,683 ± 1,532a	12,180 ± 4,977a	247.4 ± 10.8a	48.5 ± 18.0ab	1.96 ± 0.15a
Medium	22.8 ± 5.2b	8,856 ± 1,705bc	1,253 ± 718b	8,662 ± 1,637b	234.8 ± 19.8ab	37.5 ± 4.9bc	1.97 ± 0.12a
High	35.0 ± 9.6c	7,551 ± 2,908c	581 ± 879b	7,335 ± 3,001b	215.6 ± 24.1b	34.3 ± 10.0c	1.86 ± 0.13a
Harvest seven							
Control	4.6 ± 1.8a	12,176 ± 6,355a	2,066 ± 1,922a	11,358 ± 6,199ab	216.8 ± 36.5b	54.2 ± 22.5a	1.66 ± 0.12a
Low	5.2 ± 1.6a	13,991 ± 3,825a	2,283 ± 1,189a	13,385 ± 3,988a	235.8 ± 33.9a	58.8 ± 13.4a	1.75 ± 0.11a
Medium	25.0 ± 5.2b	8,017 ± 3,519b	851 ± 849ab	7,435 ± 3,463bc	220.0 ± 30.5b	35.8 ± 14.3b	1.62 ± 0.12a
High	45.0 ± 10.0c	5,580 ± 4,074c	178 ± 279b	5,195 ± 4,140c	196.2 ± 24.9c	29.0 ± 21.9b	1.61 ± 0.22a
Total harvest ($\bar{x} \pm SEM$)							
Control	4.6 ± 1.8a	149,480 ± 3,013a	53,162 ± 1,967a	139,290 ± 2,959a	340.4 ± 7.3a	445.2 ± 5.7a	2.22 ± 0.04a
Low	5.2 ± 1.6a	141,150 ± 2,404a	50,987 ± 1,640a	129,753 ± 2,356a	344.9 ± 7.0a	419.5 ± 4.5a	2.22 ± 0.06a
Medium	25.0 ± 5.2b	141,437 ± 3,650a	49,228 ± 1,960a	131,650 ± 3,650a	333.0 ± 7.0a	412.7 ± 7.4a	2.19 ± 0.07a
High	45.0 ± 10.0c	134,703 ± 3,836a	44,780 ± 1,951a	125,462 ± 3,646a	316.1 ± 6.5a	409.2 ± 8.4a	2.18 ± 0.05a

Means within a column within a single harvest interval followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Wilkinson 1986]).

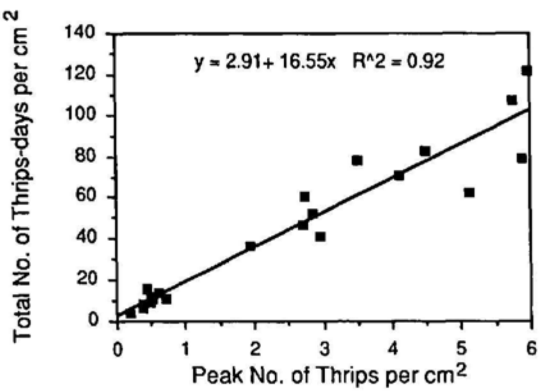

Fig. 2. Relationship between number of thrips per cm² at peak densities versus total number of accumulated thrips-days.

vented a similar increase in the number of thrips-days per cm². After the transition from rapid vegetative growth was completed, the continuing increase in melon thrips population density caused the numbers of thrips per cm² to increase. Feeding damage from the thrips may have further reduced plant growth rates, thus compounding the relative adverse effects of the thrips infestation. Additional information about thrips' dispersal rates into cucumber fields is necessary before the relative contributions of immigration and growth of resident populations to the overall rate of population increase can be understood.

Yield. No significant differences between treatments in the number of plants per plot were observed on any of the three sample dates ($F = 0.55$–1.11; df = 3, 15; $P = 0.38$–0.66). Yield data are presented on a weekly basis to minimize the variation due to differences in estimation of fruit maturity by various fruit harvesters. No significant changes in total yield ($F = 0.90$–1.05; df = 3, 15; $P = 0.34$–0.47), mean fruit size ($F = 0.41$–1.30; df = 3, 15; $P = 0.06$–0.75), total number of fruit ($F = 0.63$–1.64; df = 3, 15; $P = 0.22$–0.61), or mean fruit quality score ($F = 0.49$–2.99; df = 3, 15; $P = 0.07$–0.69) were observed for the first four harvests. The lack of significant differences between treatments for the first four harvests is not surprising if the timing of attack by the thrips is considered. As shown in Fig. 3, the populations of thrips are just starting to increase significantly by Julian date 298 after 70% of the total seasonal fruit production was harvested.

Because cucumber fruits only require about 10 d between flowering and fruit maturation (58% of 93 fruit tagged as open flowers were harvested within 9 d), fruiting after Julian date 292 may have reflected the decreased supply of photosynthates for the previous 10-d period due to increasing thrips damage.

Seasonal trends in fruit production within the four treatments are shown (Fig. 4). Total fruit

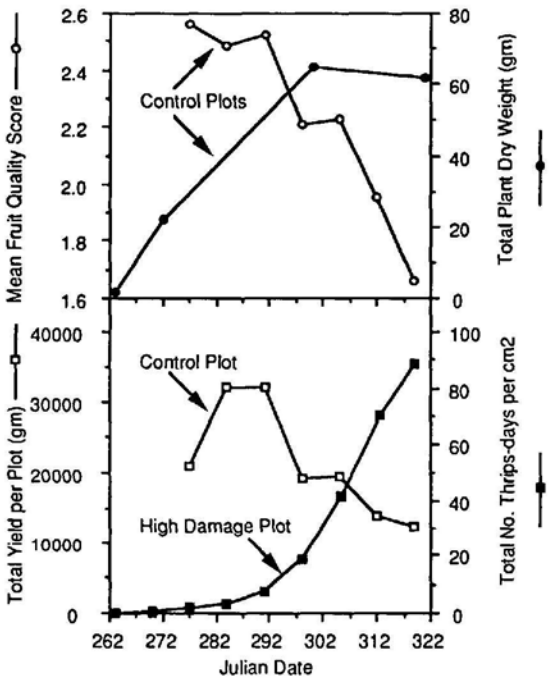

Fig. 3. Seasonal phenology of the mean fruit quality score, total yield per plot, and total plant dry weight for the undamaged control treatment as well as the total number of thrips-days per cm² for the high-damage treatment.

weight for each treatment is expressed as a percentage of the control treatment for each harvest date. The first four harvests did not show any consistent trends between treatments. As the season progressed and the number of thrips-days increased in the medium- and high-damage treatments, the relative effect of the treatment regimes

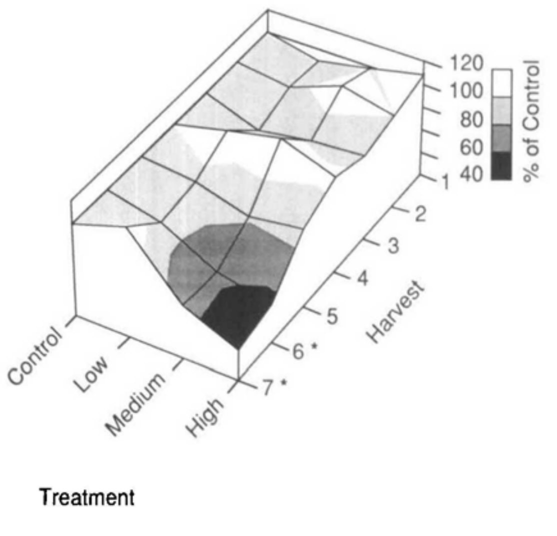

Fig. 4. Total fruit weight per treatment at each harvest date. The symbol * adjacent to the harvest date indicates that treatment means are significantly different ($P < 0.05$; Duncan's multiple range test [Wilkinson 1986]).

became increasingly severe. No significant differences were observed at harvest five on Julian date 305 for total fruit weight per plot, total number of fruit per plot, mean fruit quality, or mean fruit weight (Table 1). However, the shift towards smaller fruit associated with increasing foliar damage was evidenced by a significantly smaller proportion of jumbo fruit ($F = 4.62$; df = 3, 15; $P = 0.02$). The high-damage treatment with 21.0 thrips-days exhibited a 40% reduction in jumbo fruit, whereas the medium-damage level of 17.0 thrips-days showed a 36.1% reduction. Because no significant difference in thrips-days per cm^2 for the medium- and high-damage treatments had developed by Julian date 305, the lack of significant differences between the two treatments for any yield variable is not surprising.

By harvest six on Julian date 312, significant depressions in all categories of fruit production were observed between the two lowest treatments and the high-damage treatment (Table 1). Total fruit weight ($F = 6.51$; df = 3, 15; $P = 0.005$), total weight of jumbo fruit ($F = 3.50$; df = 3, 15; $P = 0.04$), total marketable fruit weight ($F = 6.67$; df = 3, 15; $P = 0.004$), mean fruit size ($F = 5.80$; df = 3, 15; $P = 0.008$), and the total number of fruit ($F = 6.04$; df = 3, 15; $P = 0.007$) were reduced significantly. The reduction in total weight for the highest level of damage at 35.0 thrips-days was 45.8%. The reduction resulted from a 15.5% reduction in mean fruit weight and a 37.1% reduction in total number of fruit per plot relative to the control plots. This shift in fruit size was most readily apparent in the 78.3% reduction in jumbo fruit.

By harvest seven on Julian date 319, reductions became even greater, with a 54.2% reduction in total fruit weight. The shift away from production of larger fruit was shown by a 91.4% reduction in jumbo fruit. The number of fruit per plot decreased by 46.5% at 45.0 thrips-days per cm^2. Mean fruit weight was reduced significantly by 9.5% compared with the control plots.

The experiment was stopped after the seventh week of harvest to avoid confounding effects from an increase in infestation by the rootknot nematode. There was no significant difference in nematode score on the third biomass sample on Julian date 305 ($F = 1.78$; df = 3, 15; $P = 0.19$); the range in mean nematode scores was 0.06–0.55. However, by the fourth biomass sample on Julian date 321, the nematode score in the control plots (0.72 ± 0.68) was significantly higher compared with the high-damage treatment (0.11 ± 0.27) ($F = 3.77$; df = 3, 15; $P = 0.03$). Using the total number of accumulated thrips-days and mean nematode scores as independent variables, multiple linear regression showed no significant relationship between any of the agronomic variables and mean nematode score. Probability values for the slope (beta coefficient) associated with mean nematode scores for harvests six and seven ranged between 0.18 and 0.99 (df = 2, 21). Because the relatively low mean nematode scores and the lack of significant relationships, we considered the influence of the nematode infestation on yield variables to be insignificant for harvests six and seven.

Whereas the effects of the damage by thrips were dramatic at the end of the season, the effect on the total production for the season (harvests one through seven) was not significant by a repeated-measure analysis of variance ($P > 0.05$; Table 1). The total weight produced per plot was reduced by 9.9% ($F = 0.59$; df = 5, 15; $P = 0.63$), whereas the total number of fruit produced was reduced by 8.1% ($F = 0.83$; df = 5, 15; $P = 0.50$). There was no detectable reduction in overall mean fruit quality ($F = 1.20$; df = 3, 15; $P = 0.34$). Significant interactions between harvest date and total fruit yield ($F = 2.85$; df = 8, 90; $P = 0.001$) or total number of fruit ($F = 3.55$; df = 18, 90; $P < 0.001$) occurred. The low levels of reductions in fruit weight or size for the season reflect the fact that the thrips populations did not increase to sufficient numbers until late in the production cycle of the cucumber plant. If the numbers of accumulated thrips-days were to increase early in the season, then the expected effects on yield for the season would probably be significant.

The economic evaluation of thrips feeding on cucumber will also have to consider the seasonal pattern in fruit quality. As shown in Fig. 3, the quality in the undamaged control treatment was initially high, yet declined steadily as the season progressed. As the plants aged, fruit size was reduced, and the percentage of symmetrical fruit decreased. Therefore, the percentage of yield reductions caused by thrips feeding damage occurred during the period of poorest fruit quality. Thus, the economic effects would be less than predicted if just fruit weight is considered.

Although the use of four predetermined treatment levels permits rigorous mean separation tests, the ability to predict the effects of thrips damage requires determination of the relationships between damage and the various agronomic variables. Multiple regression analyses with each of the 24 plots as a data point and block number and accumulated thrips-days as independent variables were performed on the various agronomic parameters. Block effects were significant late in the season because of a sloping grade in the field. No significant block × thrips-days interactions were detected ($P > 0.05$). No significant relationships were detected for any variable for the first four harvests ($P > 0.05$). At harvest five, effects of thrips feeding on total weight of fruit, total marketable fruit weight, mean fruit weight, and total number of fruit per plot did not show any significant relationships with thrips-days (Table 2). Only total weight of jumbo fruit exhibited a significant, but weakly negative, linear relationship. All measures of agricultural productivity showed significant negative linear relationships with thrips-days by harvest six. The most severe reductions were observed

Table 2. Multiple linear regression analysis of the influence of thrips-days per cm^2 and block position[a] on dependent variables

Dependent variable	Harvest	Thrips-days		
		B ± SE	P^b	Multiple R
Total fruit weight, g	5	−113.8 ± 79.4	0.170	0.30
	6	−156.4 ± 45.0	0.002	0.72
	7	−170.0 ± 41.6	0.001	0.79
Total weight of jumbo fruit, g	5	−163.6 ± 51.8	0.004	0.60
	6	−42.2 ± 18.0	0.030	0.51
	7	−45.4 ± 13.0	0.002	0.70
Total weight of marketable fruit, g	5	−118.8 ± 77.2	0.140	0.32
	6	−152.8 ± 45.2	0.003	0.71
	7	−163.0 ± 41.4	0.001	0.79
Mean fruit weight, g	5	−1.86 ± 1.6	0.260	0.36
	6	−0.92 ± 0.2	0.002	0.65
	7	−0.72 ± 0.036	0.061	0.48
Total no. fruit	5	−0.06 ± 0.2	0.800	0.21
	6	−0.50 ± 0.16	0.004	0.71
	7	−0.64 ± 0.16	0.001	0.80
Mean fruit quality score	5	−0.0006 ± 0.002	0.830	0.11
	6	−0.002 ± 0.002	0.326	0.71
	7	−0.002 ± 0.002	0.311	0.64

[a] Regression coefficients for block effects are not presented.
[b] P value reported for thrips-days variable.

by the seventh harvest as shown by the increasing negative slopes (beta coefficient). Significant negative linear relationships were demonstrated between thrips-days and total fruit weight produced per plot, total jumbo fruit weight, total marketable fruit weight, and total fruit number per plot. Mean fruit weight was also reduced, but was significant only at $P = 0.06$. The percentage of the variance explained by the multiple regression increased over time. No significant regressions were obtained between mean fruit quality score and thrips-days for any harvest.

Carbon Allocation Patterns. As the season progressed and thrips damage increased, the total dry weight per plant decreased relative to the treated controls (Fig. 5). No significant differences in total dry weight per plant was observed for any sample date ($F = 0.17$–2.13; df = 3, 15; $P = 0.14$–0.80). The fourth sample on Julian date 321 showed significant shifts in the relative allocation to the various plant components. The proportion of dry weight allocated to leaves was significantly reduced from 0.53 in the low-damage treatment to 0.45 in the high-damage treatment (Table 3, $F = 3.40$; df = 3, 15; $P = 0.05$). Absolute dry weight allocated to leaves decreased similarly from 31.77 g in the control treatment to 23.58 in the high-damage treatment ($F = 2.94$; df = 3, 15; $P = 0.07$). The relative proportion allocated to shoots ($F = 4.14$; df = 3, 15; $P = 0.025$) increased significantly, but

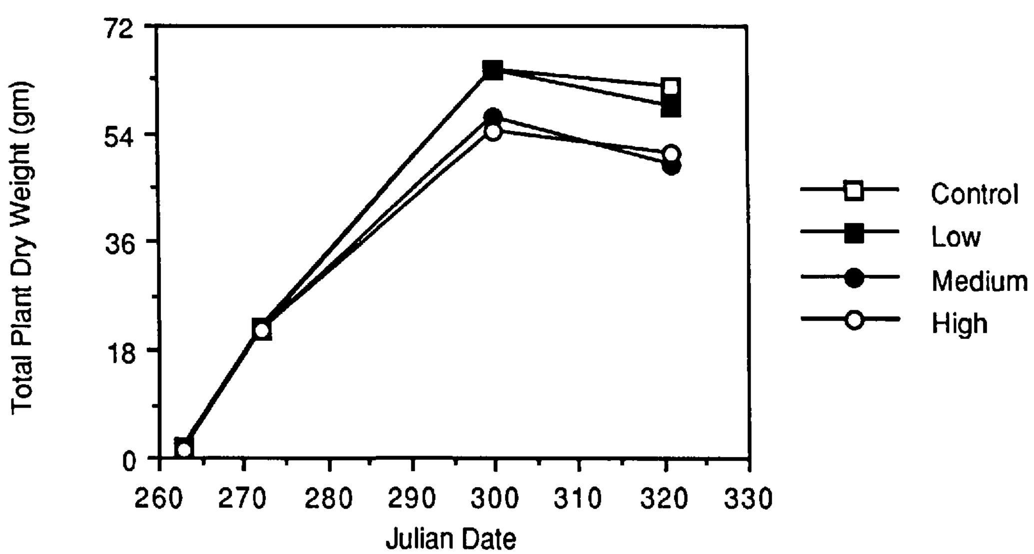

Fig. 5. Seasonal phenology of the total plant dry weight for the four damage treatment levels.

Table 3. Effect of feeding damage by mixed populations of thrips species on carbon allocation to nonreproductive structures in cucumber[a]

	Leaf		Root		Shoot		Petiole	
	Dry wt[b]	Proportion[c]	Dry wt[b]	Proportion[c]	Dry wt[b]	Proportion[c]	Dry wt[b]	Proportion[c]
Sample 3								
Control	38.70 ± 11.94a	0.63a	2.43 ± 0.84a	0.04a	14.48 ± 3.80a	0.24a	5.87 ± 1.47a	0.10a
Low	40.02 ± 11.59a	0.64a	2.38 ± 0.57a	0.04a	14.09 ± 3.95a	0.23a	5.87 ± 1.64a	0.09a
Medium	33.08 ± 8.59a	0.62a	2:02 ± 0.57a	0.04a	12.53 ± 3.62a	0.23a	5.80 ± 2.04a	0.11a
High	28.95 ± 7.96a	0.58b	3.61 ± 3.34a	0.07a	12.67 ± 2.06a	0.25a	5.08 ± 1.41a	0.10a
Sample 4								
Control	31.77 ± 10.77a	0.53ab	4.19 ± 2.80a	0.07a	18.00 ± 2.96a	0.30b	6.46 ± 1.27a	0.11a
Low	31.32 ± 9.62a	0.55a	2.50 ± 1.47b	0.04b	17.29 ± 3.09a	0.30b	6.24 ± 1.62a	0.11a
Medium	22.26 ± 8.79a	0.47b	2.35 ± 1.85b	0.05b	16.98 ± 2.16a	0.36a	5.77 ± 1.23a	0.12a
High	23.58 ± 8.91a	0.47b	1.90 ± 0.75b	0.04b	18.16 ± 2.73a	0.36a	6.46 ± 1.84a	0.13a

Means within a column within a single harvest interval followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Wilkinson 1986]).
[a] Mean of three plants per replicate.
[b] Dry weight (g; $\bar{x}$ + SD).
[c] Proportion of total dry weight for nonreproductive structures.

no apparent pattern in the absolute dry weights occurred. The apparent decrease in allocation to leaf production may not arise directly from the effects of thrips feeding on allocation patterns. On Julian date 309 a severe tropical storm that was accompanied by strong winds was responsible for additional leaf loss. Leaves damaged by thrips became brittle and were more susceptible to removal by wind. Damaged leaf blades were either torn off between the leaf veins or removed entirely. Therefore, the relatively smaller allocation to leaf dry weight may be an indirect effect of feeding damage by thrips.

Linear regression that indicated highly significant relationships between leaf dry weights (x) and leaf area (y) were developed for all four sample dates. Similar lines were obtained for the first three sample dates (sample 1: $y = 7.2 + 238.3x$; df = 1, 21; $r = 0.98$, sample 2: $y = -44.5 + 268.4x$; df = 1, 21; $r = 0.98$, sample 3: $y = 216.4 + 193.7x$; df = 1, 21; $r = 0.98$). By sample 4, the leaves were older and heavier per unit leaf area as indicated by the flattened slope of the regression ($y = 195.3 + 100.9x$; df = 1, 21; $r = 0.91$). These regressions can be used to estimate the leaf canopy development at any biomass sample date.

Allocation of dry weight to fruit was the largest component of plant production. The regression between fruit fresh weight and fruit dry weight was highly significant (dry weight = 1.58 + 0.0233 × fresh weight; $P < 0.001$; df = 1, 13; $r = 0.99$). Based on the regression function and seasonal fresh weight production, total dry weight for fruit produced for the entire season was 3,484, 3,290, 3,297 and 3,140 g, for the control, low-, medium-, and high-damage treatments, respectively. Total dry fruit weight produced per plant for the control, low-, medium-, and high-damage treatments were 56.1, 53.5, 52.3, and 51.9 g, respectively. Thus, the dry weight allocation to fruit was about equal to the allocation to vegetative growth.

Mean Leaf Size. The average leaf size increased early in the season, then reached a plateau by Julian date 298 (Fig. 6). Until that day, no consistent trends between treatments were observed. Early in the season, the medium level of damage was significantly higher than the undamaged control treatment ($F = 4.49$; df = 3, 15; $P = 0.02$), yet this pattern disappeared by the next sample date. After Julian date 298, plots with medium or high levels of thrips damage consistently produced the smallest leaves. However, these differences were only significant on Julian date 312 ($F = 6.05$; df = 3, 15; $P = 0.007$). The most heavily damaged treatment at 45.0 thrips-days/cm^2 produced leaves that were 22.5% smaller than the control treatment on Julian date 312.

Discussion

Whether *T. palmi* is a significant pest of cucumbers appears to depend on the timing of the infestation as well as the relative levels of damage. Despite the fact that thrips damage reached 45.0 thrips-days/cm^2, we observed an insignificant reduction of 9.9% in total yield for the season. However, substantial reductions of 54% in total fruit weight late in the season also demonstrated the potential adverse effects of high population levels. Therefore, *T. palmi* is apparently a pest that can cause economical and significant reductions if infestations are allowed to develop to high levels early in the season. Our results suggest that growers should protect their crops from damage levels >9.4 thrips-days/cm^2 (94.5 thrips/leaf) early in the season when the highest quality fruit and most of the total weight are produced. The threshold of 9.4 thrips-days/cm^2 was incurred by the high-damage plots at the fourth harvest (Fig. 3) without any detectable loss in yield or quality. The threshold of 94.5 thrips/leaf was calculated by converting number of thrips-

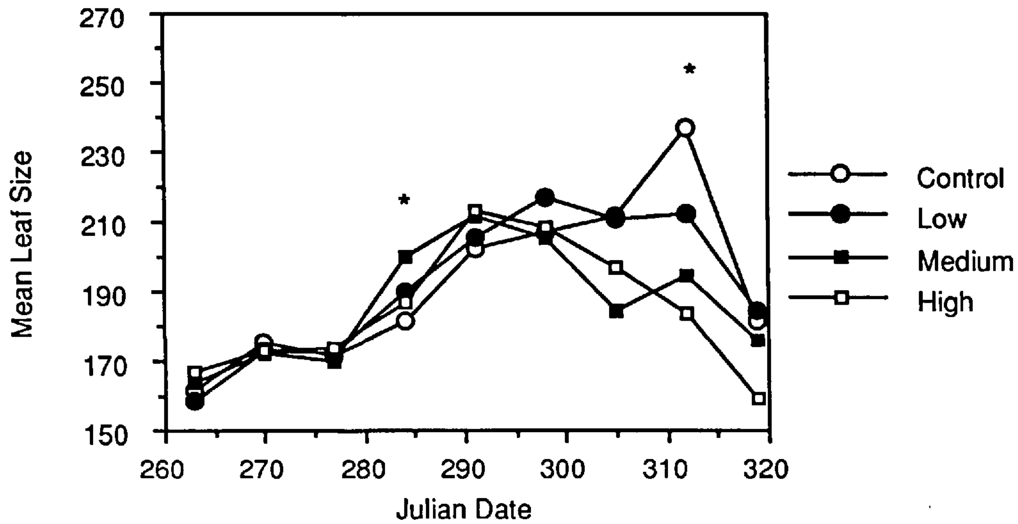

Fig. 6. Seasonal phenology of the mean leaf size (single leaf surface) for the four damage treatment levels. The symbol * over the sample date indicates that the treatment means are significantly different ($P < 0.05$; Duncan's multiple range test [Wilkinson 1986]).

days per cm^2 to thrips number per cm^2 with the linear regression (Fig. 1) and multiplying by an average leaf size of 200 cm^2 (single surface only). Given the rapid rate of development for new foliage early in the season, relatively high densities of thrips at the fifth leaf may be rare before heavy fruit production.

The development of economic injury levels for cucumbers will also depend on the current market. The relative demand for cucumbers at any time determines whether fruit will be accepted or rejected as unmarketable because of shape or size. The overall weight reduction per field by the thrips is more easily predicted. If growers wish to incur <10% losses for the season because of thrips feeding damage, then levels as high as 45.0 thrips-days/cm^2 can be tolerated at the end of the season.

The current practice of weekly applications of pesticides to suppress infestations of *T. palmi* early in the season is not warranted when densities are low to moderate. The elimination of pesticide applications early in the season should result in decreased production costs as well as limit the disruption of any potential biological control and the development of insecticide resistance.

The discrepancies between our results and the lower economic injury level of Suzuki & Miyara (1983) may reflect differences, such as cultivar type, timing of infestation between treatments, or contrasts between greenhouse and field trails. The apparent discrepancy between our results and those of Kawai (1986) may be explained several ways. Kawai (1986) pruned the cucumber plants after the plant developed 25 nodes. Kawai (1986) changed the ratio of supply (presumably linked to photosynthetically active leaf area) and demand (both vegetative and reproductive). Because the level of fruiting was not reduced by Kawai (1986), the author may have dropped the ratio of supply/demand below limiting levels for a fixed level of fruiting. Reduction in leaf area may have made the cucumber plants more susceptible to thrips damage as the remaining leaf tissue became relatively more important. Differences in relative allocation to fruiting versus vegetative growth may have important implications for predicting the susceptibility of different cultivars of cucumbers to thrips damage. Cultivars with high allocation of foliage relative to fruit may be more tolerant of equal levels of thrips damage, whereas high yielding or pruned cultivars may be more susceptible. Similarly, the ratio of available photosynthate supply relative to fruit demands also may be important for determining the relative susceptibility of different crops to thrips or other foliage feeders. Further research with manipulated levels of foliage and fruiting will be necessary to test these hypotheses.

We converted the data from Fig. 3 in Kawai (1986) to thrips-days per cm^2. Assuming average leaf size to be roughly similar between our experiments and those of Kawai (1986), the total number of accumulated thrips-days were divided by the average number of cm^2 obtained for both leaf surfaces within our trial (400 cm^2). Thus, the two most damaged plots (I and II) in Kawai (1986) had 62.2 and 32.8 thrips-days/cm^2, respectively. Plots I and II had 43.6 and 71% reductions in yield. The reduction in yield for plots I and II are similar to the losses in yield observed within the high damage plots at harvest seven, when damage levels reached as high as 45 thrips-days/cm^2. Therefore, the data are not inconsistent between the two experiments, but differ primarily in the thresholds selected. Kawai (1986) maintained constant densities throughout the experiment with different pesticide regimes, whereas thrips populations within our experiment were allowed to develop unchecked until particular damage levels were obtained. Given the differences in population growth rates between the two experiments, the relationships between thrips per cm^2 and thrips-days per cm^2 would not be expected to be similar. The development of the thrips infestation within our experiment was more typical of thrips population growth rates in the field than a fixed density over time. Thus, our threshold of 94 thrips/leaf early in the season seems to be more typical of the situation that growers face in Hawaii.

Acknowledgment

We acknowledge the technical assistance of Lois Caprio and Sandy Janus (University of Hawaii) and the careful review of an anonymous reviewer. The research was supported by the United States Department of Agriculture under CSRS Special Grant 86-CRSR-2-2827 and/or 88-34135-3506, managed by the Pacific Basin Advisory Group (PBAG). This manuscript is Journal Series 3438 of the Hawaii Institute of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.

References Cited

Hamasaki, R. T. 1987. Impact of insecticides and a predatory mite on the melon thrips, *Thrips palmi* Karny. M.S. thesis, University of Hawaii, Manoa.

Johnson, M. W. 1986. Population trends of a newly introduced species, *Thrips palmi* (Thysanoptera: Thripidae), on commercial watermelon plantings in Hawaii. J. Econ. Entomol. 79: 718–720.

Kawai, A. 1986. Studies on population ecology of *Thrips palmi* Karny. XI. Analysis of damage to cucumber. Jpn. J. Appl. Entomol. Zool. 204: 107–117.

McNally, P. S., C. Fogg, J. Flynn & J. Horenstein. 1985. Effects of thrips (Thysanoptera: Thripidae) on shoot growth and berry maturity of 'Chenin Blanc' grapes. J. Econ. Entomol. 78: 69–72.

Rosenheim, J. A., S. C. Welter, M. W. Johnson, L. R. Gusukuma-Minuto & R. F. L. Mau. 1990. Direct feeding damage on cucumber by mixed species infestations of two thrips, *Thrips palmi* and *Frankliniella occidentalis* (Thysanoptera: Thripidae). J. Econ. Entomol. 83(4): 1519–1525.

Suzuki, H. & A. Miyara. 1983. Integrated control of *Thrips palmi* using silver-colored materials 1. Loss assessment on cucumber. Proc. Assoc. Plant Prot. Kyushu 29: 77–80 (in Japanese).

Terry, L. I. & B. B. Barstow. 1988. Susceptibility of early season cotton floral bud types to thrips (Thysanoptera: Thripidae) damage. J. Econ. Entomol. 81: 1785–1791.

Waterhouse, D. F. 1987. Biological control: pacific prospects. Inkata Press, Melbourne.

Wilkinson, L. 1986. SYSTAT: the system for statistics. Systat, Evanston, Ill.

Received for publication 6 September 1989; accepted 17 April 1990.