Influences of fertilization on population abundance, distribution, and control of *Frankliniella occidentalis* on chrysanthemum

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Abstract

We examined the effects of fertilization on population abundance and within-plant distribution of western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae), on potted chrysanthemum, *Dendranthema grandiflora* (Tzvelev). We also investigated the effects of fertilization on the number of insecticide applications needed to control *F. occidentalis* on potted chrysanthemum. Under greenhouse conditions, rate of change in population abundance of *F. occidentalis* increased with fertilization levels from 0 to 100% of the standard fertilization level (375 ppm N) and was four times higher on plants fertilized with the standard level (rate of change = 0.14) than on plants fertilized with 0% during the first 4 weeks after thrips inoculation. Within-plant distribution of *F. occidentalis* was influenced by the phenology of the plants rather than total nitrogen content of plant tissues. Prior to flower opening, more *F. occidentalis* were found in the middle region of the plants. When the flowers began to open, more thrips were found feeding inside the flowers than on the leaves. We further showed that production time, the time from transplantation to flower opening, shortened considerably with increased fertilization level. Production time was shortest, 12 weeks, for plants fertilized with 100% of the standard fertilization level. When the fertilization level was reduced to 20%, production time lengthened to 13 weeks. When fertilization level was reduced to 0%, production time lengthened to 14 weeks. Increased fertilization from 0 to 100% of the standard level did not result in higher numbers of insecticide applications. All three insecticides (acephate, bifenthrin, and spinosad) were effective in keeping the thrips infestation below a predetermined level, five thrips per plant, but bifenthrin required the most number of applications to do so. For chrysanthemum, a fast-growing crop and heavy utilizer of fertilizer, fertilization influenced not only the population growth of pest insects but also plant production time. As a result, optimizing fertilization level to reduce pest population growth may be a useful tactic in an Integrated Pest Management program for managing *F. occidentalis* on potted chrysanthemum. However, the effect of fertilization on production time and plant quality should also be considered when implementing this tactic.

Introduction

Western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae), is a serious, worldwide pest of greenhouse crops (Tommasini & Maini, 1995; Lewis, 1997). It is extremely polyphagous and can damage over 200 species of vegetables and ornamentals through direct feeding and vectoring of plant diseases (Robb, 1989; Childers & Achor, 1995). This insect pest is very difficult to control because of its biology and behavior (Robb, 1989; Brødsgaard, 2004). It prefers to feed within flowers and buds, which protect the thrips from insecticides and natural enemies. Where insecticide use is prevalent, *F. occidentalis* rapidly develop and maintain insecticide resistance (Immaraju et al., 1992; Jensen, 2000; Kiers et al., 2000).

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Effective control of *F. occidentalis* necessitates integrated management tactics such as biological control (Berndt et al., 2004), host plant resistance (Bergh & Le Blanc, 1997; de Kogel et al., 1998), cultural practices (Schuch et al., 1998; Stavisky et al., 2002), and the judicious use of insecticides.

In greenhouse ornamental production, fertilization and pesticide application remain as vital agronomic practices for producing high quality and aesthetic crops. Chemical fertilizers elevate plant nitrate and amino acid levels (Mengel & Kirkby, 2001) but inadvertently increase the nutritional quality and attractiveness of plants to phytophagous insects (van Emden, 1966; Minkenberg & Fredrix, 1989; Bentz & Larew, 1992; Bentz et al., 1995). Higher levels of leaf nitrogen may enhance both growth and reproduction of herbivorous insects (Mattson, 1980; Larsson, 1989; Waring & Cobb, 1992) and reduce their susceptibility to some insecticides (McKenzie et al., 1995). Most studies on the effect of fertilization on pest populations have focused on aphids. Responses of aphids to fertilization vary greatly. Some studies found that fertilization does not affect either aphid fecundity or number (Archer et al., 1995; Bethke et al., 1998), while other studies showed that aphid fecundity increases with fertilization (van Emden, 1966; Rosenheim et al., 1994; Nevo & Coll, 2001). Chau et al. (2005) showed that population growth rate of *Aphis gossypii* Glover on potted chrysanthemum, *Dendranthema grandiflora* (Tzvelev), increases with fertilization levels from 0 to 38 ppm N and reaches a plateau from 38 to 488 ppm N. Effects of fertilization on aphid population growth can only be detected at very low fertilization levels in chrysanthemum. Crop-specific responses could explain, in part, the inconsistent detection of fertilization effects on aphid growth and development in some studies. In comparison with the aphid literature, few studies have examined the effect of fertilization on thrips populations. On field-grown tomatoes, the abundance of *F. occidentalis* increases with increasing rates of fertilization (Brodbeck et al., 2001; Stavisky et al., 2002). Conversely, Reitz (2002) showed that nitrogen fertilization has no effect on the abundance of *Frankliniella* spp. on the same crop. Schuch et al. (1998) found twice as many *F. occidentalis* infesting chrysanthemums fertilized for 10 weeks with 240 ppm N than on plants fertilized with 80 ppm N. Whether differences in *F. occidentalis* abundance were due to thrips aggregation on highly fertilized plants or elevated reproductive rates was undetermined.

Although *F. occidentalis* appears to prefer flowers and is more abundant on flowering ornamentals with flowers than those without flowers (de Jager et al., 1993; Gerin et al., 1999), it also readily feeds on leaves and stems (Schuch et al., 1998; Brødsgaard, 2004). On greenhouse cucumber, females of *F. occidentalis* deposit most of their eggs in the leaves rather than the stems or flowers (Kiers et al., 2000) and prefer younger leaves to older leaves for oviposition (de Kogel et al., 1997). In a previous study, Chau et al. (2005) found higher leaf nitrogen content in both newly unfurled leaves and physiologically mature leaves than older, basal leaves of chrysanthemum. If *F. occidentalis* responds to nutrient availability within plants, the nutrient quality of the foliage should influence the distribution of this insect within the canopy prior to flower opening. When flowers become available, *F. occidentalis* should be found mostly inside the flowers.

In the United States, environmental concerns and governmental regulation such as the Federal Clean Water Act have prompted the need to develop best management practices that optimize inputs and minimize runoff for production agriculture (Yeager et al., 1997; Lea-Cox, 2001). As a result, fertilizer usage has been modified for a number of ornamental crops such as roses, poinsettias, and hydroponically grown chrysanthemum (Kageyama et al., 1991; Cabrera et al., 1993; Rose & White, 1994). However, strategies are needed for optimizing fertilization to a level that maintains plant marketability, minimizes thrips population growth, and reduces insecticide usage.

In this study, we used *F. occidentalis* and potted chrysanthemum, *D. grandiflora*, as our experimental system. Our three objectives were (1) to determine the effect of fertilization on population abundance of *F. occidentalis* on chrysanthemum under controlled conditions in growth chambers, (2) to investigate the effect of fertilization on population abundance and within-plant distribution of *F. occidentalis* under greenhouse conditions, and (3) to evaluate whether increasing fertilization would affect the number of insecticide applications needed to control *F. occidentalis* on chrysanthemum.

Materials and methods

Chrysanthemum cultivation

We followed commercial cultural practices to produce potted chrysanthemum for our studies (Yoder Brothers Inc., 2001). A soil-less potting mix (Sunshine Mix#1, Sun Gro Horticulture Canada Ltd, Bellevue, WA, USA) was used as growing medium. Single rooted chrysanthemum cuttings (cv. 'Charm') were transplanted into individual pots (15.5 cm diameter × 10.5 cm height, Dillen Products, Middlefield, OH, USA). To maximize applicability to chrysanthemum growers, a water-soluble, complete commercial fertilizer [Peters Professional Peat-lite special, 15-16-17 (15 N-6.7 P-14.1K), Scotts-Sierra Horticultural Products Company, Marysville, OH, USA] was used as the

source of nutrients. Chrysanthemum requires elevated and balanced levels of nitrogen and potassium for proper vegetative growth (Crater, 1992). We used a fertilizer that provides equal amounts of nitrogen and potassium with 53% N in nitrate form, 20.4% N in ammoniacal form, and 26.1% N in urea form. This formulation is recommended by propagators to improve growth, reduce leaf yellowing, and increase plant longevity (Yoder Brothers Inc., 2001).

The recommended fertilizer rate for pulse or periodic feeding of potted chrysanthemum, based on nitrogen, is 350–400 ppm N (Scotts-Sierra Horticultural Products Company); therefore, 375 ppm N was used as the standard level (100%) for our studies. The amount of phosphorous and potassium in 375 ppm N fertilizer solution is 175 and 354 ppm, respectively. Each fertilization treatment was made with the same complete fertilizer. To keep the ratio of all macro- and micronutrients the same, we varied only the strength of the fertilizer to the levels specified in each experiment. Reverse-osmosis-filtered tap water (RO water) was used to water the plants and make the fertilizer solutions. Fertilization began right after transplantation. Plants were fertilized twice a week and watered as needed between fertilizations. Depending on the fertilization levels, we applied 200 ml of fertilizer solution or RO water (for no fertilization) to each pot.

We pinched each plant back to seven laterals after 2–2.5 cm of new plant growth. Daminozide, a plant growth regulator (B-Nine WSG, Uniroyal Chemical Company Inc., Middlebury, CT, USA), was applied to all pots at the concentration of 3500 ppm to reduce internode elongation (Yoder Brothers Inc., 2001) following another 3–3.5 cm of new growth after the pinch. We inoculated the 4-week-old plants with thrips on the day after daminozide application.

Insect rearing

The laboratory colony of *F. occidentalis* was maintained at 26 °C, 65% r.h., and under a L14:D10 photoperiod on kidney bean, *Phaseolus vulgaris* L., using the rearing method described by Arthurs & Heinz (2002). Freshly excised chrysanthemum leaves and inflorescences (flower heads) were added to the thrips colonies 2 days prior to experiments to feed newly emerged adult thrips.

Effect of fertilization level on *Frankliniella occidentalis* in a controlled environment

We hypothesized that *F. occidentalis* abundance would increase with higher host-plant quality. We manipulated host-plant quality by treating plants with one of four different fertilization levels: 0, 10, 20, and 100% of the standard level (375 ppm N). Davies et al. (2004) demonstrated that plants fertilized with these four

fertilization levels differ in their micro- and macro-nutrient content, ranging from severely deficient to sufficient. Thirty-six cuttings were transplanted into 36 pots. Each pot served as a replicate and we used a randomized complete block design with three replications per fertilization level in each of the three blocks (chambers), totaling nine replicates per fertilization level. Differences in thrips abundance could result from either aggregation or elevated growth rate of thrips on highly fertilized plants. Therefore, cages were used to prevent movement of *F. occidentalis* between pots so that the effect of fertilization on the rate of change in population abundance of *F. occidentalis* could be quantified. Individual pots were enclosed in cylindrical cages (36 cm diameter × 61 cm height) constructed with clear Lexan® film (GE Polymershapes, Hunterville, NC, USA), with sealed tops and bottoms (40.6 cm diameter clear plastic saucers, Ivex Packaging Corporation, Bridgeview IL, USA). Two openings (20 cm diameter) were cut on the side and one opening on the top (36 cm diameter) and covered with nylon organdy cloth for ventilation. Clear PVC tubing (0.95 cm diameter × 30 cm length) (VWR International, Suwanee, GA, USA) was attached to each cage for fertilization. The caged plants were maintained in growth chambers at 24 °C day/20 °C night and 75% r.h. The photoperiod was L16:D8 for approximately 3 weeks and then switched to L11:D13 for the remainder of the experiment to induce flower production. The average photosynthetically active radiation at plant canopy inside the cages was 650 µmol m^{-2} s^{-1} (Davies et al., 2005).

On the day after daminozide application, we isolated five adult female *F. occidentalis* in a 1.5 ml microcentrifuge tube (USA Scientific Inc., Ocala, FL, USA) and released the thrips from the tube near the base of the plant in each pot. Flowering times of plants varied with fertilization level. Hence, we harvested all the plants in a given treatment when flowers on 80% of the plants were fully open. Flowers that are heavily damaged by thrips do not open fully; therefore, we planted additional pots (nine per fertilization level) and kept these pots free of thrips for the duration of the experiment to determine when to harvest the plants. Each plant was cut at soil level and placed in a sealed plastic container (25 × 25 × 10 cm; Rubbermaid Home Products, Wooster, OH, USA). The container was vigorously shaken to dislodge any thrips that were on the plants. Individual ray flowers were also taken apart to dislodge any thrips that were feeding inside. All thrips were removed using an aspirator and stored in 70% alcohol. We later counted and recorded the total number of thrips collected from each pot. The observed differences in thrips numbers at harvest may be influenced by both fertilization level and time to harvest. To separate these factors, we

calculated the rate of change in the number of *F. occidentalis* per day using the following equation:

The rate of change in thrips number per day $= \dfrac{N_t - N_0}{t}$,(1)

with N_t as the population size at harvest, N_0 as the initial number of thrips at the start of the experiment, and t as the time from thrips inoculation to harvest (days).

Effect of fertilization level on *Frankliniella occidentalis* under greenhouse conditions

We further investigated the effect of fertilization levels on *F. occidentalis* population abundance and within-plant distribution on chrysanthemum under greenhouse conditions that approximated commercial production in Texas. We tested the propositions that population abundance and within-plant distribution of *F. occidentalis* would vary with fertilization level. The experimental design was modified from the previous experiment. Pots were placed on three greenhouse benches. We used a randomized complete block design with the three greenhouse benches as blocks and individual pots as replicates. There were three replications per fertilization level on two of the three benches and four replications on the third bench, for a total of 10 replicates per fertilization level. To prevent other insects from contaminating our experiments, we enclosed individual greenhouse benches with cages ($94 \times 285 \times 107$ cm) constructed with PVC frames and covered with Reemay® polyester (Reemay, Inc., Old Hickory, TN, USA). We inoculated each pot with *F. occidentalis* as described earlier and allowed the thrips to settle and reproduce on the plants to stimulate an infestation. We visually counted all thrips in each pot at weekly intervals. To examine the within-plant distribution of *F. occidentalis*, we divided the plant in each pot into three strata: apical (apical meristem and two newly unfurled leaves), middle (physiologically mature leaves between apical and basal regions), and basal (postphysiologically mature leaves from the oldest remaining 2–3 laterals just above the soil line). The number of thrips in each stratum was recorded separately. We planted five additional pots per fertilization level and kept these pots free of thrips for the duration of the experiment to determine when to harvest the plants and also measure the levels of total nitrogen and total carbon content of plant tissues. At the time of harvest, five leaves from each plant stratum and five flower heads (disk and ray flowers) were taken from each of the thrips-free plants to determine the effect of fertilization levels on host plant quality. We oven-dried the flower tissues and leaves at 80 °C for 48 h. Total nitrogen and total carbon contents in the leaf and flower tissue were analyzed by Analytical Chemistry Laboratory (Institute of Ecology, University of Georgia, Athens, GA, USA) using Micro-Dumas Combustion Analysis. We also estimated the rate of change in population number of *F. occidentalis* by first transforming thrips counts to their natural logarithms (ln-transformed) and plotting them against sampling dates. If there is a linear increase of ln-transformed thrips counts with time, the slope of the regression line can be used to estimate the rate of change in population number. We compared the slopes of the regression lines among fertilization levels to test for fertilization effect. The experiment was conducted from August 28 to December 3, 2002. Temperature and relative humidity inside the enclosed benches were monitored for the duration of the experiment with HOBO®H8 Pro Series data loggers (Onset Computer Corporation, Bourne, MA, USA) recording at 4 h intervals (daily mean ± SEM: 26.28 ± 0.39 °C and 60.11 ± 1.59% r.h.; n = 98 day). Daily temperature and relative humidity fluctuations were 8.53 ± 0.41 °C and 28.18 ± 1.56% r.h. (mean ± SEM; n = 98 day). Day length during this period at College Station, TX, USA (latitude N30.6°, longitude W96.3°) was calculated from the data on sunrise and sunset provided by the Astronomical Applications Department, U.S. Naval Observatory, Washington, DC, USA (daily mean ± SEM: 11.48 ± 0.08 h).

Effect of fertilization on insecticide usage for controlling *Frankliniella occidentalis*

We tested whether the number of insecticide applications needed to suppress thrips populations would vary with the level of fertilization applied to the host plants. Our previous study showed that the rate of change in population abundance of *F. occidentalis* increased with increasing fertilization; consequently, we predicted that greater numbers of insecticide applications would be needed to suppress the infestations. We examined the interactive effects of three fertilization levels (0, 20, and 100% of the standard level) and three insecticides (acephate, bifenthrin, and spinosad) currently registered for control of *F. occidentalis* on potted chrysanthemum. The three insecticides were selected for their different modes of action. Acephate (Orthene® Turf, Tree & Ornamental Spray 97, Valent USA Corp., Greenville, MS, USA) is an organophosphate with some systemic activities. Bifenthrin (Talstar® Flowable, FMC Corporation, Philadelphia, PA, USA) is a contact pyrethroid. Spinosad (Conserve® SC, Dow AgroSciences LLC, Indianapolis, IN, USA) is a microbially derived insecticide that also has systemic properties. The study was designed as a 3×3 factorial experiment that yielded nine treatment combinations. We used a randomized complete block design with the four greenhouse benches as blocks and individual pots as replicates. Three replications

per treatment were placed on two of the four benches and two replications on the other two benches, for a total of 10 replicates per treatment. The study was conducted from 24 January to 3 April, 2003. Temperature and relative humidity inside the enclosed benches were 21.88 ± 2.63 °C and $53.22 \pm 6.41\%$ r.h. (mean $\pm$ SEM; n = 69 day). Daily temperature and relative humidity fluctuations were 8.54 ± 1.03 °C and $23.79 \pm 2.86\%$ r.h. (mean $\pm$ SEM; n = 69 day). Day length during this period was 11.51 ± 1.39 h.

Five adult female *F. occidentalis* were transferred, as described in the first experiment, to the plants on the day after daminozide application. We allowed the thrips to settle and reproduce on the plants to simulate an early thrips infestation. *Frankliniella occidentalis* leaves distinct feeding damage that may greatly reduce the marketability of ornamental crops and vectors a number of viruses, such as tomato spotted wilt virus, that are detrimental to ornamentals. Although tolerance for *F. occidentalis* is low (Murphy & Broadbent, 2004), no recommendations were available on the action threshold for *F. occidentalis* on potted chrysanthemum. On cut chrysanthemum, Brødsgaard (2004) suggested that 2–7 *F. occidentalis* per chrysanthemum leaf was too high for this crop. In the absence of any diseases, we decided to use five thrips per pot as the action threshold for insecticide treatments. Based on earlier observations, plant damage by *F. occidentalis* was not conspicuous at this density level. We visually counted the number of live thrips on each pot at weekly intervals. Whenever the number of thrips for a pot exceeded five, we applied the assigned insecticide to that pot. Pots were removed for insecticide treatment and returned to their original location after treatment. According to the recommendations on the product labels, we applied acephate at a rate of 0.60 g l^{-1}, bifenthrin at a rate of 2.34 ml l^{-1}, and spinosad at a rate of 0.53 ml l^{-1}. Treatment sprays were applied at 414 kPa using a Solo® 15.1-liter capacity backpack sprayer (Model #475, Solo Inc., Newport News, VA, USA) equipped with a standard adjustable hollow-cone spray head. Insecticides were applied to upper and lower leaf surfaces until runoff. We terminated the experiment when the flowers of plants fertilized with the standard level were fully open.

Statistical analyses

For the growth chamber study, thrips abundance was analyzed using the Scheirer–Ray–Hare two-way ANOVA of ranks test with growth chamber and fertilization level as main factors (Sokal & Rohlf, 1995). The effect of fertilization on the rate of population change was analyzed using the Kruskal–Wallis test. For the greenhouse studies, the effect of fertilization on thrips abundance for the first 6 weeks after thrips inoculation was ln-transformed and then analyzed using repeated measures two-way ANOVA with greenhouse bench and fertilization level as main factors. Linear regression analysis was performed on each replicate to estimate the slope. The slopes (rate of change in population abundance) were then analyzed using one-way ANOVA for the effect of fertilization level. Within-plant distribution of thrips was first tested with the log-linear model test to determine the degree of association between sampling date, fertilization level, and plant strata. The G-test of independence for multiway table, often called R × C-test of independence (Sokal & Rohlf, 1995), was used to test the effect of sampling date on within-plant distribution of thrips for each fertilization level. In all cases, G-values were adjusted with William's correction (Sokal & Rohlf, 1995). Both total nitrogen content and total carbon content of plant tissues were first ln-transformed and then analysed using two-way ANOVA with fertilization level and plant tissues as main factors. Number of insecticide applications was first transformed to their square roots ($\sqrt{X + 0.5}$) and analyzed using one-way ANOVA to determine the effect of greenhouse benches. Then, the effects of fertilization level and insecticide on the number of insecticide applications were analyzed using the Scheirer–Ray–Hare two-way ANOVA of ranks test with fertilization level and insecticide as the main effects. We used the Games and Howell method to determine significance between pairs following non-parametric tests. Tukey's honestly significant difference test was also used to determine significant differences between pairs following parametric tests.

Results

Effect of fertilization level on *Frankliniella occidentalis* in a controlled environment

The number of thrips increased significantly with higher fertilization level (Scheirer–Ray–Hare test: H = 122.98, d.f. = 3, P<0.001). We found no significant chamber effect or significant interaction between fertilization level and chamber effect (Scheirer–Ray–Hare test: H = 2.65, d.f. = 2, P = 0.27 and H = 2.68, d.f. = 6, P = 0.85, respectively). Therefore, we pooled the data across the chambers for all further analyses. Thrips number was highest on plants fertilized with the standard level (mean $\pm$ SEM: 600.22 ± 69.92) and lowest on plants without fertilization (mean $\pm$ SEM: 54.00 ± 22.82). The number of thrips on plants fertilized either with 10 or 20% of the standard level (mean $\pm$ SEM: 322.67 ± 52.73 and 337.44 ± 31.09, respectively) was between the two aforementioned groups.

The time from thrips inoculation to harvest varied considerably with fertilization level and confounded the
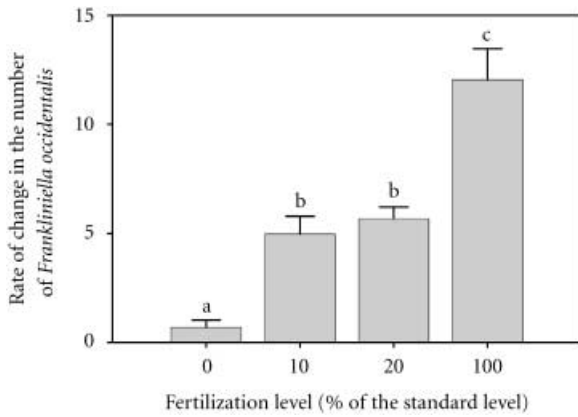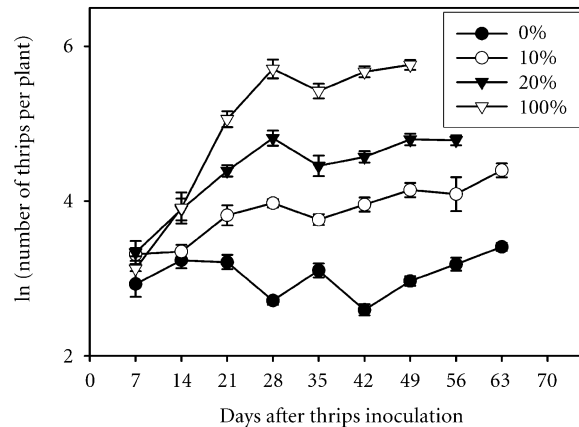
Figure 1 Mean rate of change (+ SEM) in the number of *Frankliniella occidentalis* per day per plant on chrysanthemums fertilized with 0, 10, 20, or 100% of the standard level (375 ppm N) and grown in growth chambers. Different letter(s) above the bars indicate significant differences among fertilization levels at P = 0.05 as determined by the Kruskal–Wallis test (H = 26.75, d.f. ≤ 3, P<0.001; n = 9) and followed by the Games and Howell method.

Figure 2 Mean ± SEM ln-transformed number of *Frankliniella occidentalis* per plant at each weekly sampling interval (day) on chrysanthemums fertilized with 0, 10, 20, or 100% of the standard level (375 ppm N) and grown under greenhouse conditions (n = 10).

observed differences in thrips numbers at harvest. We calculated the mean rate of change in thrips number per day for each fertilization level and found that thrips number increased 17 times faster on plants fertilized with the standard level than on plants without fertilization and about 2.1–2.4 faster on plants fertilized with the other two levels (Figure 1) (Kruskal–Wallis test: H = 26.75, d.f. = 3, P<0.001). The results demonstrated that the rate of change in the number of *F. occidentalis* increased with fertilization level.

Effect of fertilization level on *Frankliniella occidentalis* under greenhouse conditions

The total number of weekly counts was different among fertilization levels because of different harvesting time (Figure 2). We compared the number of thrips among fertilization levels only for the first 6 weeks, before flowers of plants fertilized with the standard level began to open. Similar to the first experiment, we found a significant fertilization effect on thrips population abundance (repeated measures two-way ANOVA: $F_{3,28} = 126.48$, P<0.001) (Figure 2). We found neither a significant bench effect (repeated measures two-way ANOVA: $F_{2,28} = 0.26$, P = 0.77) nor a significant interaction between bench and fertilization level (repeated measures two-way ANOVA: $F_{6,28} = 0.34$, P = 0.91). Therefore, we pooled the data across the benches for all further analyses. Thrips number (average across the first 6 weeks) was highest on plants fertilized with the standard level and lowest on plants

without fertilization [back-transformed means (95% confidence interval): 123.47 (106.91–142.59) and 19.36 (16.76–22.35), respectively]. The number of thrips on plants fertilized with 20% of the standard level was higher than on plants fertilized with 10% of the standard level [back-transformed means (95% confidence interval): 70.39 (60.95–81.29) and 40.25 (34.85–46.48), respectively] and these two groups were significantly different from the other two treatments.

There was a linear increase of thrips population for only the first 4 weeks (Figure 2). After week 4, thrips population growth was limited and no longer linear with time. To estimate the rate of change in population number, we calculated the slope of regression for each replicate in each fertilization level using only the first 4 weeks of data. We showed that rate of change in population number differed significantly with fertilization level (one-way ANOVA: $F_{3,36} = 250.32$, P<0.001) (Figure 3).

The time from transplantation to flower opening was reduced considerably with increased fertilization. The time to flower opening was shortest, 11.9 weeks, for plants fertilized with 100% of the standard level, and longest, 13.9 weeks, for plants without fertilization. The time to flower opening was 12.9 weeks for plants fertilized with 20% and 13.4 weeks for plants fertilized with 10%.

We compared the number of thrips within each plant stratum only for the first 7 weeks because of different harvesting time. Our results showed that there was a significant three-way interaction between sampling date, fertilization level, and plant strata ($G_{adj} = 605.70$, d.f. = 36, P<0.001) (Figure 4). A significant three-way interaction
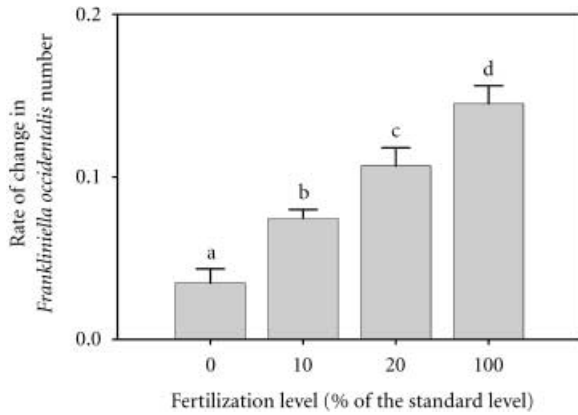
Figure 3 Mean rate of change (+ SEM) in *Frankliniella occidentalis* number on chrysanthemums fertilized with 0, 10, 20, or 100% of the standard level (375 ppm N) and grown under greenhouse conditions. Rates of change in thrips number were estimated from the slopes of regression lines that were calculated from ln-transformed thrips count of individual replicates against time (the first 4 weeks after thrips inoculation).

indicated that within-plant distribution of *F. occidentalis* was influenced by fertilization level but the degree of influence differed among sampling dates. For each fertilization level, we showed that within-plant distribution of *F. occidentalis* was not independent of sampling dates (G_{adj} values range from 65.11 to 3788.56, d.f. = 12, all P-values were smaller than 0.001) (Figure 4). We detected three distinct patterns of distribution. Before the flowers opened, more thrips (>65%) were found in the middle region of the plants than either the apical or bottom region, regardless of fertilization levels or sampling dates (Figure 4). Once the flowers began to open, more thrips were found in the apical region of the plants than the other two regions. At harvest, almost all thrips were found inside the opened flowers of the apical region.

Total nitrogen content of plant tissues increased with increased fertilization, however, total carbon content of plant tissues showed an opposite trend. Total nitrogen content was significantly different among fertilization levels and plant tissues (Table 1) (two-way ANOVA: $F_{3,64} = 259.29$, P<0.001 and $F_{3,64} = 235.85$, P<0.001, respectively). There was a significant interaction between fertilization level and plant tissue (two-way ANOVA: $F_{9,64} = 10.99$, P<0.001). Total nitrogen content was higher in leaf tissues than flower tissues when plants were fertilized with 10% of the standard level or greater. Regardless of plant tissues, total nitrogen content was highest on plants fertilized with 100% of the standard level and lowest on plants fertilized with 0% (Table 1). Plants fertilized either with 10 or 20% had total nitrogen content in
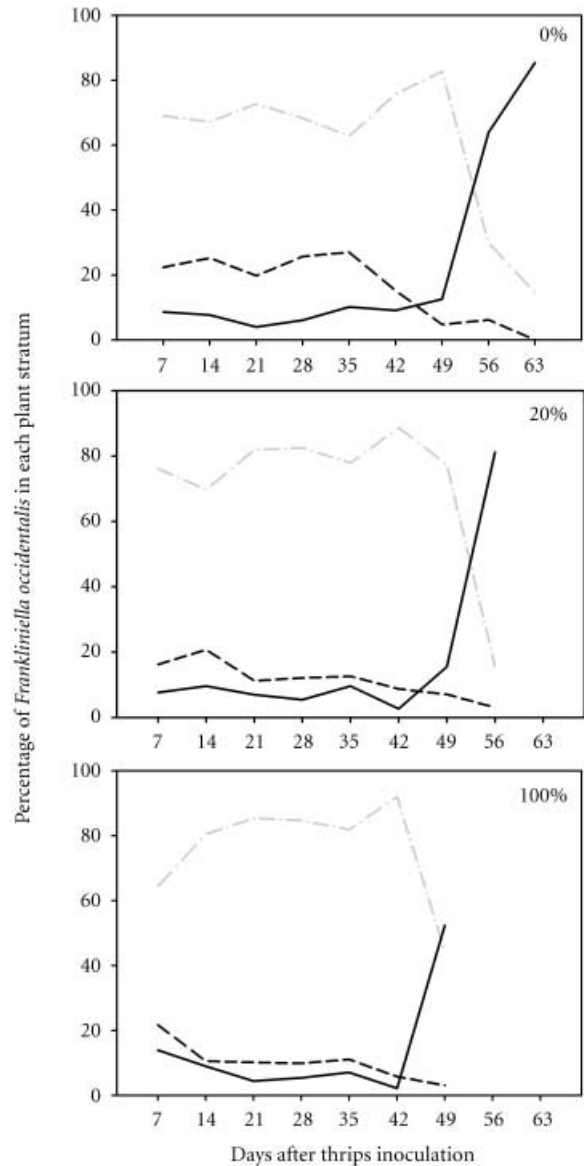
Figure 4 Percentage of *Frankliniella occidentalis* within the apical (——), middle (— · —) or basal (---) stratum of plants fertilized with 0, 20, or 100% of the standard level (375 ppm N).

between these two groups (Table 1). Leaf nitrogen content was also significantly different among the plant strata being consistently higher in the apical region rather than the basal region of the plant. Leaf nitrogen content in the middle region was not significantly different from the apical region when plants were fertilized with 20% of the standard level or higher but was significantly different from the apical region when plants were fertilized with 10% or lower. Flower nitrogen content was highest from plants fertilized with 100% of the standard level but was

Table 1 Total nitrogen and total carbon content of plant tissues taken from chrysanthemums (without thrips) fertilized with 0, 10, 20, or 100% of the standard level (375 ppm N). Leaf tissues were taken from the apical, middle, and basal strata of plants. Flower tissues included disk and ray flowers only

	Plant Tissues				
	Leaf tissues taken from the three strata			Disk and ray	
Fertilization level	Apical	Middle	Basal	Flowers	Fertilization effect[c]
	Back-transformed means (95% confidence interval) (g kg^{-1})[b]				
Total nitrogen content[a]					
0	29.90	20.35	21.74	18.16	22.13
	(27.41–32.62)	(18.63–22.20)	(19.93–23.71)	(16.64–19.81)	(21.20–23.13)a
10	43.82	34.47	29.52	19.75	30.63
	(40.17–47.80)	(31.60–37.60)	(27.06–32.23)	(18.10–21.54)	(29.34–32.01)b
20	51.57	44.52	36.86	19.99	36.05
	(47.28–56.26)	(40.81–48.57)	(33.78–40.25)	(18.32–21.80)	(34.54–37.68)c
100	69.55	63.69	57.63	27.55	51.52
	(63.75–75.87)	(58.38–69.55)	(52.83–62.87)	(25.23–30.05)	(49.30–53.79)d
Plant tissue effect[d]	46.57	37.56	34.19	21.07	
	(44.57–48.62)A	(35.95–40.29)B	(32.72–35.69)C	(20.19–22.02)D	
Total carbon content					
0	422.84	417.37	431.38	494.72	440.54
	(418.64–427.52)	(412.82–422.00)	(426.67–435.72)	(489.84–500.20)	(438.34–442.75)a
10	417.38	411.99	422.42	513.89	439.66
	(412.82–422.00)	(407.89–416.55)	(417.80–427.09)	(508.26–519.57)	(437.47–441.86)a
20	410.76	402.62	412.40	507.25	431.38
	(406.67–415.30)	(398.62–407.08)	(407.89–416.96)	(502.20–512.86)	(429.23–433.55)b
100	380.32	365.77	376.15	491.27	400.21
	(376.15–384.14)	(361.77–369.81)	(372.41–380.32)	(485.90–496.21)	(398.22–402.62)c
Plant tissue effect[d]	407.48	399.02	409.94	501.70	
	(405.45–409.53)A	(397.03–401.02)B	(407.89–412.40)A	(499.20–504.21)C	

[a]An adequate range of nitrogen in physiologically mature leaf tissue is considered to be from 45 to 60 g kg^{-1} and a deficient (severe to moderate) range is 15–30 g kg^{-1} (modified from Lunt et al., 1964).

[b]Each mean value and its 95% confidence interval are based on a sample size of five.

[c]The fertilization effect means were calculated by pooling across the plant tissues. Each mean and its 95% confidence interval were based on a sample size of 20. Differences between means within a column sharing the same lower case letter(s) are not significantly different (P>0.05) as determined by two-way ANOVA and followed by Tukey's honestly significant difference test (for total nitrogen content: $F_{3,64} = 259.29$, P<0.001; total carbon content: $F_{3,64} = 285.72$, P<0.001).

[d]The plant tissue effect means were calculated by pooling across the fertilization levels. Each mean and its 95% confidence interval were based on a sample size of 20. Differences between means within row sharing the same capital letter(s) are not significantly different (P>0.05) as determined by two-way ANOVA and followed by Tukey's honestly significant difference test (for total nitrogen content: $F_{3,64} = 235.85$, P<0.001; total carbon content: $F_{3,64} = 1624.07$, P<0.001).

the same among plants fertilized with 0, 10, or 20% (Table 1).

Total carbon content was also significantly different among fertilization levels and plant tissues (Table 1) (two-way ANOVA: $F_{3,64} = 285.72$, P<0.001 and $F_{3,64} = 1624.07$, P<0.001, respectively). Again, there was a significant interaction between fertilization level and plant tissue (two-way ANOVA: $F_{9,64} = 21.77$, P<0.001). Total carbon content was higher in flower tissues than leaf tissues regardless of fertilization levels (Table 1). Flower carbon content was higher from plants fertilized with 10% of the standard level or lower and lowest on plants fertilized with 100% of the standard level (Table 1).

Effect of fertilization on insecticide usage for controlling *Frankliniella occidentalis*

We found no significant greenhouse bench effects on the total number of insecticide applications needed to control *F. occidentalis* (one-way ANOVA: $F_{3,86} = 1.05$, P = 0.37). Therefore, we pooled the data across all benches for further
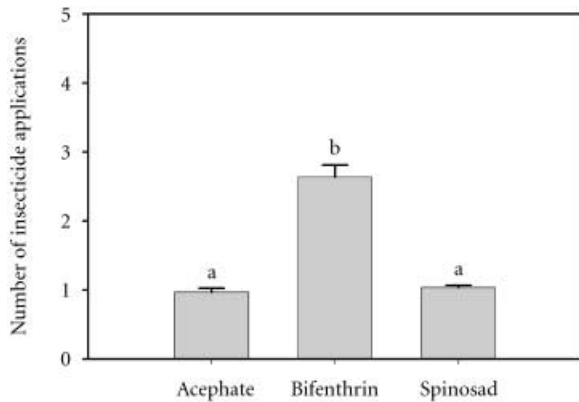
Figure 5 Mean number (+ SEM) of acephate, bifenthrin, or spinosad applications needed to keep *Frankliniella occidentalis* below the threshold of five thrips per pot. Bars sharing the same letter(s) are not significantly different (P>0.05) as determined by the Scheirer–Ray–Hare test and followed by the Games and Howell method (Scheirer-Ray-Hare test for insecticide treatments: H = 43.55, d.f. = 2, P<0.001; fertilization levels: H = 4.73, d.f. = 2, P = 0.09; and interactions between fertilization level and insecticide treatment: H = 1.99, d.f. = 4, P = 0.74).

analyses. We showed that the number of insecticide applications needed to suppress *F. occidentalis* varied with the type of insecticide but not with fertilization level (Scheirer–Ray–Hare tests: H = 43.55, d.f. = 2, P<0.001 and H = 4.73, d.f. = 2, P = 0.09, respectively). Again, there was no significant interaction between fertilization level and insecticide treatment (Scheirer–Ray–Hare tests: H = 1.99, d.f. = 4, P = 0.74). Bifenthrin required the most applications to keep the thrips number below the action threshold (Figure 5). Acephate and spinosad required only one-third of the number of applications as bifenthrin. Regardless of the type of insecticide, increased fertilization did not result in greater number of insecticide applications.

Discussion

Our studies demonstrated that population abundance of *F. occidentalis* increased with fertilization levels. Within-plant distribution of *F. occidentalis* was influenced by the phenology of the plants rather than fertilization levels. Time from transplantation to flower opening of chrysanthemums was shortened with increased fertilization. Furthermore, increased fertilization did not result in higher number of insecticide applications. The rate of change in abundance of *F. occidentalis* increased with fertilization levels ranging from 0 to 100% of the standard level in both the growth chamber and the greenhouse

studies. On plants fertilized with 10% of the standard level or greater in our greenhouse study, we found that the rate of change in population abundance of *F. occidentalis* increased rapidly for the first 4 weeks but began to level off after week 4. It is possible that the rate of change in population abundance of *F. occidentalis* was limited by the developmental stage of chrysanthemum. Guldemond et al. (1998) showed that population growth rate of *Aphis gossypii* Glover on chrysanthemum, estimated at the population level, is higher on flowering plants than young vegetative plants. Kirk (1997) and Brodbeck et al. (2001) suggested that *F. occidentalis* prefers to feed on flowers rather than leaves because pollen has high nitrogen content. When flowers are present, *F. occidentalis* populations may increase at a much higher rate than when flowers are unavailable or absent. In our study, we harvested the plants when their flowers were just fully open (marketable stage). If our experiment had continued past the marketable stage, we might have detected an accelerated change in population abundance because the thrips would have fed substantially on flower pollen.

Population growth rate of *F. occidentalis* varies considerably on edible crops and ranges from 0.02 on peanut (Lowry et al., 1992) to 0.17 on susceptible cucumber (van Rijn et al., 1995). On ornamentals, population growth rate of *F. occidentalis* ranges from 0.13 on petunia (Wijkamp, 1995) to 0.17 on chrysanthemums (cv. 'Hurricane') (Robb, 1989). When resources are unlimited and the age distribution is stable, population growth is constant (Southwood, 1978) and may be estimated from regression (Vehrs et al., 1992). In our greenhouse study, the rate of change in population abundance of *F. occidentalis* was estimated to be around 0.14 (on plants fertilized with the standard level) for a population initiated with only adult thrips. The rate of change in population abundance that we obtained would probably differ from the growth rate estimated for a population with a stable age distribution. The rate of change in population abundance might also be influenced by thrips movement. Although *F. occidentalis* adults are relatively weak fliers, they are able to disperse between pots within a greenhouse at a rate of 0.05–0.17 m per day (Rhainds & Shipp, 2004). We designed the growth chamber experiment specifically to address the possible influence of thrips movement on thrips abundance. The effect of fertilization on the rate of change in thrips number was detected in our growth chamber study when thrips were unable to move between pots. The same effect was also detected in our greenhouse study when thrips movement was not inhibited. Furthermore, flowers on plants fertilized with the standard level began to open earlier than other treatments. If thrips were attracted to these flowers,

the rate of change in population number should have increased dramatically on plants fertilized with the standard level and decreased on plants treated with lower fertilization levels (Figure 2). However, these trends were not found, thus it is unlikely that thrips movement was not uniform across all treatments. Our results are more representative of a production greenhouse where crop plants are invaded by adult thrips that move freely within and between pots.

Although we found higher nitrogen content in leaves from both the apical and the middle region of the plants than those from the basal region, we did not find significantly more thrips in the apical area prior to flower opening. Within-plant distribution of *F. occidentalis* was influenced by the phenology of the plants. Prior to flower opening, more thrips were found in the middle region than in the other two regions of plants and the pattern of distribution was not consistent with the levels of total leaf nitrogen content. If *F. occidentalis* responds to nitrogen availability within the plants, one would expect to find more thrips in both the apical and middle regions of the plants where the total nitrogen content was highest. When the flowers began to open, the distribution pattern of *F. occidentalis* changed dramatically (Figure 4). More thrips were found in the apical region, where the flowers were, instead of the other two regions. When the flowers were fully opened, we noticed that almost all the thrips were found feeding inside the flowers and very few thrips were found on the leaves. Studies have shown that pollen feeding increases reproductive fitness of many insects, including *F. occidentalis* (Gilbert, 1972; Pesho & van Houten, 1982; Kirk, 1985; Trichilo & Leigh, 1988). However, in addition to feeding on pollen, *F. occidentalis* will also feed on flower and leaf tissues (de Jager et al., 1993; Bergh & Le Blanc, 1997; Brodbeck et al., 2001). De Jager et al. (1993) showed that pollen production per flower head differs significantly among chrysanthemum cultivars and that cultivars with higher pollen production do not always support higher number of *F. occidentalis*. Instead of pollen nitrogen, we examined the total nitrogen and carbon content of the flower heads (disk and ray flowers) which would be more representative of the flowers' nutritional value. Our results showed that total nitrogen content of flower head tissues was much lower than that of leaf tissues, but it was the reverse for total carbon content. *Frankliniella occidentalis* may be responding to factors such as carbohydrate availability, secondary metabolites, and amino acid profiles rather than total nitrogen content. Responses of *F. occidentalis* to nutrient availability might be more complex because this insect feeds on a wide range of plant tissue types and can even be predacious (Trichilo & Leigh, 1986, 1988; Mound & Teulon, 1995).

We found that the recommended level of fertilization did not lead to a need for increased insecticide applications for thrips control relative to lower levels of fertilization. However, the number of insecticide applications needed to suppress populations of *F. occidentalis* varied with insecticide treatments. The three insecticides were effective in keeping *F. occidentalis* populations below the action threshold but bifenthrin required the most applications to do so. Our experiment ended when flowers on plants fertilized with the standard level (375 ppm N) were fully open. At that time, flowers on plants fertilized with 20% of the standard level were just beginning to show color and those on plants fertilized with 0% were just breaking out from the buds. We suspect that additional insecticide applications would be needed to control *F. occidentalis* populations on plants grown under reduced fertilization because of longer production time due to delayed flowering.

We showed that increased fertilization did not result in a higher number of insecticide applications. Our results were based on a total of 90 pots in our greenhouse study. This small sample size may not be representative of the 15 000 pots produced by an average commercial greenhouse. Post hoc sample size calculations based upon Pearson & Hartley's (1951) power curves and associated equations (Sokal & Rohlf, 1995) were applied to insecticide application data to determine the magnitude of differences that could be detected among fertilization treatments with 5000 or more replicates. Based on the post hoc sample size calculations, we estimated that a difference as small as 0.06 sprays per pot would be detected with 5593 replicates per treatment by setting the power of the F-test at 0.90 and the type I error (α) at 0.05. By increasing the power of the F-test to 0.99, 5501 replicates per treatment would allow us to detect a difference of 0.08 sprays per pot. These calculations suggest that at production scale characteristic of commercial greenhouse, we would likely find statistically significant fertilization effects on insecticide input.

We showed that the time from transplantation to flower opening shortened considerably with increased fertilization level. The time to flowering was shortest, 11.9 weeks, for plants fertilized with the standard level (375 ppm N). When fertilization level was reduced to 20%, the time to flowering lengthened to 12.9 weeks. When fertilization level was reduced to 0%, the time to flowering extended to 13.9 weeks. In a recent growth chamber study, Chau et al. (2004) showed that population growth rate of *F. occidentalis* does not increase with fertilization level beyond the standard level (375 ppm N). In fact, increased fertilization to 200% not only shortens production by 1 week but also reduces *F. occidentalis* population growth. Time to flowering is crucial to growers because shorter production

time often means higher profit to cost ratio, faster turn over time, and possibly less pesticide input. Optimizing fertilization level to reduce pest population growth may facilitate management of *F. occidentalis* on potted chrysanthemums but the effect of fertilization on production time and plant quality should also be considered when implementing this tactic.

Acknowledgements

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