Fertiliser application affects susceptibility of chrysanthemum to western flower thrips – abundance and influence on plant growth, photosynthesis and stomatal conductance

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SUMMARY
We report the influence of plant fertility, principally nitrogen (N) levels, on plant growth, gas exchange and herbivore abundance in chrysanthemum (Dendranthema grandiflora Tzvelev ‘Charm’) infested with western flower thrips [WFT; Frankliniella occidentalis (Pergande)]. Four levels of a commercial, soluble fertiliser “15-16-17” (elemental analysis: 15N-6.7P-14.1K) were tested at: 0, 28, 75 and 375 mg l⁻¹ N [0N, 35N, 75N, 375N], which represented 0%, 10%, 20% and 100% of the recommended N-fertilisation rate, respectively. Adult and immature WFT were most abundant at the highest fertility level (375N). At moderate (38N and 75N) to high fertility (375N), WFT infestation depressed plant vegetative and reproductive growth, and altered carbohydrate partitioning. WFT-infested plants had reduced flower bud dry mass (DM) and flower bud number compared to uninfested plants. While WFT infestation reduced leaf area and leaf mass, the specific leaf area (SLA; i.e., leaf thickness) was not affected. However, high fertility plants had greater reproductive and vegetative biomass, greater leaf elemental levels (N, P, Ca, Mg, B, Fe, Mn, Cu and Zn) and a higher SLA (i.e., thinner leaves) than low fertility (0N) plants. Leaf stomatal conductance (g) was more sensitive to WFT damage than net photosynthesis (Pn). WFT damage caused a reduction in Pn in young and physiologically mature leaves at the highest fertility level, whereas g was reduced in young, physiologically mature and older basal leaves of plants damaged by WFT at moderate to high fertility. WFT infestation had no effect on leaf macro- and micro-elements, ethylene production or chlorophyll levels. WFT damage reduced vegetative and reproductive growth primarily through reduced Pn and g.

Western flower thrips [WFT; Frankliniella occidentalis (Pergande)] are one of the most detrimental pests of greenhouse crops such as chrysanthemum (Dendranthema grandiflora Tzvelev; De Jager et al., 1995). WFT usually feed on actively growing tissues such as young leaves and flower buds by rasping and sucking fluids from individual plant cells. In wheat, thrips [Limothrips ceralium (Halliday)] remove the contents of mesophyll cells, which leads to collapse of the surrounding epidermal cells (Chisholm and Lewis, 1984). More extensive damage can disrupt leaf cell structure, leading to desiccation of mesophyll and epidermal cells. WFT feeding on young, developing tissue also causes leaf distortion, as affected cells are unable to expand. 'Silver damage' occurs when WFT feed on expanding leaves, causing cells to become filled with air (De Jager et al., 1995). WFT can also act as vectors carrying and transmitting plant viruses that cause severe economic damage to floral crops (Allen and Broadbent, 1986). WFT are difficult to control chemically, in part due to their affinity for enclosed spaces, such as floral buds, and because they deposit their eggs into sub-epidermal tissues. There is generally a low tolerance for WFT in greenhouse production and zero tolerance for export crops (Van Lenteren and Woets, 1988). However, crops grown for both foliage and flowers can have higher acceptable numbers, compared to those grown primarily for flowers, since WFT damage to flowers is the main commercial concern (Cloyd and Sadof, 2003).

High population densities of WFT can occur throughout the chrysanthemum production cycle because of favourable greenhouse growing environments and the high reproduction rates of WFT. Chrysanthemum cultivars differ in their susceptibility to WFT (De Jager et al., 1995; Schuch et al., 1998; van Dijken et al., 1994), and susceptibility is influenced by irrigation and fertilisation practices (Schuch et al., 1998). The morphology and physiological status of the host crop also determines WFT susceptibility to control measures. Greenhouse environments and cultural conditions contribute to host-plant resistance or susceptibility (Waring and Cobb, 1992). Greenhouse photoperiod (long-days) (Brodsgaard, 1994), higher temperature (Sites and Chambers, 1990), high N fertility (Mattson, 1980; White, 1984) and host plant water status (Buntin et al., 1988) all affect WFT reproduction.

Strategies to optimise fertilisation of greenhouse chrysanthemum and manage WFT development through chemical and biological controls have had mixed results (Bethke et al., 1998; Heinz and Parella, 1990). Fertilisers used in nursery/greenhouse industries are an important

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Susceptibility of chrysanthemum to WFT

Source of essential elements for both chrysanthemums and WFT. Optimal plant fertility is important for plant growth and development. Nitrogen (N) fertility can indirectly influence the uptake of other ions, chlorophyll synthesis, photosynthesis and levels of photosynthates. Some photosynthates are allocated to secondary metabolism (e.g., the production of phenolics) that can increase the ability of the plant to tolerate herbivory (Bryant et al., 1987; Larsson et al., 1987). High N-fertility can also increase insect population growth rates and decrease total phenolics, with minimal effects on cinnamic acids, benzoic acids or flavonoids (Muzika and Pregitzer, 1992). However, phytochemical-based host plant resistance may not be the primary factor determining plant tolerance to herbivores. Rather, herbivore tolerance may be partially or fully compensated for by increased plant growth in response to herbivore pressures (Herms and Mattson, 1992; McNaughton, 1983). Increased growth may allow plants to recover faster from WFT damage. During commercial production, chrysanthemums are fertilised heavily, except for the last several weeks of production when fertility is discontinued to enhance post-harvest flower quality (Yoder Brothers Inc., 2005).

As part of best management practices (BMP), optimisation of fertiliser usage and subsequent reduction in fertiliser run-off has caused changes in the usage of macroelements such as N and phosphorus (P) for a number of ornamental crops (Cabrera et al., 1993; Yeager et al., 1997). The U.S. Environmental Protection Agency (EPA), in enforcing the 1972 Federal Clean Water Act, requires all States to implement a total maximum daily load (TMDL) programme for all watersheds (Lea-Cox, 2001). Knowing the influence of fertiliser application on host plant quality and pest populations may lead to optimised fertilisation that maintains high crop quality, while minimising insect damage and the need for intensive pesticide use, with associated chemical phytotoxicity (Spiers et al., 2004). Precision chemical usage can also reduce fertiliser and pesticide run-off and contamination of surface and ground water (Yeager et al., 1997). Hence, this study tested the hypothesis that moderate levels of fertiliser, principally N application could control the abundance of WFT on

Fig. 1
Effect of western flower thrips (WFT, Frankliniella occidentalis) and fertiliser applications, based on nitrogen concentration, on chrysanthemum (Dendranthema grandiflora var. Charm). Panel A, female adult WFT (arrow); Panel B, large acetate cylindrical cages containing WFT. Plants on the left and right are, respectively, under high or low fertilisation regimes. Panels C and D, blooms and foliage of plants without WFT. Panels E and F, foliage damage caused by WFT (arrows).
chrysanthemums. While WFT are known to reduce plant quality, there have been few comprehensive studies on plant responses to WFT. This study details the effects of WFT population dynamics on plant growth and development, leaf elemental levels, gas exchange and ethylene production.

MATERIALS AND METHODS

Plant cultural conditions

Twenty-four rooted cuttings of chrysanthemum (D. grandiflora var. Charm) were transplanted into 15.5 cm standard pots. Sunshine Mix®1 (Sun Gro Horticulture Inc., Pine Bluff, AZ, USA) was used as potting medium. One rooted cutting was planted per pot so that cages containing WFT could be used without foliage touching the cage walls. Each pot was enclosed in a large acetate cylindrical cage (36 cm diameter, 61 cm high) constructed with Lexan® film (GE Polymershapes, Huntsville, NC, USA) with a sealed top and bottom (Figure 1A-F). Two openings (20 cm diameter) were cut and covered with nylon organdy cloth for ventilation. Clear PVC tubing (0.95 cm diameter, 30 cm long, VWR International, Suwanee, GA, USA) was attached to each cage for irrigation and fumigation. Caged plants were kept in growth chambers at 24°C day/20°C night and 75% RH, initially under long-day (LD) conditions (16 h photoperiod). The recommended range of N application for potted chrysanthemum is around 375 mg l⁻¹ N for pulse feeding (Scotts-Sierra Horticultural Products Company, Marysville, OH, USA). Plants were fertilised twice weekly and irrigated with reverse-osmosis treated water as needed. Plants were fertilised with 200 ml of Peters Professional Peat-lite special “15-16-17” (elemental analysis: 15N-6.7P-14.1K; Scotts-Sierra Horticultural Products Company, Marysville, OH, USA) at 0, 38, 75 or 375 mg l⁻¹ N (referred to as 0N, 38N, 75N, 375N) which are, respectively, 0%, 10%, 20% or 100% of the recommended rate (Yoder Brothers Inc., 2005).

After 2–2.5 cm of new growth, each plant was “soft-pinched” to approx. seven laterals (14 d after transplanting). After a further 7 d of LD conditions, when there was 1.3–2.5 cm of new growth, plants were put under SD conditions (11 h photoperiod) to initiate flower primordia. Seven d after switching to SD, the growth retardant B-9 (Uniroyal Chemical Company Inc., Middlebury, CT, USA) was applied to all pots at 3.5 g l⁻¹, to run-off, to reduce internode elongation.

WFT culture, inoculation and determination

Colonies of WFT [F occidentalis (Pergande)] were established and maintained in the Texas A&M University Biological Control Laboratory at 26°C, 65% RH with a 14 h photoperiod on D. grandiflora ‘Charm’. The day after B-9 treatment, plants were caged and inoculated with WFT. Plants were approximately 5 weeks-old (35 d). Five adult female WFT in a 1.5 ml micro-centrifuge tube (Scientific Inc., Ocala, FL, USA) were released near the base of the plant in each pot. All treatments, including uninfested plants, were checked weekly for WFT – which entailed counts of adults by sex, pupae (fourth instar) and nymphs. Any WFT found on control plants were removed to keep the control plants free of WFT damage. The average photosynthetic photon flux (PPF) at the plant canopy in the cages was 650 μmol m⁻² s⁻¹, regardless of photoperiod.

The experiment was initiated on 30 May 2003, and terminated after 97 d (4 September 2003). Treatments were terminated differentially and final WFT counts determined based on floral development (i.e., all plants of a given treatment were harvested when flowers were fully open and had reached anthesis). Hence, the high fertility (375N) treatment matured first and was harvested at 76 d, 75N at 83 d, 38N at 90 d and 0N at 97 d. Flowers of individual plants (n = 3) were placed in sealed plastic containers (25 cm long × 25 cm wide × 10 cm deep). Containers were shaken and individual ray flowers were dissected to dislodge any WFT. All WFT were removed using an aspirator, stored in 70% alcohol and counted.

Stages of leaf development

To determine plant development, leaf gas exchange (photosynthesis and stomatal conductance), ethylene evolution and leaf chlorophyll levels, leaves were sampled from three regions: (a) two-to-three newly unfurled young leaves from the apical region; (b) physiologically mature leaves; and (c) basal, post-physiologically mature leaves from the oldest remaining to three laterals just above the soil line (Figure 2).

Plant growth measurements

To characterise plant growth, leaf area, plant height, flower bud number, specific leaf area (SLA; cm² g⁻¹ DM

![Fig. 2](Schematic diagram of a chrysanthemum plant with leaf locations used for analysis of leaf gas exchange. The three regions were (a) young leaves, two or three newly unfurled leaves from the apical region; (b) physiologically mature leaves; and (c) older, basal leaves, post-physiologically mature leaves from the oldest one-to-three laterals above the soil surface.)
of leaves) and the DM of leaves, shoots, flower buds and stems were measured at the termination of each fertility treatment on the same day that plants were harvested for WFT.

**Macro- and micro-nutrient analysis**

Physiologically mature leaf tissues were harvested at the end of the experiment using leaves from individually potted plants (n = 3). The mineral status of plants was then determined on a DM basis. Dry leaves were ground in a Wiley mill. Nitrogen content was determined using the Kjeldahl procedure (Rund, 1984). The remaining samples were digested in wet acid (Jones et al., 1991) and macro- and micro-element determinations were made on an inductively coupled plasma atomic emission spectrophotometer (3510 ICP) at a commercial lab (J.R. Peters/Scott's Testing Laboratory, Allentown, PA, USA) using the procedures of Munter and Grande (1981).

**Chlorophyll determination**

Leaf chlorophyll was determined with a SPAD-502 portable chlorophyll meter (Minolta Camera Co., Ltd., Tokyo, Japan). Meter readings were correlated with a chlorophyll content prediction equation:

\[ y = -0.001x^2 + 0.104x - 1.730x + 11.702 \]

where \( y \) = chlorophyll content (\( \mu g \text{ cm}^{-2} \)), \( x \) = meter reading (\( r^2 = 0.98 \)).

This equation was obtained by running a linear regression analysis between the SPAD-502 readings obtained from physiologically mature leaves from two or three pots of each fertility level, and the total chlorophyll content of the same pair of leaves. Leaf chlorophyll was extracted with N,N-dimethylformamide (DMF) and the total content was determined from the optical density of the filtered aqueous supernatant at 647 nm and 664 nm (Moran, 1982). During the experiment, two leaves from three pots per treatment were selected at random from each of the three leaf regions in each pot and measured weekly with a SPAD-502 (n = 6). Only the final data are reported.

**Net photosynthesis and stomatal conductance**

Net photosynthesis (\( Pn \)) and stomatal conductance (\( g \)) measurements of photosynthetically mature, individual leaves were taken between 0900h - 1300h on the final (harvest) day for each fertility treatment, using an LI-6400 Portable Photosynthesis System (LI-COR Inc., Lincoln, NE, USA). The LI-6400 was programmed with a constant leaf chamber block temperature at 25°C. The fixed substrate level of 360 \( \mu l \text{ l}^{-1} \text{ CO}_2 \) was provided with a 12 g cartridge, and the light source was an LED 6400 R/B at a PPF of 300 \( \mu \text{ mol m}^{-2} \text{ s}^{-1} \). Each leaf was a single replication, and there were three replications per treatment (n = 3).

**Ethylene determination**

Young, physiologically mature and older leaves (Figure 2) were harvested at the end of the experiment using leaves from three individual pots per treatment (n = 3). These samples were transferred immediately to 10 ml glass vials and sealed with a rubber serum stopper. After 10 min incubation at room temperature (20°C), 1 ml of gas was withdrawn with a needle and syringe and immediately injected into a Photovac 10 plus digital gas chromatograph (PhotoVac Inc., Waltham, MA, USA) with a photodetector. Compressed air (Ultra Zero Grade, Praxair Inc., Danbury, CT, USA) was the carrier gas. Ethylene concentrations were determined using a standard ethylene curve programmed in the GC.

**Experimental design**

The experiment was arranged as a “four fertility \( \times \) two (\( \pm \) WFT infestation)” factorial for plant growth, leaf macro- and micro-elements and WFT population data. Each pot contained one established, rooted cutting as a single replicate. There were three replications (n = 3) arranged in a completely randomised design. Data were analysed using analysis of variance (ANOVA; SAS Institute Inc., 2000), with WFT infestation levels and
fertiliser concentrations as the main treatment effects. For stomatal conductance, net photosynthesis, leaf chlorophyll and ethylene determination, the experiment was arranged as a "four fertility × two (± WFT infestation) × three (leaf positions: young, physiologically mature, old)" factorial using ANOVA (n = 3). WFT-infested and uninfested (control) plants were grown in two separate chambers to avoid cross-contamination. The experiment was repeated and chambers switched between WFT treatments to avoid possible chamber effects. There were none. As the experiment was repeated twice, only results from the second experiment are presented as they mirrored the results from the first experiment.

RESULTS

WFT abundance

The total number of WFT increased at higher fertility levels from 3.3 at ON to 560.3 at 375N (P ≤ 0.001; Figure 3). WFT counts, in order of increasing abundance, were pupa, adult males, adult females and nymphs. At the highest fertiliser level (375N), pupa, adult males, adult females and nymphs averaged 2, 11, 257 and 295, respectively. None of the uninfested (control) plants had WFT. At 38N (10% of the recommended fertiliser rate) there was a 90% reduction the in total WFT population compared to 375N plants. Likewise, at 75N (20% of the recommended level) there was a 43% reduction in WFT population compared to 375N plants.

Plant growth

WFT infestation depressed plant vegetative and reproductive growth, and altered carbohydrate partitioning. WFT-infested plants had reduced flower bud DM, and flower bud number at increased fertiliser levels when compared to uninfested plants (P ≤ 0.01; Figures 4 and 5; Table 1). With increasing fertility (38N, 75N and 375N), WFT damage decreased total top (i.e., above ground) DM, including leaf, flower and flower bud DM (P ≤ 0.01). WFT caused no significant damage on ON plants, in part because of low vegetative and reproductive plant growth; therefore, a decreased food source for WFT contributed to the inability of more than 3.3 WFT to survive, from the initial inoculation of five WFT per plant. Nutritional deficiency (Table II) led
to reduced growth in low fertility plants. WFT feeding reduced leaf area and leaf mass, but did not affect specific leaf area (SLA), which is a measure of leaf thickness (Figure 5). However, high fertility plants had significantly greater ($P \leq 0.001$) reproductive and vegetative biomass, greater leaf nutritional values (Table II) and higher SLA (i.e., thinner leaves), than low fertility plants.

**Leaf macro- and micro-nutrient analysis**

Except for an increase in boron (B) levels ($P \leq 0.001$), WFT feeding had no effect on leaf macro- or micro-nutrient status (Table II). At 37SN, P was higher in WFT-infested plants. Increasing fertiliser application increased leaf N concentration ($P \leq 0.001$). Plants at 0N, 38N and 75N were deficient in leaf N, whereas 37SN plants were N sufficient (Table II). Plants at 37SN were also sufficient in Ca, Mg, B, Fe, Mn, Cu and Zn; whereas plants at 0N were deficient in N, Ca, Fe, Mn, Cu and Zn. Except for 0N all plants were sufficient in P, Ca, Mg, B, Mn and Cu. In general, increasing fertilisation significantly increased ($P \leq 0.001$) macro- and micro-nutrient levels.

**Leaf chlorophyll and ethylene levels**

Neither feeding by WFT, fertiliser application, nor their interaction, had any significant effect on leaf chlorophyll or ethylene production (data not shown).

**Net photosynthesis and stomatal conductance**

Leaf stomatal conductance ($g_s$) was more sensitive to WFT damage than net photosynthesis ($Pn$; Figures 6 and 7). The main treatment effects of thrips, fertiliser level and leaf position were significant on $g_s$ and $Pn$ ($P \leq 0.001$; Table III). WFT reduced $g_s$ in young leaves from 38N to 37SN, and the $g_s$ of physiologically mature and older, basal leaves at 75N and 37SN (Figure 6). Conversely, WFT feeding had no effect on $Pn$ of basal, older leaves, and only reduced $Pn$ in young and physiologically mature leaves at the highest fertiliser level (Figure 7). Both $g_s$ and $Pn$ increased at higher fertility levels.

**DISCUSSION**

We report on the susceptibility of chrysanthemum to WFT damage, detailing the influence of fertiliser, principally N application, on herbivore abundance, plant growth, stomatal conductance and photosynthesis. We hypothesised that moderate levels of fertility would improve the management of WFT populations. By reducing fertiliser applications, total WFT population levels were reduced by 43%, 76% and 99%, respectively, at 75N, 38N and 0N, compared to the higher, commercially recommended rate of 37SN (Figure 3). The greater abundance of WFT at the highest fertility level led to a sharp reduction in plant reproductive and vegetative biomass (Figures 4 and 5), and in plant quality, as indicated by the high level of WFT-induced foliar damage (Figure 1).

One basic question in this research was how do WFT populations influence plant growth, and is this altered by plant nutrition at different fertility levels? WFT populations significantly influenced carbohydrate partitioning of chrysanthemum via a reduction of reproductive (flower DM and flower bud number) and vegetative growth, particularly at higher fertiliser levels.

### Table I

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### Table II

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<th>WFT K (kg kg$^{-1}$)</th>
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*Mean and standard error. Physiologically mature leaves were sampled ($n = 3$).
In an earlier chrysanthemum study with aphids (Davies et al., 2004), total plant biomass was not reduced, unlike the current work using WFT. Aphids reduced reproductive growth through lower flower bud number and total flower bud DM, and decreased leaf biomass.

Phenotypic plasticity is the ability of a plant to modify its physiology and/or morphology in response to biotic and abiotic stimuli. The biotic and abiotic influences, respectively, of WFT infestation and plant nutrition, triggered morphological changes in leaf development by increasing SLA (i.e., thinner leaves) at higher fertility, while WFT feeding decreased leaf area. In a study of non-flowering chrysanthemum cultivars, WFT damage resulted in reductions of leaf area and plant height (plant DM was not reported) to varying degrees among chrysanthemum genotypes that differed in their susceptibility to WFT (Van Dijcken et al., 1994). Conversely, in another study, aphids increased leaf area and SLA in chrysanthemum at high fertiliser levels (Davies et al., 2003). A higher SLA indicates that fewer leaf mesophyll cells develop and that biomass is reduced per unit leaf area (Hunt and Lloyd, 1987; McDonald, 1990). Differences in SLA can also be caused by increased light, as well as increases in water content and cell size, and altered thickness of leaves and veins (Dijkstra, 1990). Chrysanthemum is a fast-growing plant with high nutritional demands. As such, fast-growing plants could benefit from a high SLA, if leaves increased their photosynthetic levels under certain environmental conditions (Van der Werf et al., 1993).

| Table I |

ANOVA P values for growth parameters of chrysanthemum-thrips study with western flower thrips (WFT), fertiliser application (Fert), and leaf position (L) as main treatments.

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NS, not significant; n = 3.
Schuch et al. (1998) reported differences in resistance to WFT among six chrysanthemum cultivars, with cultivars supporting differing threshold population levels of WFT. Populations of WFT were greatest under high fertiliser-low irrigation levels; but only non-floral, vegetative growth was reported during a 10-week crop cycle. As Schuch et al. (1998) allowed natural infestations to occur in the greenhouse, there were no WFT-free, true control plants (c.f. our caged system for containing WFT populations). Hence, the impact of herbivory on the growth and physiology of chrysanthemum could be compared in the current study with and without WFT infestation.

WFT damage had no significant effect on macro- or micro-nutrient levels, except for higher B. However, all treatments were considered B-sufficient (Jones et al., 1991). Likewise, higher P occurred in WFT-infested plants at 0N and 375N, but all P levels were sufficient, regardless of treatment. Plants are conservative with P and can reduce growth, leaf mass and leaf area to avoid P-deficiency (Davies et al., 1993).

The recommended range of N for potted chrysanthemum is around 375N for pulse feeding (Yoder Brothers, 2005). The commercial fertiliser used was a “15-16-17” (elemental analysis: 15N-6.7P-14.1K). 0N plants were deficient in N, Ca, Fe, Mn and Zn (Jones et al., 1991), while 35N and 75N plants were sufficient in P, Ca, Mg, B, Mn, Cu and Zn. Only the highest fertility (375N) plants were sufficient in N. 375N plants had 4.2-fold higher leaf elemental N than 0N plants. Hence, while other macro- and micro-elements are important, increased fertilisation and its phenotypic effects on WFT infestation of chrysanthemum were principally due to increased elemental N levels in plant tissues.

In another study, aphid-infested chrysanthemums (compared to aphid-free plants) had reduced total N at high fertility in both young and physiologically mature leaves, but not in older leaves (Davies et al., 2004). Leaf N is a crude index of available nitrogen. However, dietary nitrogen, principally in the form of amino acids in the phloem, is an important factor influencing aphid development (Douglas, 1993). Hence, aphid consumption of soluble nitrogen via amino acids in phloem tissue probably contributed to the decline in total N. Conversely, WFT feeding targets individual cells and causes more tissue damage than phloem-feeding aphids, but without a reduction in tissue N per se, as shown by our data.

Why is there an increased WFT population at higher fertiliser levels? Higher soluble N in plant tissues can cause outbreaks of phytophagous invertebrates (van Emden and Bashford, 1969; Mattson, 1980; White, 1984) such as WFT (Hermes, 1989; Pettit et al., 1994). While increasing N-fertilisation can increase plant growth (biomass), decreases can also occur in carbon-based defensive chemicals, such as phenolics, tannins and terpenes (Muzika and Pregitzer, 1992). Phenolics represent a large and structurally diverse class of compounds, second only to carbohydrates in their abundance in higher plants. Phenolics are ubiquitous and have antibiotic and antimicrobial activity (Harborne, 1985). Consequently many phenolics have levels of toxicity which may play a role in plant defense, and reduced levels of these allelochemicals at high N application rates may contribute to increased WFT populations. Insects such as beetles consume five-times more leaf tissue in plants low in carbon and rich in N (Larsson et al., 1986). The reduced PN in WFT-damaged plants may have also contributed to a lower C:N ratio.

Pulse vs constant feed fertilisation can also affect WFT populations. For example, Schuch et al. (1998), reported 710 WFT per plant at 240N constant feed (daily fertilisation) after 10 weeks, compared to our twice-weekly pulse fertilisation rate of 375N with 560 total WFT per plant. At 80N, they reported 302 WFT per plant compared to our pulse fertilisation of 75N with 318 WFT per plant (Figure 3). Chau et al. (2004) had 70% fewer WFT at 750N (twice the recommended pulse fertilisation rate) at 404 WFT per plant, compared to 375N plants with 1446 WFT per plant. They observed that 750N reduced chrysanthemum production time to 12 weeks, compared to 13 weeks for 375N. Soluble salt accumulation [e.g., higher electrical conductivity (EC)] was not a cultural problem with the pulse fertilisation system (data not presented) compared to the high constant feed level (240N) and subsequent high EC of Schuch et al. (1998).

At higher fertiliser levels, g, and Pn increased. Leaf chlorophyll may vary with light conditions (Pospisilova et al., 1997) and other factors such as plant mineral status (Taiz and Zeiger, 1998). While WFT did not reduce leaf chlorophyll, as was the case with aphid damage (Davies et al., 2004), there were reductions in g, and Pn at moderate and high fertiliser levels (375N) in WFT-damaged leaves. There was also a reduction in Pn (but not in g,) in young leaves with feeding aphids, but not in physiologically mature or old leaves.

The WFT-induced reduction of g, occurred at all leaf stages at intermediate and high N-fertility levels. In contrast, WFT infestation decreased Pn only at high fertility in young and physiologically mature leaves. The g, values of plants experiencing nutritional stress, water stress (Davies et al., 1993) or chemical toxicity (Davies et al., 2001) frequently show a more rapid initial reduction than Pn. In another study, thrips (Ectinotrips americanus Morgan) were reported to decrease Pn in Impatiens (Impatiens wallerana Hook f.) and peach (Prunus persica L. Batsch). However, thrips infestation increased the g, of Impatiens and had no effect on the g, of peach (Buntin et al., 1988). They concluded that leaf injury by thrips was similar to leaf injury caused by spider mites (Chisom and Lewis, 1984). Spider mites can reduce Pn and g, in strawberry. The initial reduction of Pn and g, was attributed to stomatal closure, with additional reductions in Pn due to prolonged mechanical injury of chlorophyll-containing mesophyll cells (Sances et al., 1979). The same mechanism of initial stomatal closure and damage of leaf mesophyll cells probably occurred in our WFT-infested chrysanthemums, leading to reduced gas exchange. While xylem water potential (Ψsat) was not measured, there were no visible signs of loss of turgor (i.e., drought) on WFT-infested chrysanthemums in our study.

WFT damage had no effect on ethylene production: a phytohormone that can arise through plant injury. However, because of the need to keep plants enclosed in cylinders within growth chambers, to prevent WFT contamination, ethylene measurements were taken only
at the end of the experiment when plants were harvested. With the onset of flower bud development, WFT populations tend to migrate from vegetative to reproductive tissue. Young, physiologically mature and older, basal leaves were selected for ethylene analysis. However, flowers and flower buds were not sampled, since they were destructively harvested for WFT damage analysis. Higher ethylene production may have occurred in WFT-damaged floral buds and leaves if the tissues had been analysed at an earlier stage. In an earlier study with chrysanthemum, aphids caused higher ethylene production in reproductive buds and young leaves of high fertility plants, but had no effect on physiologically mature or older leaves (Davies et al., 2004). Phloem-feeding aphids (and whiteflies) produce only minor injury to plant foliage, but this damage can activate ethylene-dependent signalling pathways often associated with pathogens (Walling, 2000).

In summary, this paper demonstrates that WFT damage can reduce plant gas exchange and decrease carbon allocation to leaves and reproductive structures of chrysanthemum. WFT infestation reduced vegetative and reproductive growth primarily through reduced PN and g s, with g s showing greater sensitivity to WFT damage than PN. This study also illustrates that WFT populations can be markedly influenced by altering levels of fertiliser application (e.g., WFT abundance increased linearly with increasing fertiliser levels). Selecting chrysanthemum cultivars with greater resistance to WFT is one approach to IPM. Controlling fertility and irrigation practices to reduce and manage WFT in chrysanthemum are other options (Schuch et al., 1998). Fine-tuning fertilisation to reduce WFT populations may reduce the number of pesticide applications and their associated chemical phytotoxicity (Spiers et al., 2004). Furthermore, the influence of WFT damage on plant growth and development could be used to establish WFT population density thresholds for pesticide application (Cloyd and Sadof, 2003). While growing plants under deficient fertility levels is not a satisfactory strategy to reduce pest populations, it is feasible to use more precise cultural practices that reduce fertility and pesticide levels, subsequently producing healthier, less stress susceptible plants.

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REFERENCES


Susceptibility of chrysanthemum to WFT


