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Effects of silverleaf whitefly feeding on tomato fruit ripening

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Abstract

Silverleaf whitefly (SLW) (*Bemisia argentifolii* Bellows and Perring) feeding on tomato (*Lycopersicon esculentum* Mill.) plants induces a disorder in the fruit known as irregular ripening. The effects of silverleaf whitefly feeding on ripening of tomato fruit both attached to and detached from the plant are described. 'Florida Petite' tomatoes free of SLW, attached to the plant, began an ethylene climacteric between 40 and 45 days after anthesis (DAA), coincident with a rapid increase in red color and loss of firmness. The ethylene climacteric began between 45 and 50 DAA in tomato fruit from plants infested with SLW, and the fruit developed less red color and softened less than did fruit from plants free of SLW. Fruit harvested 45 DAA from plants free of SLW reached the respiratory and ethylene climacteric peak 3 days after harvest, developed normal red color, and softened similar to fruit ripened on the plant. In contrast, fruit harvested 45, 50 or 55 DAA from SLW-infested plants showed no respiratory or ethylene climacteric, had poor color development, and did not soften to the same extent as did fruit from plants free of SLW. Published by Elsevier B.V.

Keywords: *Lycopersicon esculentum*; Cherry tomato; *Bemisia argentifolii*; *Bemisia tabaci*; Irregular ripening; Respiration; Ethylene; Fruit color; Fruit firmness

1. Introduction

Silverleaf whitefly (SLW), *Bemisia argentifolii* Bellows and Perring, is a significant pest of many commercially produced vegetable crops. A number of physiological disorders, including silvering of squash (Maynard and Cantliffe, 1989; Yokomi et al., 1990), chlorotic streak of bell peppers (Summers and Estrada, 1996) and irregular ripening of tomatoes (Maynard and Cantliffe, 1989; Schuster et al., 1990; Schuster, 2001) have been attributed to feeding by the SLW. Although the relationship between SLW feeding and the development of these physiological disorders have been established, the physiological bases of the disorders are not completely understood.

The most pronounced symptom of tomato irregular ripening is non-uniform color development in the

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pericarp, both internal and external (Schuster et al., 1990; Hanif-Kahn et al., 1999). Inhibition of fruit softening has also been reported to occur in fruit harvested from SLW-infested plants (Hanif-Kahn et al., 1999). The symptoms of irregular ripening are very similar to ripening of fruit from transgenic plants with suppressed ethylene evolution (Klee et al., 1991; Klee, 1993; Oeller et al., 1991; Picton et al., 1993), suggesting that the disorder may be related to ethylene synthesis, action, or both.

Ethylene plays a key role in the regulation of tomato fruit ripening (Hobson and Grierson, 1993) and inhibiting ethylene biosynthesis results in the inhibition of a number of ripening related changes, including color development (Hamilton et al., 1990; Oeller et al., 1991; Picton et al., 1993) and fruit softening (Oeller et al., 1991). Klee (1993) reported that fruit from transgenic tomato plants with reduced ethylene biosynthesis conferred by expression of 1-aminocyclopropane-1carboxylic acid (ACC) deaminase harvested early in the ripening phase ripened significantly more slowly than did control fruit. In addition, fruit from the transgenic plants produced significantly more ethylene when ripened attached to the plant than when ripened detached from the plant. Murry et al. (1993) found that transgenic tomatoes with reduced ethylene biosynthesis conferred by expression of antisense RNA to ACC oxidase did not differ from wild type plants in the duration between anthesis and color break, however, after color break the rate of color change was reduced in the fruit in the transgenics as compared to the wild type.

The objective of the work presented in this report was to determine the effects of SLW feeding on ripening physiology of tomatoes. Specifically, we measured CO_2 and C_2H_4 evolution, color, and firmness of tomatoes harvested from plants that were grown either in the absence of or infested with SLW. We followed these changes in fruit attached to the plant as well as in fruit detached and ripened off the plant.

2. Materials and methods

2.1. Plant and insect materials

Dwarf cherry tomatoes (*Lycopersicon esculentum* cv. Florida Petite) seeds were sown in trays filled with a peat-lite medium (Vergro Container Mix A; VJ Growers, Apopka, FL). Seedlings were maintained in a growth room for 4 weeks and then transplanted into 11.7-l plastic pots filled with the same peat-lite mix. Tomato seedlings were then transferred to insect-proof, screened cages (1.8 m × 1.8 m × 1.8 m, Mumite; BioQuip, Gardena, CA) (four pots per cage) within a polyethylene covered greenhouse. Plants were monitored daily to ensure that they were not contaminated with insects. Plants were watered by drip irrigation and fertilized with a combination of controlled release material (Multicote, VJ Growers, Apopka, FL) and 20N–20P–20K (2.5 g/l) applied each week through the drip irrigation system. Sulfur and fungicides were sprayed as needed to control diseases.

Bemisia argentifolii Bellows and Perring (*Bemisia tabaci* Type B, the silverleaf whitefly) were reared in a separate greenhouse in insect-proof cages on tomato plants.

2.2. Insect infestations

Prior to the appearance of flower buds, two cages (four plants per cage) were infested with adult whiteflies and the insect populations were allowed to increase until the end of the experiment.

Plants in the non-infested cages were treated with imidachloprid (Bayer Corp., Kansas City, MO) both as a drench (Admire) and as a spray (Pravado) at recommended rates (Powell and Stofella, 1998) to ensure no contamination by whiteflies.

2.3. Flower tagging and fruit sampling

Flowers at anthesis were tagged on each plant every other day. Fruit were harvested at 5 days interval between 30 and 75 days after anthesis (DAA). Typically 3–5 fruits were harvested on a specific day from both control and SLW infested plants. Additional sets of fruit were harvested 45, 50, and 55 DAA. These fruit were held at 20 °C and CO_2, C_2H_4, and color were measured daily to follow ripening off the plant. After 7 days at 20 °C, firmness of these fruit was determined. There were three to four harvests for each number of DAA for each treatment. Individual fruit were treated as replicates and there were ca. 10 fruit from any one treatment and DAA.

2.4. Carbon dioxide and ethylene measurements

Evolution of carbon dioxide and ethylene was determined at 20 °C. Individual fruit were sealed in glass jars with lids that had been fitted with rubber serum stoppers. Samples of the headspace atmosphere were collected with gas tight syringes following 30 min (CO_2) and 60 min (ethylene). Analyses of carbon dioxide and ethylene were conducted using standard gas chromatographic methods.

2.5. Color measurements

Fruit color was measured using Commission Internationale de l'Eclairage L^*, a^*, and b^* color space coordinates obtained with a chromameter (11 mm view port) (model CR-300; Minolta, Ramsey, NJ). There were two measurements per fruit made on opposite sides of the equator.

2.6. Firmness measurements

Fruit firmness (resistance to compression) was measured with an Instron Universal Testing machine (model 3200; Instron Inc., Canton, MA) fitted with a 9 cm-diameter, round flat-faced anvil. The amount of force required to compress the radial pericarp surface 3 mm at a constant speed of 5 mm s^{-1} was recorded.

3. Results

Our objective was to determine the effects of silverleaf whitefly feeding on ripening of tomato fruit. Tomato plants were grown either free of SLW (control) or infested with SLW. Flowers on plants from each group were tagged on the day of anthesis. Fruits were sampled from each group at 5 days interval between 30 and 75 days after anthesis in order to follow ripening of fruit attached to the plant. In addition, fruit were harvested 45, 50 and 55 DAA and held at 20 °C to ripen detached from the plant. Rates of CO_2 and C_2H_4 evolution, color and firmness were measured.

4. Fruit ripened on the plant

Rates of CO_2 production were similar for fruit from control and SLW-infested plants during most of the 30–75 DAA sampling period (Fig. 1A). At 30 DAA, CO_2 production was about 27 μg kg^{-1} s^{-1}. Rates of CO_2 production decreased to about 15 μg kg^{-1} s^{-1} between 30 and 35 DAA. Between 35 and 50 DAA, respiration rates fluctuated between 12 and 17 μg kg^{-1} s^{-1}. Between 55 and 75 DAA, respiratory rates of fruit from control plants increased from less than 12–17 μg kg^{-1} s^{-1} whereas the rate in fruit from SLW-infested plants remained at about 8 μg kg^{-1} s^{-1}. Rates of ethylene evolution from control fruit between 30 and 40 DAA were less than 0.03 ng kg^{-1} s^{-1} (Fig. 1B). At 45 DAA ethylene production from control fruit had reached a peak of about 0.26 ng kg^{-1} s^{-1}. Following the peak in ethylene evolution at 45 DAA, ethylene evolution rate decreased fairly consistently to about 0.05 ng kg^{-1} h^{-1} at 75 DAA. Fruit from SLW-infested plants had a different pattern of ethylene evolution than did fruit from control plants. As with the control fruit, ethylene evolution was low in the early samples. However, the rate of ethylene evolution did not increase until between 45 and 50 DAA in fruit from SLW-infested plants. The maximum rate of ethylene evolution was similar for fruit from control and SLW-infested plants. Although the maximum rates of ethylene were similar for fruit from control and SLW-infested plants, ethylene evolution remained elevated in fruit from SLW-infested plants compared with fruit from control plants.

The effects of SLW feeding on the color of tomato fruit during ripening on the plant is presented in Fig. 1C. Between 30 and 40 DAA there was no difference in color between fruit from control and SLW-infested plants. Between 40 and 45 DAA there was an increase in the a/b ratio (red color) of fruit from control plants and values were significantly higher than for fruit from SLW-infested plants. Fruit from control plants attained their highest a/b values (ca. 1.25) 55 DAA and this remained fairly constant for the remainder of the sampling period. Fruit from SLW-infested plants had a more gradual increase in color than did those from control plants and never reached as high an a/b ratio as did control plants.

The effects of SLW feeding on firmness of tomato fruit are presented in Fig. 1D. At 35 and 40 DAA there was no difference in the firmness of fruit from control and SLW-infested plants. At 50 DAA firmness of control fruit had decreased significantly as compared to fruit from SLW-infested plants. Between

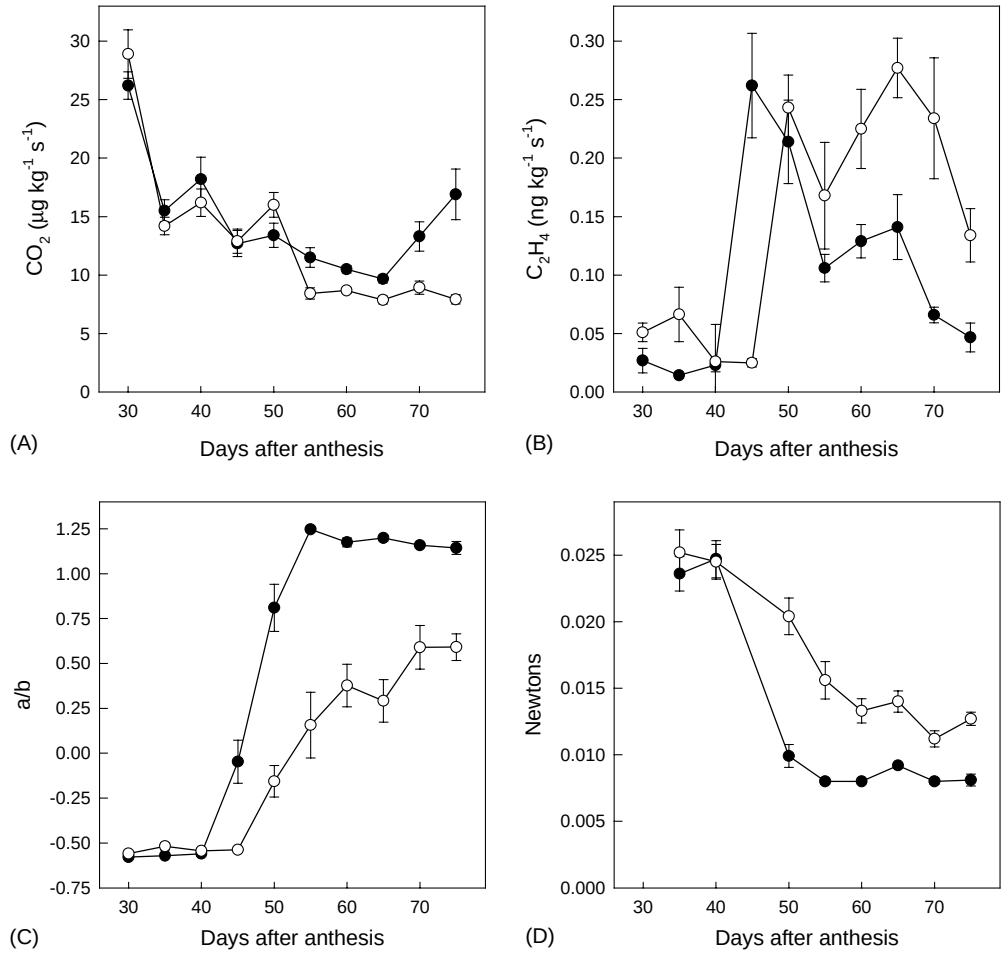

Fig. 1. Changes during development in CO_2 (A), C_2H_4 (B), color (C), and firmness (D) of Florida Petite tomatoes from plants not infested (●) or infested (○) with silverleaf whiteflies. Error bars indicate standard error of the mean.

40 and 50 DAA, there was a major decrease in the firmness of fruit from control plants. Between 50 and 75 DAA firmness of fruit from control plants was fairly consistent. In contrast to fruit from control plants, firmness of fruit from SLW-infested plants had a fairly continuous decrease between 45 and 75 DAA, however, fruit from SLW-infested plants were consistently firmer than were fruit from control plants.

5. Fruit ripened off the plant

A second method of evaluating the effects of SLW feeding on tomato fruit ripening was to harvest fruit at 45, 50, and 55 DAA and allow them to ripen off the plant. Evolution of CO_2 and C_2H_4, and color of the fruit were measured daily following harvest for 7 days. On the seventh day following harvest, firmness of the fruit was measured.

5.1. Fruit harvested 45 DAA

Rates of CO_2 production for fruit from control and SLW-infested plants harvested 45 DAA were similar (ca. 10–11 $\mu g\,kg^{-1}\,s^{-1}$) 1 day after harvest (Fig. 2A). However, 2–5 days after harvest rates of CO_2 production from control fruit (ca. 12 $\mu g\,kg^{-1}\,s^{-1}$) increased and were higher than fruit from SLW infested plants

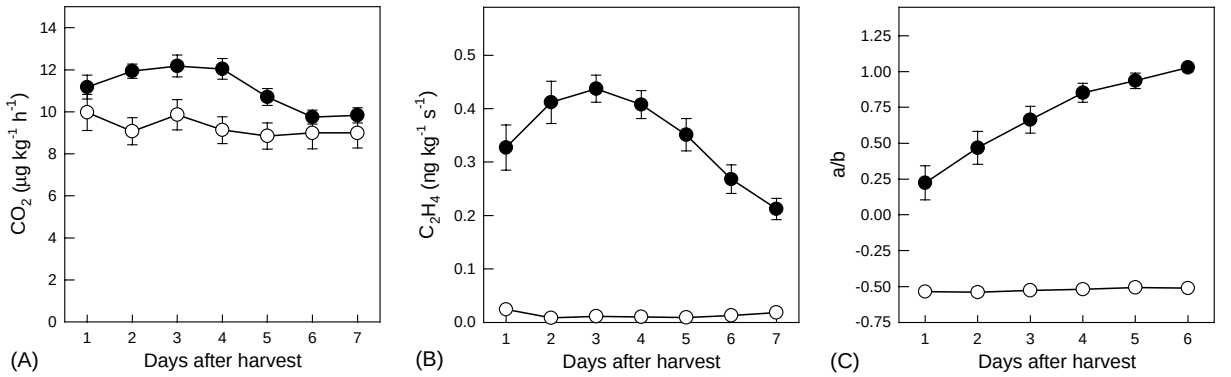

Fig. 2. Changes in CO_2 (A), C_2H_4 (B), color (C) of Florida Petite tomatoes during ripening off the plant at 20 °C. Fruit were harvested 45 days after anthesis from plants not infested (●) or infested (○) with silverleaf whiteflies. Error bars indicate standard error of the mean.

(ca. 9 $\mu g\,kg^{-1}\,s^{-1}$). After 4 days at 20 °C, the rate of CO_2 production from control fruit began to subside. By 6 days after harvest, the rates of CO_2 production for fruit from control and SLW-infested plants were similar.

Control fruit harvested 45 DAA had significantly higher rates of ethylene evolution than did fruit from plants infested with SLW (Fig. 2B). One day after harvest, fruit from control plants were producing ca. C_2H_4 0.3 $ng\,kg^{-1}\,s^{-1}$ as compared to less than 0.01 $ng\,kg^{-1}\,s^{-1}$ for fruit from SLW-infested plants. The rate of C_2H_4 evolution from control fruit harvested 45 DAA increased to about 0.45 $ng\,kg^{-1}\,s^{-1}$ 3 days after harvest, and then decreased for the next 4 days. Fruit harvested 45 DAA from plants that had been infested with SLW produced very low levels of C_2H_4 ($<0.01\,ng\,kg^{-1}\,s^{-1}$) during the 7 days following harvest.

Color (*a*/*b* ratio) of fruit harvested 45 DAA and ripened off the plant are presented in Fig. 2C. Fruit from control plants had significantly higher *a*/*b* ratios than fruit from SLW-infested plants at 45 DAA. The *a*/*b* ratio of fruit harvested 45 DAA from control plants increased continuously during the 7 days following harvest, whereas the *a*/*b* ratios of fruit from SLW-infested plants remained essentially constant.

Firmness of fruit harvested 45 DAA and allowed to ripen off the plant for 7 days was significantly lower for fruit from control plants than for fruit from SLW-infested plants (Fig. 5).

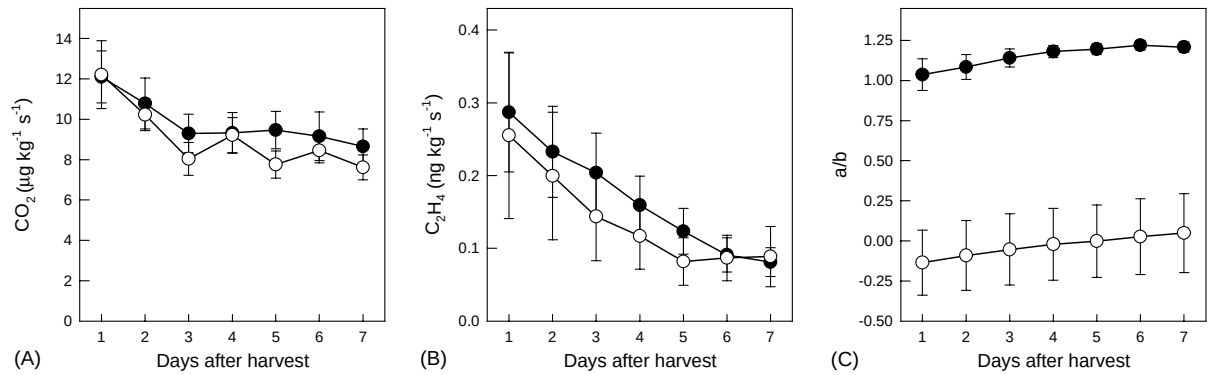

Fig. 3. Changes in CO_2 (A), C_2H_4 (B), color (C) of Florida Petite tomatoes during ripening off the plant at 20 °C. Fruit were harvested 50 days after anthesis from plants not infested (●) or infested (○) with silverleaf whiteflies. Error bars indicate standard error of the mean.

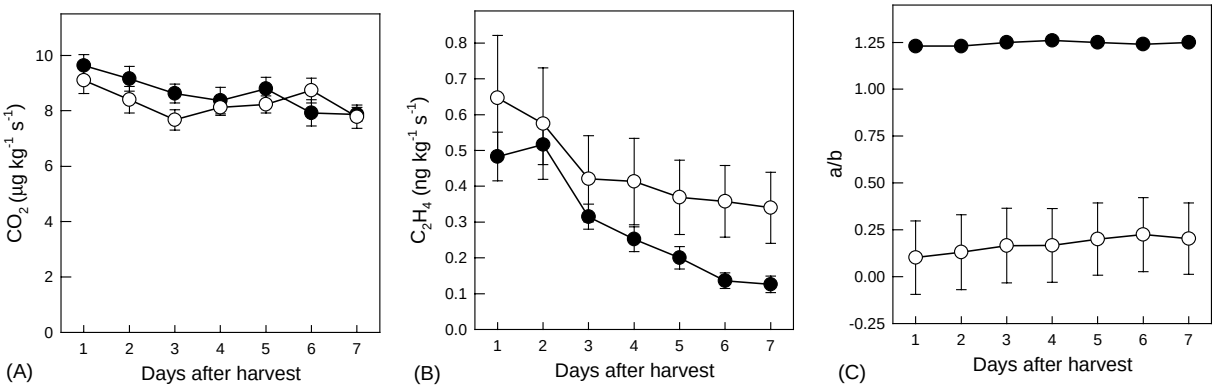

Fig. 4. Changes in CO_2 (A), C_2H_4 (B), color (C) of Florida Petite tomatoes during ripening off the plant at 20 °C. Fruit were harvested 55 days after anthesis from plants not infested (●) or infested (○) with silverleaf whiteflies. Error bars indicate standard error of the mean.

5.2. Fruit harvested 50 DAA

Rates of CO_2 and C_2H_4 production from fruit harvested 50 DAA from control and SLW-infested plants and allowed to ripen off the plant were similar (Fig. 3A and B). Rates of CO_2 production from both groups of fruit averaged about 12 $\mu g\,kg^{-1}\,s^{-1}$ at the time of harvest and decreased to about 8 $\mu g\,kg^{-1}\,s^{-1}$ following 7 days at 20 °C. Rates of C_2H_4 production from both groups of fruit averaged about 0.28 $ng\,kg^{-1}\,s^{-1}$ at the time of harvest and decreased to about 0.08 $ng\,kg^{-1}\,s^{-1}$ after 7 days at 20 °C.

Fruit from control plants harvested 50 DAA had higher *a*/*b* ratios and more uniform color than did fruit from SLW-infested plants (Fig. 3C). In contrast to the fruit harvested 45 DAA, *a*/*b* ratios of control fruit increased only slightly during 7 days of ripening. Firmness of fruit harvested 50 DAA and allowed to ripen for 7 days was significantly lower for fruit from control plants that for fruit from SLW-infested plants (Fig. 5).

5.3. Fruit harvested 55 DAA

Rates of CO_2 and C_2H_4 production from fruit harvested 55 DAA are presented in Figs. 4A and B. Rates of CO_2 production did not differ significantly between fruit from control and SLW-infested plants (Fig. 4A). Rates of CO_2 production were ca. 9.5 $\mu g\,kg^{-1}\,s^{-1}$ 1 day after harvest and decreased to ca. 8 $\mu g\,kg^{-1}\,s^{-1}$ 7 days after harvest. Ethylene evolution was similar for fruit harvested 55 DAA from control and SLW-infested plants at about 0.55 $ng\,kg^{-1}\,s^{-1}$ (Fig. 4B). However, 5–7 days after harvest the rate of ethylene production was slightly higher in fruit from SLW-infested plants (ca. 0.3 $ng\,kg^{-1}\,s^{-1}$) than in fruit from control plants (<0.2 $ng\,kg^{-1}\,s^{-1}$). Fruit harvested 55 DAA from control plants had higher *a*/*b* ratios than did fruit from SLW-infested plants (Fig. 4C). In addition, there was minimal change in color for fruit from either group of plants during 7 days after harvest. Fruit harvested from plants infested with SLW had much less uniform color than did fruit from control plants. As with fruit

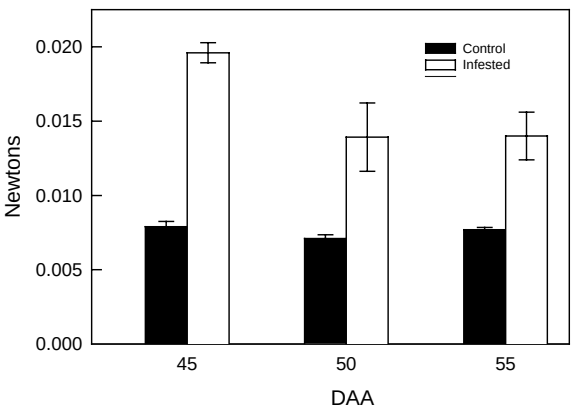

Fig. 5. Firmness of Florida Petite tomatoes harvestd at 45, 50 or 55 DAA and ripened at 20 °C for 7 days. Error bars indicate standard error of the mean.

harvested 45 and 50 DAA, firmness of fruit from control plants was less than fruit from SLW-infested plants (Fig. 5).

6. Discussion

We have determined the effects of silverleaf whitefly feeding on ripening behavior of 'Florida Petite' tomatoes either attached to or detached from the plant. Fruit were sampled based on the number of days after anthesis rather than the appearance of fruit color. This method of fruit sampling facilitated a comparison of fruit of identical age and thereby determine the temporal effects of SLW feeding on ripening. If sampling was based on the appearance of fruit color it is clear that fruit of different chronological ages would have been sampled (Fig. 1C) and this would have confounded the effects of SLW feeding (Hanif-Khan et al., 1998).

Neither fruit from control nor SLW-infested plants had a pronounced respiratory climacteric in this study. Rates of CO_2 production were highest in fruit harvested at 30 DAA, and did not differ between control and SLW-infested plants. At 40 DAA in fruit from control plants and at 50 DAA in fruit from SLW plants there were slight increases in the rates of CO_2 production (Fig. 1A). However, these increases were not of the magnitude reported in other studies (Andrews, 1995; Lyons and Pratt, 1964; Oeller et al., 1991). Fruit from control plants harvested 45 DAA had a very slight increase in the rate of CO_2 production following harvest, but neither fruit from control nor SLW-infested plants harvested 50 or 55 DAA had an increase in CO_2 production following harvest.

In a previous report concerned with the effects of SLW feeding on tomato fruit ripening (Hanif-Kahn et al., 1999), fruit were sampled when they were "mature green", and there was essentially no difference in ethylene production detected between fruit from control and SLW-infested plants; however, as pointed out by Lyons and Pratt (1964) prior to the breaker stage there is no way to identify maturity accurately by appearance. In the current study, we were able to show that SLW feeding results in a delay of the ethylene climacteric in fruit attached to the plant (Fig. 1B) and a suppression of the climacteric in fruit ripened off the plant (Figs. 2B, 3B, and 4B). The rise in ethylene production between 40 and 45 DAA in fruit from control plants is in very close agreement with previously published reports on tomato fruit ripening (Klee, 1993; Lyons and Pratt, 1964; Oeller et al., 1991).

The effects of SLW feeding on firmness of tomato fruit whether ripened on or off the vine were pronounced (Figs. 1D and 5). One enzyme that has been related to softening of tomato fruit is polygalacturonase (PG; EC 3.2.1.15). PG activity and the abundance of PG protein (Western blot analysis) were determined and no significant difference between fruit from control and whitefly infested plants was detected (data not shown). Oeller et al. (1991) reported that tomato fruit from antisense ACC synthase transgenic plants produced PG mRNA comparable to control plants. These results indicate that tomato fruit softening is not dependent on PG activity, in agreement with other reports (Schuch et al., 1991).

Powell and Stoffella (1995) suggested that harvesting tomatoes at the mature green stage from plants infested with SLW may have exacerbated the development of irregular ripening. This is consistent with our current results; fruit from plants infested with SLW developed more red color and softened more extensively if they were allowed to ripen on the plant (Fig. 1C and D) than if they were harvested and ripened off the plant (Figs. 2C, 3C, 4C and 5). Fruit from plants free of SLW harvested 45 DAA developed color and firmness similar to those ripened on the plant. Because ripening was essentially complete in fruit from control plants by 50 DAA, there was minimal change in color and firmness in fruit harvested 50 and 55 DAA and held for an additional 7 days at 20 °C.

In conclusion, our results indicate that SLW feeding on tomatoes has an impact on ethylene biosynthesis and perhaps action in the fruit. This effect is apparently magnified if the fruit are harvested early in the ripening process. According to Maynard and Cantliffe (1989), treatment of tomato fruit with ethylene does not eliminate symptoms of irregular ripening. This is in contrast to results seen with transgenic tomatoes with suppressed ethylene production; treatment of these fruit results in normal ripening (Oeller et al., 1991). Development of red color and softening, ripening related changes known to be regulated by ethylene in tomato fruit, are suppressed in fruit from plants that are infested by SLW.

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