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Strawberry (*Fragaria ×ananassa* Duch.) Growth and Productivity as Affected by Temperature

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Abstract. **Thermotolerance of photosynthesis and productivity in 'Chandler' and 'Sweet Charlie' strawberry plants (*Fragaria ×ananassa* Duch.) exposed to three temperature regimes was studied. Net CO_2 assimilation rate (A), variable chlorophyll fluorescence (Fv), efficiency of photosystem II (Fv/Fm), relative chlorophyll content, plant growth, and fruit yield and quality were measured. High temperature (40 °C day/35 °C night) was more detrimental to photosynthesis and productivity than the moderate or low temperature (30/25 or 20/15 °C). Net CO_2 assimilation rate in both cultivars was markedly reduced by 40/35 °C, although there was slight decline in 'Sweet Charlie' at 30/25 °C. 'Chandler' maintained significantly higher A rates than 'Sweet Charlie' for at least three weeks of heat stress, indicating that 'Chandler' might tolerate longer exposure to high temperature. In parallel to the decrease in A rate, intercellular CO_2 concentration (C_i) and instantaneous water use efficiency (WUE) were significantly decreased at high temperature. 'Chandler' leaves were cooler and transpired more than 'Sweet Charlie' leaves, suggesting that each cultivar adopted different heat resistance mechanisms at 40/35 °C. There were changes in Fv and Fv/Fm with increasing temperature, indicating irreversible damage to photosystem II at 40/35 °C might have occurred. The trend of reduction in stomatal conductance (g_S) in both cultivars at high temperature did not coincide with the reduction in A rates. Decline in A rates at high temperature was more related to changes in Fv/Fm than to g_S activity. The optimal temperature for vegetative growth was 30/25 °C. Reduction in A rate at high temperature resulted in reduction in total leaf area (LA), shoot, root, and leaf biomasses. Strawberry roots were more responsive than shoot growth to temperatures above 20/15 °C. Fruit yield for 'Chandler' was higher at 20/15 °C than at 30/25 °C, suggesting that 'Chandler' might have a higher source-to-sink relationship at 20/15 °C than at 30/25 °C. Fruit skin color was temperature dependent only for 'Chandler'. A quadratic relationship between flower development and duration of exposure to 30/25 °C for both cultivars was observed; more than two weeks of 30/25 °C can be detrimental to flower development. Regardless of the cultivar and duration of exposure, 40/35 °C was the temperature regime most detrimental to fruit set.**

Strawberry cultivars grown in specific areas are adapted to the day length and temperatures of that region. Nevertheless, heat stress is one of the challenges that face strawberry production. Reduction in plant growth by high temperatures is well established in horticultural crops such as tomato (*Solanum lycopersicum* L.) (Adams et al., 2001), grape (*Vitis* spp.) (Chaumont et al., 1997), and strawberry (Renquist et al., 1983). Damage to crops by high temperatures has been reported in many regions around the world and Kansas is no exception; temperatures above 35 °C are common during the growing season.

High temperature adversely affects vegetative growth and fruit quality of tomato (Adams et al., 2001; Mulholland et al., 2003) and reproductive systems of peanut (*Arachis hypogaea* L.) (Vara-Prasad et al., 1999). Heat stress affects photosynthesis, which is highly sensitive to thermal inhibition (Henning and Brown, 1986) whether stress occurs early or late in the growing season. High temperature inhibits thylakoid activities, especially near the photosystem II (PSII) reaction center (Berry and Björkman, 1980).

There have been reports on responses of strawberry cells and whole plants to various temperatures. Strawberry cells subjected to 30 °C grew slowly and did not proliferate normally in suspension cultures (Zang et al., 1997). Strawberry vegetative growth (Hellman and Travis, 1988), root growth (Fukuda and Matsumoto, 1988), fruit set (Nishiyama et al., 2003), pollen viability (Ledesma and Sugiyama, 2005), fruit weight (Mori, 1998), fruit quality (Polito et al., 2002), and leaf protein expression (Gulen and Eris, 2004; Ledesma et al., 2004) were negatively affected by high temperatures. However, strawberry plants resistant to high temperature have the ability to maintain high rates of photosynthesis, stabilize proteins, and synthesize new proteins (Gulen and Eris, 2004).

It has been established that the critical temperature range for strawberry growth inhibition is between 35 and 40 °C and that development of runners is inhibited by 3 d of exposure to 40 °C (Hellman and Travis, 1988). Nevertheless, the mechanism involved in heat stress is not well defined, and information related to strawberry varietal response to heat stress manifested in direct effect on photosynthetic rate and indirect effect on the photosynthesis process is limited. Annual temperature fluctuation occurs frequently in Kansas from late spring through midsummer, a period characterized by high temperatures and long exposure that severely impact growth and production of strawberries.

In this respect, our objective was to investigate the effects of low, moderate, and high temperatures on physiological characteristics and productivity of 'Chandler' and 'Sweet Charlie' strawberry plants. Specific objectives were to identify the optimal temperatures for photosynthesis and chlorophyll fluorescence, determine the influence of high temperature on photosynthesis and efficiency of PSII, and to assess growth response and productivity of strawberry plants under three temperature treatments.

Materials and Methods

Plant materials and treatments. Two new June-bearing strawberry cultivars were selected to replace the old cultivars in Kansas. 'Chandler' and 'Sweet Charlie' are chosen for their early production, high yield, and quality fruits. Plug plants of 'Chandler' and 'Sweet Charlie' (Davon Crest Farms LLC, Hurlock, Md.) strawberry (*Fragaria ×ananassa*) were planted 6 Aug. 2003 in polyethylene pots (16.25 × 16.25 × 12.5 cm) containing a mixture of 1 soil:1 peatmoss:1 perlite (by volume). Each pot had six drainage holes to facilitate water drainage. Plants were grown for 4 weeks under greenhouse conditions of 22/17 ± 3 °C day/night (D/N) temperatures, 50 ± 10% relative humidity (RH), and 16/8-h light/dark (L/D) photoperiods with 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPF* density (*PPFD*) (400–700 nm, measured with LI-188B Integrating Quantum/Radiometer/Photometer and LI-190sB sensor; LI-COR, Inc., Lincoln, Nebr.) on a horizontal plane above the plant canopy. Supplemental light was provided by Hydrofarm grow lights with 400-W, high-pressure sodium, S-51-type lamps (Hydrofarm Products, Petaluma, Calif.). Plants were irrigated

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as needed with deionized distilled water to full pot capacity (Olson et al., 2000). Full pot capacity was determined by saturating the dry soil with water and then measuring the increase in weight after water drained by gravity from the pot. Moisture was maintained by weighing the pots and replenishing water to full pot capacity. Plants were fertilized weekly with a commercial fertilizer containing 300 $\mu g \cdot L^{-1}$ nitrogen (N), 250 $\mu g \cdot L^{-1}$ phosphorus (P), and 220 $\mu g \cdot L^{-1}$ potassium (K) (Miracle-Gro; Scotts Miracle-Gro Products, Port Washington, N.Y.).

Four weeks later, and before temperature treatments, the most recently fully expanded leaflet was measured to determine gas exchange, relative chlorophyll content, and chlorophyll fluorescence. Nine plants of each cultivar were randomly distributed into one of the three growth chambers (Conviron CMP 3244, Asheville, N.C.) set at 20/15 ± 1 °C, 30/25 ± 1 °C, or 40/35 ± 1 °C D/N temperatures, 16/8-h L/D photoperiods with 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD*, and 70% RH. Growth chamber lights were turned off between 10:00 PM and 6:00 AM. Plants were watered as needed to full pot capacity with deionized distilled water. Pest control was carried out according to strawberry pest control recommendations (Kadir et al., 2006).

Gas exchange, chlorophyll fluorescence, and relative chlorophyll content of the most recently fully expanded leaflet were measured at weekly intervals for 4 weeks between 9:00 AM and 11:00 AM. Open flower number was recorded and percentage of dead flower was calculated at weekly intervals. Total fruit yield and fruit quality were recorded as the strawberry plants grow; vegetative and root growth was determined after 4 weeks of exposure.

Leaf gas exchange measurement. Gas exchange was measured with an LI-6400 open system portable photosynthesis meter (LI-COR Inc.). Net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), and leaf temperature were determined. Instantaneous water use efficiency (WUE) was calculated as the ratio between the photosynthetic and transpiration rates (A/E). A leaf sample was placed in the leaf chamber (6.0 cm^2) and exposed to 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPFD* and a CO_2 concentration of 400 $\mu L \cdot L^{-1}$. Data were recorded after 30 to 45 s, when CO_2 and g_S stabilized.

Leaf chlorophyll fluorescence measurement. Leaf chlorophyll fluorescence was determined by using a pulse-modulated fluorometer (Fluorescence Monitoring System [FMS-1]; Hansatech Instruments Ltd., Norfolk, U.K.). The FMS-1 requires no dark adaptation of the leaf because it uses modulated fluorometry to separate actinic light from the fluorescence signal. During measurements, a tissue sample is exposed to a pulsed amber LED light source causing excitation of a pulsed fluorescence signal in the absence of actinic light. The machine was operated in the Fv/Fm mode, and the fluorescence was measured with a photodiode in the 710- to 760-nm range. The fluorometer probe was placed 5 mm away from the leaf, and measurements were made at a steady state of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and a saturating state of 5000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 0.8 s. Fluorescence parameters of initial fluorescence (Fo), maximal fluorescence (Fm), variable fluorescence (Fv = Fm – Fo), and quantum yield efficiency of PSII (Fv/Fm) were recorded from the fluorescence LCD display. Three readings from locations between the veins were averaged to represent one observation.

Relative chlorophyll content measurement. An indirect index of chlorophyll content was measured with a leaf chlorophyll meter (SPAD-501; Minolta Corp., Osaka, Japan) at weekly intervals. Three SPAD measurements (38 mm^2 total leaf area) from locations between the veins were averaged to represent one observation.

Plant growth and productivity. Individual plants were harvested after 4 weeks of temperature treatments and leaf, crown, and runner numbers were recorded. Total leaf area (LA) per plant was measured with the LI-3100 leaf area meter (LI-COR Inc.). Roots were extracted from the soil, washed with deionized distilled water, and placed on paper towels in the greenhouse for one day. Leaves, shoots (crowns and petioles), and roots were dried at 70 °C ± 2 for 72 h and were weighed.

Weekly observation of flower development was conducted in each growth chamber. Open flower number was recorded and percentage of dead flower was calculated based on total flower number per week in each temperature. Percentage of dead flower was determined by dividing total number of flower by number of dead flower and multiplying by 100.

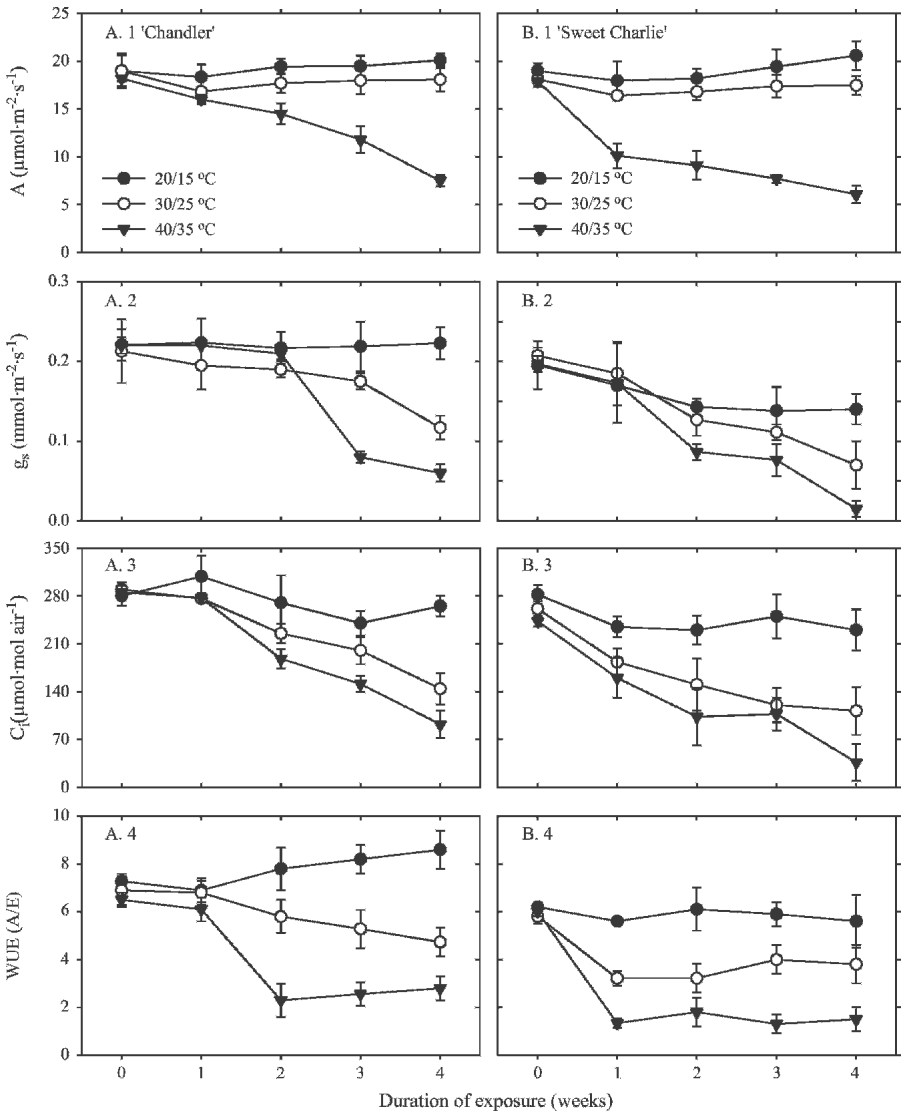

Fig. 1. Effect of three temperature regimes (20/15, 30/25, or 40/35 °C day/night [D/N] and 16/8-h photoperiod for 4 weeks) on net CO_2 assimilation rate (A) (A.1 and B.1), g_S (g_s) (A.2 and B.2), intercellular CO_2 (C_i) (A.3 and B.3), and instantaneous water use efficiency (WUE) (A.4 and B.4) of newly fully developed leaflet on 4-week-old 'Chandler' (A 1–4) and 'Sweet Charlie' (B 1–4) plants. Measurements were obtained at CO_2 concentration of 400 $\mu L \cdot L^{-1}$ at weekly intervals. Vertical bars through data points are standard errors; values smaller than symbols are not shown. Data represent means of nine plants grown in the same temperature regime.

Fruits were harvested at full maturity (more than 90% skin color). Fruit yield per plant and average fresh fruit weight were recorded. Soluble solids concentration (SSC) was measured from extracted juice with a handheld sugar refractometer (Atago No. 41385; Leslie Ratay, New Gardens, N.Y.) and a sucrose scale calibrated at 20 °C. Three external fruit color measurements were taken with a Chromameter (CR-310; Minolta, Japan) according to the Hunter '*a*', '*L*', '*b*' system and the results were averaged. The machine was calibrated with a white standard (L = 97.83, a = –0.38, b = 1.94). The "*a*" value represents greenish to redness, lightness coefficient "*L*" represents brightness and darkness, and "*b*" value represents blueish to yellowish. Hue value (°h) measures fruit color intensity and was calculated from a combination of Hunter "*a*" and "*b*" values (Hunter and Harold, 1987); the lowest °h represents the greatest degree of red skin color.

The experiment was a randomized complete block design with a factorial arrangement of cultivar × temperature × time. Temperature treatments were replicated two times; for the second replication, strawberry plants were planted in the greenhouse on 10 Jan. 2004; there was no interaction between treatments and replications; thus, data are averaged across replications. Temperature treatment response was determined by analysis of variance according to General Linear Models Procedure (SAS Institute, Cary, N.C.). Least significant differences (LSD) among means were tested at $P = 0.05$. Standard errors of the means were calculated. Person correlation coefficients (r) between selected parameters were established. Appropriate data were subjected to regression analysis to establish the coefficient of determination (r^2) for the best model.

Results and Discussion

Gas exchange. Temperature and duration of exposure significantly interacted with cultivar to influence gas exchange parameters (Fig. 1). High temperature (40/35 °C) was more detrimental to photosynthesis than moderate or low temperature (20/15 or 30/25 °C). Net CO_2 assimilation rates (A) of 'Chandler' (Fig. 1, A.1) and 'Sweet Charlie' (Fig. 1, B.1) in 20/15 °C were the same as those of plants in 30/25 °C, although a 15% decline was observed in 'Sweet Charlie' after 4 weeks of exposure to 30/25 °C. Regardless of the cultivar, plants grown in 40/35 °C showed early decline in A rates. One and 2 weeks of exposure reduced A rates by 44% and 20% in 'Sweet Charlie' and 'Chandler', respectively, compared with the control. Photosynthetic rate in 40/35 °C at the end of the experiment was practically the same for both cultivars, but 'Chandler' maintained significantly higher A rates for at least 3 weeks of high temperature than 'Sweet Charlie'. These results indicate that photosynthetic rate in 'Chandler' remained higher at warm temperatures than that in 'Sweet Charlie'; the former might survive longer exposure to high temperature.

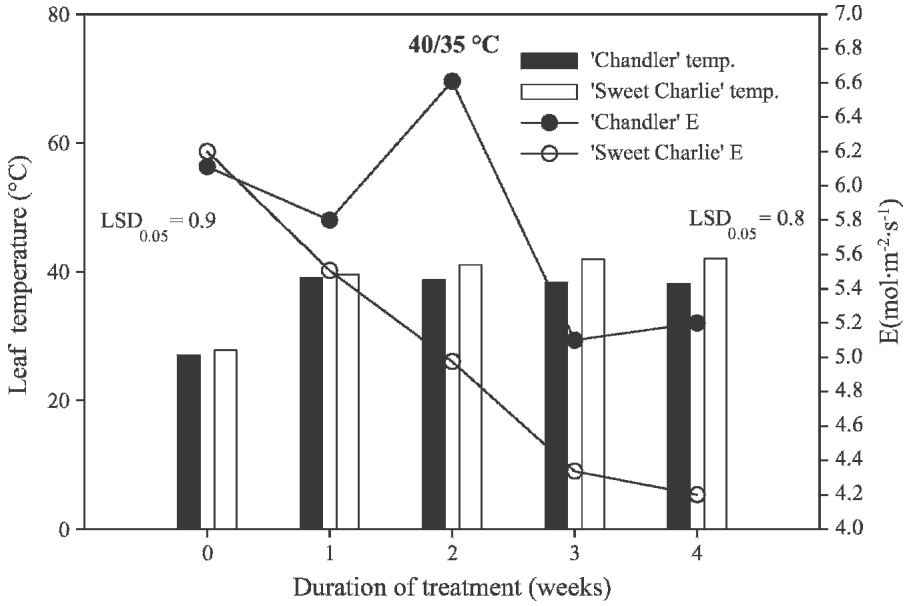

Fig. 2. Effect of high temperature (40/35 °C day/night [D/N] and 16/8-h photoperiod for 4 weeks) on leaf temperature (bars) and transpiration rate (E) (circles) of newly fully developed leaflet on 4-week-old 'Chandler' (solid circles and bars) and 'Sweet Charlie' (open circles and bars) plants. Measurements were obtained at CO_2 concentration of 400 µL·L^{-1} at weekly intervals. Data represent means of nine plants grown in the same temperature regime.

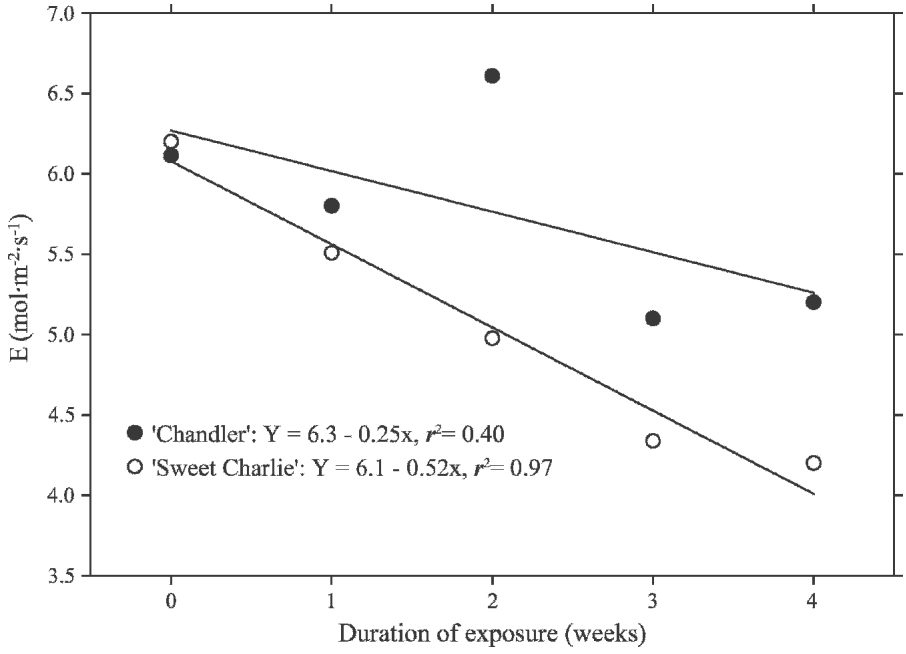

Fig. 3. Relationship between duration of exposure to high temperature (40/35 °C day/night [D/N]) and 16/8-h photoperiod for 4 weeks) and transpiration rate (E) of newly fully developed leaflet on 4-week-old 'Chandler' (•) and 'Sweet Charlie' (X) plants. Measurements were obtained at CO_2 concentration of 400 µL·L^{-1} at weekly intervals. Lines represent linear regression analysis of the means. Data represent means of nine plants.

Initially, g_S (g_s) of both cultivars was the same, but reduction occurred in the 40/35 °C treatment after 2 and 3 weeks of exposure in 'Sweet Charlie' (Fig. 1, B.2) and 'Chandler' (Fig. 1, A.2), respectively. Four weeks of exposure to high temperature reduced g_s in 'Sweet Charlie' by 92% compared with 72% in 'Chandler'. Nevertheless, the g_s of 'Chandler' was significantly higher than that of 'Sweet Charlie' at the end of the experiment, which might indicate that g_s of 'Chandler' is relatively less responsive to high temperature than that of 'Sweet Charlie'. In both cultivars, a decline in g_s at high temperature did not correspond to a decline in A rates. Different reduction trends of A rate and g_s at high

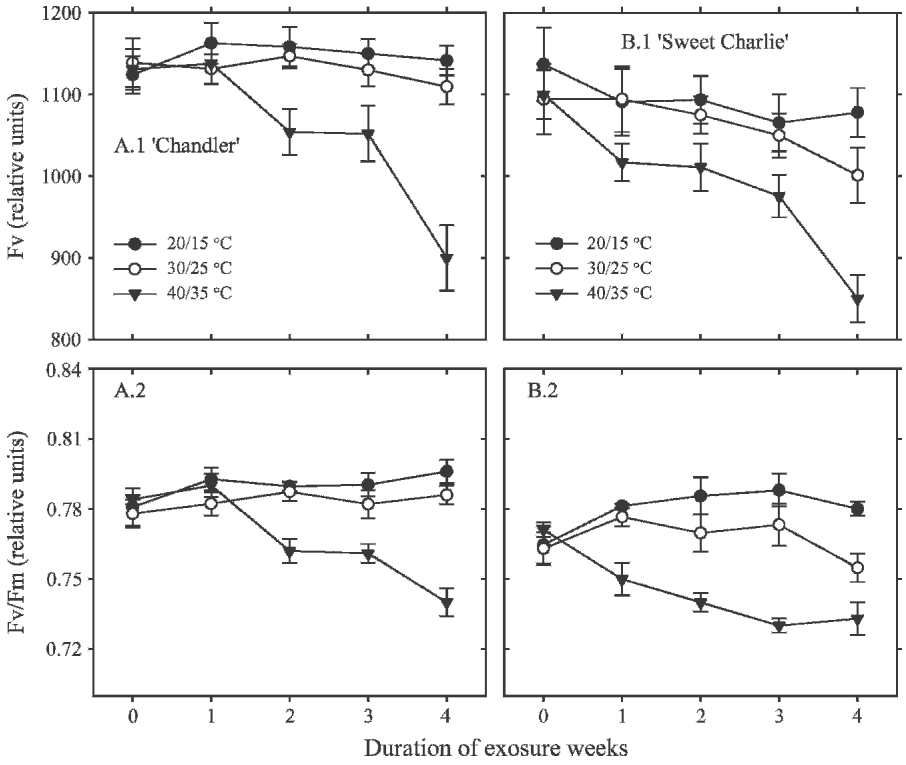

Fig. 4. Effect of three temperature regimes [20/15, 30/25, or 40/35 °C day/night (D/N) and 16/8-h photoperiod for 4 weeks] on variable fluorescence (Fv) and quantum yield efficiency of photosystem II (Fv/Fm) ratio of newly fully developed leaflet on 4-week-old 'Chandler' (A 1–2) and 'Sweet Charlie' (B 1–2) plants. Chlorophyll fluorescence was measured as described in the "Materials and Methods" at weekly intervals. Vertical bars through data points are standard errors; values smaller than symbols are not shown. Data represent means of nine plants grown in the same temperature regime.

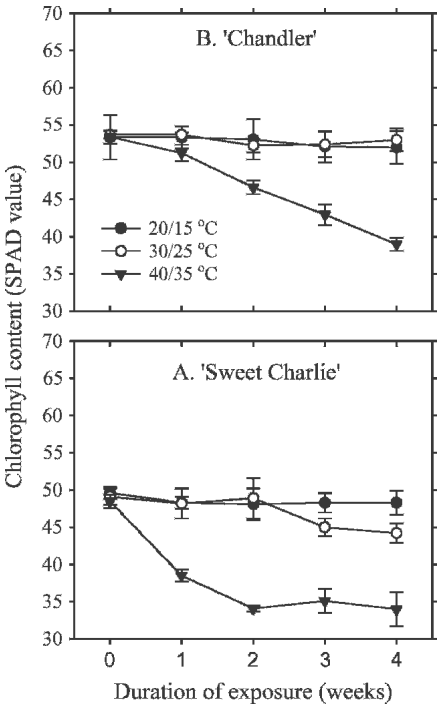

Fig. 5. Effect of three temperature regimes (20/15, 30/25, or 40/35 °C day/night [D/N] and 16/8-h photoperiod for 4 weeks) on relative chlorophyll content (SPAD value) of newly fully developed leaflet on 4-week-old 'Chandler' and 'Sweet Charlie' plants. Chlorophyll content was measured with the leaf chlorophyll meter at weekly intervals. Vertical bars through data points are standard errors; values smaller than symbols are not shown. Data represent means of nine plants grown in the same temperature regime.

temperature suggest that high temperature directly acts on limitation factors related to photosynthesis processes other than g_s activities. This agrees with earlier report that g_s usually is not involved in temperature effects on photosynthesis (Paulsen, 1994). High temperature affects photosynthetic processes through nonstomatal activities such as enzymatic activity during photosynthesis (Medrano et al., 2003).

Low temperature (20/15 °C) had no influence on intercellular CO_2 (C_i) concentrations in either cultivar. However, in 30/25 and 40/35 °C, C_i was reduced 1 week earlier in 'Sweet Charlie' (Fig. 1, B.3) than in 'Chandler' (Fig. 1, A.3). In contrast to 'Sweet Charlie', 'Chandler' maintained significantly higher C_i concentrations for at least 3 weeks at 30/25 °C. A linear decline for 'Sweet Charlie' and Chandler' in 40/35 °C was recorded after 1 and 2 weeks of exposure, respectively. After 4 weeks of high temperature, reduction was more severe in 'Sweet Charlie' (87%) than 'Chandler' (68%) compared with the control plants. Results indicate that timing of C_i reduction in both cultivars coincided with a decrease in A rates but not g_s. This suggests that decline in C_i, which results in a decline in A rate, might also be related to factors other than g_S such as a decrease in mesophyll conductance (Candolfi-Vasconcelos and Koblet, 1991).

Instantaneous WUE measures the efficiency of carbon fixation per unit water loss. For both cultivars, the rate of carbon gain was almost always higher than water loss (higher WUE) in 20/15 and 30/25 °C than in 40/35 °C. The declining trend of WUE at high temperature was similar to the trend of A rates and C_i concentrations in both cultivars; WUE in 'Sweet Charlie' (Fig. 1, B.4) decreased by 79% after 1 week and by 64% in 'Chandler' after 2 weeks of high temperature (Fig. 1, A.4). 'Chandler' had 46% higher WUE after 4 weeks of high temperature than 'Sweet Charlie'. These results suggest that 'Chandler' has higher A to E ratio under high temperature condition than 'Sweet Charlie'.

Responses of leaf temperatures and transpiration rates (E) to 40/35 °C are shown in Figure 2. No treatment impact on leaf temperatures or E rates was observed for 20/15 °C, whereas 30/25 °C exerted a trend (data not shown) similar to that for 40/35 °C. Leaf temperatures increased in both cultivars after 1 week of exposure to high temperature; average leaf temperature was 39.3 °C. Trends of reduction in transpiration were similar to those of g_s for both cultivars; E rate was reduced after 2 and 3 weeks in 'Sweet Charlie' and 'Chandler', respectively. 'Chandler' plants showed constant E rates for 2 weeks but declined thereafter by an average of 16%. Leaf temperature, however, remained constant throughout the duration of the experiment with an average of 38.5 °C. In contrast, 'Sweet Charlie' plants showed an average decline in E rate of 28% after 2 weeks, which resulted in an average of 2.1 °C increase in leaf temperature. After 4 weeks of exposure, 'Chandler' leaves transpired ≈20% more and leaf temperature was ≈4 °C cooler than 'Sweet Charlie' leaves. Results showed that 'Sweet Charlie' had higher leaf temperature and lower E rate under high temperature than 'Chandler'. Transpiration rate of 'Sweet Charlie' was negatively related to leaf temperature (r = –0.90) and positively related to g_s (r = 0.95); nonetheless, E rate of 'Chandler' was not significantly related to leaf temperature (r = 0.57) and was less related to g_s rate (r = 0.86) than 'Sweet Charlie'. This suggests that different mechanisms for heat resistance might have been adopted by each cultivar. In contrast to 'Sweet Charlie', 'Chandler' leaves under heat stress managed to maintain constant g_s, resulting in cooler leaf temperature as a result of high transpiration. When transpiration rate of 'Sweet Charlie' (Fig. 3) was regressed against duration of exposure, there was a negative linear relationship between transpiration and time. The relationship explained most (97%) of the variation in E rate with increasing time of exposure. 'Chandler', on the other hand, showed a negative linear relationship between transpiration and time although with low r^2 (0.40).

Table 1. Response of total leaf area (LA); shoot, leaf, and root biomasses; and leaf, crown, and runner numbers of 4-week-old strawberry plants to 20/15, 30/25, or 40/35 °C day/night (D/N) and 16/8-h photoperiod for 4 weeks of exposure.[z]

	Temp (°C)		
Parameter	20/15	30/25	40/35
LA (cm^2)	581 b[y]	765 a	209 c
Shoot biomass (g)[x]	8.4 a	8.8 a	6.1 b
Leaf biomass (g)	8.2 b	10.0 a	6.6 c
Root biomass (g)	11.3 a	9.4 b	8.2 c
Leaves (no.)	32 ab	37 a	28 b
Crowns (no.)	2.9 b	3.4 a	1.1 c
Runners (no.)	2.2 b	3.1 a	—[w]

[z]There was no significant difference between the cultivars; thus, data are averaged across cultivars for statistical analysis.
[y]Values are means of 18 plants grown in the same temperature regime. Means within parameter followed by different letter are significantly different at $P \leq 0.05$ using Fisher's protected LSD.
[x]Shoot biomass includes crowns and petioles.
[w]No runners.

Table 2. Response of yield, fruit size, soluble solids concentration (SSC), and skin color (°h) of 'Chandler' and 'Sweet Charlie' 4-week-old plants to 20/15 and 30/25 °C day/night (D/N) and 16/8-h photoperiod for 4 weeks of exposure.

Cultivar	Temp (C)[z]	Yield (g/plant)	Fruit size (g)	SSC (%)	Hue[y] (°h)
	20/15				
Chandler		9.2 a[x]	3.1 a	6.9[NS]	15 d
Sweet Charlie		9.3 a	5.0 a	6.7[NS]	44 bc
	30/25				
Chandler		3.0 b	1.0 b	5.4[NS]	56 a
Sweet Charlie		6.0 ab	3.2 a	6.4[NS]	37 c

[z]No fruits in 40/35 °C.
[y]Values (Atan b/a) calculated from a combination of Hunter *a* and *b* values.
[x]Means of nine plants grown in the same temperature regime. Means within column followed by different letter are significantly different at $P \leq 0.05$ using Fisher's protected LSD.
[NS]Nonsignificant at $P \leq 0.05$.

Chlorophyll fluorescence. Temperature and duration of exposure significantly interacted with cultivar to influence chlorophyll fluorescence. Variable chlorophyll fluorescence (Fv = Fm – Fo) and quantum yield efficiency of PSII (Fv/Fm) are shown in Figure 4. The Fv of both cultivars (Fig. 4, A.1 and B.1) followed the same trend as net CO_2 assimilation rates (Fig. 1, A.1 and B.1); throughout the duration of exposure, low or medium temperature had no influence on Fv, although 7% decline in Fv was observed in 'Sweet Charlie' (Fig. 4, B.1) after 4 weeks of exposure to 30/25 °C. Regardless of the cultivar, plants grown in 40/35 °C showed early Fv decline. After 1 and 2 weeks of exposure, Fv declined in 'Sweet Charlie' (8%) and 'Chandler' (6%) (Fig. 4, A.1), respectively; nonetheless, there was no significant difference between the two cultivars after 4 weeks of exposure to high temperature.

Quantum yield efficiency of PSII is the function of Fv and Fm. At any time, Fv/Fm followed the trends of Fv (Fig. 4, A.1 and B.1) and A rates (Fig. 1, A.1 and B.1). Reduction of Fv/Fm at 40/35 °C was the result of increase in Fo and decline in Fm rates (data not shown) in both cultivars, although there was significant difference between the cultivars. Efficiency of PSII in 'Chandler' (Fig. 4, A.2) was significantly higher at 3 weeks of exposure than that of 'Sweet Charlie' (Fig. 4, B.2). Collective results indicate that, under heat stress, 'Chandler' PSII is marginally more efficient than the PSII of 'Sweet Charlie'. The photosynthetic rate of 'Chandler' was positively related to Fv ($r = 0.97$) and Fv/Fm ($r = 0.94$) compared with Fv ($r = 0.92$) and Fv/Fm ($r = 0.86$) of 'Sweet Charlie'. The stronger relationship between A rates and Fv/Fm in 'Chandler' might indicate that PSII is more thermostable that of 'Sweet Charlie'.

These findings confirm that temperatures above 30 °C reduce photosynthetic rate as a result of a reduction in PSII efficiency rather than a reduction in g_S.

Chlorophyll content. Three-way interaction of cultivar by temperature by time was found for relative chlorophyll content. Regardless of temperature treatments, relative chlorophyll content (SPAD value) of 'Chandler' leaves was higher than that of 'Sweet Charlie' (Fig. 5). Throughout the test period, neither 20/15 nor 30/25 °C treatments affected chlorophyll content of 'Chandler' leaves, but 30/25 °C reduced chlorophyll content of 'Sweet Charlie' by an average of 10% after 3 weeks of exposure. High temperature reduced chlorophyll content of both cultivars. Chlorophyll content of 'Sweet Charlie' leaves was reduced by 21% after 1 week exposure to 40/35 °C; 13% reduction was observed for 'Chandler' after 2 weeks. Both 'Sweet Charlie' and 'Chandler' plants in 40/35 °C showed a constant decline over time, although 'Chandler' leaves had 13% greater relative chlorophyll content at the end of the experiment. Chlorophyll content of different plant species under high temperature has shown mixed results. This study showed a decline under heat stress, which agrees with a decline reported in grapevines grown in a controlled environment (Fukuda and Matsumoto, 1988) and in mulberry (*Morus* spp. L.) plants exposed to high temperature for a short period of time (Chaitanya et al., 2001). Higher chlorophyll content was detected for heat-stressed grapevines in open air (Fukuda and Matsumoto, 1988). It was suggested that increase in chlorophyll content could be attributed to time of exposure and difference in plant species (Gulen and Eris, 2003), strength and source of stress (Dekov et al., 2000), or increase in leaf thickness, which led to concentration of more chlorophyll content (Abdelrahman, 1984). It has been suggested that longer exposure time of strawberry (Gulen and Eris, 2003) and tomato (Romero-Aranda et al., 2001) plants to high temperature increased chlorophyll content.

Plant growth, yield, and fruit quality. Cultivar had no impact on total leaf area (LA); shoot, leaf, and root biomasses; and leaf, crown, and runner numbers, so data were averaged across cultivars (Table 1). Reduction in A (Fig. 1, A.1 and B.1) was more pronounced in 40/35 °C as indicated by declines in LA and in shoot and leaf biomasses. The optimal temperature for plant growth was 30/25 °C as was 20/15 °C. Plants at 30/25 °C maintained greater LA, which generally paralleled leaf chlorophyll content (Fig. 5). Total leaf area of plants grown in 30/25 °C was 24% and 73% greater than that of plants in 20/15 and 40/35 °C, respectively. Runner development was inhibited by high temperature, whereas plants in 30/25 °C had 29% more runners than in 20/15 °C. These findings are in agreement with Smeets's (1982) report that runner development was inhibited by 14 or 20 °C, whereas 26 °C was the optimal temperature. Leaf biomass was the highest in 30/25 °C, but number of leaves was not significantly different from at 20/15 °C, which resulted in similar shoot biomass in both temperatures. Leaf number and leaf biomass in 40/35 °C were reduced by 24% and 34%, respectively, which resulted in 31% reduction in shoot biomass. Results indicate that dry matter accumulation was directly related to A rates, which agrees with earlier report (Ferrini et al., 1995) that positive correlation was found between the two variables. Plants in 30/25 °C, followed by those in 20/15 °C, produced more crowns than plants in 40/35 °C. Root growth was sensitive to temperatures above 20/15 °C; greatest growth was produced in 20/15 °C (11.3 g) followed by 9.4 g in 30/25 °C. The least root biomass was observed in plants grown at 40/35 °C. These results indicate that strawberry roots are more sensitive to high temperature than shoot growth. Strawberry root growth in Hoagland solution was severely inhibited when plants were subjected to temperatures above 35 °C (Abdelrahman, 1984; Geater et al., 1997). Most of the growth inhibition of strawberry plants subjected to high root-zone temperature were associated with reduction in transpiration and leaf water potential (Geater et al., 1997).

A three-way interaction of cultivar by temperature by time was found for total marketable fruit yield and quality. Regardless of the cultivar, 40/35 °C treatment inhibited fruit development (Table 2). There were no nonmarketable fruits (disease or misshape) in either the 20/15 °C or the 30/25 °C treatment. Fruit yield for 'Chandler' was higher (67%) at 20/15 °C than at 30/25 °C, whereas no significant difference between the two temperatures was found for 'Sweet Charlie'. This suggests that 'Chandler' might have higher source-to-sink relationship at 20/15 °C than

at 30/25 °C. More fruit transpiration or a low rate of dry matter accumulation in fruits (Miura et al., 1994) might also have occurred at 30/25 °C, which reduced fruit yield of 'Chandler' as a result of reduction of fruit size. The difference between 'Chandler' and 'Sweet Charlie' suggests that high temperature effect on strawberry fruit yield and size is cultivar-dependent. Yield and fresh fruit weight are negatively related to increase in temperature (Mori, 1998). High temperature negatively affects fruit set in strawberries, depending on the cultivar, by reducing pollen viability and inhibiting pollen tube growth and elongation of pollen tube growth (Ledesma and Sugiyama, 2005). There was no significant reduction in 'Sweet Charlie' yield between 20/15 and 30/25 °C, suggesting that 'Sweet Charlie' flowers might have produced heat-tolerant pollen (Ledesma and Sugiyama, 2005) that can survive 30/25 °C. These findings suggest that the optimal temperature for 'Chandler' fruit yield and size was 20/15 °C, whereas 'Sweet Charlie' can produce comparable yield and fruit size in 30/25 °C to those of plants in 20/15 °C. There was no significant difference in fruit size between the cultivars in 20/15 °C, but 'Sweet Charlie' produced larger fruits in 30/25 °C than 'Chandler'. No temperature impact was found on fruit SSC in either cultivar, which disagrees with Hardh and Hardh (1977) who reported that sugar content was reduced by high temperature. The discrepancy might be the result of differences in the environmental conditions and cultivars of the two experiments.

Fruit color of strawberries, skin redness, is one of the important fruit quality characteristics that determine differences between temperature treatments. This characteristic is measured by determining the hue value (°h) from a combination of Hunter "*a*" and "*b*" values (data not shown). The lowest °h value or the greatest degree of redness was observed in 'Chandler' fruits in 20/15 °C; in contrast, 'Sweet Charlie' plants produced redder fruits in 30/25 °C. Within cultivar at the two temperatures, 'Chandler' fruits in 20/15 °C were 73% redder than those in 30/25 °C, whereas no significant difference was observed in 'Sweet Charlie' fruits. Between the cultivars, 'Chandler' fruits in 20/15 °C were 66% redder than 'Sweet Charlie' fruits. Contrasting results occurred in 30/25 °C; 'Sweet Charlie' fruits were 34% redder than 'Chandler' fruits. Strawberry skin redness was temperature dependent only for 'Chandler'. Although high temperature reduced color intensity of strawberry fruits (Hardh and Hardh, 1977), results of this study suggest that temperature effect on skin redness is cultivar-dependent.

Flower development. A significant interaction between cultivar, temperature, and time was found for open flower number and percentage of dead flower. Relationships between time of exposure to three temperature regimes and open flower number of 'Chandler' and 'Sweet Charlie' are shown in Figure 6. Quadratic relationships were observed at 30/25 °C, but positive and negative linear relationships were observed at 20/15 and 40/35 °C, respectively. Flowers developed in the 20/15 °C treatment as time of exposure increased, although a stronger relationship with time was observed in 'Chandler' (r^2 = 0.95) than in 'Sweet Charlie' (r^2 = 0.66), which resulted in higher yield in 20/15 °C (Table 2). At 30/25 °C, maximum open flower number for 'Chandler' was at 2 weeks, whereas maximum number for 'Sweet Charlie' was at 1 week exposure, but the number declined thereafter in both cultivars. For instance, increasing time of exposure to 4 weeks reduced open flower number by 24% and 45% in 'Chandler' and 'Sweet Charlie', respectively. Both cultivars exhibited a negative linear relationship between open flower number and time of exposure to 40/35 °C. For example, the number was reduced from 4.8 and 3.2 for 'Chandler' and 'Sweet Charlie', respectively, to no flowers as time of exposure to high temperature increased from 1 to 2 weeks. Results of this study show that, despite a positive linear relationship in 20/15 °C, more flowers were produced in 30/25 °C. Nevertheless, more than 2 weeks at 30/25 °C can be detrimental to flower development for both cultivars. Strawberry flower initiation was delayed at 20 °C and 16-h photoperiod, whereas 26 °C initiated early and more flowers (Smeets, 1982). Continuous flowering at 30/25 °C in 'Chandler' for 2 weeks compared with 1 week in 'Sweet Charlie' suggests that flower initiation is dependent on the ability of a cultivar to form flower buds in response to temperature under long-day conditions (Heide, 1977). Biosynthesis of a flowering inhibitor (Vince-Prue et al., 1976) might have increased to a level that led to inhibition of flower initiation or flower bud formation in 'Chandler' and 'Sweet Charlie' after 2 weeks and 1 week of 30/25 °C, respectively.

Time of exposure to 30/25 and 40/35 °C increased percentage of dead flower in both cultivars (Fig. 7). 'Chandler' was not influenced by 2 weeks of exposure to 30/25 °C (Fig. 7), but the value increased by 64% as time of exposure increased from 2 to 3 weeks.

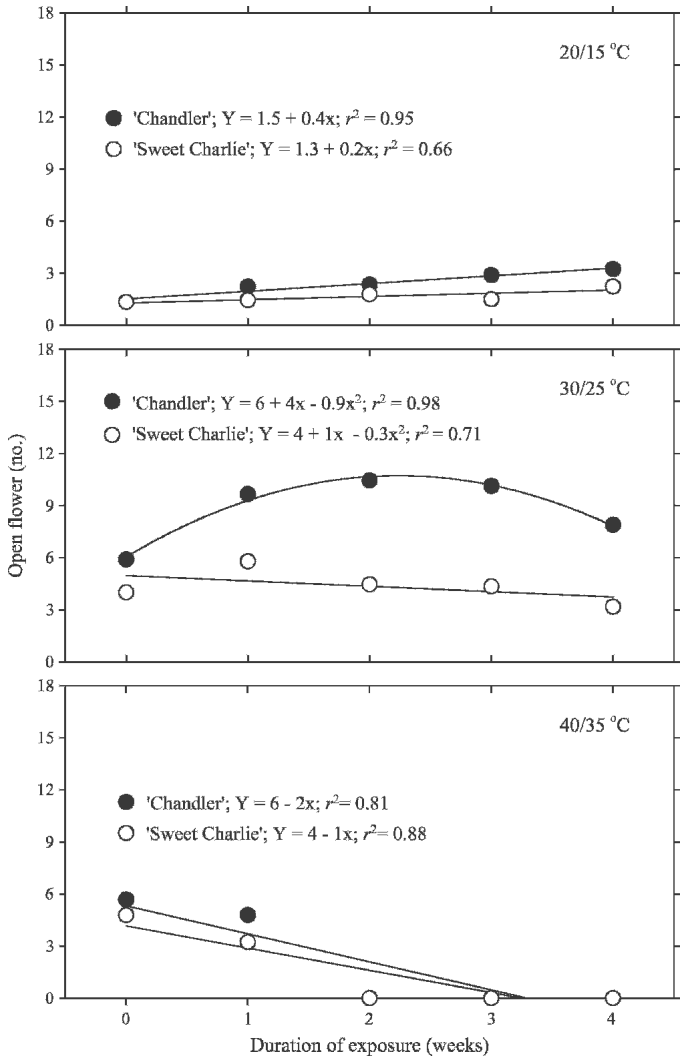

Fig. 6. Relationship between duration of exposure to three temperature regimes (20/15, 30/25, or 40/35 °C day/night [D/N]) and 16/8-h photoperiod for 4 weeks) and open flower number of 4-week-old 'Chandler' (•) and 'Sweet Charlie' (X) plants. Data collected at weekly intervals. Lines represent linear regression analysis of the means. Data represent means of nine plants grown in the same temperature regime.

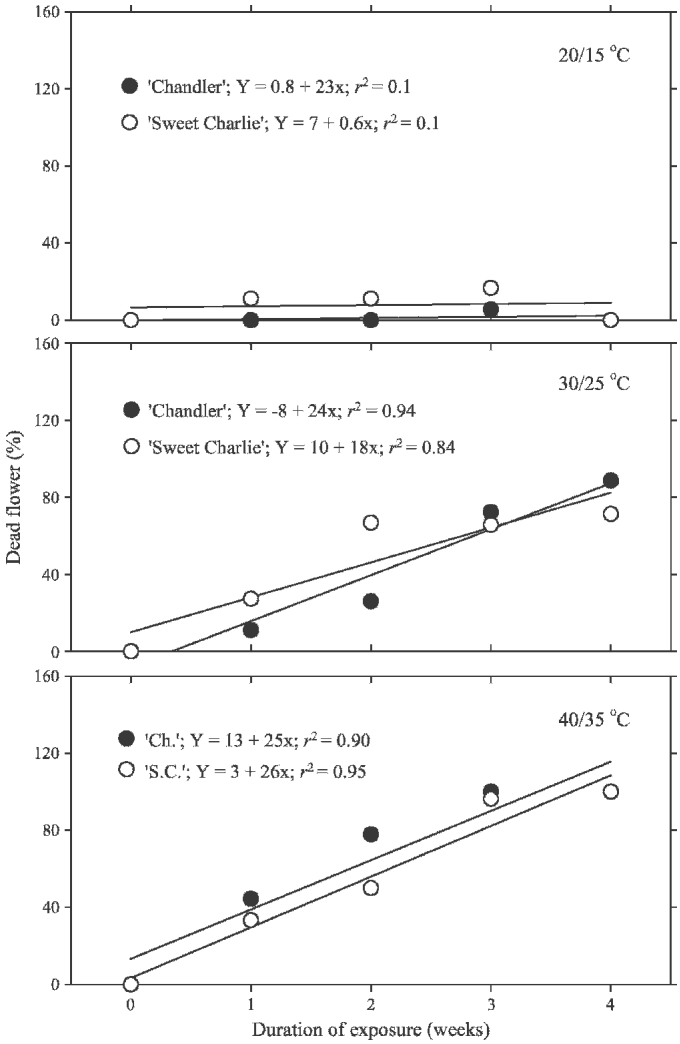

Fig. 7. Relationship between duration of exposure to three temperature regimes (20/15, 30/25, or 40/35 °C day/night [D/N] and 16/8-h photoperiod for 4 weeks) and percentage of dead flower of 4-week-old 'Chandler' (•) and 'Sweet Charlie' (X) plants. Data collected at weekly intervals. Lines represent linear regression analysis of the means. Data represent means of nine plants grown in the same temperature regime.

Earlier increase in the percentage of dead flower of 'Sweet Charlie' was observed as time of exposure increased. For example, there was an increase from 27% to 67% as time of exposure increased from 1 to 2 weeks. In contrast, the rate at 40/35 °C increased from 44% and 33% to 78% and 50% in 'Chandler' and 'Sweet Charlie', respectively, as time of exposure increased from 1 to 2 weeks. Regardless of cultivar and time of exposure, high temperature was the most detrimental to flower initiation, whereas 20/15 °C was the least. Interaction between cultivar and time of exposure impacted flower survival at 30/25 °C. For example, in week 2, percentage of dead flower for 'Chandler' was 26% compared with 67% for Sweet Charlie, which suggests that 30/25 °C affects flower initiation and survival but that the effect is cultivar-dependent.

In conclusion, high temperature severely reduced strawberry growth and yield. Photosynthesis inhibition was a primary factor of injury from high temperature, and strawberry cultivars differed in their response to heat stress. Plant growth at moderately high temperature (30/25 °C) hardly contributed to the reduction in photosynthesis; reduction was associated with relatively no change in Fv/Fm, suggesting that there was no damage to PSII in 30/25 °C. The 40/35 °C treatment caused more reduction in thermostability of the photosynthesis apparatus of the relatively heat-sensitive 'Sweet Charlie' than it caused in 'Chandler'. Results of this study show that the main factor for photosynthesis reduction was more related to changes in the efficiency of PSII than to stomatal activities. There was no cultivar impact on shoot or root growth and 30/25 °C was the optimal temperature for shoot growth but 20/15 °C was the optimal temperature for root growth. 'Chandler' plants had higher WUE, suggesting that, under heat stress, 'Chandler' might have higher ratio of photosynthetic rate to transpiration than 'Sweet Charlie'. High temperature inhibited flower and fruit set in both cultivars. The 20/15 °C was the optimal temperature for fruit yield and fruit size in 'Chandler', whereas 'Sweet Charlie' produced yield and fruit size in 30/25 °C comparable to that of plants in 20/15 °C. Strawberry skin redness was temperature dependent only for 'Chandler'. Despite a positive linear relationship between flower development and duration of exposure to 20/15 °C in both cultivars, a quadratic relationship occurred for 30/25 °C. More than 2 weeks of 30/25 °C can be detrimental to flower development, suggesting that 30/25 °C affects flower initiation and survival but that the effect of duration of exposure is cultivar-dependent.

Although 'Chandler' is more resistant to high temperature, future investigations involving comparison of the two cultivars will be needed for a better understanding of high temperature effect during the development of reproductive stages. Effect of chemicals and evaporative cooling system to alleviate heat stress should also be considered in investigations of heat tolerance during the reproductive stages.

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