Flower Production, Fruit Set, and Physiology of Bell Pepper during Elevated Temperature and Vapor Pressure Deficit

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ABSTRACT. High temperature reduces fruit set in bell pepper [*Capsicum annuum* L. var. *annuum* (Grossum Group)], and reduction of pepper productivity, resulting from high temperature, may be a direct effect of temperature or an indirect effect of water stress induced by increased vapor pressure deficits (VPDs) at high temperature. We evaluated responses of plant growth, reproduction, net photosynthesis (P_N), chlorophyll fluorescence, predawn respiration, leaf water potential, and stomatal conductance of 'Ace' and 'Bell Boy' bell pepper to elevated temperature (33 °C) with increased VPD (2.1 kPa) or elevated temperature with no increase in VPD (1.1 kPa). VPD had no effect on flower number or fruit set and did not adversely influence the physiological processes measured. Therefore, deleterious effects of high temperature on pepper fruit set does not appear to be temperature induced water stress, but is more likely a direct temperature response. Elevated temperature decreased fruit set but not flower production. Gas exchange measurements suggest failure to set fruit was not due to reduced leaf photosynthesis.

Reduced fruit set during periods of high temperature has been documented for a wide variety of plant species including pepper (*Capsicum annuum* L.) (Khah and Passam, 1992; Konsens et al., 1991). In pepper, reduced fruit set is common when day temperatures are ≥ 32 °C (Rylski and Spigelman, 1982). Abscission of reproductive structures in pepper during periods of high temperatures reduces yield in the northeastern United States (Wien, 1990), Israel (Rylski and Spigelman, 1982), and Greece (Khah and Passam, 1992), where peppers are commonly grown in plastic or glass greenhouses year round.

High temperature influences many aspects of plant physiology and growth, which in turn may have a direct or indirect effect on fruit set. In tomato (*Lycopersicon esculentum* Mill.) and cowpea [*Vigna unguiculata* (L.) Walp. ssp. *unguiculata*], high temperature affects pollen development resulting in nonviable pollen and failure to set fruit (Peet and Bartholomew, 1996; Sato et al., 2000; Warrag and Hall, 1984). In pepper, reduced fruit set at high temperature has been associated with decreased concentrations of reducing sugars in flower buds and flowers (Aloni et al., 1991) and increased ethylene production (Aloni et al., 1994).

High temperature may reduce fruit set indirectly by increasing vapor pressure deficits (VPDs), which can result in water deficits. Increased VPD results in increased evaporation and transpiration from leaf surfaces (Larcher, 1995). If the VPD creates a water deficit within the plant, stomata will close and leaf water potential will decrease resulting in decreased photosynthesis (Nilsen and Orcutt, 1996). There is a paucity of research on effects of water deficit on pepper fruit set (Katerji et al., 1993). However, research on other crops such as wheat (*Triticum aestivum* L.) and soybean (*Glycine max* L.) has demonstrated reproductive sensitivity to water deficit during flower development and fruit set (Lalonde et

al., 1997; Westgate and Peterson, 1993) resulting in reduced grain yield and pod biomass, respectively. Determining whether increased VPD at high temperature contributes to losses in fruit production in pepper will provide impetus for studying mechanisms responsible for reduced yield resulting from high temperature, and may provide strategies for preventing pepper fruit loss. Therefore, the following experiments were conducted to determine A) whether reduced pepper fruit set is a direct result of high temperature or increased VPD induced by high temperature, B) if reduced fruit set at high temperature is due to decreased flower bud production, increased flower bud abscission, or increased flower abscission, and C) whether high temperatures and/or increased VPD have a detrimental influence on plant gas exchange and water relations.

Materials and Methods

PLANT MATERIALS. 'Ace' and 'Bell Boy' bell peppers [*Capsicum annuum* var. *annuum* (Grossum Group)] were used in this investigation. 'Ace' was chosen for recognized heat tolerance (Turner and Wien, 1994; Wien et al., 1989), and 'Bell Boy', a commonly grown cultivar, was chosen for comparison. Seeds of 'Ace' and 'Bell Boy' were sown in 20 cm³ plug trays with Strong-Lite Germination media (Strong-Lite, Sepeca, Ill.) and germinated under mist at 25 ± 4 °C. After germination, seedlings were transplanted individually into 0.5-L pots in Strong-Lite Soilless Universal Mix (Strong-Lite) and were grown in a greenhouse at day/nights of 25/21 °C, under ambient light supplemented with 400 W high pressure sodium, high intensity discharge lighting for 14 h daily. Plants were watered bi-weekly and fertilized weekly with 1.1 g/plant of a 20.0N–4.4P–16.6K water soluble fertilizer (Peter's Lite, Fogelsville, Pa.). After temperature/VPD treatments commenced, as described in the treatment section, plants were watered daily and fertilized bi-weekly.

TREATMENTS. The experiment was conducted twice (Expt. 1 and Expt. 2) in different growth chambers over two time periods. Three growth chambers were used for each experiment with treatment settings of 25 °C with a VPD of 1.1 kPa [60% relative humidity (RH)], 33 °C with a VPD of 1.1 kPa (75% RH), and 33 °C with a VPD of 2.1 kPa (60% RH). When the first flower buds

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reached anthesis, ≈ 4 to 6 weeks after germination, 15 (Expt. 1) or 18 (Expt. 2) plants of each cultivar were potted into 3.2-L pots with Strong-Lite Soilless Universal Mix (Strong-Lite) and arranged randomly into three growth chambers (E15; Conviron, Controlled Environments, Inc., Winnipeg, Canada) with five (Expt. 1) or six (Expt. 2) plants per chamber. The three growth chambers were set initially at constant temperatures of $25 \pm 0.2^\circ\text{C}$ with a 12-h photoperiod of $650 \pm 50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux as measured at canopy level with a quantum flux sensor (LI-189; LI-COR, Inc., Lincoln, Nebr.). Irradiation sources in each chamber consisted of a combination of two 1000-W metal halide and two 1000-W sodium high-intensity-discharge lamps. RH inside the chambers was $60\% \pm 10\%$, equivalent to a VPD of 1.1 kPa. Plants were allowed to acclimatize to the growth chamber environment for 1 week (Expt. 1) or 3 weeks (Expt. 2) before treatment initiation.

The effect of high temperature with stable or increased VPD was investigated by increasing temperatures to 33°C in two chambers with increased VPD of 2.1 kPa in one of the high temperature chambers. Temperature and RH were stable within the growth chambers with a SD of 0.5°C and 4%, respectively. Light, temperature, and RH were monitored regularly to verify treatment conditions. Sample size was five plants of each cultivar per treatment (Expt. 1) and six plants of each cultivar per treatment (Expt. 2). Treatment duration was increased from 18 d in Expt. 1 to 25 d in Expt. 2 to allow more time for fruit set.

GROWTH ANALYSIS. Reproductive structures were recorded every 3 to 5 d. Data collected consisted of flower buds (visible buds which had not opened), mature flowers (flowers which were open, at anthesis or senescing), or fruit (fruitlets ≥ 2 cm in length).

To measure plant growth, leaf expansion was followed nondestructively by measuring the length and width of a leaf (tagged at 2 cm^2 from the second or third node from the apical growing point at the initiation of experiment) for each plant throughout the experiment in Expt. 1 only. Leaf area was determined using established regressions of length $\times$ width against leaf area, obtained with a leaf area meter (LI-3000; LI-COR, Inc.).

PHYSIOLOGICAL ANALYSIS. Leaf water potential and stomatal conductance were measured to determine whether high temperature and increased VPD changed plant water relations. Net photosynthesis (P_N), chlorophyll fluorescence, and dark respiration were measured to determine if carbon limitation and injury to the photosynthetic apparatus occurred under the high temperature and/or increased VPD. These were recorded from the youngest, fully expanded leaves, one measurement per leaf and four measurements per leaf for chlorophyll fluorescence.

WATER STATUS. Water potential was determined using a Scholander-type pressure bomb (Soil Moisture Equip. Corp., Santa Barbara, Calif.). One leaf per plant of equal size from the third to fourth node from the apical growing point was collected 6 h into the photoperiod (middle of photoperiod) and placed immediately into a plastic bag, which was then sealed. Water potentials were determined on days 5 and 12 (Expt. 1) and days 3 and 11 (Expt. 2).

Stomatal conductance was determined using an AP4 Porometer (Delta-T Devices, Ltd., Cambridge, United Kingdom) in Expt. 1 or a Ciras-1 Portable Photosynthesis System (PP Systems, Haverhill, Mass.) in Expt. 2. Measurements were taken from one leaf per plant between hours 2 (1000 HR) and 5 (1300 HR) of the 12 h photoperiod on day 18 for Expt. 1 and on days 3 and 11 during Expt. 2.

PHOTOSYNTHESIS. Photosynthetic measurements were made in

Expt. 2 only. Rates of CO_2 exchange were measured with a portable infrared gas analyzer (Ciras-1 Portable Photosynthesis System) to determine net photosynthetic rates (P_N). Data were collected from one leaf of each plant between hours 2 and 5 of the 12-h photoperiod on days 3 and 11.

Chlorophyll fluorescence yield was determined with an OS-500 OPTI-Sciences Modulated Fluorometer (PP Systems). Fluorescence yield, also termed the potential yield of photochemistry, is the difference between the level of chlorophyll fluorescence when all Photosystem II (PSII) centers are open (F_m) and the maximum level of chlorophyll fluorescence when all PSII centers are closed (F_o), divided by F_m [i.e., $(F_o - F_m)/F_m$] (Horton and Bowyer, 1990). Fluorometer parameters were set at a modulation of 180, saturation of 230 with a duration of 0.8 s, and a detector gain of 65. Photosynthetically active radiation and temperature sensors were also used. Data were collected from four leaves for each plant during the middle of the photoperiod under full light conditions on days 3 and 11.

PREDAWN DARK RESPIRATION. Dark respiration was determined only in Expt. 2 by measuring rates of CO_2 exchange in predawn conditions, using a portable infrared gas analyzer (LI-6400; LI-COR). Data were collected from one leaf per plant on days 14 and 19. All measurements were taken 1 to 2 hours before dawn.

STATISTICAL ANALYSIS. Floral data for Expts. 1 and 2 were analyzed separately due to age differences of the plants. Without replication of treatments, the error term for temperature and VPD is underestimated (Potvin and Tardif, 1988). Therefore, only treatment effects, which were significant for both experiments were considered significant. Flower bud number, mature flower number, fruit number, and number of total reproductive structures from days 0 to day 15 were analyzed with a repeated measure multivariate analysis of variance (MANOVA). Pillai's Trace was used to determine significant factor effects (von Ende, 1993). Only 4 d were included in the analysis to increase power of the test. For Expt. 1 days 0, 3, 9, and 15 were used, and in Expt. 2 days 0, 5, 9, and 15 were used. Treatments of 33°C at a VPD of 1.1 kPa and 33°C at a VPD of 2.1 kPa were compared in a separate repeated MANOVA, as were treatments 25°C at a VPD of 1.1 kPa and 33°C at a VPD of 1.1 kPa to separate VPD and temperature effects. A Bonferroni adjustment, $\alpha = 0.05/2 = 0.025$, was used to determine significant effects (Scheiner, 1993).

Leaf growth was analyzed with a two-way (cultivar $\times$ treatment) repeated-measure analysis of variance (ANOVA). Leaf water potential, recorded in both experiments, was pooled as replicates and analyzed with a two-way repeated measure ANOVA. Stomatal conductance was log transformed to normalize the distribution prior to analysis. Tukey-Kramer HSD was used for all pairwise comparisons with a $P < 0.05$. Tukey-Kramer HSD comparison uses a higher quantile for calculation of least significant difference (LSD) values, and thus is more conservative than Tukey's studentized range test (Sall and Lehman, 1996). All analyses were completed using statistical analysis software JMP version 3 (SAS Inst., Inc., Cary, N.C.).

Results

FLOWER AND FRUIT PRODUCTION. VPD did not influence the number of flower buds, mature flowers, total reproductive structures, or fruit (Table 1). Temperature, however, significantly affected fruit set (Table 2). Plants grown at 33°C at either VPD failed to set fruit, while plants grown at 25°C began to set fruit within 9 d of the beginning of the experiment and continued

setting fruit up to termination of the experiment (Fig. 1). Flower bud number (Fig. 2), mature flower number (Fig. 3), and total reproductive structures (data not presented) were not affected by temperature, when temperature was considered for the entire experiment (Table 2; between subjects).

To determine if lack of fruit set at the high temperature treatments was due to a delay of fruit production, plants in Expt. 2 were grown for a longer period at the treatment temperatures to allow more time for fruit production. While plants at 25 °C with a VPD at 1.1 kPa in Expt. 2 continued to produce fruit, the number of flower buds decreased greatly from a mean of 102.3/plant for 'Ace' 5 d before fruit set (day 9) to a mean of 23.8/plant 7 d after fruit set had begun (day 22). 'Bell Boy' responded similarly with an increase in fruit set and a great decrease in flower bud number at the control temperature of 25 °C with a VPD at 1.1 kPa. Plants at 33 °C continued producing flower buds throughout the experiment. 'Ace,' grown at 33 °C with a VPD of 1.1 kPa, had a mean

of 92.2 flower buds/plant on day 22, and 'Bell Boy' grown at the same temperature had a mean of 63.7 flower buds on day 22. Both cultivars failed to set fruit at 33 °C even after 25 d of temperature exposure (data not presented).

LEAF AREA. Leaf area of tagged leaves measured throughout Expt. 1 as shown in Fig. 4 did not differ significantly among treatments ($P=0.32$). Leaves continued to expand at the same rate until day 14 for all treatments. Leaves of 'Bell Boy' expanded at

Table 1. MANOVA of flower bud number, mature flower number, and total reproductive structures per plant of 'Ace' and 'Bell Boy' bell pepper for the treatment period with repeated measure of Expts. 1 and 2, comparing treatments of 33 °C at a VPD of 1.1 kPa vs. 33 °C at a VPD of 2.1 kPa. Individual plants are subjects. No fruit were produced at the 33 °C treatments. Values presented are P values with the numerator/denominator df. Bonferroni adjustment maintains that $\alpha = 0.025$ (Scheiner, 1993).

Source	Treatment (temp/VPD)	
	33 °C/1.1 kPa	vs. 33 °C/2.1 kPa
	Expt. 1 [P value (df)]	Expt. 2 [P value (df)]
Flower buds		
Between subjects		
Treatment (Trt)	0.220 (1/16)	0.341 (1/20)
Cultivar (Cv)	0.002 (1/16)	0.030 (1/20)
Trt $\times$ Cv	0.322 (1/16)	0.050 (1/20)
Within subjects		
Time (T)	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.117 (3/14)	0.378 (3/18)
T $\times$ Cv	0.008 (3/14)	<0.001 (3/18)
T $\times$ Trt $\times$ Cv	0.430 (3/14)	0.359 (3/18)
Mature flowers		
Between subjects		
Trt	0.611 (1/16)	0.686 (1/20)
Cv	0.008 (1/16)	0.005 (1/20)
Trt $\times$ Cv	0.048 (1/16)	0.075 (1/20)
Within subjects		
T	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.609 (3/14)	0.530 (3/18)
T $\times$ Cv	0.092 (3/14)	0.002 (3/18)
T $\times$ Trt $\times$ Cv	0.392 (3/14)	0.143 (3/18)
Total reproductive structures		
Between subjects		
Trt	0.276 (1/16)	0.538 (1/20)
Cv	0.001 (1/16)	0.117 (1/20)
Trt $\times$ Cv	0.242 (1/16)	0.060 (1/20)
Within subjects		
T	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.101 (3/14)	0.382 (3/18)
T $\times$ Cv	<0.001 (3/14)	0.076 (3/18)
T $\times$ Trt $\times$ Cv	0.405 (3/14)	0.486 (3/18)

Table 2. MANOVA of flower bud number, mature flower number, total reproductive structures, and fruit number per plant of 'Ace' and 'Bell Boy' bell pepper for the treatment period with repeated measure of Expts. 1 and 2, comparing temperature treatments of 25 °C at a VPD of 1.1 kPa vs. 33 °C at a VPD of 1.1 kPa. Individual plants are subjects. No fruit were produced at the 33 °C treatment. Values shown are P values with the numerator/denominator df. Bonferroni adjustment maintains that $\alpha = 0.025$ (Scheiner, 1993).

Source	Treatment (temp/VPD)	
	33 °C/1.1 kPa	vs. 33 °C/2.1 kPa
	Expt. 1 [P value (df)]	Expt. 2 [P value (df)]
Flower buds		
Between subjects		
Treatment (Trt)	0.127 (1/16)	0.208 (1/20)
Cultivar (Cv)	0.014 (1/16)	0.038 (1/20)
Trt $\times$ Cv	0.470 (1/16)	0.321 (1/20)
Within subjects		
Time (T)	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.493 (3/14)	<0.001 (3/18)
T $\times$ Cv	0.035 (3/14)	0.265 (3/18)
T $\times$ Trt $\times$ Cv	0.681 (3/14)	0.003 (3/18)
Mature flowers		
Between subjects		
Trt	0.168 (1/16)	0.284 (1/20)
Cv	0.255 (1/16)	0.284 (1/20)
Trt $\times$ Cv	0.699 (1/16)	0.038 (1/20)
Within subjects		
T	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.200 (3/14)	<0.001 (3/18)
T $\times$ Cv	0.126 (3/14)	0.240 (3/18)
T $\times$ Trt $\times$ Cv	0.965 (3/14)	0.019 (3/18)
Total reproductive structures		
Between subjects		
Trt	0.115 (1/16)	0.174 (1/20)
Cv	0.009 (1/16)	0.051 (1/20)
Trt $\times$ Cv	0.488 (1/16)	0.674 (1/20)
Within subjects		
T	<0.001 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.491 (3/14)	0.002 (3/18)
T $\times$ Cv	0.014 (3/14)	0.398 (3/18)
T $\times$ Trt $\times$ Cv	0.489 (3/14)	0.223 (3/18)
Fruit number		
Between subjects		
Trt	<0.001 (1/16)	<0.001 (1/20)
Cv	0.444 (1/16)	0.068 (1/20)
Trt $\times$ Cv	0.444 (1/16)	0.035 (1/20)
Within subjects		
T	0.004 (3/14)	<0.001 (3/18)
T $\times$ Trt	0.004 (3/14)	<0.001 (3/18)
T $\times$ Cv	0.004 (3/14)	0.191 (3/18)
T $\times$ Trt $\times$ Cv	0.004 (3/14)	0.238 (3/18)

Fig. 1. Fruit number per plant of 'Ace' and 'Bell Boy' bell peppers grown at 25 °C with a VPD of 1.1 kPa (□), 33 °C with a VPD of 1.1 kPa (●), or 33 °C with a VPD of 2.1 kPa (▲) in two experiments. Fruit number from treatments 33 °C with a VPD of 1.1 kPa and 33 °C with a VPD of 2.1 kPa are identical and, thus, shown with the same symbol. Vertical bars = SE (Expt. 1: n = five plants; Expt. 2: n = six plants).

Fig. 2. Flower bud number per plant of 'Ace' and 'Bell Boy' bell peppers grown at 25 °C with a VPD of 1.1 kPa (□), 33 °C with a VPD of 1.1 kPa (●), or 33 °C with a VPD of 2.1 kPa (▲) in two experiments. Vertical bars = SE (Expt. 1: n = five plants; Expt. 2: n = six plants).

Fig. 3. Mature flower number per plant of 'Ace' and 'Bell Boy' bell peppers grown at 25 °C with a VPD of 1.1 kPa (□), 33 °C with a VPD of 1.1 kPa (●), or 33 °C with a VPD of 2.1 kPa (▲) in two experiments. Vertical bars = SE (Expt. 1: n = five plants; Expt. 2: n = six plants).

a slightly higher rate than 'Ace', (day $\times$ cultivar, $P < 0.001$).

WATER STATUS. Water potentials were significantly more negative at the higher temperature ($P < 0.001$) from a mean of -0.59 MPa at 25 °C to -0.9 MPa at 33 °C (Table 3). Date of data

Fig. 4. Leaf area of 'Ace' (solid symbols, solid lines) and 'Bell Boy' (open symbols, dashed lines) bell pepper plants over the course of 21 d at 25 °C with a VPD of 1.1 kPa (■), 33 °C with a VPD of 1.1 kPa (●), or 33 °C with a VPD of 2.1 kPa (▲). Vertical bars = SE (n = five plants).

collection did not interact with treatment effects ($P = 0.39$), and cultivars responded similarly to the treatments (cultivar $\times$ treatment, $P = 0.44$). Data for the 2 d as well as the two cultivars were pooled for pairwise comparison. Water potentials did not significantly differ between the two VPDs at high temperatures.

For both experiments, stomatal conductance of plants at 33 °C was higher than that at 25 °C ($P < 0.001$), but did not differ consistently between either VPD (Table 3). 'Ace' and 'Bell Boy' responded similarly [$P = 0.68$ (Expt. 1); $P = 0.69$ (Expt. 2)] and cultivar data were pooled for analysis.

PHOTOSYNTHETIC MEASUREMENTS. Net photosynthetic rates were significantly higher at the high temperature ($P < 0.001$)

Table 3. Leaf water potential (Ψ) and nontransformed stomatal conductance of youngest, fully expanded leaves of 'Ace' and 'Bell Boy' bell pepper grown at 25 °C at a VPD of 1.1 kPa, 33 °C at a VPD of 1.1 kPa, or 33 °C at a VPD of 2.1 kPa.

Treatment (temp/VPD)	Water potential (Ψ) (MPa) ^z	Stomatal conductance (H ₂ O, mmol·m ⁻² ·s ⁻¹) ^y	
		Expt. 1	Expt. 2
25 °C/1.1 kPa	-0.59 a ^x	345.1 a	163.3 a
33 °C/1.1 kPa	-0.90 b	571.7 a	691.1 c
33 °C/2.1 kPa	-0.88 b	1184.5 b	420.8 b

^zWater potential values are means of one-way ANOVA of treatments with pooled data from 2 d of data collection of two experiments with 'Ace' and 'Bell Boy' bell pepper.

^yStomatal conductance values are means from one-way ANOVA of treatments with pooled data from 2 d of data collection with the two cultivars, but the two experiments are kept separate due to a significant experiment × treatment interaction.

^xMean separation within columns by Tukey-Kramer HSD ($P < 0.05$) (Sall and Lehman, 1996).

Table 4. Net photosynthesis (P_N) and chlorophyll fluorescence (yield) of youngest, fully expanded leaves of 'Ace' and 'Bell Boy' bell pepper grown at 25 °C at a VPD of 1.1 kPa, 33 °C at a VPD of 1.1 kPa, or 33 °C at a VPD of 2.1 kPa. Values are pooled means from cultivars and 2 d of data collection.

Treatment (temp/VPD)	P_N (CO ₂ , μmol·m ⁻² ·s ⁻¹)	Chlorophyll fluorescence (yield)
25 °C/1.1 kPa	9.7 a ^z	0.64 a
33 °C/1.1 kPa	11.6 b	0.67 b
33 °C/2.1 kPa	13.2 c	0.67 b

^zMean separation within columns by Tukey-Kramer HSD ($P < 0.05$) (Sall and Lehman, 1996).

Table 5. Predawn dark respiration responses of youngest, fully expanded leaves of 'Ace' and 'Bell Boy' bell peppers grown at 25 °C with a VPD of 1.1 kPa, 33 °C with a VPD of 1.1 kPa, or 33 °C with a VPD of 2.1 kPa. Values are means of six plants.

Cultivar	Treatment (temp/VPD)	Respiration rate (CO ₂ , μmol·m ⁻² ·s ⁻¹)	
		14 DAT ^z	19 DAT
Ace	25 °C /1.1 kPa	1.7 a ^y	1.8 a
	33 °C /1.1 kPa	1.2 b	1.8 a
	33 °C / 2.1 kPa	1.3 b	1.6 a
Bell Boy	25 °C /1.1 kPa	2.0 a	1.9 a
	33 °C /1.1 kPa	1.1 b	1.3 b
	33 °C / 2.1 kPa	1.3 b	1.2 b

^zDAT = days after treatment began.

^yMean separation within columns for a cultivar by Tukey-Kramer HSD ($P < 0.05$) (Sall and Lehman, 1996).

(Table 4). Cultivars responded similarly ($P = 0.11$), and P_N was not affected by time ($P = 0.59$). P_N increased from 25 °C by 18% at 33 °C with a VPD of 1.1 kPa and by 35% at 33 °C with a VPD of 2.1 kPa.

CHLOROPHYLL FLUORESCENCE MEASUREMENTS. Chlorophyll fluorescence yield increased by 5% at the higher temperatures ($P < 0.001$) (Table 4). Yields did not differ among VPD treatments. Cultivars responded similarly to treatments ($P = 0.28$), and fluorescence was not affected by time ($P = 0.06$).

DARK RESPIRATION MEASUREMENTS. Predawn leaf dark respiration rates decreased from 8% to 38% at 33 °C ($P < 0.001$) (Table 5). However, respiration rates did not differ between VPD treatments. Respiration rates responded differently to the treatment between the 2 d of data collection (treatment × day, $P < 0.001$). Therefore, results are presented separately for the 2 d and two cultivars.

Discussion

No effect of increased VPD on flower production, fruit set, or leaf expansion of 'Ace' and 'Bell Boy' bell pepper was observed at 33 °C. High temperature influenced leaf water potential, stomatal conductance, P_N , chlorophyll fluorescence, and predawn leaf respiration, and it completely inhibited fruit set, independently of VPD.

Although flower bud number was similar at 33 °C (Fig. 2), and many buds reached the mature flower stage (Fig. 3), fruit set was inhibited completely (Fig. 1). While flowers developing at high temperature generally opened fully, the flowers did not shed pollen. Failure of peppers to set fruit at 33 °C was due to abscission of mature flowers, possibly after a malfunction in flower development, such as incomplete microspore meiosis, resulting in nonfertilized flowers.

Plant water status was affected more by high temperature than VPD. Decreased water potentials suggest that plants were under some water stress at the high temperature (Table 3). However, stomatal conductances increased (Table 3), suggesting water was not limiting. Increases in stomatal conductances were most likely related to increases in P_N at the high temperature (Table 4).

Dark respiration increases exponentially with increased temperatures (Larcher, 1995). However, our observations of an increase in P_N and the decrease in predawn dark respiration at high temperatures (Table 5) are contrary. One explanation for the lower predawn dark respiration rates in the elevated temperature treatments may be that carbohydrate reserves were depleted by the end of the dark period. Respiration rates are dependent in part on carbohydrate availability; subsequently our measurements of predawn dark respiration suggest that carbohydrate availability may have been limiting by the end of the dark period. Therefore, the increase in P_N may have been in response to increased demand for carbon assimilation in plants growing at high temperature. The increase in fluorescence yield suggests a change in the efficiency of photosynthesis at the high temperature. Direct measurements of diurnal carbohydrate levels and further examination of chlorophyll fluorescence are needed to test these hypotheses.

Plant organ respiration, assimilate levels, and partitioning have been associated with stress induced flower bud and flower abscission. Turner and Wien (1994) reported that dark respiration rates of flower buds decreased further under stress conditions in pepper cultivars susceptible to stress induced flower bud and flower abscission than respiration rates of stress resistant cultivars. Respiration rates of expanded leaves were higher under both control and stress conditions for stress susceptible cultivars than for stress resistant cultivars. Aloni et al. (1991) did not observe an effect of high day or night temperatures on photosynthetic rates of source leaves of pepper but observed that partitioning of [¹⁴C] sucrose to flower buds and flowers was reduced, while importation to young leaves increased. The presence of developing fruit further decreased sucrose importation to flowers. Our observation of increased P_N of expanded leaves at 33 °C and the decrease

of predawn dark respiration of leaves at 33 °C may support the hypothesis of Aloni et al. (1991) that leaves at high temperature maintain their assimilation rate at the expense of developing reproductive structures.

Data herein indicate that in bell pepper high temperature inhibits fruit set independently from VPD at the levels studied and at constant high temperature of 33 °C. Vapor pressure deficits may have an effect on pepper productivity at lower temperatures, but the stress caused by the high temperature treatment masked any effect of the increased VPD. Inhibition of fruit set at high temperature is due primarily to abscission of mature flowers. We have observed (unpublished data) that high temperature directly affects pollen development. Although, carbon assimilation may play an important role in flower bud and flower abscission, we hypothesize that inhibition of fruit set at high temperature is most likely a direct effect of high temperature on flower development and perhaps fertilization.

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