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High Temperature Effects on Growth and Floral Development of Chrysanthemum

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Abstract. **Pinched plants of *Chrysanthemum morifolium* Ramat. 'Orange Bowl' and 'Surf' grown in a chamber maintained at 22° day/18°C night were transferred to 30° day/26° night at the beginning of week 1, 3, 5, or 7 after start of photoinduction period (15-hr nyctoperiod). Plants remained at high temperatures for 2, 4, 6, 8, or 10 weeks and then were returned to the 22°/18° chamber. Exposure to high temperatures during the first 4 weeks of short days increased the number of nodes, leaf area, stem length, and dry weight of leaves and stems. Rate of floret initiation and perianth differentiation decreased when exposed to high temperatures during the first 4 weeks of short days in 'Orange Bowl' but not in 'Surf'. 'Orange Bowl' exposed to high temperatures for 10 weeks from the start of short days flowered 12 days later than plants grown at lower temperatures and formed bracteate buds. Flowering of 'Orange Bowl' grown at 22°/18° during the first 4 weeks of short days, then transferred to high temperatures, was not substantially delayed and flowers developed normally. Flowering was delayed 3 days when 'Surf' was exposed to high temperatures for 8 weeks from the start of short days. Exposure to high temperatures did not cause bracteate bud formation in 'Surf'. With both cultivars, increasing the duration of high temperature exposure increased the time to flowering.**

High temperatures during production can delay flowering and induce abnormal inflorescence development in chrysanthemums (9). This phenomenon is commonly referred to as "heat delay" and has been shown to be induced by temperatures in the range of 27° to 32°C (1–3, 9). The severity of heat delay depends to a large extent on the tolerance or sensitivity of various chrysanthemum cultivars to high temperatures.

Discrepancy exists in the literature on the effects of high temperatures on chrysanthemum growth and floral development. Based on dates of visible bud and flowering, Post and Lacey (9) reported that high temperatures did not affect bud initiation (time from start of short days to visible bud), but delayed bud development (time from visible bud to flower). Moreover, they observed bract formation and a large number of developed florets on the capitulum in response to high temperatures. Cathey (1) found that high temperatures enhanced bud initiation but delayed bud development. However, Cathey and Borthwick (2) later reported that floral initiation was slightly delayed by increased temperatures. Cockshull (3) has observed an increase in leaf production and a delay in capitulum initiation in response to high temperatures; however, these studies were conducted under continuous lighting, which precluded floret initiation. The objectives of this study were to determine the most sensitive stage(s) of floral development and to investigate the duration effect of high temperatures by comparing a sensitive to a tolerant cultivar as determined by commercial producers.

Materials and Methods

Rooted chrysanthemum cuttings of 'Orange Bowl' (10-week response, high temperature sensitive) and 'Surf' (9-week response, high temperature tolerant) were planted in a soilless medium (Metro Mix 300, W.R. Grace, Cambridge, Mass.) in 225-ml styrofoam cups. Plants were placed in a chamber (8.9 m^2) in the Southeastern Plant Environment Laboratory (phytotron) at North Carolina State Univ., Raleigh, at a plant density of 86.5 plants/m^2. Cool-white fluorescent and incandescent lamps provided a photosynthetic photon flux (PPF) of ≈640–650 $\mu mol \cdot s^{-1} \cdot m^{-2}$ at wavelengths of 400–700 nm for 9 hr/day. Plants were exposed to a 3-hr night interruption (2300–0200 HR) of 11–12 $\mu mol \cdot s^{-1} \cdot m^{-2}$ at wavelengths of 400–700 nm from incandescent filament lamps (5). Two weeks after planting, short-day photoinductive periods were initiated by providing a 15-hr nyctoperiod from 1700 to 0800 HR. Ambient temperatures of 22° ± 0.25°C day and 18° ± 0.25° night were

Table 1. Duration and timing of high temperature treatments on 'Orange Bowl' and 'Surf' chrysanthemums.

Treatment[z]	No. short days after start of short days					
	1	14	28	42	56	70
1-2	XXXXXXX[y]					
1-4	XXXXXXXXXXXXX					
1-6	XXXXXXXXXXXXXXXXX					
1-8	XXXXXXXXXXXXXXXXXXXXXX					
1-10[x]	XXXXXXXXXXXXXXXXXXXXXXXXXXXXX					
3-2		XXXXXXX				
3-4		XXXXXXXXXXXX				
3-6		XXXXXXXXXXXXXXXXX				
3-8[x]		XXXXXXXXXXXXXXXXXXXXXXXX				
5-2			XXXXXXX			
5-4			XXXXXXXXXXXX			
5-6[x]			XXXXXXXXXXXXXXXXX			
7-2				XXXXXXX		
7-4[x]				XXXXXXXXXXXX		

[z]First number refers to week at which high temperature treatments were initiated and second number refers to length in weeks of high temperature exposure.
[y]Duration in high temperature chamber.
[x]'Orange Bowl' only, as 'Surf' is classified as a 9-week response cultivar and 'Orange Bowl' is classified as a 10-week response cultivar.

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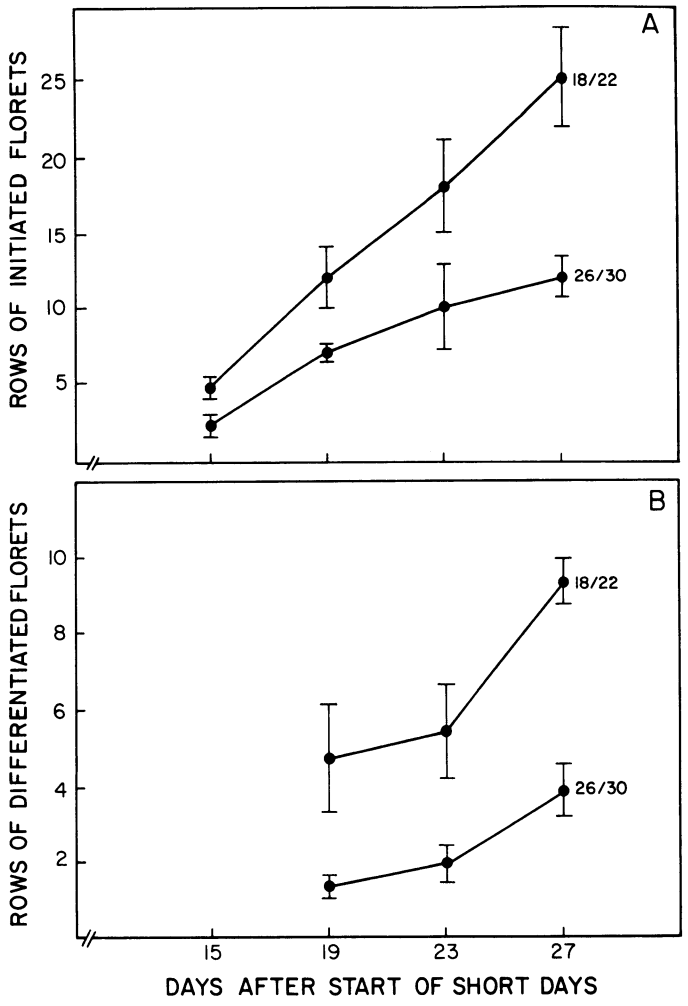

Fig. 1. Effect of high (30°/26°C) and low (22°/18°) temperatures during short days on number of rows of florets initiated (**A**) and number of rows of florets with differentiated perianth (**B**) for 'Orange Bowl' chrysanthemums. Vertical bars represent SE.

Table 2. Effect of high (30°/26°C) and low (22°/18°) temperature treatments during short days on leaf, stem, and inflorescence final dry weights of the lateral shoot for 'Orange Bowl' and 'Surf' chrysanthemums.

Treatment[z]	Leaf dry wt (g)	Stem dry wt (g)	Inflorescence dry wt (g)	Total dry wt (g)
		Orange Bowl		
1-2[z]	1.17	1.05	1.60	3.81
1-4	1.74	1.51	1.38	4.63
1-6	1.89	1.61	1.26	4.76
1-8	1.58	1.49	1.13	4.20
3-2	1.16	0.97	1.07	3.19
3-4	1.29	1.07	1.12	3.47
3-6	1.16	1.06	1.20	3.43
5-2	0.88	0.75	1.30	2.93
5-4	0.93	0.73	1.07	2.73
7-2	0.82	0.69	1.48	3.00
Control	0.76	0.66	1.37	2.78
Waller–Duncan at 5% level	0.34	0.23	0.43	0.48
		Surf		
1-2	1.06	0.65	1.44	3.35
1-4	1.04	0.64	1.41	3.40
1-6	1.17	0.71	1.35	3.23
1-8	1.22	0.69	1.22	3.18
3-2	0.76	0.46	1.28	2.50
3-4	0.78	0.41	1.02	2.21
3-6	0.79	0.44	0.96	2.19
5-2	0.62	0.37	1.04	2.03
5-4	0.70	0.31	0.97	1.88
7-2	0.74	0.33	0.99	2.06
Control	0.65	0.36	1.19	2.22
Waller–Duncan at 5% level	0.18	0.12	0.28	0.44

[z]First number refers to week at which high temperature treatments were initiated and second number refers to length in weeks of high temperature exposure.

maintained in one chamber that served as the low temperature or control chamber, and another chamber maintained at 30° ± 0.25° day and 26° ± 0.25° night was used for the high temperature treatments. Temperatures were monitored with a type T (copper–constantan) thermocouple in a shielded aspirated housing (5). Temperatures selected for this study were based upon a previous study conducted in the phytotron that involved exposing plants of both cultivars at the start of short days to day/night temperatures of 18°/14°, 22°/18°, 26°/22°, and 30°/26° until stage of flower maturation.

Plants were irrigated daily with 300 ml/plant of a modified Hoagland's solution (7.6 mM N) and 300 ml deionized water (5). Plants were pinched 1 week after planting and pruned to one lateral shoot when shoots were 3 cm in length. Leaves below the pinch were pruned to four per plant for 'Orange Bowl' and five per plant for 'Surf'. Plants were divided randomly into 15 subgroups (treatments) for 'Orange Bowl' and 11 treatments for 'Surf'. Treatments consisted of exposing plants to high temperatures at the start of short days (week 1), and 2 (week 3), 4 (week 5), or 6 weeks (week 7) after the start of short days for 2, 4, 6, 8, or 10 weeks (Table 1). Each cultivar was in separate experiments that were incomplete factorials in a randomized complete block design with three replicates over time using six plants per replicate/treatment/cultivar.

Leaf area, stem length, and leaf, stem, and inflorescence dry weights of the lateral shoot were determined each week for two plants per treatment/replicate. Number of short days to first flower color (showing-color) and to the time that the outer rows of florets were perpendicular to the pedicel (open-flower) was determined. Inflorescences were evaluated for abnormal development, floret color, and number of florets at open flower.

Flower development was observed on plants exposed to either low or high temperature treatments from the start of short days. At 3, 7, 11, 15, 19, 23, and 27 days after the start of short days, six meristems from plants at low or high temperatures were fixed in formalin–glacial acetic acid–95% ethanol (FAA) and observed with a dissecting light microscope. Meristem diameter, appearance of involucral bract primordia, number of rows of initiated florets, and number of rows of florets with differentiated perianth were determined. For electron microscopy, selected meristems were dehydrated in a graded alcohol series, critical-point-dried, coated with Au/Pd in a Technics Hummer V sputter coater, and viewed with a Hitachi S-450 scanning electron microscope.

An additional study was conducted simultaneously at the Ornamental Horticulture Dept. Greenhouses of the Univ. of Florida, Gainesville. Cultivars and treatments were identical to the

Table 3. Effect of high (30°/26°C) and low (22°/18°) temperatures during short days on selected growth parameters of 'Orange Bowl' and 'Surf' chrysanthemums. Plants exposed to high or low temperatures from start of short days until week 8.

Cultivar	Treatment	No. leaves ± SE	Leaf area/ leaf (cm) ± SE	Internode length (cm^2) ± SE	Total leaf area (cm^2) ± SE	Stem length (cm) ± SE
Orange Bowl	30/26[z]	20 ± 1	12 ± 0.5	1.1 ± 0.2	245 ± 14	22.6 ± 1.0
	22/18	16 ± 1	9 ± 0.5	1.0 ± 0.1	138 ± 5	15.4 ± 0.4
Surf	30/26	19 ± 1	11 ± 0.5	0.6 ± 0.1	214 ± 9	12.0 ± 0.5
	22/18	16 ± 1	9 ± 0.5	0.7 ± 0.1	147 ± 6	11.4 ± 0.6

[z]Day/night temperatures (°C).

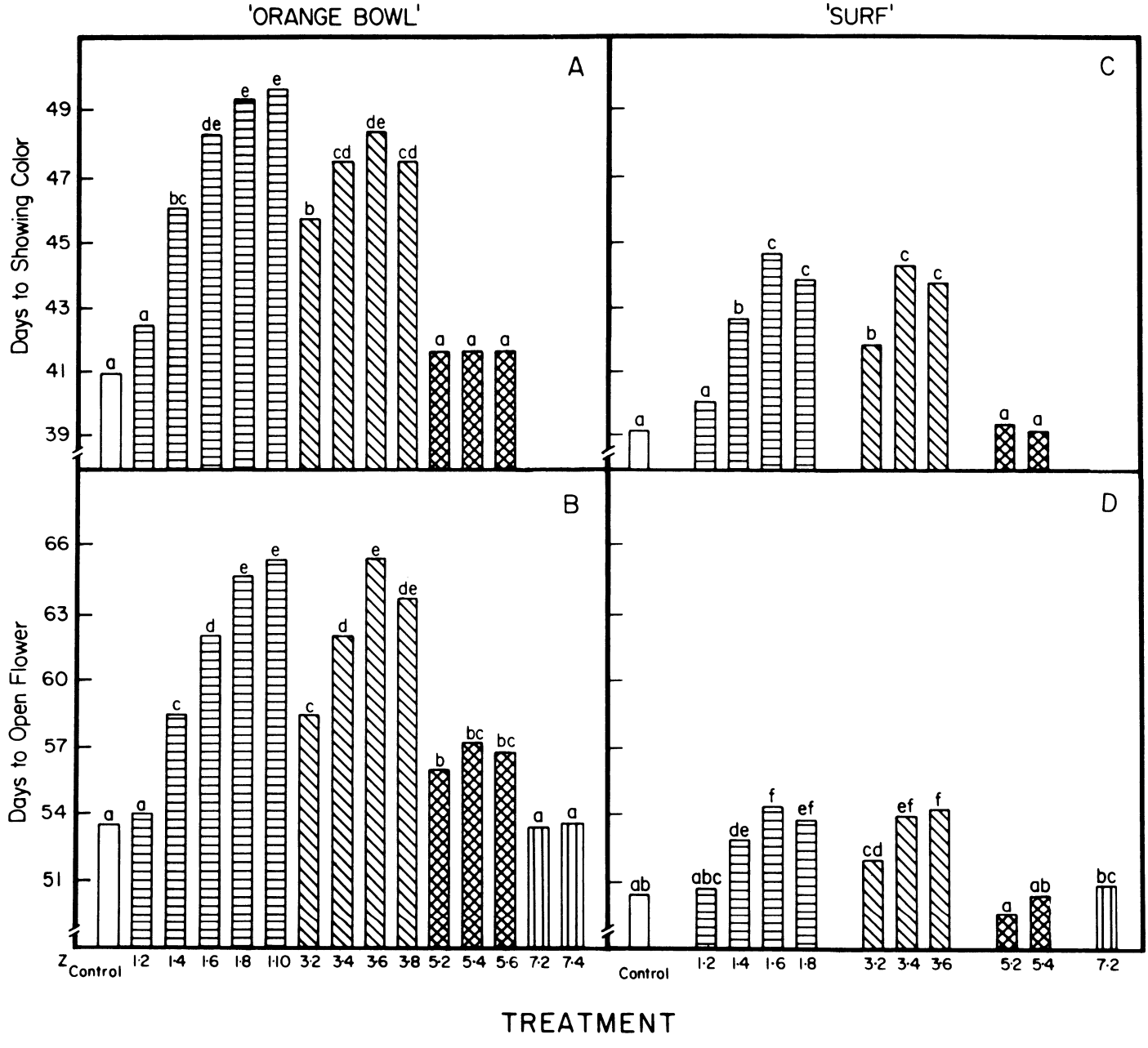

Fig. 2. Effect of high (30°/26°C) and low (22°/18°) temperature treatments during short days on time to stage of showing-color and open-flower for 'Orange Bowl' and 'Surf' chrysanthemums. Bars with different letters are significantly different at the 5% level according to Waller–Duncan multiple range test. [z]First number refers to week at which high temperature treatments were initiated and second number refers to length in weeks of high temperature exposure.

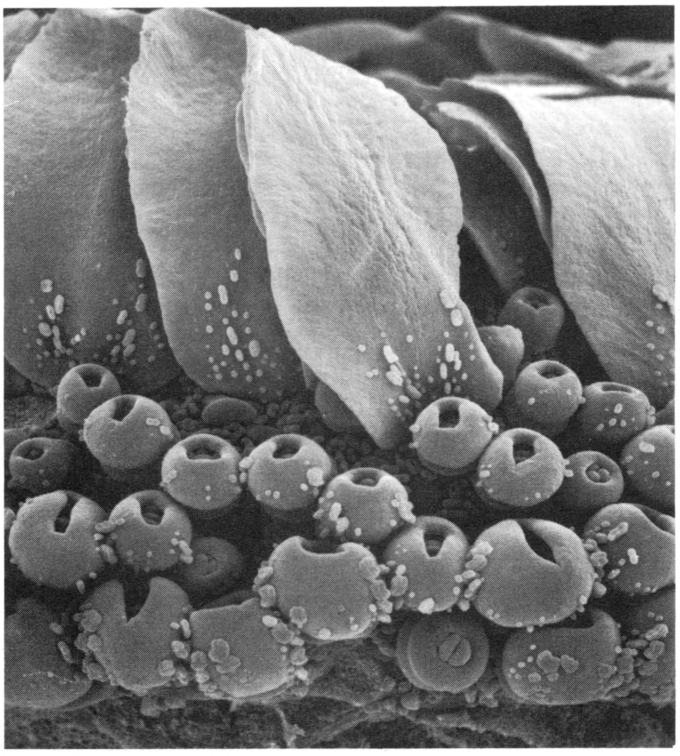

Fig. 3. Meristem of 'Orange Bowl' chrysanthemum exposed to high (30°/26°C) temperatures for first four weeks of short days. Outer rows of florets are disorganized and anomalous bracts are evident.

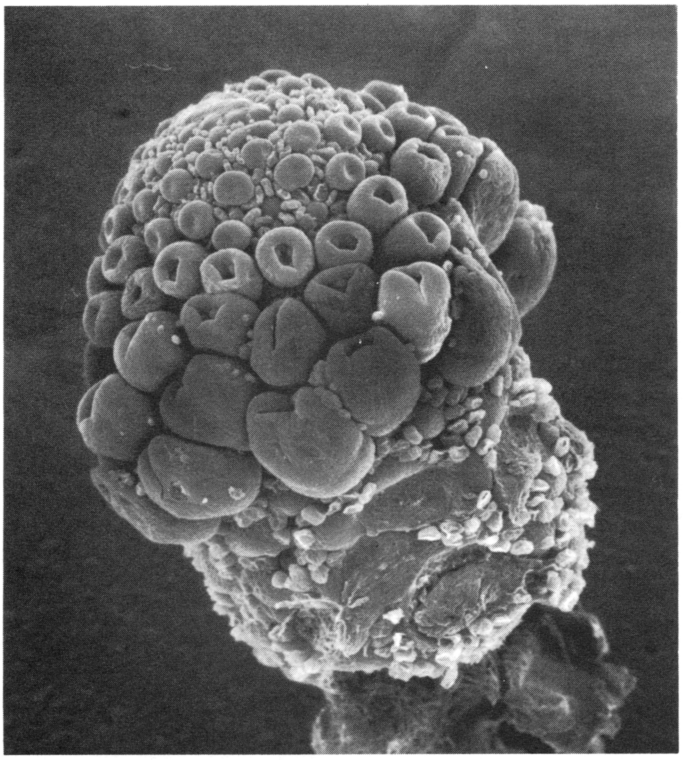

Fig. 4. Secondary inflorescence formed on a receptacle of 'Orange Bowl' chrysanthemum exposed to high temperatures (30°/26°C) from start of short days until week 10.

experiment previously described. As the results obtained from this study were similar to those of the phytotron, only the phytotron results will be reported.

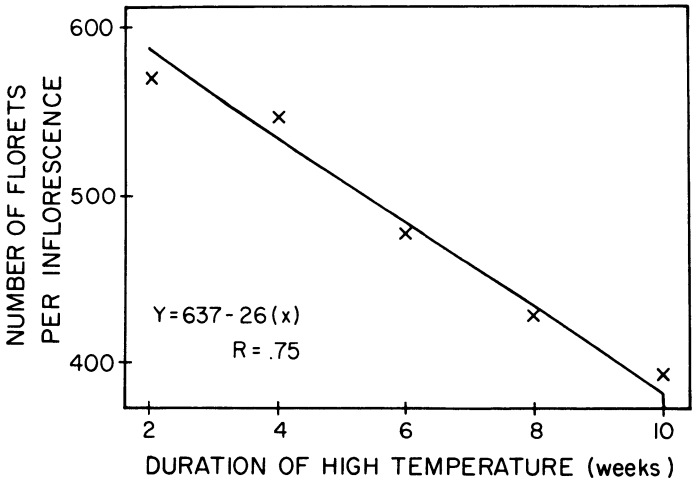

Fig. 5. Effect of increasing duration of high (30°/26°C) temperatures during short days on mean number of florets per inflorescence for 'Orange Bowl'. Plants were exposed to high temperatures at start of short days for 2, 4, 6, 8, or 10 weeks. Points represent treatment means with 6 inflorescences per treatment.

Results and Discussion

Effect of high temperature on growth. High temperature treatments initiated at the start of short days or at week 3 (treatments 1-2, 1-4, 1-6, 1-8, 3-2, 3-4, and 3-6) increased leaf and stem dry weights in 'Orange Bowl' compared to the control (Table 2). High temperature treatments initiated at week 5 or 7 (treatments 5-2, 5-4, and 7-2) did not increase lateral shoot dry weights substantially compared to the control. At open flower, stem and leaf dry weights accounted for 51% and 73% of the total lateral shoot dry weight for 'Orange Bowl' plants exposed to low and high temperatures for the entire short-day period (control and treatment 1-8), respectively.

Stem and leaf dry weights of 'Surf' plants were greater when exposed to high temperatures at the start of short days (treatments 1-2, 1-4, 1-6, and 1-8) compared to plants exposed to high temperatures after week 3 or remaining at low temperature until open flower (Table 2). Stem and leaf dry weights of 'Surf' plants exposed to low or high temperatures (control or treatment 1-8) accounted for 46% and 62% of total lateral shoot dry weight, respectively. The increase in shoot dry weight in both cultivars was attributable to an increase in leaf and stem growth, as temperature treatments had little effect on final inflorescence dry weight (Table 2).

High temperatures caused an increase in total leaf area and stem length (Table 3). Increased leaf area was a result of an increase in leaf size and number. Increase in stem length was a function of increased node number as the mean internode length was not affected.

Effect of high temperature on floret initiation and differentiation. High temperatures delayed meristem transition to the reproductive state and rates of floret initiation and differentiation in 'Orange Bowl'. Involucral bract primordia, indicative of transition to the reproductive state, were evident at 7 and 11 days after the start of short days for 'Orange Bowl' plants exposed to low and high temperatures, respectively. Statistical differences in meristem diameter between the temperature treatments were not evident for 'Orange Bowl' plants. High temperatures decreased developmental rate from 1.7 rows of florets (control) initiated per day to 0.8 rows/day (Fig. 1A). Exposure to high temperatures decreased the rate of perianth differentiation from

0.6 rows of florets per day (control) to 0.3 rows/day (Fig. 1B). Transition to the reproductive state and rates of floret initiation and differentiation in 'Surf' were not significantly affected by high temperature treatments.

Effect of high temperature on flowering. High temperature treatments beginning with week 1 or 3 of short days (treatments 1-4, 1-6, 1-8, 1-10, 3-2, 3-4, 3-6, and 3-8) increased the number of days to showing-color and to open-flower for plants of 'Orange Bowl' and 'Surf' (Fig. 2). Increasing the duration of the high temperature exposure increased the number of days to showing-color and open-flower. The most sensitive 2-week period was weeks 3 and 4 of short days. For treatments that provided only two weeks of high temperature exposure (treatments 1-2, 3-2, 5-2, and 7-2), treatment 3-2 caused the most delay. The amount of delay caused by treatment 1-4 was equaled by treatment 3-2, which overlapped the last two weeks of the 1-4 treatment. Flowering was not delayed in plants of either cultivar exposed to high temperatures during the first two weeks of short days (treatment 1-2). Exposure to high temperatures, starting with week 5 of short days (treatments 5-2, 5-4, 5-6), delayed flower opening in plants of 'Orange Bowl', but not of 'Surf'.

Cultivars differed in degree of developmental delay. 'Orange Bowl' plants exposed to high temperatures from the start of short days until open-flower (treatment 1-10) flowered 12 days later than plants at low temperatures during the same period (Fig. 2B). In comparison, 'Surf' plants exposed to high temperatures from start of short days to open-flower (treatment 1-8) flowered 3 days later than plants at low temperatures during the same period (Fig. 2D).

Treatments that included high temperatures during the third and fourth weeks of short days (treatments 1-4, 1-6, 1-8, 1-10, 3-2, 3-4, 3-6, and 3-8) resulted in bract formation interior to the outer rows of florets of 'Orange Bowl' plants (Fig. 3). 'Orange Bowl' plants exposed to high temperatures at the start of or at the third week of short days until flower (treatments 1-10 and 3-8) formed bracteate buds; i.e., only the outer rows of florets developed and the receptacle was covered with noninvolucral bracts. Secondary inflorescences arising from individual florets were also observed (Fig. 4). Increasing duration of exposure to high temperature increased the degree of teratological modifications. Concomitant with the increase in number of bracts was a decrease in the number of florets per inflorescence. Number of florets per inflorescence decreased with increasing duration of high temperature exposure (Fig. 5). No teratological modifications were noted on 'Surf' plants.

Floret color of 'Orange Bowl' plants was affected by exposure to high temperatures after the seventh week of short days. Florets of plants exposed to high temperature at this time (treatments 1-8, 1-10, 3-6, 3-8, 5-4, 5-6, 7-2, and 7-4) were yellow (Royal Horticultural Society color group 12A) rather than the normal orange-yellow (Royal Horticultural Society color group 14B) typical of the cultivar. Increasing duration had an observable effect.

Our studies indicate that high temperatures during the short-day photoinductive period enhanced vegetative growth and retarded floral development. The high temperature-sensitive cultivar was delayed in rate of floret initiation and differentiation by high production temperatures. Moreover, the supraoptimal temperatures used in this study perturbed floral development as evident in the induction of anomalous bracts on the receptacle and the decrease in the number of developed florets. The diminution in floret color may be attributable to either a decrease in synthesis or an increase in degradation of anthocyanins or carotenoids. The difference in tolerance or sensitivity to high temperatures is relative, since 'Surf' was significantly delayed by high temperature treatments, but not as severely as 'Orange Bowl', and abnormal development did not occur in 'Surf'.

Inhibition of floret initiation and/or development is a manifestation of indirect heat injury as defined by Levitt (8). Specific chemical and/or physical reactions may be inhibited or enhanced at supraoptimal temperatures. Exposure to high temperatures (38°C) have been shown to alter the endogenous auxin and gibberellin levels in tomato flowers and result in poor or inhibited fruit set (7). These high temperature effects may be due to altered or inhibited assimilate transport (4). Kinet (6) has suggested that the inhibition of inflorescence development may be the result of competition for available assimilates between reproductive and vegetative growth. The redistribution of assimilates may be affected by various plant growth substances. It is thus hypothesized that the physical permutations of normal inflorescence development and the enhancement of vegetative growth in chrysanthemum may be attributed to pertubations in the normal balances of endogenous plant growth substances as a result of high temperatures.

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