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Development Rate during Four Phases of Chrysanthemum Growth as Determined by Preceding and Prevailing Temperatures

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Abstract. **Time required to complete four developmental phases in chrysanthemum 'Bright Golden Anne' (*Dendranthema grandiflora* Tzvelev.) was determined under greenhouse conditions at constant temperature setpoints of 10, 15, 20, 25, 30, or 20 day/16C night. The four developmental phases were: I—start of short days to visible bud (2-mm-diameter terminal flower bud), II—visible bud to disbud (10-mm-diameter terminal flower bud), III—disbud to color (flower bud showing first color), and IV—color to flower. Plants either remained at the same temperature during all four phases or were moved to one other constant temperature regime after phase I, II, or III. Fastest development during all phases occurred at 20 day/16C night or constant 20C. Temperature of previous phases had less of an effect on future phases as plant development progressed. Low temperature (10C) during phase I delayed development in phase II, and high temperature (30C) during phase I and II delayed development during phase III. The length of each phase could be predicted based on the temperature preceding and during the phase. Optimum temperatures for fastest development during the four phases were calculated as 21.3, 20.3, 23.1, and 19.1C, respectively.**

Optimum temperature for growth and development of many plant species varies as the plant develops (2, 3, 8, 18, 21, 26). Sachs (21) studied temperature effects during germination, seedling growth, vegetative growth, flowering, and fruiting of several species, including *Zea mays*, *Curcubita pepo*, and *Pisum sativum*. Each phase exhibited a minimum, optimum, and maximum temperature for growth. Temperatures above or below the optimum temperature delayed growth. The shortest time to complete development could be determined when the optimum temperature requirements were known for each phase.

Changes in optimum temperature requirements during development have been observed in chrysanthemum. Temperatures above 16C favored rapid development before the visible bud stage, but temperatures below 16C hastened development after the visible bud stage in the cultivars Revelation and Satellite (3). At 10C the number of leaves formed before flower initiation increased, but delayed development compared to 16C in the cultivars Balcombe Perfection, Crensa, and Mayford Crimson (25). Low temperatures (5 or 10C) after buds were visible caused only small delays in time to flower (25). Reproductive development was delayed in 'Bright Golden Anne' above 20C after disbud, although the rate of dry weight gain increased (14).

The temperature during one phase of development can influence response to the environment during subsequent phases. 'Revelation' chrysanthemum grown at 21C under long days (LD), then shifted to 16C at the start of short days (SD), flowered 7 days later than plants grown at 16C during both LD and SD (3). Exposure to 5 or 10C compared to 16C during the LD period delayed subsequent development of 'Balcombe Perfection', 'Crensa', and 'Mayford Crimson' chrysanthemum under SD at 16C. The 10C LD treatment also increased the number of leaves on flowering shoots (25). Chrysanthemum cuttings of 'Revelation' taken from stock plants grown at 27, 21, or 16C flowered after 107, 101, and 110 days, respectively, when held at 10C from planting to flowering (3). 'Annette Hegg Lady' poinsettia cuttings taken from stock plants maintained at 12 or 15C initiated flowers faster when allowed to develop at 21C than cuttings taken from stock plants held above 15C (11).

Knowledge of the relationships between temperature and plant growth is essential for appropriate temperature adjustments in greenhouse production. This study was initiated to determine optimum temperatures for maximum chrysanthemum growth rates during four developmental phases and to determine the importance of temperature during early developmental phases on the subsequent growth rate.

Materials and Methods

One thousand rooted cuttings of 'Bright Golden Anne' chrysanthemum (1) were planted individually in 10-cm pots (450 cm^3) on 31 Oct. 1985 and placed in a greenhouse at 20 ± 2C (24-hr average temperature). The natural daylength was extended to 16 hr/day with incandescent lamps. After 7 days (on 7 Nov.), 810 plants were selected for uniformity, pinched to six leaves, and transferred to greenhouse sections with heating set points of 20C day temperature (DT) and 16C night temperature (NT) or constant 10, 15, 20, 25, or 30C (cooling setpoints were 2 degrees higher than the heating setpoints). A short photoperiod (minimum 10-hr length) was also initiated, and maintained through flowering by pulling an opaque curtain at 1800 HR and retracting it at 0800 HR. The actual photoperiod was <10 hr (minimum 9 hr 2 min) from 10 Nov. to 1 Feb. due to the time of sunrise and sunset at lat.42°N. Plants were randomized in each greenhouse section at a spacing of 44 plants/m^2.

Plants were grown in a commercial peat-lite medium (Michigan Peat Co.) and watered as required to avoid stress. Nutrition consisted of 14.3 mM N and 5.1 mM K at every watering using ammonium nitrate and potassium nitrate. Daminozide was applied at 15.6 mM as a foliar spray 7 and 14 days after the start of SD (7).

Greenhouse temperatures were controlled using a greenhouse climate control computer (Oglevee Computer Systems, Connelsville, Pa.) and monitored by a datalogger (Digistrip III, Kaye Instruments Co., New Bedford, Conn.) using aspirated

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iron/constantan thermocouples. All plants were within 2 m of the temperature sensors during the experiment. Photosynthetic photon flux (PPF) was monitored with a LI-190SB quantum sensor (LI-COR). Actual temperatures and PPF levels were measured every 10 sec. and averaged to provide hourly mean values. Average temperatures and PPF levels incurred during the experiment in the different greenhouse sections were calculated from the hourly means and used in the analyses (Table 1). Difference in PPF within a developmental phase and among temperatures were caused by the length of time plants were within a phase under the different temperatures and changes in seasonal PPF.

The four defined developmental phases were: phase I—from start of SD to visible bud (VB, 2-mm-diameter terminal flower bud), phase II—from VB to disbud (DB, 10-mm-diameter terminal flower bud), phase III—from DB to color (first appearance of color on flower bud), and phase IV—from color to flower (outermost petals had reflexed to a horizontal position). A plant was considered at a specific developmental stage when at least one shoot on the plant had developed the desired characteristic.

Ten plants, randomly preselected, from each greenhouse section were moved to each of the other sections at VB, DB, and color. The plants remained in the second greenhouse section (temperature) until flowering. Plants were moved from, but not to, the 20/16C section. The number of days from start of SD was recorded as each developmental stage was reached.

Functional relationships were developed for prediction of time required to complete a phase of development with the temperatures before and during the phase as the independent variables. An optimum temperature for development was expected, with delayed development as the temperature deviated from the optimum (3, 21). This type of growth response can be described in multiple linear regression analysis by second-order terms. Therefore, forward stepwise regression analysis (19) was performed using linear and second-order terms with significance levels for addition and deletion at 0.05. In an effort to improve the developed equations, higher-order terms were also considered. These were rejected, as their addition only slightly improved the coefficients of determination while decreasing the F values of the equations. Furthermore, they did not improve the prediction in any of the developmental phases. Surface graphs were created using the selected functions and the Surfer graphing program (12).

The experiment was repeated with SD starting on 11 Mar. 1986. Results and trends were similar in the two experiments. Greenhouse temperatures were better-controlled during the first experiment and, therefore, only those results are presented.

Results and Discussion

Time to flower followed a parabolic temperature response curve, with most rapid development occurring in plants grown in the 20/16C and 20C treatments (Table 2). Flowering in plants grown at the lowest (10C) and the highest (30C) temperatures, was delayed ≈60 days (Table 2). Temperature response curves for 21 chrysanthemum cultivars were also found to be parabolic, with an optimum temperature range for fastest development (9). Flowering in the 21 cultivars occurred fastest at temperatures between 17C and 21C. Our results agree with these findings, as the fastest flowering occurred at 20/16C (17.7C average temperature) and 20C (Table 2).

The time required by plants to complete a developmental phase depended on the phase and temperature during that phase. Time required to complete phase I averaged 40%, phase II 35%, phase III 10%, and phase IV 15% of total time to flower, based on the data in Table 2.

Plant response to nonoptimal high and low temperatures changed as plants developed from phase I to phase IV. While plants took longer to complete phase I at 10 than 30C, the reverse was true during phase IV; i.e., development was faster at 10 than 30C. In phase II and III, the rate of development was similar at 10 and 30C. Earlier experiments indicated that low temperature (<20C) slowed development in phase I, while not prolonging subsequent development (14).

Table 1. Temperature and photosynthetic photon flux during the four experimental phases of chrysanthemum development defined in this study.

Setpoint temp (°C)	Phase[z] I	II	III	IV	I–IV
	Actual average temp (°C)[y]				
10	11.0 ± 0.1	11.4 ± 0.2	11.4 ± 0.2	10.5 ± 0.5	11.1 ± 0.1
15	14.6 ± 0.2	15.9 ± 0.1	17.1 ± 0.3	16.8 ± 0.2	15.6 ± 0.2
20/16[x]	18.5 ± 0.1	18.7 ± 0.1	18.9 ± 0.5	19.6 ± 0.4	18.8 ± 0.1
20	20.1 ± 0.1	20.4 ± 0.2	19.9 ± 0.6	21.0 ± 0.2	20.3 ± 0.1
25	26.3 ± 0.3	27.7 ± 0.3	25.9 ± 0.1	25.3 ± 0.1	26.5 ± 0.2
30	31.2 ± 0.2	30.7 ± 0.3	32.7 ± 0.2	31.1 ± 0.2	31.1 ± 0.2
	Average photosynthetic photon flux ($mol \cdot day^{-1} \cdot m^{-2}$)[y]				
10	3.9 ± 0.3	6.2 ± 0.4	11.7 ± 1.1	11.5 ± 1.6	6.6 ± 0.4
15	3.4 ± 0.3	5.3 ± 0.4	7.0 ± 1.0	5.3 ± 0.8	4.6 ± 0.3
20/16[x]	3.4 ± 0.4	5.3 ± 0.4	8.0 ± 0.3	6.5 ± 0.8	4.5 ± 0.3
20	3.4 ± 0.4	4.3 ± 0.3	7.8 ± 0.3	6.4 ± 0.8	4.5 ± 0.3
25	3.4 ± 0.3	5.4 ± 0.4	5.7 ± 1.0	6.0 ± 0.9	4.8 ± 0.3
30	3.8 ± 0.3	6.0 ± 0.4	10.5 ± 1.2	11.5 ± 1.3	6.6 ± 0.4

[z]Phase I was from start of short days to visible bud (VB), phase II from VB to removal of lateral flower buds (disbud, DB), phase III from DB to buds showing first color (C), and phase IV from C to flower.
[y]±SE.
[x]Day/night temperature.

Table 2. Effects of various constant temperatures on duration of four developmental phases and leaf number per shoot for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

Temperature (°C)	Days of development[z]					Leaf number per shoot
	Phase I	Phase II	Phase III	Phase IV	Total	
10	52	53	16	17	138	12
15	38	27	7	14	86	10
20/16[y]	34	25	6	12	77	10
20	33	25	6	14	78	10
25	37	31	11	17	96	12
30	48	52	15	22	137	15
LSD (0.001)	2.1	3.6	1.5	2.6	5.2	1.6

[z]Phase I was from start of short days to visible bud (VB), phase II from VB to removal of lateral flower buds (disbud, DB), phase III from DB to buds showing first color (C), and phase IV from C to flower.
[y]Day/night temperature.

The delay in development at 10C during phase I was probably due to a different growth response than the delay at 30C, because more leaves were formed at 30C. Plants grown at 30C formed five more leaves than plants grown at 15–20C and three more leaves than plants at 10 or 25C, indicating delayed flower initiation (Table 2). The delay in development at low temperatures during phase I is probably the result of a combination of delayed flower initiation and slower bud development (24).

Delayed flowering in chrysanthemum at low temperatures has been observed both with and without an increase in leaf number (25). Four to five more leaves were formed below the flower when plants were grown under 2.9 rather than 5.8 $mol\cdot day^{-1}m\cdot^{-2}$ PPF (4). Flower initiation and development in chrysanthemum are affected by interactions between PPF and temperatures (5, 13, 15, 22, 25). The low PPF during phase I in our experiment (3.9 $mol\cdot day^{-1}\cdot m^{-2}$, Table 1) may be responsible for the increase in leaf number at 10C.

Increased leaf number and delayed development at high temperature is commonly referred to as "heat delay" in chrysanthemum. Such an increase in leaf number appears to be independent of prevailing PPF. The cultivar Bright Golden Anne grown under 5.8 or 17.6 $mol\cdot day^{-1}\cdot m^{-2}$ PPF formed four or five more leaves at 26C than at 14C (15). The high-temperature-tolerant cultivar Surf formed three more leaves and the high-temperature-sensitive cultivar Orange Bowl four more leaves at a PPF of 21 $mol\cdot day^{-1}\cdot m^{-2}$ when the temperatures were changed from 22C DT/18C NT to 30C DT/26C NT (27).

Rate of leaf unfolding in several plant species increases linearly to some maximum rate as temperature increases (6, 10, 16, 20, 23). Based on the data of Cockshull et al. (6), the average leaf unfolding rate in chrysanthemum can be calculated as 0.20 leaves/day at 10C and 0.53 leaves/day at 20C. The delay in development at low temperatures during phase I is probably the result of a combination of delayed flower initiation and slower bud development (24).

Even though plants grown at 30C in this study produced more leaves, the length of the leaf unfolding period can be expected to be similar to that of 20C due to the increased leaf unfolding rate at 30C (6). The delayed development during phase I at 30C was attributed to delayed flower development after flower initiation rather than to delayed flower initiation (27).

The effects of temperature during early phases on developmental rate during later phases were studied by shifting plants to a second temperature at the start of each phase. Time to flower could not be shortened by shifting plants from 20/16C to a second temperature (Fig. 1). Fastest development occurred when plants were maintained at 20/16 or 20C, or were shifted to 15C from 20/16 or 20C. Transfer of plants to 10, 25, or 30C from 15, 20/16, or 20C delayed development compared to plants maintained at 15, 20/16, or 20C. Shifting plants at VB from a less favorable temperature (e.g., 10 or 30C) to 15 or 20C resulted in faster flowering than comparable shifts at DB or color.

Functional relationships between time of development in a phase and temperature before and during that phase were developed (Table 3). Only the direct effect of temperature was evaluated during phase I, since all plants were grown at constant 20C before the start of the experiment. Response to temperature during phase I was parabolic, with a predicted optimal temperature of 21.3C (Fig. 2). Lepage et al. (17) reported that the time from start of SD to VB was linearly related to the average daily temperature in the range from 10 to 18C for 'Accent', 'Boston', 'Lapana', 'Pink Gin', 'Rewilo', and 'White Spider' chrysanthemums. VB occurred an average of 17 days earlier at 18 than 10C (17), which is comparable to this study, where VB occurred 19 days earlier at 20 than at 10C (Table 2, Fig. 2). Since Lepage et al. (17) limited the upper temperature to 18C, the parabolic shape of the response observed here could not be distinguished in their study.

Table 3. Regression coefficients for functions relating temperature (T) to the duration of four developmental phases in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

Regression[z] variable	Phase[y]			
	I	II	III	IV
Constant	107.6160	105.6318	44.6060	30.6927
T_1	−7.0448	−2.0318	−1.9315	−0.2680
T_2	---	−3.2967	−1.8386	−1.6791
$(T_1)^2$	0.1650	0.0305	0.0500	0.0279
$(T_2)^2$	---	0.1337	0.0403	0.0291
$T_1 \times T_2$	---	−0.2039	0.0054	---
$T_1 \times (T_2)^2$	---	---	−0.0001	0.0017
$(T_2)^2 \times T_2$	---	0.0049	---	−0.0018
r^2	0.92	0.82	0.82	0.75

[z]T_1 = temperature from start of SD to beginning of the considered phase, T_2 = temperature during the considered phase.
[y]Phase I was from start of short days to visible bud (VB), phase II from VB to removal of lateral flower buds (disbud, DB), phase III from DB to buds showing first color (C), and phase IV from C to flower.

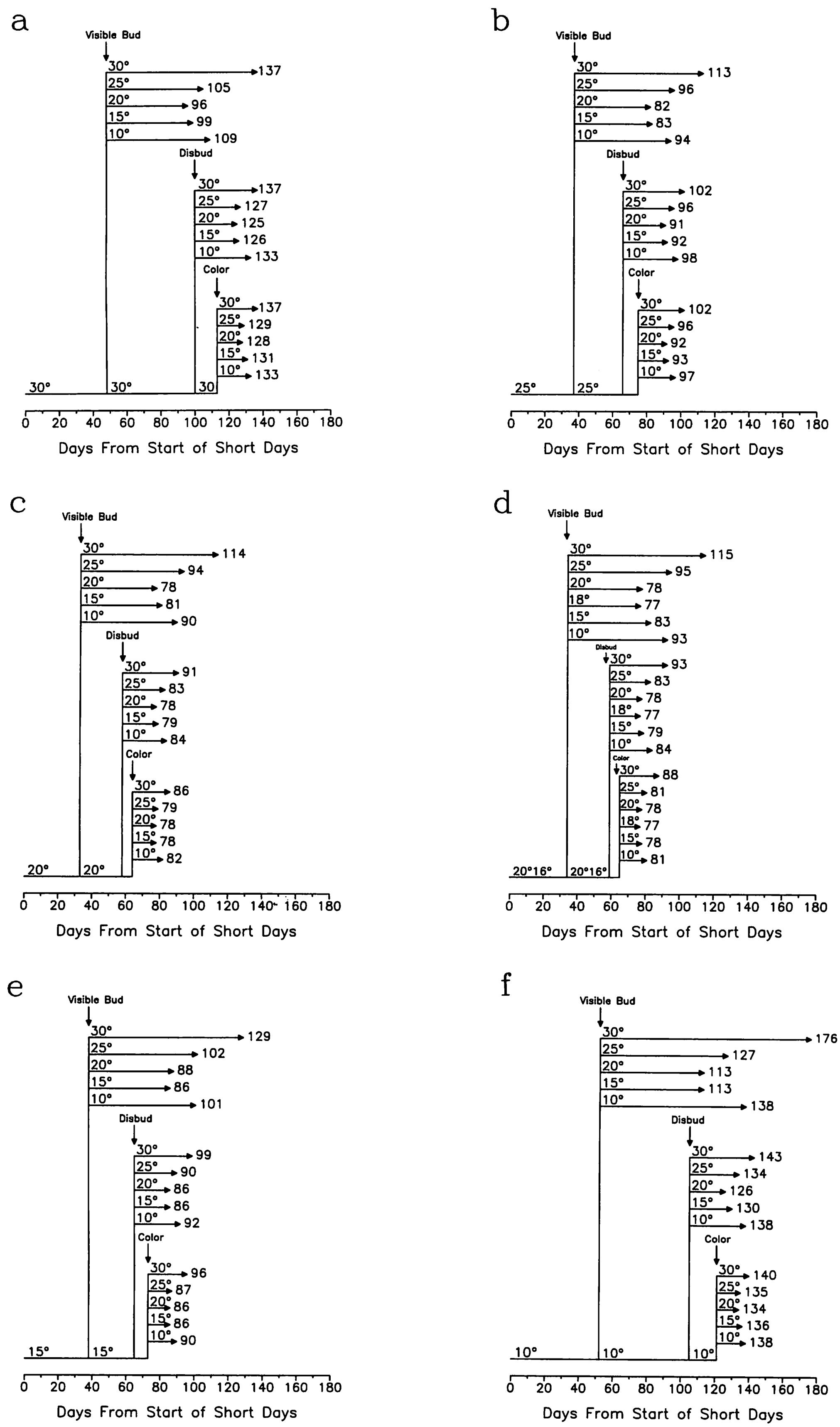

Fig. 1. Effect of temperature on total number of days to flower from beginning of short days for *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'. Initial temperature at (**a**) 30C, (**b**) 25C, (**c**) 20C, (**d**) 20C day and 16C night, (**e**) 15C, and (**f**) 10C.

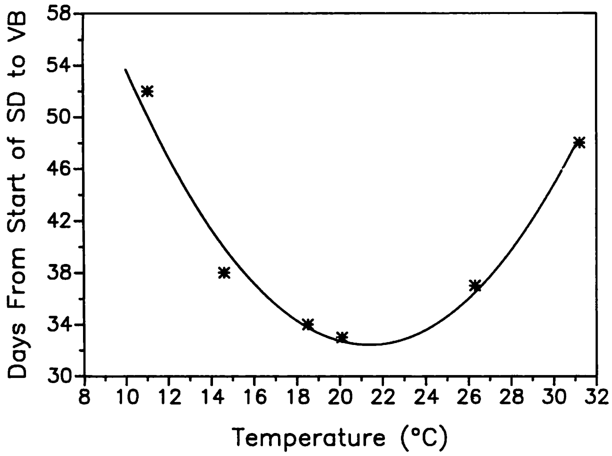

Fig. 2. Effect of temperature on rate of development during phase I in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'. Observed times of development illustrated by asterisks (n = 10).

The number of days required to complete phase II varied from 25 to 40 days at 20C, depending on the previous temperature treatment (Table 4). Phase II development at 20C was delayed more in plants grown at 10C than at 30C during phase I (Table 4, Fig. 3a). Using 15C in phase I delayed development more than 20/16, 20, or 25C when combined with 25 or 30C in phase II.

In contrast to the development in phase II, development rate during phase III was not greatly influenced by low temperature before phase III. High temperature (30C) before phase III, however, delayed development under all temperatures during phase III (Table 4, Fig. 3b). Temperature exposure before phase IV had only a small effect on time of development during phase IV (Table 4, Fig. 3c).

Optimum temperature for each phase was calculated using the developed functions. The calculated optimum temperature was 21.3C for phase I. The optimum temperatures for phase II, III, and IV were calculated as 20.3, 23.1, and 19.1C when the calculated optimum temperatures for earlier phases were used as the previous temperatures.

For practical purposes, the temperatures for fastest development may be expressed as an optimum range rather than a specific temperature. The developed function for phase I predicted 32 days as the fastest rate of development to VB at 21.3C. Predicting time of development during phase I to within 1 day of the minimum 32 days was possible with temperatures from 18.8 to 23.8C. Predicting time of development during phases II, III, and IV within 1 day of the minima (21, 6, and 14 days, respectively) was possible with temperatures of 17.1 to 23.5C, 17.2 to 29.0C, and 14.8 to 23.4C. These wide ranges of optimum temperature for each phase provide flexibility in greenhouse temperature control. Temperatures within the range will result in similar number of days to complete development.

Optimum temperatures for development often decrease with plant age (3, 18, 26). Preliminary experiments showed that DT and NT >20C accelerated development until VB in chrysanthemum, but slowed development during later phases (14). Optimum temperatures for development in this study decreased with plant age, except for phase III. The third phase was shortest (10% of time required for flowering) and had the widest range of temperatures allowing developmental rates within 1 day of the optimum rate. The short duration of phase III resulted in difficulties in distinguishing small differences in rate of development. Measurements could only be made with an accuracy of 1 day. The predicted increase in optimum temperature for phase III compared to phase II may therefore not be valid. Regression analysis of time required to complete development from VB to flower (phases II, III, and IV) as a function of temperature gave an equation with an optimum temperature of 19.3C, a value intermediate to the 20.3 and 19.1C optimum calculated for phases II and IV, respectively.

Cathey (3) reported that development in chrysanthemum occurs faster above 16C before VB and below 16C after VB. We found a similar lowering of the optimum temperature after VB, but not to the extent observed by Cathey. The calculated optimum temperature for the development from VB to flower (phases II, III, and IV) was 19.3C, a decrease of 2 degrees in optimum temperature compared to phase I. Although the optimum tem-

Table 4. Effect on phase length of temperature before and during a particular phase of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'.

Temperature (°C)		Length of phase[z] (days)		
Initial[y]	Final[y]	II	III	IV
10	10	53	16	17
15	10	34	12	17
20/16[x]	10	32	10	16
20	10	32	11	18
25	10	30	15	20
30	10	33	20	20
LSD (0.001)		3.0	1.9	2.2
10	15	39	10	15
15	15	27	7	14
20/16[x]	15	28	7	13
20	15	27	8	14
25	15	25	11	16
30	15	27	14	18
LSD (0.001)		3.3	1.5	1.6
10	20	40	9	13
15	20	29	7	13
20/16[x]	20	25	6	13
20	20	25	6	14
25	20	25	10	15
30	20	27	13	15
LSD (0.001)		3.4	2.0	1.2
10	25	48	10	14
15	25	38	8	14
20/16[x]	25	31	7	16
20	25	32	8	15
25	25	31	11	17
30	25	33	14	16
LSD (0.001)		3.9	1.9	1.9
10	30	69	11	19
15	30	47	9	23
20/16[x]	30	41	8	23
20	30	42	9	22
25	30	41	11	23
30	30	52	15	22
LSD (0.001)		3.3	1.8	2.6

[z]Phase II was from VB to removal of lateral flower buds (disbud, DB), phase III from DB to buds showing first color (C), and phase IV from C to flower.
[y]Initial temperature from start of SD to beginning of the considered phase, final temperature during phase II, III or IV, respectively.
[x]Day/night temperature.

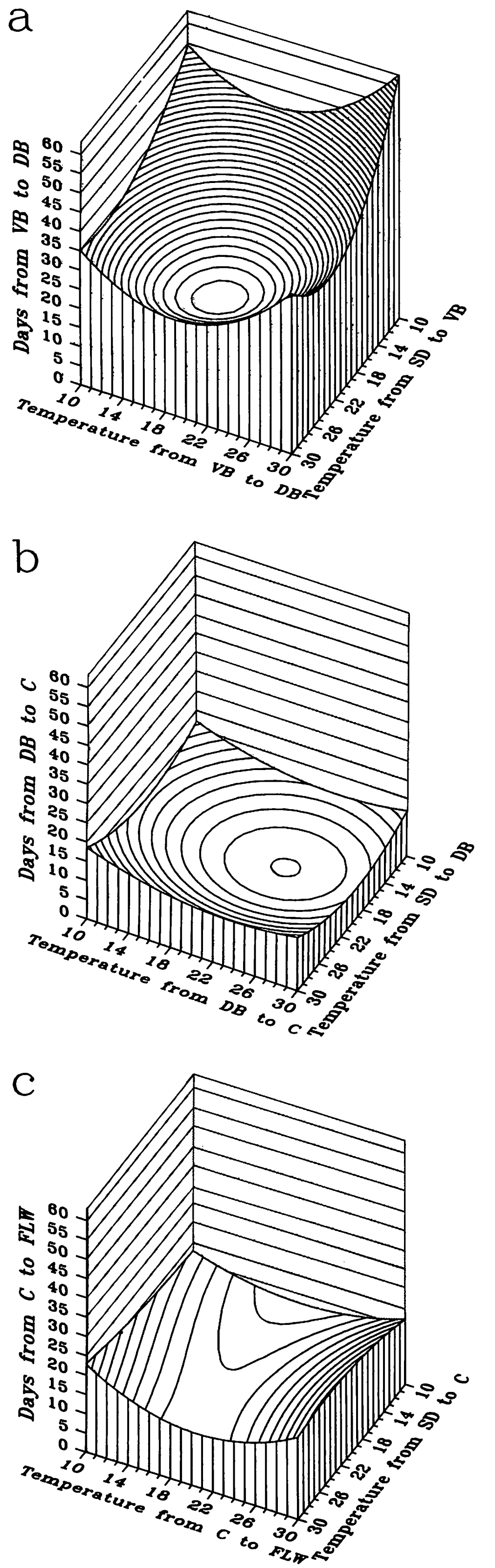

Fig. 3. Effect of temperature and time of exposure on rate of development in *Dendranthema grandiflora* Tzvelev. 'Bright Golden Anne'. The four phases studied were from start of short days to visible bud (VB), from VB to removal of lateral flower buds (disbud; DB), from DB to a flower bud showing color (C), and from C to flower (FLW). (**a**) Effect of temperature during phases I and II on duration of phase II. (**b**) Effect of temperature during phases I and II, and III on duration of phase III. (**c**) Effect of temperature during phases I, II, III and phase IV on duration of phase IV.

perature decreased, it was still >16C. The difference between our results and Cathey's (3) could be due to differences in cultivars, environmental conditions before SD, or irradiance conditions.

The results presented on rate of development indicate that chrysanthemum undergoes temperature conditioning. Rate of development during phase II and III varied, depending on previous temperature exposure (Fig. 3 a and b). Unfavorable temperatures for development in phase I, such as 10 or 30C, cannot be totally negated by maintaining an optimum temperature in phase II. Similarly, the effects of an unfavorable temperature during phases I and II were carried over to phase III. During phase IV, the plants exhibited less temperature conditioning, and time required to complete development was primarily determined by the temperature of that phase.

Minimum, optimum, and maximum temperatures for different phases of growth and development (21) can be modified by previous temperature exposure. In chrysanthemum, temperature conditioning alters response to later temperatures. Phasic development in chrysanthemum can therefore only be predicted if the preceding temperature conditions are known.

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