HortScience 33(4):663–667. 1998.

Effect of Forcing Temperature on Time to Flower of *Coreopsis grandiflora*, *Gaillardia* ×*grandiflora*, *Leucanthemum* ×*superbum*, and *Rudbeckia fulgida*

Mei Yuan[1], William H. Carlson[2], Royal D. Heins[2], and Arthur C. Cameron[2]

Department of Horticulture, Michigan State University, East Lansing, MI 48824

Additional index words. base temperature, blanket flower, coneflower, degree-day, herbaceous perennial, Shasta daisy, tickseed

Abstract. **Scheduling crops to flower on specific dates requires a knowledge of the relationship between temperature and time to flower. Our objective was to quantify the effect of temperature on time to flower and plant appearance of four herbaceous perennials. Field-grown, bare-root *Coreopsis grandiflora* (Hogg ex Sweet.) 'Sunray', *Gaillardia* ×*grandiflora* (Van Houtte) 'Goblin', and *Rudbeckia fulgida* (Ait.) 'Goldsturm', and tissue culture–propagated *Leucanthemum* ×*superbum* (Bergman ex J. Ingram) 'Snowcap' plants were exposed to 5 °C for 10 weeks and then grown in greenhouse sections set at 15, 18, 21, 24, or 27 °C under 4-hour night-interruption lighting until plants reached anthesis. Days to visible bud (VB), days to anthesis (FLW), and days from VB to FLW decreased as temperature increased. The rate of progress toward FLW increased linearly with temperature, and base temperatures and degree-days of each developmental stage were calculated. For *Coreopsis, Leucanthemum,* and *Rudbeckia*, flower size, flower-bud number, and plant height decreased as temperature increased from 15 to 26 °C.**

Temperature is one of the critical factors controlling plant developmental processes, such as flowering. As forcing temperature increases, time to flower usually decreases until it reaches a minimum. In many circumstances, in the absence of the effects of other factors, such as photoperiod, the rate of development increases linearly with temperature (Roberts and Summerfield, 1987). Thus, the relationship between the rate of development toward flowering (1/DTF, where DTF is the days to flower) and temperature can be described as follows:

$$1/DTF = b_0 + b_1 * T \qquad [1]$$

Using the constants b_0 and b_1, the base temperature, T_b, and degree-days (°days) can be calculated as follows:

$$T_b = - b_0/b_1 \qquad [2]$$

$$°days = 1/b_1 \qquad [3]$$

Base temperature is the temperature at, or below which, the rate of progress toward flowering is zero. Degree-days represent the thermal time required for flowering.

Temperature influences not only time to flower, but also plant appearance. For instance, stem length, spike length, and floret number of *Antirrhinum majus* L. 'Jackpot' increased as temperature was decreased from 21 to 10 °C (Maginnes and Langhans, 1961). Flowers of *Lysimachia congestiflora* Hemsl. grown at 18 °C lasted longer than those grown at 26 °C (Zhang et al., 1995). Temperature also affects morphological characteristics such as height and leaf color in *Dicentra spectabilis* (L.) Lem (Lopes and Weiler, 1977).

Growing herbaceous perennials as flowering potted plants is a new trend in the horticulture industry. *Coreopsis grandiflora* 'Sunray', *G.* ×*grandiflora* 'Goblin', *L.* ×*superbum* 'Snowcap', and *R. fulgida* 'Goldsturm' are popular, commercially grown, herbaceous perennial plants. *Coreopsis*, *Leucanthemum*, and *Rudbeckia* ranked among the top 10 best-selling perennials in 1992 and 1993 (Rhodus, 1995). *Coreopsis grandiflora*, *G.* ×*grandiflora*, *L.* ×*superbum*, and *Rudbeckia* are reported to be long-day plants, and cold treatments enhance flowering of *Coreopsis* and *Gaillardia* (Engle, 1994; Evans and Lyons, 1988; Ketellaper and Barbaro, 1966; Tanimoto and Harada, 1985). Another cultivar of Shasta daisy, 'G. Marconi', required ≈4 weeks to reach VB after cold treatments under long days (LD) (Shedron and Weiler, 1982a). However, there is little information on the effect of forcing temperature on time to flower of these species. Scheduling crops to flower on a specific date is usually desirable in greenhouse production and requires knowledge of the relationship between forcing temperature and time to flower. The objectives of these experiments were to quantify the effects of forcing temperature on time to flower and plant appearance (flower size, flower bud number, and plant height) of *C. grandiflora* 'Sunray', *G.* ×*grandiflora* 'Goblin', *L.* ×*superbum* 'Snowcap', and *R. fulgida* 'Goldsturm' to provide crop production scheduling data.

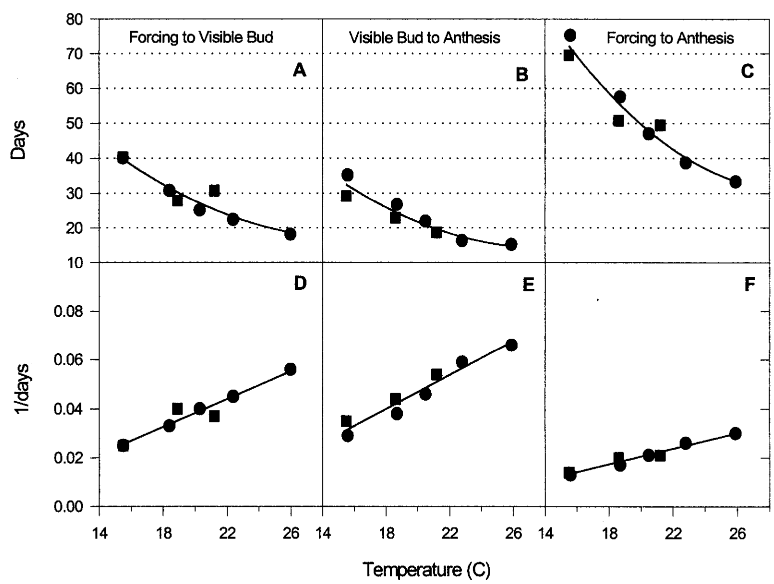

Fig. 1. Effects of temperature on time to (**A**, **B**, **C**) and rate of progress toward flowering (**D**, **E**, **F**) in *Coreopsis grandiflora* 'Sunray' for year 1 (■) and year 2 (●). The parameters of linear regression lines are presented in Table 1. The quadratic regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F.

Received for publication 8 Apr. 1997. Accepted for publication 5 Dec. 1997. We gratefully acknowledge the financial support of the Agricultural Experiment Station of Michigan State Univ. and greenhouse growers supportive of Michigan State Univ. floricultural research. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

[1]Former Graduate Assistant.

[2]Professor.

Materials and Methods

Experiments were conducted twice over 2 years. The 1st year, field-grown, bare-root *C. grandiflora* 'Sunray' and *R. fulgida* 'Goldsturm', and tissue culture–propagated *L.* ×*superbum* 'Snowcap' and *G.* ×*grandiflora* 'Goblin', both growing in 5.7-cm square pots (1090 cm^3), were received from a commercial grower and transplanted into 15-cm-diameter (2570 cm^3) round pots on 24 Oct. 1993. Plants were grown in a commercial soilless medium containing composted pine bark, horticultural vermiculite, Canadian sphagnum peat, processed bark ash, and washed sand (MetroMix 510, Scotts-Sierra Horticultural Products Company, Marysville, Ohio). Plants were placed under LD [9-h daylength plus a 4-h night interruption provided by incandescent light bulbs at a photosynthetic photon flux (*PPF*) of ≈3 to 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$] at 20 °C for 3 weeks. They then were exposed to 5 °C for 10 weeks in coolers illuminated for 9 $h \cdot d^{-1}$ by cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.) at ≈20 $\mu mol \cdot m^{-2} \cdot s^{-1}$. After cold treatment, 10 plants of each species were placed in greenhouse sections set at 15, 18, 21, 24, and 27 °C. Supplemental lighting (high-pressure sodium lamps providing ≈90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant level) was initiated automatically by an environmental control computer when ambient *PPF* dropped below 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and terminated when *PPF* exceeded 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants received natural daylengths with a 4-h night interruption from 2200 to 0200 HR, provided by high-pressure sodium lamps that delivered ≈90 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The 2nd year, similar plant material was used, except for *Gaillardia* (bare-root plants instead of potted plants). Bare-root plants were dug from the field on 11 Nov. 1994. They then were sealed in boxes and held at 0 °C for 10 weeks; *Leucanthemum* was held at 5 °C. Plants were transplanted into 3402 cm^3 (1 gal. U.S.) pots after cold treatments and grown under the same conditions as those during the 1st year.

The dates of VB and FLW were recorded for each plant both years. The diameter of the first opened flower, number of unopened flower buds, and plant height also were recorded at FLW the second year.

The experimental designs for both years were completely randomized. Data were analyzed using the SAS (SAS Institute, Cary, N.C.) general linear models procedure (PROC GLM) for analysis of variance and linear regression procedure (PROC REG) for the regression models. Mean days to VB and to FLW , and from VB to FLW, were used to calculate regression models.

Temperatures in each greenhouse section were controlled with a Priva environmental computer. The actual temperature for each treatment was recorded every 15 min by a CR-10 datalogger, and average temperatures from the start of forcing to VB and to FLW and from VB to FLW were calculated for each species and used in data analyses. The difference between day and night temperature (DIF) for each treatment was calculated also.

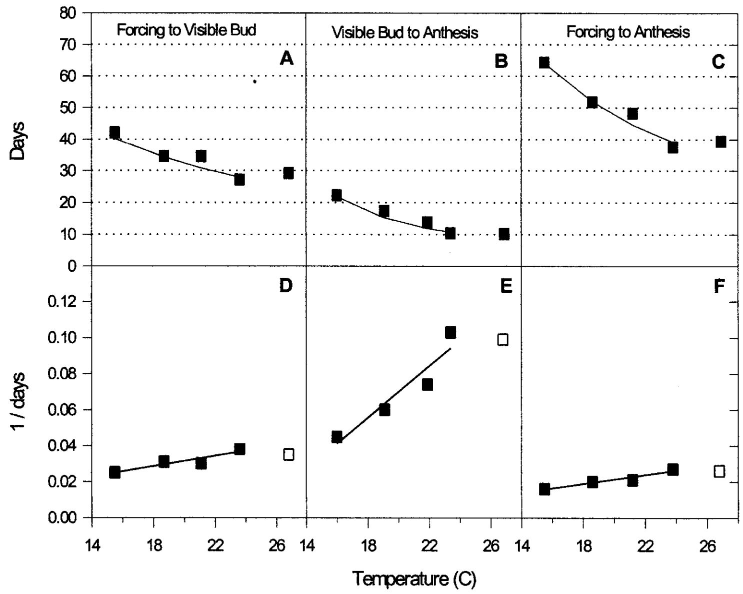

Fig. 2. Effects of temperature on time to (**A**, **B**, **C**) and rate of progress toward flowering (**D**, **E**, **F**) in *Gaillardia* ×*grandiflora* 'Goblin' for year 1. The parameters of linear regression lines are presented in Table 1. Data represented by ❑ were not included in the regression analysis. The quadratic regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F.

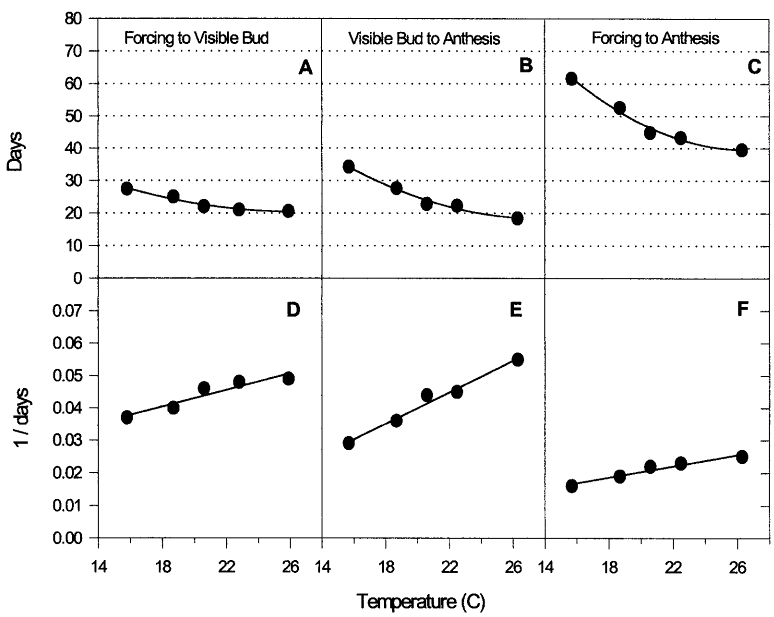

Fig. 3. Effects of temperature on time to (**A**, **B**, **C**) and rate of progress toward flowering (**D**, **E**, **F**) in *Leucanthemum* ×*superbum* 'Snowcap' for year 2. The parameters of linear regression lines are presented in Table 1. The quadratic regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F.

The bare-root *Gaillardia* plants did not tolerate cold storage, and more than half died in the coolers. The surviving plants lacked vigor throughout the entire experiment. Therefore, only the first year's (1994) data on *Gaillardia* are presented.

Results and Discussion

Days to VB, days from VB to FLW, and days to FLW of all species decreased as temperature increased. The relationship between temperature and time to VB, and to FLW, and from VB to FLW generally followed a quadratic pattern (Figs. 1–4, graphs A, B, and C). For all species, increasing temperature from 15 to 21 °C accelerated flowering more than increasing it from 21 to 27 °C. For example, days to FLW for *Coreopsis* decreased from 75 to 47 (Δ = 28 d) as temperature increased from 15.5 to 20.3 °C, but decreased from 47 to 33 (Δ = 14 d) as temperature increased from 20.3 to 25.9 °C (Fig. 1C). In these experiments, all plants flowered. The effect of temperature on

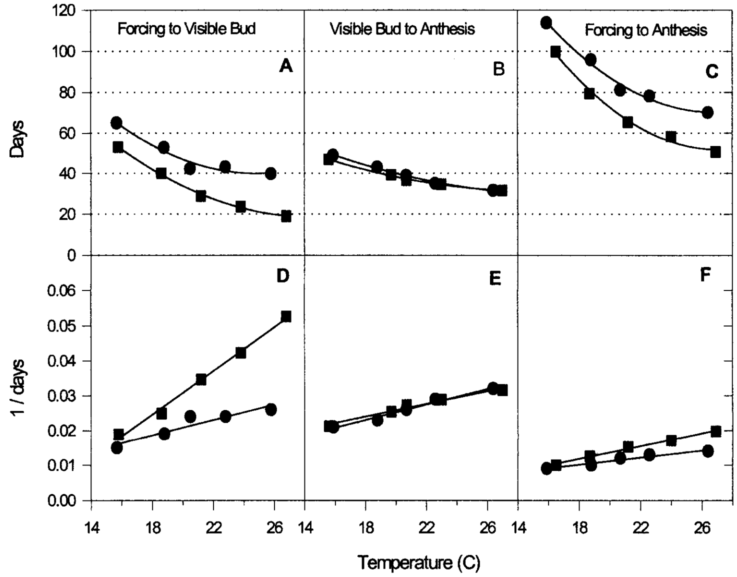

Fig. 4. Effects of temperature on time to (**A**, **B**, **C**) and rate of progress toward flowering (**D**, **E**, **F**) in *Rudbeckia fulgida* 'Goldsturm' for year 1 (■) and year 2 (●). The parameters of linear regression lines are presented in Table 2. The quadratic regression lines in graphs A, B, and C are the reciprocals of correlated linear regression lines in graphs D, E, and F.

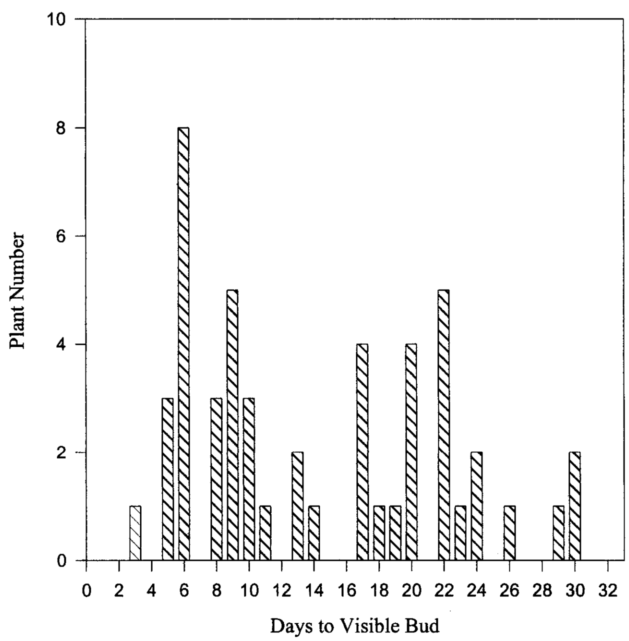

Fig. 5. Distribution of *Leucanthemum* ×*superbum* 'Snowcap' plants relating to days to visible bud after 10 weeks of cold treatment at 5 °C.

time to FLW was species-dependent. Increasing temperature from 15 to 26 °C reduced days to FLW ≈40, 25, 20, and 50 d for *Coreopsis, Gaillardia, Leucanthemum*, and *Rudbeckia*, respectively.

In the 1st year, some *Leucanthemum* plants showed great variability in time to VB. Some plants reached VB in a few days (one plant in only 3 d) from the end of cold treatment (Fig. 5). The distribution of response was more binomial than normal (Fig. 5). *Leucanthemum* ×*superbum* vary greatly in their flowering requirements (Shedron and Weiler, 1982a). Some clones require cold to flower, and some do not; however, all usually respond to LD (Engle, 1994). Yuan (1995) showed that 'Snowcap' does not require cold treatment for flowering. In the 1st year's experiment, some plants must have initiated flowers before or during cold treatments, since they showed VB shortly after being returned to warm temperatures. Since the goal of this experiment was to quantify the time from the start of vegetative plant forcing to FLW, only the 2nd year's data were used to estimate base temperature and degree-days.

There were linear relationships between temperature and rate of progress toward FLW of all species in the studied temperature range (Figs. 1–4, graphs D, E, and F). For *Coreopsis*, the regression analysis was based on combined data for 2 years (Fig. 1), and the parameters of the equation are given in Table 1. In *Gaillardia*, times to VB, and to FLW, and from VB to FLW were longer at 27 °C than at 24 °C (Fig. 2). Since the rate to FLW increases linearly with temperature only at suboptimal ranges (Roberts and Summerfield, 1987), the data at 27 °C were excluded from regression analysis (Fig. 2). For *Rudbeckia*, regression lines for each year were calculated and their slopes and intercepts were compared statistically (Table 2). Although the slopes and intercepts for equations relating the rate of progress to VB and FLW differed between years, the rate of progress from VB to FLW was the same. When the reciprocal of the linear regression function was plotted against original data, it matched well, suggesting that linear regression lines describe the relationship between temperature and developmental rate well and can be used to predict time to FLW.

Base temperatures and degree-days for each developmental stage of each species were determined using Eqs. [2] and [3]. For *Coreopsis*, results were similar for the different growth phases. The estimated base temperature ranged from 6.6 to 6.8 °C. The degree-days to FLW were 645 when days to FLW data were used alone, and 652 when data for days from emergence to VB and days from VB to FLW were combined. For *Rudbeckia*, the estimated base temperature ranged from 5.2 to 10.2 °C the 1st year and from –1.3 to 5.1 °C the 2nd year. Base temperature (T_b) and degree-days can be used to predict the FLW date in commercial greenhouse environments in which temperatures fluctuate. A developmental process requires a certain amount of thermal time (degree-days) above the base temperature. If the average daily temperature is T_a, the days necessary to complete a growth phase can be calculated as °days/($T_a - T_b$). Using this method, the time required to complete a developmental stage can be obtained for these species when the average forcing temperature is available. The predicted days to complete a developmental stage are similar to the observed days in all species.

The rate of progress toward VB and FLW differed between the 2 years for *Rudbeckia* (Fig. 4). In year 1, plants had grown for 3 weeks under LD before cold treatment, and flowered ≈20 d earlier than plants in year 2. Rudbeckia is an obligate LD plant that does not require vernalization for flower induction (Yuan, 1995). We speculate that plants were induced the 1st year during the 3 weeks of LD before the cold treatment. When they were returned to warm temperatures after cold treatment, development continued normally and they flowered faster than noninduced plants from the 2nd year. The average time to FLW after the cold treatment was 20 d less the 1st year, which is similar to the duration of the pre-cold growth period under LD. In other words, the total growing time after the start of LD was the same both years. The developmental-rate models for year 2 are most appropriate for *Rudbeckia* scheduling.

Table 1. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB) and to anthesis (FLW), and from VB to FLW in *Coreopsis grandiflora* 'Sunray', *Gaillardia ×grandiflora* 'Goblin', and *Leucanthemum ×superbum* 'Snowcap'. Intercept and slope were used to calculate base temperature (T_b) and degree-days (°days).

Developmental stage (d)	Intercept (b_0) 1/d	Slope (b_1) (1/d)/C	T_b(°C)	°days	r^2
		Coreopsis			
Forcing to VB	−1.81E-2 ± 7.50E-3[z]	2.75E-3 ± 3.74E-4	6.6	364	0.94***
VB to FLW	−2.35E-2 ± 8.07E-3	3.47E-3 ± 4.0E-4	6.8	288	0.90***
Forcing to FLW	−1.05E-2 ± 2.75E-3	1.55E-3 ± 1.37E-4	6.8	645	0.96***
		Gaillardia			
Forcing to VB	8.39E-4 ± 7.46E-3	1.46E-3 ± 3.74E-4	−0.5	685	0.88*
VB to FLW	−6.21E-2 ± 2.84E-2	6.46E-3 ± 1.40E-3	9.6	155	0.91*
Forcing to FLW	−4.28E-3 ± 4.49E-3	1.25E-3 ± 2.24E-4	3.3	800	0.94*
		Leucanthemum			
Forcing to VB	1.71E-2 ± 5.08E-3	1.28E-3 ± 2.41E-4	−13.1	781	0.90*
VB to FLW	−4.17E-3 ± 4.75E-3	2.19E-3 ± 2.23E-4	0.9	457	0.95**
Forcing to FLW	3.06E-3 ± 2.51E-3	8.74E-4 ± 1.19E-4	−3.4	1144	0.97**

[z]Standard error.

*, **, ***Significant at $P < 0.05$, 0.01, or 0.001, respectively.

Table 2. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud (VB) and to anthesis (FLW), and from VB to FLW in *Rudbeckia fulgida* 'Goldsturm'. Intercept and slope were used to calculate base temperature (T_b) and degree-days (°days).

	Developmental stage (d)	Intercept (b_0) 1/d	Slope (b_1) (1/d)/C	T_b(°C)	°days	r^2
Year 1	Forcing to VB	−3.17E-2 ± 2.92E-3[z]	3.12E-3 ± 1.35E-4	10.2	321	0.99***
Year 2	Forcing to VB	1.26E-3 ± 4.76E-3	9.65E-4 ± 2.27E-4	−1.3	1036	0.86*
Comparison		F = 6.81*	F = 71.23**			
Year 1	VB to FLW	7.65E-3 ± 1.76E-3	9.09E-4 ± 8.19E-5	8.4	1100	0.99***
Year 2	VB to FLW	5.14E-3 ± 1.91E-3	9.85E-4 ± 8.91E-5	5.1	1015	0.98**
Comparison		F = 1.81[NS]	F = 0.38[NS]			
Year 1	Forcing to FLW	−4.73E-3 ± 1.14E-3	9.17E-4 ± 5.25E-5	5.2	1091	0.98***
Year 2	Forcing to FLW	6.87E-4 ± 1.37E-3	5.28E-4 ± 6.48E-5	−1.3	1894	0.96**
Comparison		F = 9.4*	F = 20.9**			

[z]Standard error.

NS, *, **, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

Table 3. The difference between day and night temperature (DIF) of plants under different forcing temperatures and three developmental stages: from forcing to visible bud (VB), from VB to anthesis (FLW), and from forcing to FLW.

	Coreopsis DIF			*Leucanthemum* DIF			*Rudbeckia* DIF		
Temp setting (°C)	Forcing to VB	VB to FLW	Forcing to FLW	Forcing to VB	VB to FLW	Forcing to FLW	Forcing to VB	VB to FLW	Forcing to FLW
27	0.1	0.5	0.3	0.3	0.1	0.3	0.3	0.2	0.3
24	0.2	0.6	0.4	0.4	1.3	0.8	0.4	1.0	0.8
21	0.2	0.0	0.1	0.1	0.4	0.2	0.2	0.2	0.2
18	0.9	1.7	1.3	1.0	1.6	1.2	1.0	1.4	1.2
15	0.5	1.1	0.9	0.8	1.2	0.9	0.9	1.3	1.1

In contrast to *Rudbeckia*, *Coreopsis grandiflora* 'Sunray' has an obligate vernalization requirement for flower initiation (Yuan, 1995). Plants cannot be induced to flower without cold treatment, even under extended LD. In the 1st year, field-grown bare-root plants were shipped to us in late October and had received little cold in the field before harvesting. Therefore, they were insensitive to LD during the 3-week pre-cold LD treatment. The 2nd year, plants were not exposed to LD before cold treatment. Time to FLW was similar in both years.

Flower-bud number of *Coreopsis, Rudbeckia*, and *Leucanthemum* decreased ≈ 80%, 75%, and 55%, respectively, as temperature increased from 16 to 26 °C (Fig. 6A). Temperature had a greater effect on flower size in *Leucanthemum* and *Rudbeckia* than in *Coreopsis* (Fig. 6B). Flower diameter decreased 2.7 cm in *Leucanthemum* and *Rudbeckia*, but only 0.9 cm in *Coreopsis* as temperature increased from 16 to 26 °C.

Height of *Rudbeckia* decreased 50% when temperature increased from 16 to 26 °C (Fig. 6C). In *Coreopsis*, only plants grown at 16 °C were significantly taller than those grown at 23 or 26 °C. Height of *Leucanthemum* decreased ≈9 cm as temperature increased. Stem elongation increases with the difference between day and night temperatures (DIF) in many species such as *Lilium, Campanula, Fuchsia*, and *Begonia ×tuberhybrida* (Erwin and Heins, 1995). The DIF to which each species was exposed differed between treatments, generally increasing as forcing temperature decreased (Table 3). The effect of DIF on stem elongation is greatest when a plant is elongating most rapidly (Erwin and Heins, 1995). In all these species, DIF was greatest during the time from VB to FLW, suggesting that DIF may have contributed to some of the differences in plant height.

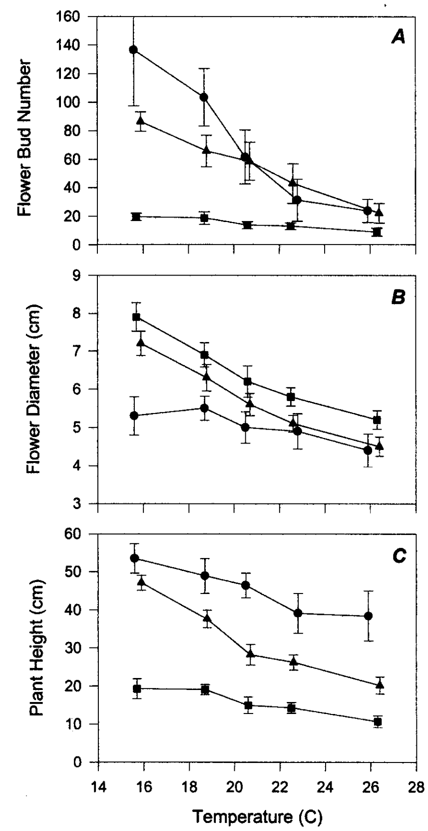

Fig. 6. Effects of temperature on (**A**) number of unopened flower buds, (**B**) flower diameter, and (**C**) plant height in *Coreopsis grandiflora* 'Sunray' (●), *Leucanthemum ×superbum* 'Snowcap' (■), and *Rudbeckia fulgida* 'Goldsturm' (▲). Error bars are 95% confidence intervals.

Overall, plants grown at cooler temperatures had more and larger flowers and were taller, but took longer to reach FLW. On the other hand, plants flowered faster at higher temperatures, but produced fewer and smaller flowers. *Leucanthemum* plants grown under the two highest temperatures were too short for 3402 cm³ (1 gal. U.S.) pots, whereas *Coreopsis* and *Rudbeckia* grown under the lowest temperature were too tall for them. Settings from 18 to 21 °C are recommended to force *C. grandiflora* 'Sunray', *G. ×grandiflora* 'Goblin', *L. ×superbum* 'Snowcap', and *R. fulgida* 'Goldsturm'. Plants flowered faster in this temperature range than did those grown at lower temperatures, and they were more attractive. The time required to bring each species to flower under the same temperature varies. For example, to schedule *Coreopsis, Gaillardia, Leucanthemum*, and *Rudbeckia* to flower on the same day when forcing at 20 °C, forcing should begin 50, 45, 45, and 85 d, respectively, before the schedule date if plants are transplanted after cold treatment.

Literature Cited

Engle, B.E. 1994. Use of light and temperature for hardening of herbaceous perennial plugs prior to storage at –2.5C. MS Thesis, Michigan State Univ., East Lansing.

Erwin, J.E. and R.D. Heins. 1995. Thermomorphogenic responses in stem and leaf development. HortScience 30:940–949.

Evans, M. and R.E. Lyons. 1988. Photoperiod and gibberellin induced growth and flowering responses of *Gaillardia* ×*grandiflora*. HortScience 23:584–586.

Ketellapper, H.J. and A. Barbaro. 1966. The role of photoperiod, vernalization and gibberellic acid in floral induction in *Coreopsis grandiflora* Nutt. Phyton 23:33–41.

Lopes, L.C. and T.C. Weiler. 1977. Light and temperature effects in the growth and flowering of *Dicentra spectabilis* (L.) Lem. J. Amer. Soc. Hort. Sci. 102:388–390.

Maginnes, E.A. and R.W. Langhans. 1961. The effect of photoperiod and temperature on initiation and flowering of snapdragon (*Antirrhinum majus*–variety Jackpot). J. Amer. Soc. Hort. Sci. 77:600–607.

Rhodus, T. 1995. Top 20 perennials. Greenhouse Grower. January, p. 80–84.

Roberts, E.H. and R.J. Summerfield. 1987. Measurement and prediction of flowering in annual crops, p. 17–50. In: J.G. Atherton (ed.). Manipulation of flowering. Butterworths, London.

Shedron, K.G and T.C. Weiler. 1982a. Regulation of growth and flowering in *Chrysanthemum* ×*superbum* Bergmans. J. Amer. Soc. Hort. Sci. 107:874–877.

Tanimoto, S. and H. Harada. 1985. Rudbeckia, p. 239–242. In: A.H. Halevy (ed.). CRC handbook of flowering, vol. 4. Boca Raton, Fla.

Yuan, M. 1995. The effect of juvenility, temperature, and cultural practices on flowering of *Coreopsis, Gaillardia, Leucanthemum, Heuchera* and *Rudbeckia*. MS Thesis, Michigan State Univ., East Lansing.

Zhang, D., A.M. Armitage, J.M. Affolter, and M.A. Dirr. 1995. Environmental control of flowering and growth of *Lysimachia congestiflora* Hemsl. HortScience 30:62–64.