Cold Treatment and Forcing Temperature Influence Flowering of *Campanula carpatica* ‘Blue Clips’

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Abstract. The influence of cold treatments on flowering in *Campanula carpatica* Jacq. ‘Blue Clips’ was determined. Plants with 10 to 12 nodes (P1) and 12 to 16 nodes (P2), in 128-cell (10-mL cell volume) and 50-cell (85-mL cell volume) trays, respectively, were stored at 5 °C for 0, 2, 4, 6, 8, 10, 12, or 14 weeks under a 9-hour photoperiod. They then were transplanted and forced in a 20 °C greenhouse under a 9-hour photoperiod with a 4-hour night interruption (NI) (2200 to 0200 HR). Time to visible bud and to flowering in P1 decreased slightly as the duration of cold treatment increased. Flowering was hastened by ≈10 days after 14 weeks at 5 °C. Cold treatments had no significant effect on time to visible bud or flower in P2. The number of flower buds on P1 did not change significantly in response to cold treatments, while flower bud count on P2 increased by up to 60% as duration of cold treatments increased. Final height at flowering of both ages decreased 10% to 20% with increasing duration of cold exposure. To determine the relationship between forcing temperature and time to flower, three plant sizes were forced under a 9-hour photoperiod with a 4-hour NI (2200 to 0200 HR) at 15, 18, 21, 24, or 27 °C. Plants flowered more quickly at higher temperatures, but the number and diameter of flowers were reduced. Days to visible bud and flowering were converted to rates, and base temperature (T_b) and thermal time to flowering (degree-days) were calculated. Average T_b for forcing to visible bud stage was 2.1 °C; for forcing to flower, 0.0 °C. Calculated degree-days to visible bud were 455; to flower, 909.

The Campanulaceae include more than 700 species of annual, biennial, and perennial plants. Many of the more than 300 species within the *Campanula* genus are popular garden plants (Liberty Hyde Bailey Hortorium, 1976). *Campanula* is one of the 25 top-selling genera of herbaceous perennials grown in the United States (Rhodus, 1995).

Campanula carpatica is a popular herbaceous perennial that grows as a compact mound with numerous blue or white bell-shaped flowers. The species is native to the Carpathian Mountains of Eastern Europe and is hardy from USDA zones 3 to 8 (Nau, 1993). *C. carpatica* is an obligate long-day plant, and recommended greenhouse forcing conditions include extending the daylength to a minimum of 16 h, or providing a 4-h night break with incandescent lamps at 2 to 4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Drushal, 1991). In North America, *C. carpatica* traditionally has been produced outdoors and is not in bloom in the spring when the majority of garden plants are sold. Con-

sumers prefer to purchase plants in flower; consequently, producers are interested in understanding the flowering requirements of this species and developing production schedules.

Exposure to a period of low temperatures is one of the environmental cues that regulates development and flowering in many plant species native to temperate latitudes (Roberts and Summerfield, 1987). Some species of herbaceous perennials require a cold treatment for further development of existing dormant flower buds, while in other cases, floral bud initiation occurs during exposure to low temperature. In other species, low temperatures hasten or are required for subsequent initiation and development of floral primordia. In this type of response, also termed “vernalization,” floral primordia are not initiated until after a return of higher temperatures, and initiation may not occur until photoperiodic requirements are also met (Chouard, 1960). Hastening of flowering can be measured directly by calculating time to flower and also has been correlated with a reduction of the number of leaves formed before flowering in grains (Chouard, 1960) and *Arabidopsis thaliana* L. (Bagnall, 1993). A cold treatment is not required for flowering in *C. carpatica*; however, Armitage (1995) reported that under a 16-h photoperiod provided with day-extension (DE) lighting, holding the cultivar White Clips at 2 °C for 12 weeks accelerated subsequent flowering by ≈50 d. In preliminary experiments, we failed to find this response to cold treatments in *C. carpatica* ‘Blue Clips’

grown under a 4-h night interruption (NI), but flowering occurred ≈10 d earlier when plants were forced under DE lighting (unpublished).

Production time for any crop is related to temperatures supplied during forcing. At temperatures below a species-specific minimum (T_b), the time to flower (f) is infinite. Temperatures above a ceiling value (T_{ce}) delay flowering. When developmental time is converted to a rate by taking the reciprocal, the relationship between mean temperature and rate of development is often linear in the range between T_b and T_{ce} (Roberts and Summerfield, 1987). Base and optimum temperatures vary within and between species and are related to climatic origin (Roberts and Summerfield, 1987).

Temperatures that result in most rapid flowering may not optimize plant appearance. Recommended forcing temperatures for *C. carpatica* are ≈13 to 17 °C (Armitage, 1994; Drushal, 1991; Madsen and Madsen, 1986; Nau, 1993); however, the effect of temperature on time to flower has not been quantified.

Information on the time required for flowering is critical for development of effective production schedules for any crop. To predict time to flower, one must know if *C. carpatica* ‘Blue Clips’ exhibits a vernalization response and how forcing temperature influences development. The objectives of these experiments were to clarify the influence of cold treatments on subsequent flowering in this species, and to determine the relationship between temperature and time to flower.

Materials and Methods

General. During forcing, plants were grown in a commercial soilless medium containing composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (MetroMix 510; Scotts-Sierra Horticultural Products, Marysville, Ohio). Plants were top-watered as necessary with 7 mm N from a 20N-4.4P-16.6K all-purpose water-soluble fertilizer (Peter’s Professional Peat-lite Special; Grace-Sierra Horticultural Products, Milpitas, Calif.). Supplemental lighting (high-pressure sodium providing ≈50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant level) was initiated at 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ambient photosynthetic photon flux (PPF) and terminated when PPF exceeded 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

All cold treatments were delivered in a 5 ± 0.5 °C cooler lit for 9 h·d⁻¹ with cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.) at ≈10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. While in the cooler, plugs were watered with well water (CaCO₃ at 340 mg·L⁻¹) acidified (93% H₂SO₄) to a titratable alkalinity of CaCO₃ at 100 mg·L⁻¹.

Seedlings with 10 to 12 nodes (P1) grown in 128-cell trays (10-mL cell volume) were received from a commercial producer 21 Dec. 1994. Seedlings with 12 to 16 nodes (P2) grown in 50-cell trays (85-mL cell volume) were received on 27 Oct. 1994.

Cold treatments (Expt. 1). Upon arrival, 10 plants of each size were removed from the plug tray, thinned to a single plant per cell (singulated), and transplanted. The P1 were

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Table 1. Actual average daily air temperatures during forcing of *Campanula carpatica* 'Blue Clips' to visible bud (VB) and to opening of the first flower (FLW). DIF was calculated as the difference between average daily day temperature and average daily night temperature, adjusted to reflect natural daylengths during the forcing period. P1 were from 128-cell trays and averaged 10 to 12 nodes at start of forcing. P2 were from 50-cell trays and averaged 12 to 16 nodes. P3 were from 5.5-cm pots.

Plant size	Force date	Temp (°C)					
		Setpoint	Forcing to VB	DIF	VB to FLW	DIF	Forcing to FLW
P1	7 Apr. 1995	15.0	16.3	1.4	17.2	1.9	16.7
		18.0	19.4	1.4	19.2	1.2	19.4
		21.0	21.1	-0.1	21.2	0.0	21.1
		24.0	23.6	0.4	23.7	0.6	23.6
		27.0	27.7	-0.2	26.9	0.1	27.4
P2	23 Jan. 1995	15.0	15.5	0.8	16.0	1.6	15.6
		18.0	18.4	1.1	19.4	1.8	18.7
		21.0	20.7	-0.1	21.3	0.2	20.9
		24.0	22.8	0.2	22.9	0.6	22.9
		27.0	25.9	0.3	26.1	0.5	25.9
P3	4 Feb. 1995	15.0	15.4	0.8	15.9	1.6	15.6
		18.0	18.5	1.1	19.1	1.8	18.8
		21.0	20.6	-0.1	21.2	0.2	20.8
		24.0	22.8	0.2	23.1	0.6	22.9
		27.0	25.8	0.3	26.6	0.5	26.1

transplanted into 10-cm (470 mL) containers; P2, into 16-cm (2.2-L) containers. Plants were placed in the greenhouse at 20 °C and grown under a 4-h NI from 2200 to 0200 HR. The NI was supplied by 60-W incandescent lamps at a PPF of 3 to 5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, as measured by a LI-COR quantum sensor model LI-189 (LI-COR, Lincoln, Neb.). Black cloth was pulled at 1700 HR and opened at 0800 HR on all benches. The remaining plants in the plug trays were placed in a 5 ± 0.5 °C cooler. Ten plugs of each size were removed from the cooler at 2-week intervals, singulated, transplanted, and placed under NI in the greenhouse. Dates of the first visible bud (flower

bud ≈ 2 mm long) and opening of the first flower were recorded for each plant, and days to visible bud and flowering were calculated. At flowering, total plant height, number of visible flower buds, and number of nodes under the terminal flower on the main stem were determined. The number of nodes formed on the main stem during forcing was calculated.

Temperature control. Air temperatures on each bench were monitored with two 36-gauge (0.127 mm) thermocouples connected to a CR-10 datalogger (Campbell Scientific, Logan, Utah). The datalogger collected temperature data every 10 s and recorded the hourly

average. Nighttime air temperatures under black cloth on solid aluminum benches can be 3.5 °C cooler than greenhouse air temperatures because of radiant heat loss to the greenhouse glazing material (Heins and Faust, 1994). To provide uniform temperature conditions, the datalogger controlled a 1500-W electric heater under each bench, which provided supplemental heat as needed throughout the night. Actual daily air mean was 20.4 °C. The maximum difference in actual daily air mean between any two treatments throughout the experiment was 0.6 °C.

Data analysis. Analysis of variance was used to determine the relationship between

Table 2. Influence of time at 5 °C on mean days to visible bud (VB), days to flower (FLW), number of nodes formed during forcing, number of flower buds present at flowering, and height at flowering of two sizes of *Campanula carpatica* 'Blue Clips'. Plants from 128-cell trays (P1) averaged 11 nodes at planting, and those from 50-cell trays (P2) averaged 13 nodes.

Weeks	Days			Nodes (no.)			Flower	Ht
at 5 °C	VB	FLW	VB to FLW	Planting	Final	New	buds (no.)	(cm)
P1 plants								
0	31	48	17	11	25	14	28	16
2	34	56	21	12	28	16	17	16
4	34	54	20	11	27	16	32	18
6	25	51	26	10	25	15	22	18
8	32	53	21	12	30	18	21'	16
10	24	42	18	10	25	14	23	14
12	25	44	19	13	29	16	26	14
14	25	42	17	12	27	15	25	16
Average	29	49	20	11	27	16	24	16
Significance								
Weeks 5 °C	***	***	***	NS	**	NS	***	**
Linear	***	***	*		NS		NS	*
Quadratic	NS	***	***		NS		NS	NS
P2 plants								
0	26	48	21	15	34	20	33	22
2	27	48	21	17	34	18	31	22
4	27	49	22	15	30	15	33	19
6	29	50	21	12	30	18	26	20
8	26	47	20	14	31	17	32	18
10	30	50	20	12	28	16	35	18
12	28	47	19	12	30	18	45	20
14	25	47	20	13	30	17	52	18
Average	27	48	20	13	31	18	36	19
Significance								
Weeks 5 °C	NS	NS	NS	*	**	NS	***	***
Linear				**	**		***	***
Quadratic				NS	*		***	*

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

Fig. 1. Influence of forcing temperature on time to flower in *Campanula carpatica* 'Blue Clips' plants from 128-cell trays (P1), 50-cell trays (P2), and 5.5-cm pots (P3). Each symbol (●, ■, or ▲) represents the mean of 10 plants. (A), (B), and (C) show days for the indicated developmental stage. The solid lines (—) represent the regression equation using pooled data for the three plant sizes. Lines in (D), (E), and (F) represent predicted values for the rate of progress (1/no. days) to the indicated developmental stage, based on linear regression. Statistical analysis and calculations are presented in Table 3.

duration of cold treatment and time to visible bud and flowering, number of buds and nodes at flowering, nodes formed during forcing, and total plant height. Trend analysis was performed using the SAS GLM procedure (SAS Institute, 1989).

Forcing temperature (Expt. 2). Three plant sizes were tested. Plants in 50-cell trays were placed in a 5 °C cooler for 13 weeks until 23 Jan. 1995, then singulated, transplanted into 13-cm (1.1 L) square containers, and moved into each of five greenhouses set to 15, 18, 21, 24, or 27 °C. Plants in 128-cell trays were placed in a 5 °C cooler for 15 weeks until 7 Apr. 1995, when they were singulated, transplanted into 10-cm containers, and placed into the various treatment zones. Field-grown plants (P3) in 5.5-cm pots (190-mL cell volume) were received on 17 Jan. 1995, transplanted into 2.2-L containers, and placed into the several greenhouses on 4 Feb. 1995. Ten plants of

each size were placed in each of the treatment zones. Plants received natural daylengths with a 4-h NI from 2200 to 0200 HR, provided by high-pressure sodium lamps that delivered $\approx 90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Temperature control. Temperatures in each greenhouse were controlled by a greenhouse climate-control computer (Priva, model CD750; De Lier, Holland). Actual air temperatures were recorded every 15 min by a CR-10 datalogger. Actual average daily air temperatures were determined (Table 1) and used in all calculations.

Data analysis. Data were recorded as described for Expt. 1, and the diameter of five open flowers per plant on P2 and P3 was measured. P1 in the greenhouse set at 27 °C became severely heat stressed, so data from those plants were not included in the analysis. Base temperature (T_b) and thermal time, or degree-days, were calculated (Roberts and

Summerfield, 1987). The mean time to flower in each treatment was converted to a rate by taking the reciprocal, and the relationship between the rate of progress to flowering ($1/f$) and the mean temperature T in °C was determined by

$$1/f = b_0 + b_1 T \quad [1]$$

where b_0 and b_1 are constants. Once b_0 and b_1 were calculated, the base temperature, T_b , was calculated as

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

and thermal time, or degree-days (°Cd), was determined by

$$^{\circ}\text{Cd} = 1/b_1 \quad [3]$$

Within each developmental stage, slopes and intercepts of regression equations for the three plant sizes were compared using the SAS REG procedure (SAS Institute, 1989).

Results

Cold treatments. Time to visible bud and flowering decreased in P1 after cold treatments, but did not change in P2 (Table 2). Cold treatment did not affect the number of new nodes formed on the main stem during forcing on either P1 or P2. The number of flower buds on P1 differed between treatments, but there were no consistent trends in response to cold treatments. The number of flower buds increased on P2 as duration of cold treatments increased. Average height at flowering in P1 and P2 decreased slightly with increasing duration of cold treatment; while statistically significant, the response was not consistent.

Forcing temperature. Plants flowered more quickly at higher temperatures (Fig. 1). Time from forcing to flowering averaged 57 d at ≈ 16 °C, and 36 d at ≈ 26 °C.

Rates of progress to visible bud and flowering were linear within the range of temperatures tested (Fig. 1). Slopes and intercepts of the regression functions within each developmental stage did not differ significantly between the three plant sizes. Since all plant sizes responded similarly to the forcing temperatures, data within each developmental stage were pooled. Base temperatures (T_b) calculated from pooled data were between -0.7 and 2.1 °C (Table 3).

Larger initial plant size resulted in more flower buds per plant in all treatments (Fig. 2).

Table 3. Parameters of linear regression analysis relating forcing temperature to rate of progress to visible bud and flowering in *Campanula carpatica* 'Blue Clips'. Intercept and slope were used in Eqs. [2] and [3] to calculate base temperature (T_b) and degree-days, or thermal time (°days). Visible bud and flowering data for P1 plants forced at setpoint 27 °C were not included in the calculations because the plants were damaged by heat stress.

Plant size	Developmental stage	Intercept (b_0) (1/days)	Slope (b_1) (1/days)/°C	T_b (°C)	Degree-days	r^2
P1 (10–12 nodes)	Forcing to visible bud	-0.0030 ± 0.0111^2	0.0022 ± 0.0005	1.4	455	0.89 ^{NS}
	Visible bud to flower	0.0062 ± 0.0115	0.0024 ± 0.0006	-2.6	417	0.90 ^{NS}
	Forcing to flower	-0.0009 ± 0.0028	0.0012 ± 0.0001	0.8	833	0.98*
P2 (12–16 nodes)	Forcing to visible bud	-0.0029 ± 0.0064	0.0020 ± 0.0003	1.5	500	0.93**
	Visible bud to flower	-0.0112 ± 0.0126	0.0031 ± 0.0006	3.6	323	0.90*
	Forcing to flower	-0.0032 ± 0.0007	0.0012 ± 0.0000	2.7	833	0.99***
P3 (5.5-cm pots)	Forcing to visible bud	-0.0041 ± 0.0021	0.0024 ± 0.0001	2.0	417	0.99***
	Visible bud to flower	0.0039 ± 0.0139	0.0023 ± 0.0006	-1.7	435	0.80**
	Forcing to flower	0.0015 ± 0.0022	0.0011 ± 0.0001	-1.4	909	0.97**
Pooled	Forcing to visible bud	-0.0025 ± 0.0046	0.0022 ± 0.0002	2.1	455	0.97**
	Visible bud to flower	0.0017 ± 0.0065	0.0025 ± 0.0030	-0.7	400	0.97*
	Forcing to flower	0.0002 ± 0.0013	0.0011 ± 0.0001	0.0	909	0.99***

²Standard error.

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

Fig. 2. Influence of forcing temperature on (A) number of flower buds visible at opening of the first flower, (B) average flower diameter, and (C) total plant height in *Campanula carpatica* 'Blue Clips' plants from 128-cell trays (P1), 50-cell trays (P2), and 5.5-cm pots (P3). For (A) and (C), each symbol (●, ■, or ▲) represents the average of 10 plants. For average flower diameter (B), each symbol (● or ■) represents the average of 50 flowers. Flowers on P1 were not measured. Error bars represent 95% confidence intervals.

The difference between P1 and P2 was much less than that between P2 and P3. Plants forced at $\approx 16^\circ\text{C}$ had more than twice the number of flower buds per plant than those forced at $\approx 26^\circ\text{C}$. Flower diameter on P2 and P3 was largest when plants were forced at $\approx 16^\circ\text{C}$. Average plant height in P2 and P3 did not vary with temperature. P1 forced at $\approx 16^\circ\text{C}$ were ≈ 4 cm taller than those in the other treatments.

Discussion

Time to visible bud and flowering for P2 did not change as duration of cold treatment increased, but that for P1 decreased slightly. Variations in forcing conditions, such as seasonal changes in light intensity, may have influenced rates of development of P1. Cold treatments did not have a consistent promotive effect on flowering. These findings contrast with those of Armitage (1995), who reported a reduction in time to flower from ≈ 150 d for

uncooled plants to ≈ 100 d after 12 weeks at 2°C for *C. carpatica* 'White Clips'. According to temperature data provided by Armitage, forcing temperatures in the greenhouse were not consistent throughout the course of his experiment. Plants that were cooled experienced warmer forcing temperatures than uncooled plants, which certainly would hasten flowering of the cooled plants. A forcing schedule for *C. carpatica* 'Karl Foerster' suggested by Madsen and Madsen (1986) states that plants will be ready for sale 8 to 10 weeks after the start of forcing under long days at 15°C , which is similar to the time to flowering we observed.

Hastening of flowering in *C. carpatica* by cold treatments may be more evident when forcing occurs under DE rather than NI treatments. Preliminary experiments indicate a reduction of ≈ 10 d in time to flowering after 15 weeks at 5°C when plants were forced under DE (9-h normal day plus 7-h extension); the reduction was ≈ 4 d when plants were forced under NI (E. Runkle, personal communication).

Flower bud count on P2 increased with cold treatment, but since time to flowering was not reduced and flowering occurred even in the absence of cold treatment, this is not a vernalization response. An increase in flower count after vernalization was reported in some species of *Dianthus*, but was accompanied by a hastening of flowering (Chouard, 1960). The increase in flower bud count reported here may reflect the higher natural light levels experienced by plants forced in the spring, although P1 did not respond similarly.

The two plant sizes tested displayed inconsistent responses to the cold treatments. However, in general, holding plugs of *C. carpatica* 'Blue Clips' at 5°C for up to 14 weeks reduced subsequent time to flower by no more than 10 d. Exposure to low temperatures had no detrimental effects on any of the characteristics evaluated in this work.

To complete a developmental process, a plant must experience a specific number of units of degree-days above the base temperature characteristic of that process (Roberts and Summerfield, 1987). Once the base temperature and the amount of thermal time required for a developmental stage are known, predicted time for completion of development can be calculated. Thermal time commonly is used to schedule planting and harvest of fruit and vegetable crops (Roberts and Summerfield, 1987). For *C. carpatica* 'Blue Clips', calculated degree-days to visible bud were 455; to flower, 909. To calculate time to visible bud or flower at any temperature between T_b and T_c , the degree-days required for that developmental stage are divided by the degrees provided above the T_b . For example, time to flower for plants forced at 20°C ($T_b = 0.0^\circ\text{C}$) is estimated to be 909 degree-days/ $20.0^\circ\text{C} = 45.5$ d. In comparison, actual time to flower for plants forced at $\approx 20^\circ\text{C}$ in Expt. 1 was ≈ 48 to 49 d.

Campanula carpatica 'Blue Clips' is native to temperate alpine regions, and the plants in this experiment were most attractive, in terms of the number and size of flowers, when

forced at or below 21°C . For growers, plant appearance must be weighed against the longer production time required with lower forcing temperatures. Forcing at 20°C will hasten flowering by ≈ 5 d compared to forcing at 18°C .

Average forcing temperature had little effect on plant height in most treatments. However, P1 plants forced at $\approx 15^\circ\text{C}$ were 3 to 4 cm taller than P1 in other treatments. Diurnal changes in temperature may have affected plant height. The difference between day temperature and night temperature (DIF) strongly influences plant height in a wide range of pot and bedding plants (Erwin and Heins, 1995; Myster and Moe, 1995). The average daily DIF in this experiment was $<2^\circ\text{C}$ in all treatments, but P1 were forced during April and May, when daytime temperatures in the $\approx 15^\circ\text{C}$ treatment periodically rose 5 to 12°C above night temperatures. Daytime temperatures fluctuated by $<6^\circ\text{C}$ in the other treatments. In many plant species, internode elongation increases as DIF increases (Erwin and Heins, 1995; Myster and Moe, 1995). P1 plants were exposed to occasional peaks of high daytime temperatures, which may have increased plant height.

P2 bloomed ≈ 5 d earlier than either the larger or smaller seedlings. The plants from 5.5-cm pots had been pruned before shipment, which apparently delayed their development. We expect that cutting back plants of any size would delay their flowering similarly. Slopes of the regression lines for each stage of development did not differ significantly between plug sizes, indicating that all plant sizes responded similarly to the forcing temperatures.

Larger plugs generally resulted in taller plants with more flowers. Seedlings from 128-cell trays (10 to 12 nodes) developed into well-proportioned flowering plants in the 10-cm containers, and plants with 12 to 16 nodes were appropriate for the 16-cm (2.2-L) containers.

In conclusion, *C. carpatica* 'Blue Clips' is an obligate long-day plant that does not require a cold treatment for flowering. Exposure to 5°C reduced time to visible bud and flowering by no more than 10 d, and had little effect on flower count or plant height. Plants forced at 26°C flowered ≈ 21 d earlier than those forced at 16°C . Flowers were most abundant and largest at 16°C .

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