Effect of Temperature and Daily Light Integral on Flower Size and Number of Campanula carpatica ‘Blue Clips’, ‘Deep Blue Clips’, and Campanula ‘Birch Hybrid’

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Abstract. The effects of temperature on flower size and number of flower buds of Campanula carpatica Jacq. ‘Blue Clips’, ‘Deep Blue Clips’, and Campanula ‘Birch Hybrid’ were investigated in four temperature and light-transfer experiments. In year 1, ‘Blue Clips’ and ‘Birch Hybrid’ plants were grown initially at 20°C and then transferred at visible flower bud (VB) to 14, 17, 20, 23, or 26°C until flower (Expt. 1). In Expt. 2, ‘Blue Clips’ and ‘Birch Hybrid’ plants were transferred from 14 to 26°C or from 26 to 14°C at various intervals after flower induction. Flower size of both species was negatively correlated with average daily temperature (ADT) after VB; flowers on plants grown at 14°C were 35% larger than those on plants grown at 26°C. In contrast, temperature before VB had only a small effect on final flower size in both species, although flower diameter of ‘Birch Hybrid’ plants grown at constant 26°C was 20% smaller than that of the plants grown initially at 20°C and then transferred to VB to 26°C. For both species, the longer the exposure to high temperature after VB, the smaller the flowers. Number of flower buds at flower in ‘Birch Hybrid’ decreased as ADT after VB increased. In year 2, ‘Deep Blue Clips’ plants were grown at constant 20°C under high or low daily light integral (DLI) of 4 mol·m⁻²·d⁻¹ until VB, and then transferred to 14, 17, 20, 23, or 26°C under high or low DLI (Expt. 3). In Expt. 4, ‘Deep Blue Clips’ plants were grown at 14, 17, 20, 23, or 26°C until VB, and then transferred to constant 20°C under high or low DLI until flower. Flower size (petal length) was negatively correlated with ADT both before and after VB, while flower bud number was negatively correlated with the ADT only after VB, regardless of DLI. In both experiments, petal length decreased by 0.3 to 0.5 mm per 1°C increase in ADT before or after VB. Flowers were larger and more numerous under high than under low DLI after VB, regardless of the DLI before VB.

The Campanulaceae include >700 species that are annual, biennial, or perennial. Campanula carpatica ‘Blue Clips’, ‘Deep Blue Clips’, and Campanula ‘Birch Hybrid’ are popular garden perennial species that have numerous, blue, bell-shaped flowers and can be grown as flowering potted plants. ‘Blue Clips’ (Whitman et al., 1997) and ‘Deep Blue Clips’ (unpublished data) plants have no vernalization requirement and have an obligate long-day requirement for flowering, while ‘Birch Hybrid’ (Finical et al., 1998) plants have an obligate vernalization requirement but are day-neutral for flowering.

Flower size and number, important quality attributes for many floral crops, generally decrease as temperature increases. This phenomenon has been noted in C. carpatica ‘Blue Clips’ (Niu et al., 2001; Whitman et al., 1997), C. ‘Birch Hybrid’ (Frane, 1999), and pansy ‘Universal Violet’ (Viola xwittrockiana Gams.) (Pearson et al., 1995). Increasing daily light integral (DLI) can compensate for the negative effect of high temperatures in many cases. More and larger flowers of C. carpatica ‘Blue Clips’ were obtained at 20 to 22°C under DLI of 10 mol·m⁻²·d⁻¹ compared to those at 16 to 18°C under DLI of 4 mol·m⁻²·d⁻¹ (Niu et al., 2001). Supplementary lighting for 22 d during greenhouse production increased the size and number of C. carpatica ‘Karl Foerster’ flowers during the marketing and postharvest periods (Serek, 1991).

Stage of growth may affect response to environmental conditions. Pearson et al. (1995) reported that increasing temperature before visible bud (VB) had little effect on flower size of pansy ‘Universal Violet’, but affected flower size in all subsequent bud developmental stages. If other species respond to temperature as does pansy, such information might be used to maintain or improve plant quality by adjusting temperature during crop development. Whether the effect of DLI on flower size and number varies with developmental stages is not known.

There are several phases during the flowering process: flower induction, which is the initial biochemical changes that lead to flowering; flower initiation, during which the flower bud or inflorescence can be first identified under a microscope; bud or inflorescence development or expansion; and, finally, anthesis. Since VB can easily be identified macroscopically, the objectives of this study were to investigate when flowers of ‘Blue Clips’, ‘Deep Blue Clips’, and ‘Birch Hybrid’ were responsive to temperature during flower development and determine how DLI before or after VB affected flower size and number of ‘Deep Blue Clips’.
The number of plants per treatment was ten for 'Blue Clips' and six for 'Birch Hybrid'. A total of nine of the 'Birch Hybrid' plants did not flower; data for those plants were not included in analyses.

Dates of the first VB and flower were recorded, as well as the diameter of the first open flower. For 'Birch Hybrid' plants, the number of flower buds per shoot at flower was recorded for two shoots.

Year 2

General plant culture. Seedlings of C. carpatica 'Deep Blue Clips' with three true leaves were received from a commercial producer in 128-cell trays on 4 Sept. 1999. Upon receipt, seedlings were placed in a greenhouse maintained at 20 ± 2 °C under natural photoperiods. When seedlings had produced an average of seven leaves, they were transplanted to 10-cm (470-mL) containers, grown in a commercial medium (Peat-Perlite Mix, Michigan Grower Products, Galesburg, Mich.), and irrigated with the same type of nutrient solution used in year 1.

In both years, greenhouse temperatures were controlled by a greenhouse climate-control computer (model CD750, Privia, De Lier, The Netherlands). Plant temperatures were measured throughout the experimental period by inserting thermocouples (chromel-constantan, 0.127 mm in diameter) into shoot tips. The thermocouples were reinserted to a new position every 1 to 2 weeks as plants grew. Vapor pressure deficit (VPD) was maintained around 0.7 KPa in all sections by injecting water vapor as needed. Actual temperatures (air and plant) and PPFD were measured at 10-s intervals, and the hourly average was recorded by a CR-10 datalogger (Campbell Scientific, Logan, Utah). The actual plant average daily temperature (ADT) from forcing to VB (majority of the plants), from VB to flower, and from forcing to flower over the entire experimental period were calculated and used in all data analyses.

Experimental design. Five greenhouse sections (4.7 × 4.1 m) were set at 14, 17, 20, or 26 °C and each section had two DLI levels. One of the three benches (high DLI bench; average 26 μmol·m⁻²·s⁻¹) from forcing to VB (majority of the plants), from VB to flower, and from forcing to flower over the entire experimental period were calculated and used in all data analyses.

Five greenhouse sections (4.7 × 4.1 m) were set at 14, 17, 20, or 26 °C and each section had two DLI levels. One of the three benches (high DLI bench; average 17 mol·m⁻³·d⁻¹) from forcing to VB (majority of the plants), from VB to flower, and from forcing to flower over the entire experimental period were calculated and used in all data analyses.

Results and Discussion

Year 1

'Blue Clips'. Flower diameter in both experiments was negatively correlated with ADT after VB (Fig. 1A). Flower diameter in Expt. 1 was largest when plants were grown at constant 14 °C or grown initially at 20 °C and then transferred to 14 or 17 °C until flower, and smallest when plants were grown at constant 26 °C or grown initially at 20 °C and then transferred to 26 °C at VB.

In Expt. 2, the diameter of plants that were transferred from 26 to 14 °C before VB (Fig. 1A) did not differ significantly from that of plants held in constant 14 °C. Similarly, flower diameter of plants that were transferred from 14 to 26 °C before VB (W1-14-26 and W3-14-26) did not differ from that in constant 26 °C.

Flower diameter of 'Blue Clips' plants that were transferred from 26 to 14 °C was smaller than that of plants held at constant 14 °C, but larger than that of those at constant 26 °C (Fig. 1A). Similarly, flower diameter of plants that were transferred to 26 °C from 14 to 60% larger at constant 14 °C than at 26 °C before VB (W1-26-14) was the same as that of plants grown at 20 °C (W1-26-20) but larger than that of plants grown at 20 °C before VB (W2-26-20). Flower diameter of 'Blue Clips' plants that were transferred from 26 to 14 °C was smaller than that of plants grown at 20 °C before VB (W1-26-20) but larger than that of plants grown at 20 °C before VB (W2-26-20). Flower diameter of 'Blue Clips' plants that were transferred from 26 to 14 °C was smaller than that of plants grown at 20 °C before VB (W1-26-20) but larger than that of plants grown at 20 °C before VB (W2-26-20).

The results indicate that when 'Blue Clips' plants were grown at cool temperatures initially and transferred to warm temperatures at or before VB, the final flower diameter was comparable to that of plants grown at warm temperatures throughout. Conversely, when plants were grown at warm temperatures initially and transferred to cool temperatures at or before VB, the flower diameter was similar to that of plants grown at a constant cool temperature. The longer the plants were exposed to warm temperatures after VB, the smaller the flower. After VB, plants grown part of the time at a cool temperature and part at a warm one had a intermediate flower size that was negatively correlated with ADT (Fig. 1A).

'Birch Hybrid'. Flower diameter increased as temperature after VB decreased. In Expt. 1, flower diameter of plants grown at constant 14 °C did not differ from that of the plants grown initially at 20 °C and then transferred to 14 °C at VB (Fig. 1B). However, flower diameter at constant 26 °C was 20% smaller than that of the plants grown initially at 20 °C and then transferred to 26 °C at VB. When plants were grown initially at 20 °C and then transferred to VB at 14, 17, 20, or 23 °C, the lower the temperature after VB, the larger the flowers. Flower diameter was 25% or 60% larger at constant 14 °C than at constant 20 or 26 °C.

In Expt. 2, flower diameter of plants grown at 26 °C for 1 week and then transferred to 14 °C (W1-26-14) was the same as that of plants grown at constant 14 °C (Fig. 1B). Flower diameter following transfer from 26 to 14 °C after VB (W2-26-14 and W3-26-14) was intermediate between those at constant 14 °C and constant 26 °C, whereas diameter following transfer from 14 to 26 °C before VB (W1-14-26) was the same as at constant.
26 °C (Fig. 1B). In W2-14-26 and W3-14-26, some plants were transferred from 14 to 26 °C after VB, so the flower diameter was larger than that at constant 26 °C.

The number of flower buds per shoot in ‘Birch Hybrid’ also decreased linearly as ADT after VB increased but the correlation was low (Fig. 1C). In ‘Blue Clips’, the number of flower buds at first flower decreased as forcing temperature increased from 14 to 26 °C (Niu et al., 2001; Whitman et al., 1997) but was not recorded in this study.

Flowers of ‘Blue Clips’ in W3-26-14, W5-26-14, W1-14-26, and constant 26 (Fig. 1A) and of ‘Birch Hybrid’ in W2-26-14, W3-26-14, W1-14-26, and constant 26 (Fig. 1B) were smaller than the average (based on the linear regression line), since some or all of the plants in the treatments were exposed to 26 °C during early flower bud development (Table 1). Generally, flowers of both species were larger in Expt. 1 than in Expt. 2 at the same ADT after VB, although differences were not significant. The tendency toward smaller flowers in Expt. 2 suggests that exposure to 26 °C from flower initiation to VB had at least some effect on final flower size.

Time from VB to flower decreased as ADT from VB to flower increased for both species (Fig. 2), which agrees with previous reports (Frame, 1999; Whitman et al., 1997). Time from VB to flower decreased ≈2 weeks as ADT increased from 15 to 20 °C (Fig. 2A and B). Frame (1999) reported that flower developmental rate in ‘Birch Hybrid’ increased as temperature increased from 17 to 24 °C but decreased as temperature continued to increase from 24 to 29 °C. In this study, time from VB to flower decreased as ADT increased from 14 to 24 °C, but did not change as ADT increased from 24 to 26 °C (Fig. 2A and B). Therefore, 26 °C is probably out of the linear range for flower development in both species. Flower developmental rate in ‘Blue Clips’ increased linearly with ADT from 14 to 25 °C, regardless of the combinations of day and night temperatures (Niu et al., 2001).

For both species, increasing the temperature hastened flower development but reduced flower size and number. Flower size was negatively correlated with the temperature after VB. Although the specific effect of all temperatures before VB on final flower size is not clear from this study, high temperature (26 °C) before VB did reduce flower size slightly.

**Year 2**

‘Deep Blue Clips’. Flower size (petal length) and number of flower buds decreased as ADT increased (Fig. 3 A and D) for plants grown at a constant temperature, irrespective of the DLI from forcing to flower. The number of flower buds was higher under higher (17 mol·m⁻²·d⁻¹) than under low DLI (5.7 mol·m⁻²·d⁻¹; Fig. 3D).

For plants grown initially at 20 °C until VB and then transferred to various temperatures (Expt. 3), flower size and number of flower buds decreased linearly as ADT after VB increased under all DLIs (Fig. 3 B and E). Differences in slopes and intercepts of the linear regression lines for flower size vs. ADT after VB were nonsignificant (Fig. 3B), provided that the DLI after VB was the same. Therefore, data were pooled under the same DLI after VB for linear regression lines (Fig. 3 B, C, and E). However, flower size and number of flower buds differed significantly when plants were grown under high (solid symbols) vs. low (open symbols) DLIs after VB (Fig. 3 B and E). Petal length decreased ≈0.5 and 0.3 mm per 1 °C increase in ADT after VB under low and high DLIs, respectively (Fig. 3B). Plants averaged five fewer flower buds for every 1 °C rise in temperature after VB (Fig. 3E). Plants had ≈100 more flower buds when grown under the high DLI after VB, regardless of the DLI before VB or temperature after VB (Fig. 3E).

Flower size of plants grown at various temperatures until VB and then transferred to 20 °C (Expt. 4) was also negatively correlated with the temperature before VB (Fig. 3C). Except for the plants grown at low DLI before VB and high DLI after VB (solid triangle symbol, r² of 0.89), the number of flower buds was not influenced by the ADT before VB (Fig. 3F). Flowers were larger and flower buds were more numerous under high DLI after VB, regardless of the DLI before VB.

Time from forcing to VB, from VB to flower, or from forcing to flower was unaffected by DLI before or after VB, and was closely correlated with ADT (Figs. 4–5). Time from VB to flower in Expt. 3 and from forcing to VB in Expt. 4 are not presented, since ADT was constant during those periods. Times from

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**Table 1. Effect of time of transferring plants from 14 to 26 °C on days to visible bud (VB) of Campanula carpatica ‘Blue Clips’ and Campanula ‘Birch Hybrid’ (Expt. 2).**

| Treatment Time (d) from ADT | ADT (°C) | Time (d) from forcing to VB |
|----------------------------|----------|-----------------------------|
| **Blue Clips**              |          |                             |
| Constant 14 °C              | ---      | 14.7                        |
| Constant 26 °C              | ---      | 25.1                        |
| Transfer from 26 to 14 °C   | 7        | 17.3                        |
| W1-26-14                    |          | 14.7                        |
| W3-26-14                    | 21       | 22.7                        |
| W5-26-14                    | 35       | 25.1                        |
| Transfer from 26 to 14 °C   | 7        | 22.3                        |
| W1-14-26                    |          | 25.1                        |
| W3-14-26                    | 21       | 17.7                        |
| W5-14-26                    | 35       | 14.7                        |
| **Birch Hybrid**            |          |                             |
| Constant 14 °C              | ---      | 14.5                        |
| Constant 26 °C              | ---      | 26.12                       |
| Transfer from 26 to 14 °C   | 7        | 18.4                        |
| W1-26-14                    |          | 14.7                        |
| W3-26-14                    | 14       | 25.4                        |
| W5-26-14                    | 21       | 25.4                        |
| Transfer from 26 to 14 °C   | 7        | 21.1                        |
| W1-14-26                    |          | 25.4                        |
| W3-14-26                    | 14       | 16.5                        |
| W5-14-26                    | 21       | 14.7                        |

*Means ± 95% confidence interval.
forcing to VB, from VB to flower, or from forcing to flower decreased as ADT during those periods increased until $24^\circ C$, but increased or did not change as ADT continued to increase above $24^\circ C$. Flower developmental rate increases linearly as temperature increases between the base temperature, at which there is no growth, and the optimum temperature, at which developmental rate is maximum (Roberts and Summerfield, 1987). Therefore, the optimum temperature for rapid flower development for ‘Deep Blue Clips’ was $24^\circ C$.

Time from flower induction (start of long days) to flower initiation and to VB and from flower initiation to VB were longest at 14 days) to flower initiation and to VB, from flower initiation to VB and from VB to flower, or from forcing to flower decreased as ADT during those periods increased until $24^\circ C$, but increased or did not change as ADT continued to increase above $24^\circ C$. Flower developmental rate increases linearly as temperature increases between the base temperature, at which there is no growth, and the optimum temperature, at which developmental rate is maximum (Roberts and Summerfield, 1987). Therefore, the optimum temperature for rapid flower development for ‘Deep Blue Clips’ was $24^\circ C$.

Time from flower induction (start of long days) to flower initiation and to VB and from flower initiation to VB were longest at 14 $^\circ C$ and shortest at 20 $^\circ C$ in the temperature range studied (Table 2). Flower bud initiation was delayed 5 d when the temperature was raised from 20 to 26 $^\circ C$.

In Expts. 3 and 4, temperature before or after VB affected flower size, but only the temperature after VB affected the number of flower buds. Pearson et al. (1995) concluded that flower size of pansy was influenced only by the temperature after VB. However, at least some of their data did show that flowers grown at constant 10 $^\circ C$ were 13% larger than those of plants grown initially at 25 $^\circ C$ and then transferred to 10 $^\circ C$ at VB. Conversely, when plants were grown at 10 $^\circ C$ until VB and then transferred to 25 $^\circ C$ until flower, flowers were 25% larger than those of plants grown at constant 25 $^\circ C$. In year 1, ‘Blue Clips’ and ‘Birch Hybrid’ plants that were exposed to high temperature before VB tended to have smaller flowers. The time from flower bud initiation to VB was 9.5, 6.5, and 7.5 d at 14, 20, and 26 $^\circ C$, respectively, for ‘Deep Blue Clips’ (Table 2). Cool temperatures from both flower bud initiation to VB and VB to flower may be critical for maximizing flower size. Time from flower bud initiation to VB may be 7 d for ‘Blue Clips’ and ‘Birch Hybrid’ at $20^\circ C$, since time to flower for these species was similar to that for ‘Deep Blue Clips’ (Frane, 1999; Whitman et al., 1997). Thus, in order to maximize flower size, plants should not be exposed to high temperatures during the week before VB.

Increasing DLI before VB did not increase flower size or number of flower buds, although the low DLI level tested was above 5 mol·m$^{-2}$·d$^{-1}$. Therefore, supplementary lighting to increase the DLI above 5 mol·m$^{-2}$·d$^{-1}$ before VB is unnecessary for ‘Deep Blue Clips’. However, supplementary lighting after VB partially compensated for the negative effect of high temperatures. For example, the number of flower buds was 40% higher under the high DLI (17 mol·m$^{-2}$·d$^{-1}$) after VB at 22 to 24 $^\circ C$ than under the low DLI (5.7 mol·m$^{-2}$·d$^{-1}$) at 14 to 16 $^\circ C$ (Fig. 3E), although flowers were larger at cooler temperatures.

Quantification of lateral branching is difficult in C. carpatica. Instead, the number of flower buds can be recorded to reflect branching status when the first flower is fully open, a high number of buds indicating more branching. Plants developed more lateral branches from their existing shoots as they elongated under high DLI after VB.

Since high DLI was obtained by supplementing natural light with HPS lamps, both light quantity and quality may have contributed to the increased number of flower buds. The ratio of red (R) to far red (FR) was 5.9 for HPS lamps (Whitman et al., 1998), but only 1.15 for sunlight (Smith, 1994). Thus, the actual R/FR ratio was higher in the high than in the low DLI treatments. High R/FR conditions enhance branching and suppress stem elongation (Smith, 1994). Plants were more compact under high than under low DLI.

Pearson et al. (1995) suggested that production of small pansy flowers at high temperature might be attributable to a reduced duration of flower development, which would limit the time for cell division or for cellular expansion. For the three species tested in our study, flower size increased linearly as the time from VB to flower increased (data not shown), indicating that the flowers were larger when the duration for flower development was longer. Since we did not measure cell number or size in flowers, we do not know which was affected.

In summary, flower size in ‘Deep Blue Clips’ decreased as the temperature before or after VB increased. The number of flower buds was not influenced by the temperature before VB, while it was negatively correlated with the temperature after VB. Increasing DLI after VB increased flower size and number, but a DLI of 5.7 to 17 mol·m$^{-2}$·d$^{-1}$ before VB did not affect flower size and number of flower buds in
Deep Blue Clips. For all species, flower size and number decreased as temperature after VB increased.

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Table 2. Time (days) to flower bud initiation and visible bud (VB) in Campanula carpatica ‘Deep Blue Clips’.

| Temp (°C)  | 14.0 | 20.0 | 26.0 |
|-----------|-----|-----|-----|
| To flower bud initiation | 29.0 | 12.0 | 17.0 |
| To VB | 38.5 | 18.5 | 24.5 |
| From flower bud initiation to VB | 9.5 | 6.5 | 7.5 |

‘Deep Blue Clips’. For all species, flower size and number decreased as temperature after VB increased.

Fig. 5. Relationship between average daily temperature (ADT) and time from visible bud (VB) to flower (A) or from forcing to flower of Campanula carpatica ‘Deep Blue Clips’ (Expt. 3); relationship between ADT and time to VB (B) or flower (Expt. 4). Symbols indicate the DLI level before/after VB: High/High (●), High/Low (○), Low/High (▲), and Low/Low (◆). The solid line represents the reciprocal of developmental rate pooled from all the combinations of DLIs before and after VB. Regression coefficients (r2) for developmental rate vs. ADT in the range of 14 to 24 °C were 0.92 (Fig. 5A, VB to flower), 0.86 (B, forcing to flower), and 0.85 (C, forcing to VB), respectively. That for developmental rate vs. ADT in the range of 16 to 20 °C was 0.76 (D, forcing to flower).