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Day and night temperatures, daily light integral, and CO_2 enrichment affect growth and flower development of *Campanula carpatica* 'Blue Clips'

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Abstract

Campanula carpatica Jacq. 'Blue Clips' plants were grown in a greenhouse under nine combinations of day and night temperatures created by moving plants every 12 h among three day/night temperatures (15, 20, and 25°C). At each temperature, there were three daily light integrals (DLI; 4.2, 10.8, and 15.8 mol m^{-2} per day, averaged over the experimental period) created with varying supplemental light, and ambient (≈400 μmol mol^{-1}) and enriched (≈600 μmol mol^{-1}) CO_2 concentrations. Time to flower was closely related to average daily temperature (ADT), and was not significantly affected by the day or night temperatures delivered to achieve a specific ADT. Time to flower was not largely affected by DLI or CO_2 enrichment. As plant ADT increased between 15 and 25°C, flower diameter decreased about 1 mm per degree and was not related to the difference between day and night temperatures (DIF). Flower diameter was smallest and least sensitive to changes in temperature at lower DLI and at ambient CO_2 levels. There were 10 less flower buds and 0.3 g less dry mass per plant at first flower for every 1° increase in plant ADT at high and medium DLIs. Flower bud number and dry mass were relatively low and less sensitive to changes in ADT at low DLI, and increased slightly with CO_2 enrichment at medium and high but not at low DLI. Plant height was not related to ADT, but increased linearly as DIF increased from −6 to 12°C at all DLIs, but the response was stronger under low DLI than high and medium DLIs. Flower bud number and dry mass were correlated closely with the ratio of DLI to daily thermal time (base temperature of 0°C). Flower bud number and dry mass were highest when *C. carpatica* plants

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were grown at 15°C with a DLI of 10–15 mol m^{-2} per day.

Keywords: CO_2 enrichment; *Campanula carpatica*; Daily light integral; DIF; Flower size; Photothermal ratio

1. Introduction

Campanula carpatica Jacq. 'Blue Clips' is a popular herbaceous perennial native to the Carpathian Mountains of Eastern Europe. *C. carpatica* 'Blue Clips' is an obligate long-day plant (Mathon, 1959) that flowers faster at higher temperatures but with smaller and fewer flower buds compared to lower temperatures (Serek, 1991a; Whitman et al., 1997). Increasing temperature also decreased flower size and flower bud number of *Coreopsis grandiflora* Hogg ex Sweet. 'Sunray', *Leucanthemum×superbum* Bergman ex J. Ingram 'Snowcap', and *Rudbeckia fulgida* Ait 'Goldsturm' (Yuan et al., 1998), *Viola×wittrockiana* Gams. (Pearson et al., 1995) and seed geraniums (Armitage et al., 1981).

The effect of altering day and night temperatures independent of average daily temperature (ADT) on plant height, flower timing, flower size and flower number is not well understood for *C. carpatica* 'Blue Clips'. For many potted and bedding plant species grown at constant ADT, stem length or plant height increases as the difference between day and night temperatures (DIF) increases (Myster and Moe, 1995). Only a few studies have examined the effects of DIF on flower number and size. Serek (1991a), using a morning 2 h temperature dip, concluded that negative DIF reduced flower area for *C. carpatica* 'Blue Clips', although the experiment was not conducted at a constant ADT. DIF influenced flower diameter in *Catharanthus roseus* 'Grape Cooler' (Pietsch et al., 1995) but not in *Begonia×hiemalis* Fotsch (Willumsen et al., 1995) and pansy (Niu et al., 2000). A better understanding of the relative effects of ADT and DIF on plant morphology and flower number and size could be useful to develop temperature management strategies to produce *C. carpatica* 'Blue Clips' plants with maximum flower size and minimum stem elongation.

Increasing daily light integral (DLI) usually increases plant dry matter (DM) accumulation, hastens development and improves final plant quality. Increasing irradiance from 40 to 100 μmol m^{-2} s^{-1} (16 h per day) for the final 22 days of greenhouse production increased the size and number of *C. carpatica* 'Karl Foerster' flowers at harvest by about 50% (Serek, 1991b). Results from experiments with higher DLI have not been reported to our knowledge for *C. carpatica* though we have observed that flower number is greatly increased when plants are forced progressively later in the spring. Increasing DLI decreased time to flower and increased flower size of chrysanthemums (Karlsson et al., 1989) and

C. roseus 'Grape Cooler' (Pietsch et al., 1995). Low light delayed developmental rate in African violet, presumably due to an insufficient supply of photosynthates (Faust and Heins, 1993).

Both temperature and light affect plant growth, development, and quality, though their effects often are described independently. Liu and Heins (1997) proposed that the ratio of radiant energy (light) to thermal energy (temperature) could be used to describe the combined effects of temperature and light on plant quality. They confirmed that poinsettia quality (bract size, plant size and flower number) was related closely to photothermal ratio (PTR) (Liu, 1999). It would be interesting to know if herbaceous perennial plant quality is also related to PTR.

The objectives of this study were to determine the relative effects of ADT, different day and night temperatures, DLI, and CO_2 concentration on flower timing, flower size and number, and stem elongation of *C. carpatica* 'Blue Clips'. The information will be useful to develop production strategies that maximize flower number and size.

2. Materials and methods

2.1. Plant material and culture

Seedlings of *C. carpatica* 'Blue Clips' with three to five true leaves were received from a commercial producer in 128-cell trays (10 ml cell volume) on 15 October 1998. Upon receipt, seedlings were placed in a greenhouse maintained at 20°C under natural day length. When seedlings reached an average of seven leaves, they were transplanted to 10 cm (470 ml) containers and grown in a commercial medium (High Porosity Mix, Strong-lite Products, Pine Bluff, AR) composed of pine bark, fibrous Canadian sphagnum peat, horticultural vermiculite, screened coarse perlite and a wetting agent. Plants were irrigated as necessary with a nutrient solution of well water (EC of 0.7 mS cm^{-1} and 105, 35, and 23 mg l^{-1} Ca, Mg, and S, respectively) acidified with H_2SO_4 to a titratable alkalinity of 130 mg l^{-1} $CaSO_3$ and water soluble fertilizer providing 125–12–125–13 mg l^{-1} N–P–K–Ca (30% ammonical N) plus 1.0–0.5–0.5–0.5–0.1–0.1 mg l^{-1} (Fe–Mn–Zn–Cu–B–Mo) (MSU Special, Greencare Fertilizers, Chicago, IL). Planting density was 101 plants m^{-2}.

2.2. Experimental design

Six greenhouse sections (4.7×4.1 m^2), each with three benches, were set at 15, 20 or 25°C. Three sections were enriched with CO_2 to a setting of 1000 μmol mol^{-1}. In each section, high-pressure sodium (HPS) lamps were used to provide 12 h supplemental lighting starting at sunrise from 19 November 1998

to January 1999 at a PPF of 0, 145 or 250 μmol m^{-2} s^{-1}. An opaque barrier was placed between the low and medium DLI-treatment benches during the day. There was one bench at each PPF level. Under each CO_2 concentration, nine combinations of day and night temperatures (DT and NT) were created by moving the flats, each with 14 plants (14 plants per treatment), every 12 h among the three sections (three temperatures: 15, 20, and 25°C). Plants maintained at constant temperature were also moved within the same bench. Therefore, there were 54 treatments in total. Night-interruption lighting was provided by one HPS lamp (minimum PPF of 4 μmol m^{-2} s^{-1}) per section from 2200 to 0200 HR to meet the long-day flowering requirement of *C. carpatica* 'Blue Clips'.

2.3. Measurement and control of the greenhouse environment

Greenhouse temperatures were controlled by a greenhouse climate-control computer (Priva, Model CD750, 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 moved to a position closer to the shoot tip every one to two weeks as the plants grew to ensure accuracy of the shoot-tip temperature measurement. The instantaneous PPF was measured at 10 s intervals at canopy level in one of the six sections using three 1 m line-quantum sensors made from 18 G2711 photodiodes (Hamamatsu, Japan), and the DLIs were then calculated. In all six sections, the CO_2 concentrations were monitored during the photoperiod by using an infra-red CO_2 analyzer (Model 2166, Valtronics, California, USA); gas sampling was switched every minute from one section to another using solenoid valves. The CO_2 analyzer was calibrated for every 4–5 days using nitrogen and CO_2 standard gases. All environmental data (air and plant temperatures, light, CO_2, and vapor pressure deficit [VPD]) were monitored or controlled (CO_2 concentration and VPD) using a Campbell Scientific CR-10 datalogger (Logan, Utah, USA). The datalogger collected data for every 10 s and recorded the hourly average. VPD was maintained around 0.7 kPa in all sections by the injection of water vapor as needed. The plant ADT and DLI for the entire experimental period were then calculated and used in data analyses.

2.4. Data collection and analysis

Dates of visible bud (VB) and first fully open flower were recorded. The experiment was terminated for each plant when the first flower was fully open. Upon termination, flower diameter, plant height (from the medium surface to the top point of the plant), and number of flower buds were recorded. The final DM of the first 10 plants to flower (excluding roots) from each treatment was determined after tissue was dried 4 days at 60°C in a forced-air oven.

PTR (mol m^{-2} per degree-day) was calculated as DLI divided by daily thermal time (per degree-day), which is calculated as plant ADT minus base temperature. The base temperature used was 0°C, according to the results of Whitman et al. (1997).

Statistical Analysis System's PROC CORR (SAS Institute, Cary, NC) was used to test the significance of correlation and PROC GLM was used to test the significance between linear regression lines. Means were used in regression analyses. The linear regression lines were presented in the graphs only when the correlation was statistically significant. Data were pooled for the regression lines when slopes and intercepts were not statistically different (e.g., in the regression line of flower diameter in response to plant ADT data were pooled from the two CO_2 concentrations). The data on plants grown at constant 15°C (setting) under the low DLI were excluded in the data analyses because temperature control to 15°C after VB was unsuccessful.

3. Results

The average actual air temperatures during the entire experimental period were 16.0, 21.1, and 25.6°C for ambient CO_2 sections, and 17.2, 22.1, and 25.7°C for CO_2 enriched sections. The average DLIs over the course of the experiment were 4.2, 10.8, and 15.8 mol m^{-2} per day. Average CO_2 concentrations measured during the light period were 595, 603, and 635 μmol mol^{-1} (enriched) and 430, 399, and 380 μmol mol^{-1} (ambient) in the 15, 20, and 25°C sections, respectively. The actual CO_2 concentrations in the CO_2 enriched sections were lower than the setting (1000 μmol mol^{-1}) because of ventilation during moderate-temperature days. Venting was unavoidably increased in part due to heat output from the HPS lamps.

Flower timing was closely related to ADT (Fig. 1) but was not significantly affected by the day or night temperatures delivered to achieve a specific ADT (data not shown). Rates of progress to VB, to flower, and from VB to flower increased linearly with increasing plant ADT (Fig. 1). Flower timing was not influenced by CO_2 concentration and data were pooled in Fig. 1. There was some indication that time to VB was increased at the lowest DLI (Fig. 1A), but the effect was not significant and could have been due to lower soil temperatures during early establishment. Flower timing was similar to that observed in our previous studies (Whitman et al., 1997).

Flower diameter was negatively correlated with plant ADT at all DLIs under both CO_2 concentrations (Fig. 2A–C) but was not significantly affected by the day or night temperatures delivered to achieve a specific ADT (data not shown). With a 1°C increase in plant ADT, flower diameter decreased about 1 mm per degree at high and medium DLIs under both CO_2 concentrations, and 0.8 or

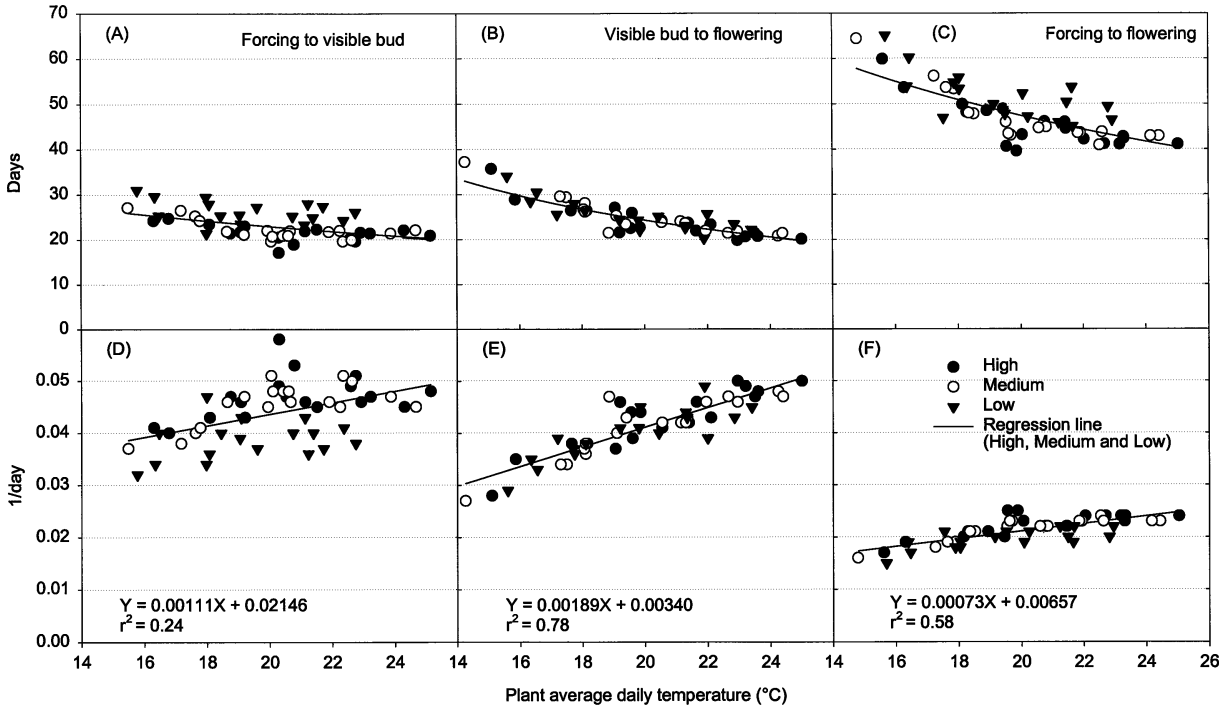

Fig. 1. (A)–(C) Effects of plant ADT on time to VB, from VB to flower, and from forcing to flower and (D)–(F) rate of progress towards VB, from VB to flower, and from forcing to flower in *Campanula carpatica* 'Blue Clips' grown at (●) high, (○) medium, and (▼) low DLIs. The solid lines in graphs (D)–(F) are linear regression lines pooled from the three DLIs. The solid lines in graphs (A)–(C) are the reciprocals of correlated linear regression lines in graphs (D)–(F), respectively.

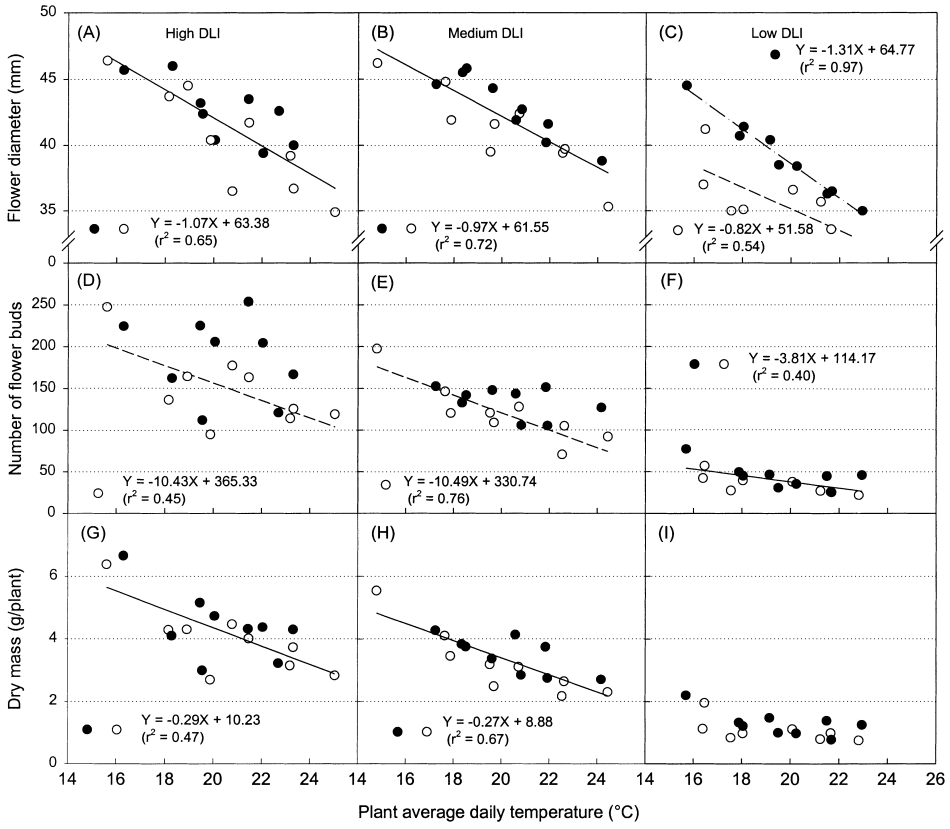

Fig. 2. (A)–(C) Effects of plant ADT on flower diameter, (D)–(F) number of flower buds, and (G–I) dry mass in *C. carpatica* 'Blue Clips' grown at three DLIs under (○) ambient, and (●) enriched CO_2 concentrations. The solid line is the regression line pooled from the two CO_2 concentrations; short-dash and dash-dotted lines are the regression lines under ambient and enriched CO_2 concentrations, respectively.

1.3 mm per degree at low DLIs under ambient or enriched CO_2 conditions, respectively. Carbon dioxide enrichment did not significantly affect the relationship between the flower diameter and plant ADT at high and medium DLIs, but on an average increased the flower diameter by ≈2 mm. Under low DLI, CO_2 enrichment increased flower diameter by ≈3 mm. On an average, flower diameter increased by 3–4 mm at comparable temperatures as DLI increased from 4.2 to 10.8 mol m^{-2} per day, while there was no further increase in flower diameter when DLI was increased from 10.8 to 15.8 mol m^{-2} per day.

The number of flower buds decreased linearly (slope, ≈−10 flowers per degree) as plant ADT increased under ambient CO_2 concentration, though there was substantial variation (Fig. 2D and E). At high and medium DLIs under CO_2 enrichment, the number of flower buds was not significantly correlated with plant

ADT (Fig. 2D and E). At low DLI, plant ADT had little effect on the number of flower buds and no difference was observed between the two CO_2 concentrations (Fig. 2F). The number of flower buds doubled when DLI was increased from 4.2 to 10.8 mol m^{-2} per day, but rose only an additional 30% when DLI increased from 10.8 to 15.8 mol m^{-2} per day. Carbon dioxide enrichment increased the number of flower buds slightly (25 and 10% at high and medium DLIs, respectively).

Dry mass (measured at first open flower) decreased linearly as plant ADT increased under high and medium DLIs, while there was no correlation between DM and plant ADT at low DLI under either CO_2 concentration (Fig. 2G–I). Dry mass was not significantly affected by the day or night temperatures delivered to achieve a specific ADT (data not shown). Dry mass was ≈8% greater on an average in the CO_2 enrichment under high and medium DLIs, though the increase was not statistically significant. Under low DLI, DM was low and unaffected by CO_2 concentration. Dry mass increased by ≈155% when DLI increased from 4.2 to 10.8 mol m^{-2} per day, but only an additional 25% when DLI was increased from 10.8 to 15.8 mol m^{-2} per day. Dry mass and number of flower buds were tightly correlated, independent of treatments (number of flower buds=0.0231DM+0.3515, r^2=0.92).

DIF significantly influenced stem elongation and plant height but not flower diameter (Fig. 3) or flower bud number (data not shown). Even at constant ADT (20°C), DIF did not affect flower diameter (data not shown). Time to flower and DM were also not affected by DIF (data not shown). Plant height increased 0.4 cm at low DLI and 0.3 cm at high and medium DLIs per 1°C increase in DIF (Fig. 3B). Plant height was unaffected by CO_2 enrichment. Plants tended to be tallest when grown at high positive DIF under low DLI.

Dry mass and flower bud number were significantly correlated with PTR, independent of CO_2 concentration (Fig. 4). However, flower diameter was only weakly correlated with PTR (Fig. 4A).

4. Discussion

Plant DM, time to flower, flower size, and flower bud number of *C. carpatica* 'Blue Clips' were influenced by plant ADT in the range 15–25°C but not by different day or night temperatures delivered to achieve a specific ADT. Conversely, plant height was positively affected by DIF but not by ADT (Fig. 2B). Serek (1991a) observed an increase in the number and size of *C. carpatica* 'Blue Clip' flowers using a 2 h morning dip to 15°C independent of ADT which suggested that DIF could have a direct effect. In the present experiments, using 12 h night temperatures between 15 and 25°C, there was no evidence for an effect of DIF on flower size or number (Fig. 3A).

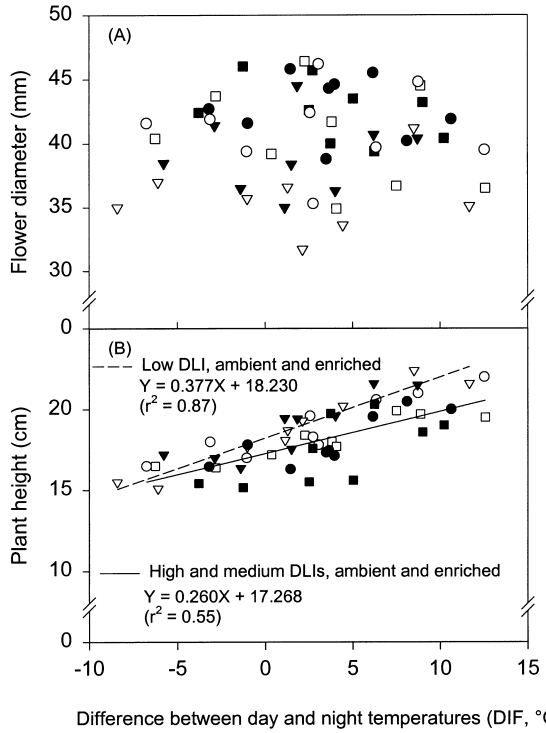

Fig. 3. Effects of the difference between day and night temperatures (DIF) on: (A) flower size, and (B) plant height of *C. carpatica* 'Blue Clips' grown at three DLIs under ambient and enriched CO_2 concentrations. Symbols (□), (○), and (▽) indicate high, medium, and low DLIs, respectively, under ambient CO_2 concentration; symbols (■), (●), and (▼) indicate high, medium, and low DLIs, respectively, under enriched CO_2 concentration.

The response of plant height to DIF was stronger under low DLI than under medium and high DLIs. We observed similar plant height and flower peduncle responses to DIF in pansy: stem and flower peduncle elongated more under low DLI than high DLI (Niu et al., 2000). Erwin and Heins (1995) found that plant height response to DIF increased as irradiance increased. In the present experiment, high and medium DLIs were obtained by supplementing sunlight with HPS lamps, which have a red (R) to far red (FR) ratio (R/FR) of 5.9 (Whitman et al., 1997), while sunlight has an R/FR ratio of only 1.15 (Smith, 1994). Thus, the actual R/FR ratios in this experiment were the highest in high DLI treatment and lowest in the low DLI (sole sunlight) treatment. Red light has been shown to reduce stem elongation whereas FR light promotes stem elongation (Smith, 1994). The response of stem elongation to DIF was also shown to be small under conditions that result in reduced stem elongation. An example is the smaller response of *Lilium longiflorum* Thunb. to DIF on short-

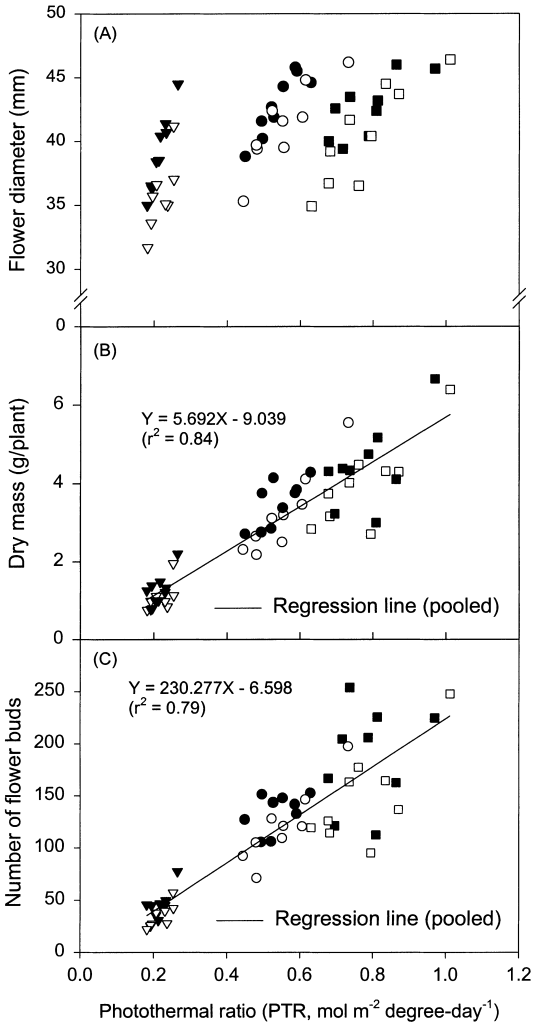

Fig. 4. The relationship between: (A) PTR and flower diameter; (B) PTR and the number of flower buds; (C) PTR and dry mass of *C. carpatica* 'Blue Clips' grown at three DLIs under ambient and enriched CO_2 concentrations. Symbols (□), (○), and (▽) indicate high, medium, and low DLIs, respectively, under ambient CO_2 concentration; symbols (■), (●), (▼) indicate high, medium, and low DLIs, respectively, under enriched CO_2 concentration.

growing, ancymidol (a growth retardant) treated plants than on non-treated plants (Erwin et al., 1989). Therefore in the present experiment, the high DLI with a high R/FR ratio reduced stem elongation, and may have contributed to the smaller stem response to DIF. We did observe more lateral branching in plants in the medium and high DLI treatments where R/FR ratio was high, although high DLI itself may be responsible for the increased lateral branching.

Low light affects development and developmental rate by limiting the supply of photosynthate (Volk and Bugbee, 1991; Faust and Heins, 1993). Based on the relatively low flower number and plant size, we suggest that 4.2 mol m^{-2} per day is below the minimum DLI required to commercially produce satisfactory *C. carpatica* 'Blue Clips', at least at an ADT>15°C. Serek (1991b), using up to 6 mol m^{-2} per day supplemental light for the last 22 days of production, found a 50% increase in the number of open flowers at harvest. In the present experiment, flower number and dry mass (measured at first open flower) generally increased 2–3-fold when DLI increased from 4.2 to 10.8 mol m^{-2} per day (Fig. 2). Flower bud number and DM increased only 20–50% as DLI increased from 10.8 to 15.8 mol m^{-2} per day. These results indicate that it would be best to produce *C. carpatica* with a DLI of 10 mol m^{-2} per day.

The number of flower buds and DM increased linearly as PTR increased. Flower size was probably correlated more with temperature than PTR, since DLI above 10 mol m^{-2} per day did not influence flower size. When light intensity is unvarying, increasing temperature increased developmental rate but decreased the number of lateral shoots and increased shoot length in petunia (Kaczperski et al., 1991). In the present experiment, the combination of high temperature and low DLI resulted in reduced vegetative growth and fewer, smaller flowers in *C. carpatica* 'Blue Clips'. Therefore when temperature is increased to hasten development, light level also should be increased accordingly to maintain quality.

Carbon dioxide enrichment can increase DM, number of flowers or leaves, and lateral branching in potted plants, cut flowers, vegetables, and forest plants (Mortensen and Ulsaker, 1985; Mortensen, 1987). In the present experiment, CO_2 enrichment to ≈600 ppm had a measurable effect on flower size at low DLIs, but did not affect time to flower. However, CO_2 enrichment had a relatively small effect on growth and flower development compared to DLI and ADT, most likely because of our limited ability to enhance CO_2 concentrations (≈600 μmol mol^{-1}).

Theoretically, increasing CO_2 concentration should decrease PTR for obtaining a similar DM, since PTR describes light energy available for photosynthesis per unit of developmental time and increasing CO_2 concentration increases the rate of photosynthesis. In the present study, CO_2 concentration did not significantly modify the relationship between the number of flower buds and PTR or between DM and PTR. However, PTR tended to be lower under enriched than ambient CO_2 concentrations for the same number of flower buds or DM (Fig. 4). Further research is needed to determine the minimum PTR before and after VB under ambient and enriched CO_2 conditions to produce high-quality *C. carpatica* 'Blue Clips' plants.

In summary, ADT but not DIF controlled plant developmental rate, DM, flower number and flower size in *C. carpatica* 'Blue Clips'. Conversely, plant height was not affected by plant ADT but increased with DIF. Increasing DLI from 4.2 to

10.8 mol m^{-2} per day markedly increased DM and flower bud number at the first open flower but had relatively little effect on flower size and no effect on flower timing. Increasing DLI from 10.8 to 15.8 mol m^{-2} per day did not increase flower developmental rate or flower size. Carbon dioxide enrichment to 600 ppm had relatively little effect on growth and flowering of *C. carpatica*.

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