Day and Night Temperatures, Daily Light Integral, and CO₂ Enrichment Affect Growth and Flower Development of Pansy (Viola ×wittrockiana)

Genhua Niu,¹ Royal D. Heins,² Arthur C. Cameron,² and William H. Carlson² Department of Horticulture, Michigan State University, East Lansing, MI 48824

Additional index words. DIF, flower size, photothermal ratio

ABSTRACT. Pansy [Viola xwittrockiana Gams. 'Delta Yellow Blotch' (Yellow) and 'Delta Primrose Blotch' (Primrose)] plants were grown in a greenhouse under two CO₂ concentrations [ambient (≈400 µmol·mol⁻¹) and enriched (≈600 µmol·mol·1], three daily light integrals (DLI; 4.1, 10.6, and 15.6 mol·m⁻²·d⁻¹), and nine combinations of day and night temperatures created by moving plants every 12 h among three temperatures (15, 20, and 25 $^{\circ}$ C). Time to flower decreased and rate of flower development increased as plant average daily temperature (ADT) increased at all DLIs for Yellow or at high and medium DLIs for Primrose. Increasing the DLI from 4.1 to 10.6 mol·m⁻²·d⁻¹ also decreased time to flower by 4 and 12 days for Yellow and Primrose, respectively. Both cultivars' flower size and Yellow's dry weight [(DW); shoot, flower bud, and total] decreased linearly as plant ADT increased at high and medium DLIs, regardless of how temperature was delivered during day and night. DW in Yellow increased 50% to 100% when DLI increased from 4.1 to 10.6 mol·m⁻²·d⁻¹ under both CO₂ concentrations. Flower size in Yellow and Primrose increased 25% under both CO₂ conditions as DLI increased from 4.1 to 10.6 mol·m⁻²·d⁻¹, but there was no increase between 10.6 and 15.6 mol·m⁻²·d⁻¹, regardless of CO₂ concentration. Plant height and flower peduncle length in Yellow increased linearly as the difference between day and night temperatures (DIF) increased; the increase was larger under lower than higher DLIs. The ratio of leaf length to width (LL/LW) and petiole length in Yellow increased as DIF increased at medium and low DLIs. Carbon dioxide enrichment increased flower size by 4% to 10% and DW by 10% to 30% except for that of the shoot at medium DLI, but did not affect flower developmental rate or morphology. DW of vegetative and reproductive parts of the plant was correlated closely with photothermal ratio, a parameter that describes the combined effect of temperature and light.

Plant developmental rate is influenced primarily by temperature. In many circumstances, flower developmental rate increases linearly as temperature increases between the base and optimum temperature (Roberts and Summerfield, 1987). For instance, flower developmental rate of 'Blue Clips' tussock bellflower (Campanula carpatica Jacq.) (Whitman et al., 1997), 'Sunray' tickseed (Coreopsis grandiflora Hagg ex Sweet.), 'Goblin' blanket flower (Gaillardia ×grandiflora Van Houtte), 'Snowcap' shasta daisy (Leucanthemum×superbum Bergman ex J. Ingram), and 'Goldsturm' coneflower (Rudbeckia fulgida Ait.) (Yuan et al., 1998) increased linearly as forcing temperatures increased from 15 to 26 °C.

Low irradiance can delay the developmental rate by limiting the supply of photosynthate (Faust and Heins, 1993; Volk and Bugbee, 1991). Time to flower decreased by up to 3 weeks in 'Snow Cloud' petunia (*Petunia* ×*hybrida* Vilm.-Andr.) as the daily light integral (DLI) increased from 6.5 to 13 mol·m⁻²·d⁻¹ (Kaczperski et al., 1991). Flowering did not occur below a DLI of 3.3 mol·m⁻²·d⁻¹, and DLIs above 17 mol·m⁻²·d⁻¹ did not affect developmental rate of flower buds in 'Red Elite' geranium (*Pelargonium*×*hortorum* Bailey) (White and Warrington, 1988). These results suggest that plant developmental rate increases as DLI increases until a threshold is reached; above that threshold, the effect of DLI on developmental rate is less and/or nonsignificant.

Temperature and DLI influence not only the rate of plant growth and development, but also plant quality. For floral crops,

plant quality can be described by parameters such as flower size, number of flower buds, plant height, dry weight (DW), etc. Increasing temperature decreased flower size and the number of flower buds of 'Sunray' tickseed, 'Snowcap' shasta daisy, 'Goldsturm' coneflower (Yuan et al., 1998), 'Blue Clips' tussock bellflower (Whitman et al., 1997), and impatiens (Impatiens wallerana Hook.) (Lee et al., 1990). For 'Grape Cooler' vinca (Catharanthus roseus L.), flowers were largest when plants were grown at 25 °C in the 15 to 35 °C range (Pietsch et al., 1995). Flower diameter of hybrid geranium was largest at 15 °C in the 10 to 32 °C range (Armitage et al., 1981). Flower size of 'Universal Violet' pansy (Viola ×wittrockiana) decreased linearly as temperature increased in the 9 to 31 °C range (Pearson et al., 1995). Increasing DLI can also increase flower size and number of flower buds. As DLI or photosynthetic photon flux (PPF) increased, flower size of 'Bright Golden Anne' chrysanthemum (Dendranthema grandiflora Tzvelev.) (Karlsson et al., 1989) and 'Grape Cooler' vinca (Pietsch et al., 1995) increased. In miniature roses (Rosa L. sp.), the total number of flowers and buds increased with increasing DLI (Mortensen and Moe, 1995).

Different combinations of temperature and light can influence plant quality. For instance, Lieth et al. (1991) showed that the optimum temperature for instantaneous growth of petunia increased from 14.6 °C at 5 mol·m⁻²·d⁻¹ to 33.5 °C at 30 mol·m⁻²·d⁻¹. Optimum temperature for flowering of 'Universal Violet' pansy decreased when the DLI fell below 6 mol·m⁻²·d⁻¹ (Adams et al., 1996). Liu and Heins (1997 and 1998) and Liu (1999) proposed that the photothermal ratio (PTR), which was defined as 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 'Freedom' poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) plant quality characteristics were related closely to PTR. Such a relationship between PTR and plant quality in pansy is unknown.

Received for publication 20 Sept. 1999. Accepted for publication 8 Mar. 2000. 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.

¹Visiting research associate.

²Professor.

In many potted and bedding plant species, stem length or plant height increases as the difference between day and night temperatures (DIF) increases, while average daily temperature remains constant (Myster and Moe, 1995). Little is known regarding DIF effect on pansy morphology.

Carbon dioxide enrichment has been applied in greenhouses and controlled environments to enhance plant growth and improve plant quality. Potted plants, cut flowers, vegetables, and tree species all show positive effects from CO₂ enrichment: increased DW, number of flowers or leaves, and lateral branching (Mortensen, 1987).

Pansy is a commercially important floricultural crop for the landscape, but information about the effects of environmental conditions on plant growth and development is limited. Therefore, the objectives of this study were to quantify the effects of different day and night temperatures, DLIs, and CO₂ concentrations on plant growth, flower development (time to flower and flower size), and morphology of pansy. The relationship between PTR and plant quality was also quantified.

Materials and Methods

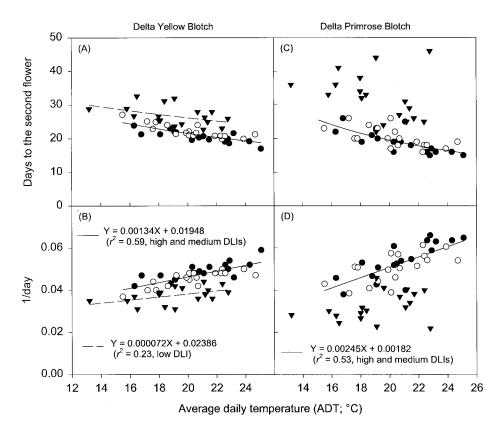
PLANT MATERIAL AND CULTURE. Seedlings of 'Delta Yellow Blotch' (Yellow) and 'Delta Primrose Blotch' (Primrose) pansy with four to five true leaves were received from a commercial producer in 512-cell trays on 20 Oct. 1998. Upon receipt, seedlings were placed in a greenhouse maintained at 20 ± 2 °C under natural sunlight. After seedlings produced an average of six leaves, they were transplanted to 10-cm (470-mL) containers and grown in a commercial medium (High Porosity Mix; Strong-Lite Products, Pine Bluff, Ark.) 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 Ca, Mg, and S, respectively, per liter) acidified with H₂SO₄ to a titratable alkalinity of 130 mg of CaSO₃/L and water soluble fertilizer providing (mg·L⁻¹) 125N–12P–125K–13Ca (30% ammonical N) plus (mg·L⁻¹) 1.0Fe–0.5Mn–0.5Zn–0.5Cu–0.1B–0.1Mo (MSU Special; Greencare Fertilizers, Chicago, Ill.).

EXPERIMENTAL DESIGN. Six greenhouse sections $(4.7 \times 4.1 \text{ m})$, each with three benches, were at 15, 20, or 25 °C (set points). Starting at sunrise from 19 Nov. to 31 Dec. 1998, each section was provided 12-h supplemental lighting from high-pressure sodium (HPS) lamps at a *PPF* of 0, 145, or 250 μ mol·m⁻²·s⁻¹. The instantaneous PPF was measured at 10-s intervals at canopy level in one of the six sections by using three quantum line sensors including 18 G2711 photodiodes (Hamamatsu Co., Hamamatsu, Japan) on a 1-m bar, and the DLIs then were calculated. One bench was lighted at each PPF level during this 12-h period. Three of the sections were enriched with CO₂ at 1000 μmol·mol⁻¹ (set point). Under each CO₂ concentration, nine combinations of day and night temperatures were created by moving the flats, each with 14 plants, every 12 h among the three sections (three temperatures: 15, 20, and 25 °C). Therefore, there were 54 treatments in total. Night-interruption lighting was provided using 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 pansy.

Greenhouse temperatures were controlled by a greenhouse climate-control computer (model CD750; Priva, De Lier, The Netherlands). Plant temperatures were measured throughout the experimental period by inserting thermocouples (Chromel-constantan, 0.127-mm diameter) into shoot tips. The inserted position of a thermocouple in the plant was moved to a position close to the shoot tip every 1 to 2 weeks as the plants grew to improve the accuracy of shoot-tip temperature measurement. By using an infrared CO₂ analyzer (Model 2166, Valtronics, Valley Springs, Calif.), all six sections' CO₂ concentrations were monitored during the photoperiod: solenoid valves switched the gas sampling from one section to another every minute. The CO₂ analyzer was calibrated every 4 to 5 d with nitrogen and CO₂ standard gases. All environmental data [air and plant temperatures, light, CO₂, and vapor pressure deficit (VPD)] were monitored or controlled (CO₂ concentration and VPD) using a Campbell Sci-

Fig. 1. Effects of plant average daily temperature (ADT) on days to the second flower and rate of progress toward the second flower of (**A** and **B**) 'Delta Yellow Blotch' pansy and (**C** and **D**) 'Delta Primrose Blotch' pansy grown at three daily light integrals (DLI; ● high, ○ medium, ▼ low). The solid line in (**B**) and (**D**) is the linear regression line pooled from the high and medium DLIs; the dashed line in (**B**) is the regression line at low DLI. The solid and dashed lines in (**A**) and solid line in (**C**) are the reciprocals of correlated linear regression lines in (**B**) and (**D**).



entific CR-10 datalogger (Logan, Utah). The datalogger collected data every 10 s and recorded the hourly average. The actual plant temperatures (shoot tip temperature) were used in all data analyses. Vapor pressure deficit was maintained around 0.7 kPa in all sections by injecting water vapor as needed.

DATA COLLECTION. Since flower buds were present on some plants at the beginning of treatments, all flower buds were removed during the first 3 d after the start of treatments. The experiment was terminated when the second (Primrose) or the third (Yellow) flower was fully expanded (4 d after anthesis). Flower size (length and width) and peduncle length on two (Primrose) or three (Yellow) flowers per plant and time to flower were recorded. Upon termination (e.g., when the third flower was fully open), Yellow's plant height (from the medium's surface to the top point of the plant), leaf length (LL), leaf width (LW), and petiole length of the third leaf associated with the third flower were recorded. The ratio of LL to LW then was calculated. DW of flower buds and shoots was determined after the tissues were dried for 4 d at 60 °C in a forced-air oven. Only time to the first and second flower formation, flower size, and peduncle length were recorded for Primrose.

DATA ANALYSIS. Photothermal ratio (mol·m⁻²·degree-day⁻¹) was calculated as DLI (mol·m⁻²·d⁻¹) divided by daily thermal time

(degree-days·d⁻¹), which was calculated as plant average daily temperature (ADT) minus base temperature. The base temperature was assumed to be 0 °C (Adams et al., 1996).

PROC CORR of SAS Institute (SAS Inst. Inc., Cary, N.C.) 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. Linear regression lines are presented in the graphs only for statistically significant correlations. 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 CO₂ concentrations in Fig. 2A–C).

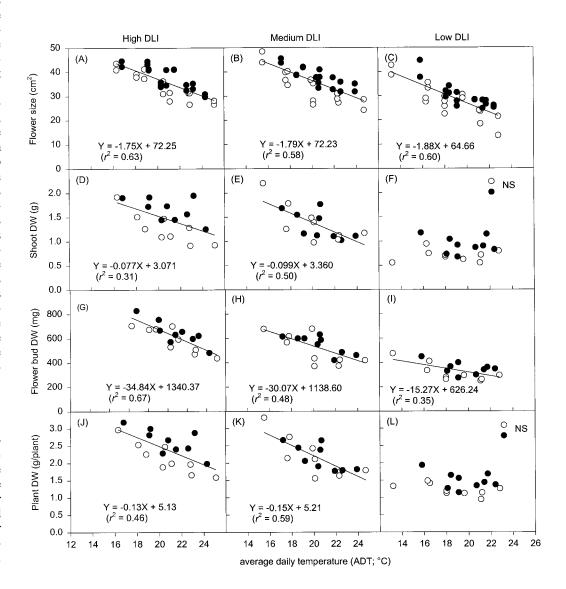
Results

Environmental conditions. Actual average air temperatures during the entire experimental period were 16.3, 20.9, and 25.7 °C for ambient CO₂ sections and 17.2, 22.3, and 25.7 °C for CO₂-enriched sections. Actual average DLIs were 4.1,

10.6, and 15.6 mol·m⁻²·d⁻¹, and actual average CO_2 concentrations measured during the light period were 576 to 638 μ mol·mol⁻¹ (enriched) and 400 to 436 μ mol·mol⁻¹ (ambient) sections, respectively. Actual CO_2 concentrations in the CO_2 -enriched sections were lower than the setting (1000 μ mol·mol⁻¹) because of ventilation on warm days.

TIME TO FLOWER AND FLOWER SIZE. Since CO_2 enrichment did not influence time to flower (days to the second flower) for each cultivar, data were pooled from the two CO_2 concentrations in Fig. 1. Time to flower decreased and rate of progress to flower (1/day) increased linearly as plant ADT increased at all DLIs in Yellow or at high and medium DLIs in Primrose (Fig. 1). Rate of progress to flower was not correlated with plant ADT in Primrose at low DLI, and was highly variable (Fig. 1C and D). Time to flower decreased on average 4 d for Yellow and 12 d for Primrose when DLI increased from 4.1 to 10.6 mol·m $^{-2}$ ·d $^{-1}$. However, there was little decrease in time to flower when DLI increased from 10.6 to 15.6 mol·m $^{-2}$ ·d $^{-1}$.

Fig. 2. Effects of plant average daily temperature (ADT) on (A–C) flower size, and DW of the (D–F) shoot, (G–I) flower bud, and (J–L) total plant of 'Delta Yellow Blotch' pansy grown at three daily light integrals (DLI; high, medium, and low) under enriched (\bullet) or ambient (\circ) CO₂ concentrations. NS in (F) and (L) indicates nonsignificance of the correlation between DW and ADT.



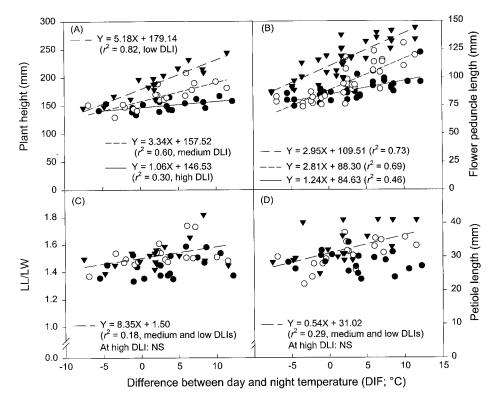


Fig. 3. Effects of the difference between day and night temperatures (DIF) on (A) plant height, (B) flower peduncle length, (C) ratio of leaf length to width (LL/LW), and (D) leaf petiole length of *Viola* ×wittrockiana at three daily light integrals (DLI; ●high, O medium, ▼low). The lines are linear regression lines: dash dot, low DLI; short dash, medium DLI; solid, high DLI; long dash, pooled from medium and low DLIs.

Flower size was correlated negatively with plant ADT (Fig. 2A–C) under both CO_2 concentrations. Flower size decreased 1.75 to 1.88 cm² per 1 °C increase in plant ADT. Flower size increased by $\approx 25\%$ when DLI increased from 4.1 to 10.6 mol·m⁻²·d⁻¹. However, there was no increase in flower size when DLI increased from 10.6 to 15.6 mol·m⁻²·d⁻¹, regardless of CO_2 concentration. Although statistically insignificant, carbon dioxide enrichment increased flower size by 10%, 8%, and 4% at high, medium, and low DLIs, respectively.

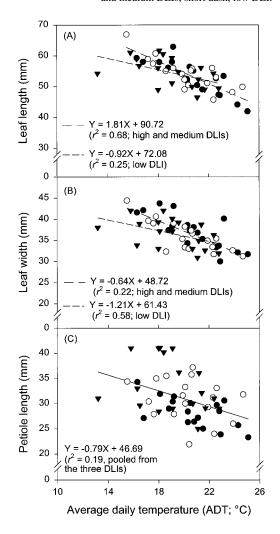
DRY WEIGHT. DW (shoot, flower bud, and total) at the third open flower decreased linearly as plant ADT increased under both CO_2 concentrations (Fig. 2D, E, G, H, I, J, and K), except for shoot and total DW at low DLI where no statistically significant relationship existed (Fig. 2F and L). As with time to flower (Fig. 1C), plant ADT had little effect on shoot and total plant DW at low DLI, regardless of CO_2 concentration. Shoot, flower bud, and total plant DW increased by $\approx 80\%$, 70%, and 40%, respectively, averaged over both CO_2 concentrations when DLI increased from 4.1 to $10.6 \, \text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Under enriched CO_2 concentration, DW increased $\approx 20\%$ when DLI increased from $10.6 \, \text{to} \, 15.6 \, \text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, while under ambient CO_2 concentration, only flower bud DW increased between $10.6 \, \text{and} \, 15.6 \, \text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Carbon dioxide enrichment increased DW by 10% to 30%, except for that of the shoot at medium DLI.

PLANT MORPHOLOGY PARAMETERS. Since CO₂ concentration did not affect plant height, flower peduncle length, LL, LW, the ratio of LL to LW (LL/LW), petiole length data were pooled from the two CO₂ concentrations in Figs. 3 and 4. Flower peduncle length data were also pooled from the two cultivars, since there

was no significant difference between them (Fig. 3B).

Plant height and flower peduncle length at all DLI increased linearly as DIF increased (Fig. 3A and B). Plant height increased approximately 1.0, 3.3, and 5.2 mm, and flower peduncle length increased approximately 1.2, 2.8, and 3.0 mm per 1 °C increase in DIF under high, medium, and low DLIs, respectively. Leaf length, leaf width, and petiole length decreased as plant ADT increased (Fig. 4A-C). The ratio of LL to LW and petiole length increased slightly with DIF under medium and low DLIs, while there was no significant correlation between LL/LW and DIF or between petiole length and DIF at high DLI (Fig. 3C and D). Other than plant height and flower peduncle length, the correlation between

Fig. 4 (**below**). Effects of plant average daily temperature (ADT) on (**A**) leaf length, (**B**) leaf width, and (**C**) petiole length of 'Delta Yellow Blotch' pansy grown at three daily light integrals (DLI; ● high, ○ medium, ▼ low). The lines are linear regression lines: solid, pooled from high, medium, and low DLIs; dash dot, pooled from high and medium DLIs; short dash, low DLI.



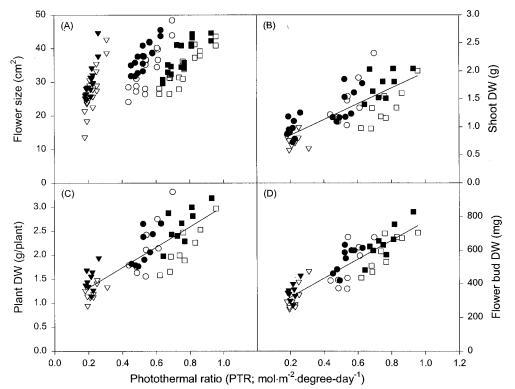


Fig. 5. The relationship between (A) flower size, (B) shoot, (C) plant, or (D) flower bud DW, and photothermal ratio (PTR) of 'Delta Yellow Blotch' pansy at three daily light integrals (DLI) under ambient or enriched CO₂ concentrations. Symbols □, ○, and ∇ indicate high, medium, and low DLIs, respectively, under ambient CO₂ concentration; symbols ■, ●, and ▼ indicate high, medium, and low DLIs, respectively, under enriched CO₂ concentration.

other parameters and DIF or ADT was generally low and was highly variable. Flower size and time to flower in both cultivars and DW in Yellow (data not presented) were not influenced by DIF.

RESPONSIVENESS TO PTR. Flower size varied greatly within a narrow PTR range at a given DLI but was not well correlated with PTR over a wide PTR range (Fig. 5A). Shoot, total, and flower bud DW (Fig. 5B–D) increased linearly as PTR increased under both CO₂ levels (Fig. 5B–D). Carbon dioxide enrichment did not affect the relationship between DW and PTR.

Discussion

TEMPERATURE AND LIGHT. Time to flower, flower size, and DW were influenced by plant ADT, regardless of the way temperature was delivered during the day and night. For both cultivars (except Primrose at low DLI), time to flower decreased as plant ADT increased. Flower size decreased linearly as plant ADT increased at all DLIs. These results are in agreement with those of Adams et al. (1997) and Pearson et al. (1995): the rate of pansy flower development and size decreased linearly as temperature increased, but is not influenced by the way temperature is delivered during the day and night.

In the present experiment, flower developmental rate and size increased as DLI increased from 4.1 to 10.6 mol·m⁻²·d⁻¹. However, for both cultivars, there was little difference in time to flower and flower size between 10.6 and 15.6 mol·m⁻²·d⁻¹. Therefore, the threshold of DLI on increasing flower developmental rate and size in pansy is probably close to 10 mol·m⁻²·d⁻¹.

Daily light integral significantly influenced DW, which increased ~70% under both CO₂ concentrations as DLI increased from

4.1 to 10.6 mol·m⁻²·d⁻¹. However, there was no further increase under ambient CO₂ concentration or an increase of only \approx 20% under enriched CO₂ concentration as DLI increased from 10.6 to 15.6 mol·m⁻²·d⁻¹. Therefore, the relationship between DW and DLI from 4.1 to 15.6 mol·m⁻²·d⁻¹ was asymptotic.

Temperature and light affected plant quality, and their combined effects could be described by PTR (Liu, 1999). Development is driven by thermal energy and determined primarily by temperature, while biomass accumulation is driven by photosynthesis and determined primarily by intercepted light. In the present experiment, DW increased linearly with PTR. The combination of high temperature and low DLI (low PTR) resulted in a low DW and small flowers. Therefore, in order to produce high-quality pansy plants, DLI also must be increased when temperature is in-

creased to hasten development.

Theoretically, the relationship between growth (DW) and PTR can be modified by CO₂ concentration, since PTR describes light energy available for photosynthesis per unit of developmental time. Elevating CO₂ concentration can increase the rate of photosynthesis at a particular *PPF* and, to maintain a similar DW, PTR should decrease. In the present study, the limited elevated CO₂ concentration (≈600 mmol·mol⁻¹) did not modify the linear regression lines between DW and PTR. However, for a similar DW (shoot, flower bud, and total) PTR tended to be lower under the enriched than the ambient CO₂ concentrations (Fig. 5). Since DW increased linearly as PTR increased, further research on pansy is warranted to determine a minimum PTR for acceptable market quality.

Plant morphology was influenced by DIF. Plant height and flower peduncle length at all DLIs and LL/LW and petiole length at medium and low DLIs increased with increasing DIF, which means that the plant internode, flower peduncle, and leaf elongated as DIF increased. The effect of DIF on plant height and peduncle length was more pronounced at the lower DLI in this experiment than at higher DLI, indicating that DLI interacted with DIF and the response to DIF increased as DLI decreased. We also observed stronger plant height response to DIF in 'Blue Clips' tussock bellflower under low DLI than high DLI (unpublished data). These results contradicted those reported by Erwin and Heins (1995) that stem elongation responses to DIF increased as irradiance increased.

Why might plant height response to DIF be less under high DLI than low DLI in this experiment while Erwin and Heins (1995) reported the opposite? The difference could be due to light quality. In the present experiment, high and medium DLIs were obtained by supplementing natural daylight with light from HPS lamps; light from HPS lamps has a high red (R) to far red (FR) ratio (R/FR) of 5.9 (Whitman et al., 1998) while sunlight only has a R/FR ratio of 1.15 (Smith, 1994). Thus, the actual R/FR ratios in this experiment were the highest in the high DLI treatment

(HPS plus sunlight) and lowest in the low DLI treatment (sunlight only). Since stem elongation in most plants decreases as both irradiance and the R/FR ratio increases (Smith, 1994), plants would be expected to be more compact in the high DLI treatments compared to low DLI treatment. One might also predict a smaller response to DIF on compact plants as the stem elongation response to DIF has been shown to be smaller under conditions that reduce total stem elongation. For example, ancymidol, a growth retardant, reduced stem elongation of Easter lily (Lilium longiflorum Thunb.), and response to DIF was less on ancymidoltreated plants than on plants elongating without an ancymidol application (Erwin et al., 1989). Therefore, since the high irradiance and high R/FR ratio already limited elongation, response to DIF in the high DLI treatment was less in this experiment than that previously reported when light quantity changes were solely due to changes in natural radiation.

CARBON DIOXIDE ENRICHMENT. Elevating CO_2 concentration generally increases plant growth and improves quality until a saturation point is reached. DW, shoot length, number of leaves, and growth of lateral breaks of 'Horim' chrysanthemum increased when CO_2 concentration was raised from ambient to 1000 mmol·mol⁻¹, while raising it from 1000 to 1600 μ mol·mol⁻¹ provided no additional benefit (Mortensen and Moe, 1983). In the present experiment, CO_2 enrichment increased vegetative growth, flower bud DW, and flower size but did not affect flower developmental rate or morphology. Overall, the magnitude of the effect of CO_2 enrichment was small, possibly because of the limited enriched concentrations (average of \approx 600 μ mol·mol⁻¹).

The effect of CO_2 enrichment on flower developmental rate varies, depending on species and other environmental conditions (Mortensen, 1987). Carbon dioxide enrichment did not affect flowering in the present study, probably because plants already had reached the reproductive phase when CO_2 was enriched, the enriched concentrations were limited, or both. It is possible that CO_2 enrichment might have promoted early flower induction if the experiment had been started at a young vegetative stage.

In summary, plant growth and flower developmental rate, flower size, and flower bud DW of pansy increased as plant ADT decreased from 25 to 15 °C, regardless of DIF, and as DLI increased from 4.1 to 10.6 mol·m⁻²·d⁻¹. Limited CO₂ enrichment enhanced plant growth and quality very little and did not affect flower developmental rate and plant morphology. Flower size under both CO₂ concentrations or DW of vegetative parts under ambient CO₂ concentration did not increase as DLI increased from 10.6 to 15.6 mol·m⁻²·d⁻¹. Plant height and flower peduncle length at all DLIs and LL/LW and petiole length at medium and low DLIs were correlated positively with DIF; the correlation was stronger under lower than high DLIs. DW of vegetative parts and flower buds was correlated closely with PTR.

Literature Cited

- Adams, S.R., S. Pearson, and P. Hadley. 1996. Modeling growth and development of pansy cv. Universal Violet in response to photo-thermal environment: Application for decision support and scheduling. Acta Hort. 417:23–32.
- Adams, S.R., S. Pearson, and P. Hadley. 1997. The effects of temperature, photoperiod and light integral on the time to flowering of pansy cv. Universal Violet (*Viola* ×wittrockiana Gams.). Ann. Bot. 80:107–112.
- Armitage, A.M., W.H. Carlson, and J.A. Flore. 1981. The effect of temperature and quantum flux density on the morphology, physiology, and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 106:643–647.
- Erwin, J.E. and R.D. Heins. 1995. Thermomorphogenic responses in stem

- and leaf development. HortScience 30:940-949.
- Erwin, J.E., R.D. Heins, and M.G. Karlsson. 1989. Thermomorphogenesis in *Lilium longiflorum*. Amer. J. Bot. 76:47–52.
- Faust, J.E. and R.D. Heins. 1993. Modeling leaf development of the African violet (*Saintpaulia ionantha* Wendl.). J. Amer. Soc. Hort. Sci. 118:747–751.
- Kaczperski, M.P., W.H. Carlson, and M.G. Karlsson. 1991. Growth and development of *Petunia* ×*hybrida* as a function of temperature and irradiance. J. Amer. Soc. Hort. Sci. 116:232–237.
- Karlsson, M.G., R.D. Heins, J.E. Erwin, R.D. Berghage, W.H. Carlson, and J.A. Biernbaum. 1989. Irradiance and temperature effects on time of development and flower size in chrysanthemum. Scientia Hort. 39:257– 267.
- Lee, W.S., J.E. Barrett, and T.A. Nell. 1990. High temperature effects on the growth and flowering of *Impatiens wallerana* cultivars. Acta Hort. 272:121–127.
- Lieth, J.H., R.H. Merrit, and H.C. Kohl. 1991. Crop productivity of petunia in relation to photosynthetically active radiation and air temperature. J. Amer. Soc. Hort. Sci. 116:623–626.
- Liu, B. 1999. Photothermal ratio: Relating plant growth and development to the ratio of light and temperature. PhD diss. Mich. State Univ., East Lansing.
- Liu, B. and R.D. Heins. 1997. Is plant quality related to the ratio of radiant energy to thermal energy? Acta Hort. 435:171–182.
- Liu, B. and R.D. Heins. 1998. Modeling poinsettia vegetative growth and development: The response to the ratio of radiant to thermal energy. Acta Hort. 456:133–142.
- Mortensen, L.M. 1987. Review: CO₂ enrichment in greenhouses. Crop responses. Scientia Hort. 33:1–25.
- Mortensen, L.M. and R. Moe. 1983. Growth responses of some greenhouse plants to environment: VI. Effect of CO₂ and artificial light on growth of *Chrysanthemum morifolium* Ramat. Scientia Hort. 19:141–147.
- Mortensen, L.M. and R. Moe. 1995. Effects of temperature, carbon dioxide concentration, day length and photon flux density on growth, morphogenesis and flowering of miniature roses. Acta Hort. 378:63–70.
- Myster, J. and R. Moe. 1995. Effect of diurnal temperature alternations on plant morphology in some greenhouse crops: A mini review. Scientia Hort. 62:205–215.
- Pearson, S., A. Parker, S.R. Adams, P. Hadley, and D.R. May. 1995. The effects of temperature on the flower size of pansy (*Viola* ×wittrockiana Gams.). J. Hort. Sci. 70:183–190.
- Pietsch, G.M., W.H. Carlson, R.D. Heins, and J.E. Faust. 1995. The effect of day and night temperature and irradiance on development of *Catharanthus roseus* L. 'Grape Cooler'. J. Amer. Soc. Hort. Sci. 120:877–881.
- 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.
- Smith, H. 1994. Sensing the light environment: The functions of the phytochrome family, p. 377–416. In: Kendrick and Kronenberg (eds.). Photomorphogenesis in Plants. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Volk, T. and B. Bugbee. 1991. Modeling light and temperature effects on leaf emergence in wheat and barley. Crop Sci. 31:1218–1224.
- White, J.W. and I.J. Warrington. 1988. Temperature and light integral effects on growth and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 113:354–359.
- Whitman, C., R.D. Heins, A.C. Cameron, and W.H. Carlson. 1997. Cold treatment and forcing temperatures influence flowering of *Campanula carpatica* 'Blue Clips'. HortScience 32:861–865.
- Whitman, C. R.D. Heins, A.C. Cameron, and W.H. Carlson. 1998. Lamp type and irradiance level for daylength extensions influence flowering of *Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', and *Coreopsis verticillata* 'Moonbeam'. J. Amer. Soc. Hort. Sci. 123:802–807.
- Yuan, M., W.H. Carlson, R.D. Heins, and A.C. Cameron. 1998. Effect of forcing temperature on time to flower of *Coreopsis grandiflora*, *Gaillardia ×grandiflora*, *Leucanthemum ×superbum*, and *Rudbeckia fulgida*. HortScience 33:663–667.