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Photoperiod and the Difference between Day and Night Temperature Influence Stem Elongation Kinetics in *Verbena bonariensis*

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Abstract. The effects of photoperiod and the difference between day temperature (DT) and night temperature (NT) (DIF) on stem elongation in *Verbena bonariensis* L. (tall verbena) were investigated. Plants were exposed to nine treatment combinations of –10, 0, or 10 °C DIF and 8-, 12-, or 16-hour photoperiods. Stem elongation was measured and analyzed by a noncontact computer-vision-based system. Total daily elongation increased as DIF increased; it also increased as photoperiod increased under positive DIF (DT > NT) and zero DIF (DT = NT), but not under negative DIF. Under positive DIF, daily elongation was 90% greater under the 16-hour photoperiod than under the 8-hour photoperiod. DIF affected elongation rate during the daily light span but not during the daily dark span. Total light-span elongation increased as DIF or photoperiod increased. Total dark-span elongation was not influenced by DIF or photoperiod. Elongation rates per hour in the light and dark were not significantly affected by photoperiod but increased in the light as DIF increased. Therefore, for a particular DIF, total elongation during 16-hour photoperiods (long days) was greater than that under 8-hour photoperiods (short days) because there were more hours of light under long days.

A technique for temperature-based height control of greenhouse crops was developed by Erwin et al. (1987) and is based on a concept that has been called DIF, where DIF is the difference between day temperature (DT) and night temperature (NT); i.e., DIF = DT – NT. Mature internode length is related quantitatively to DIF in many plant species; therefore, controlling plant height is possible by controlling DIF. The internode length of *Lilium longiflorum* Ramat. (Easter lily) was described as an exponential function of DIF, where shortest internodes occurred under negative DIF (DT < NT), and the longest developed under positive (DT > NT) (Erwin et al., 1989a). Results similar to those found by Erwin et al. (1987) have been reported for a wide range of plant species (Myster and Moe, 1995), including *Dendranthema ×grandiflora* Kitam. (syn. *Chrysanthemum ×morifolium* Ramat.) (chrysanthemum) (Karlsson et al., 1989; Ludolph, 1992), *Euphorbia pulcherrima* Willd. ex Klotzsch (poinsettia) (Berghage and Heins, 1991), *Xanthium pensylvanicum* L. (cocklebur) (Erwin, 1991), *Streptocarpus nobilis* C.B. Clarke (cape primrose) (Erwin, 1991), *Campanula isophylla* Moretti (Italian bellflower) (Moe and Heins, 1990; Moe et al., 1991), *Begonia ×cheimantha* Everett ex. C. Weber (Christmas begonia) (Jacobson et al., 1991), *Begonia ×hiemalis* Fotsch (winter flowering begonia) (Moe and Mortensen, 1992), *Codiaeum* A. Juss (croton) (Kresten-Jensen and Andersen., 1992), and *Solanum tuberosum* L. (white potato) (Kozai et al., 1992). Since DIF can potentially control plant height with fewer chemical growth regulators, the effects of DIF on greenhouse energy consumption (Amsen and Nielsen, 1991), crop production time (Jacobson et al., 1991; Kresten-Jensen and Andersen, 1992), interactions with light quality (Moe and Mortensen, 1992), economics (Erwin, 1992), yield of *Cucumis sativus* L. (cucumber) (Grimstad and Frimandslund, 1993), placement of high night temperatures (Kresten-Jensen, 1993), and timing of low-temperature pulses (Erwin et al., 1989b; Grimstad, 1993) have been studied. We have observed an interaction with photoperiod, noting that *Dendranthema* x*grandiflora* plants in the same DIF treatment were taller under long days than under short days (unpublished data). Since DIF was introduced to greenhouse growers (Heins and Carlson, 1990; Heins and Erwin, 1990), its use to attain desired plant height has become widespread (Erwin and Heins, 1995; McCann, 1991; Myster and Moe, 1995; Roberts, 1991).

Measurements of plant elongation rate are made because the elongation of a plant stem can be an important expression of physiological events (Christ, 1987). Linear voltage displacement transducers (LVDTs) generally are used to measure plant elongation (Aimi, 1969; Barlow and Boersma, 1972; Christ, 1987; Gallagher et al., 1976; Penny et al., 1974; Tutty et al., 1994; Watts, 1974). One disadvantage of LVDTs is that they must be connected to the plant's shoot tip, potentially affecting stem elongation because of mechanical stimulation or girdling of the shoot as it expands in a clip or string noose.

A noncontact system using images eliminates the aforementioned problems. Because of video and microprocessor technology, personal computers have become powerful enough to process image data. Image-processing techniques can potentially measure and analyze objects in a nondestructive, noncontact manner and therefore are starting to be used in agriculture (Meyer and Davison, 1987; Shimizu and Oshita, 1991; Trooien and Heermann, 1992; Wolfe et al., 1992).

We have developed a noncontact computer-vision-based system for measuring stem elongation in the light and dark (Shimizu and Heins, 1995). The objective of this research was to quantify stem elongation kinetics of *Verbena bonariensis* during a 24-h cycle under different DIF and photoperiod conditions using this noncontact measuring system. *Verbena bonariensis*, a long-day

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plant, was selected for this research because it has long internodes that make measurement of elongation easier.

Materials and Methods

Stem cuttings of *Verbena bonariensis* were rooted in a commercial propagation medium (Oasis) (Smithers-Oasis, Kent, Ohio) and then transplanted to a soilless medium in 15-cm (1.2-L) pots. Plants were grown at 20 to 24 °C in a glass greenhouse for ≈20 d under natural light levels and photoperiods from September to March. Plants were top-watered as necessary with 7 mM N, 0.7 mM P, and 2 mM K from a 20N–4.4P–16.6K all-purpose water-soluble fertilizer (Peter's professional Peat-lite special; Grace-Sierra Horticultural Products Co., Milpitas, Calif.). Supplemental photosynthetic lighting [photosynthetic photon flux (*PPF*)] was provided for 9 h each day at 50 mmol·m^{-2}·s^{-1} from high-pressure sodium lamps, and the night was interrupted with a 4-h light break from incandescent lamps at 5 mmol·m^{-2}·s^{-1} as measured by a quantum sensor (LI-289; LI-COR, Lincoln, Neb.).

Mean values and 95% confidence intervals for stem elongation rates of 10 plants randomly sampled following transplanting are illustrated in Fig. 1. The elongation rates were calculated by numerical differentiation of a Richards function (Richards, 1959), which was fitted to the stem length data obtained by measuring internode lengths between 0900 and 1000 HR every morning for 30 d. Since stem elongation in *Verbena bonariensis* approximated a sigmoid pattern and the growth rate was not constant (Fig. 1), a group of plants at the same growth stage were selected for further experimentation.

The stage at which the first flower opens is easily recognizable by its external appearance. Several uniform plants ≈3 d from flower were selected and placed for 2 or 3 d in a growth chamber set to one of the experimental conditions described below. One plant per treatment then was selected and placed in the proper position in a measurement system for image acquisition (Shimizu and Heins, 1995). Since plants respond quickly to DIF, (Heins and Erwin, 1990) a 3-d period was considered adequate for data collection. During the experiments, plants were placed on a tray containing water to ensure that they did not experience water stress.

Treatments. Stem elongation was quantified for plants exposed to nine combinations of photoperiod and DIF. Photoperiods consisted of 8, 12 or 16 h of light. Day and night air-temperature settings within each photoperiod treatment were selected to provide 10, 0, or –10 °C DIF using 15, 20, and 25 °C. Actual temperature of the shoot tip varied from air settings because of thermal heating from the lamps. Measured bud temperatures (0.127-mm thermocouple) were 28.4 °C (DT) and 16.4 °C (NT) for the 10 DIF treatment (actual DIF of 12 °C), 24.6 °C (DT) and 20.7 °C (NT) for the 0 DIF treatment (actual DIF of 3.9 °C), and 18.9 °C (DT) and 24.9 °C (NT) for the –10 DIF treatment (actual DIF of –6.0 °C). For simplicity, DIF treatments will be referred to as positive, zero, and negative throughout this paper, even though the zero DIF was actually positive.

PPF at canopy level was ≈364, 243, and 182 μmol·m^{-2}·s^{-1} in the three photoperiod treatments (8, 12 or 16 h of light, respectively), provided by adjusting the distance between the fluorescent lamps and the plant canopy, which resulted in a daily integrated *PPF* of 10.5 mol·m^{-2}·d^{-1} for each treatment. Lights were turned on at 0800 HR in each experiment. A vapor-pressure deficit of 0.8 kPa was maintained in all treatments. Each temperature–photoperiod treatment was replicated four times.

The measurement system used an image processing technique in which three-dimensional plant elongation could be measured remotely (Shimizu and Heins, 1995). Front and side images of a plant were captured simultaneously by using a mirror and a charge-coupled device (CCD) camera, and were stored on a magneto-optical disk. Images were obtained at night by irradiating plants with wavelengths of 800 nm and greater. Images were captured automatically and saved every 12 min for 3 d, and plant stem lengths then were computed by the developed image-processing algorithms (Shimizu and Heins, 1995). The length data were filtered by a Fast Fourier Transformation (FFT) to transform time domain data to frequency domain data, allowing us to reduce high-frequency noise and smooth the data series. The size of the window function in FFT operation was selected empirically. Elongation rate then was calculated by numerical differentiation.

Results

Stem elongation rate (SER) during a daily light–dark cycle was influenced by photoperiod and DIF as shown in Fig. 2. For plants in the positive DIF treatments, elongation rate was always slowest during the dark span and fastest during the light span. For plants in the negative DIF treatment, there was little difference in the elongation rate between the light and dark spans. The patterns of elongation were similar among replications within a treatment.

When integrated over a 24-h cycle, DIF and photoperiod interacted to affect daily stem elongation as shown in Fig. 3. Photoperiod had little or no influence on daily elongation of plants grown under

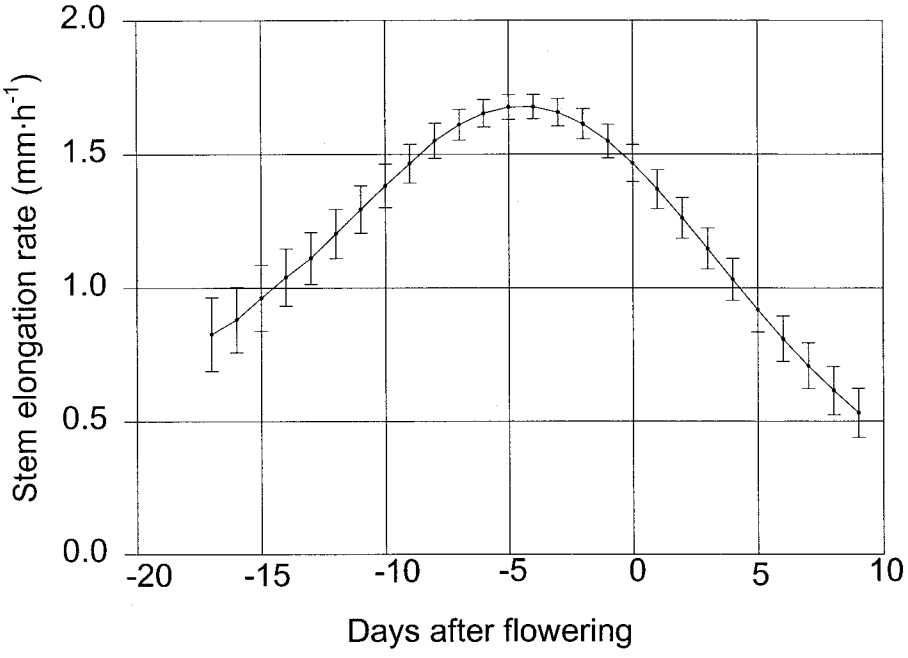


Fig. 1. Mean stem elongation rate in *Verbena bonariensis* under zero DIF air temperatures (20 °C DT/20 °C NT). Supplemental photosynthetic lighting from high-pressure sodium lights was provided for 9 h each day at 50 μmol·m^{-2}·s^{-1}, and the night was interrupted with a 4-h light break from incandescent lamps at 5 μmol·m^{-2}·s^{-1}. Vertical bars indicate 95% confidence intervals of the means.

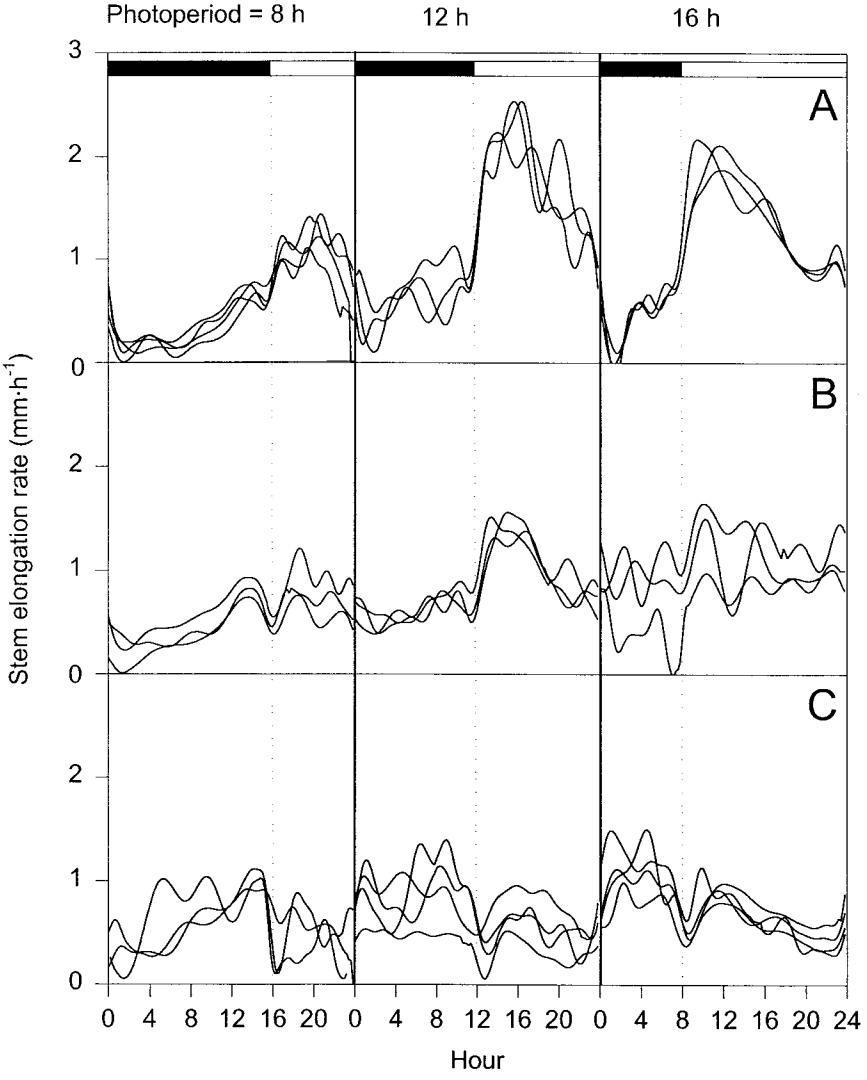


Fig. 2. Stem elongation rates of *Verbena bonariensis* grown under (**A**) positive DIF, (**B**) zero DIF, and (**C**) negative DIF. Air temperature DIF values were 10, 0, and –10 °C while measured bud temperature DIF values were 12, 3.9, and –6 °C, respectively. The dark bar over each graph column represents the period of darkness during the 24-h cycle. Each line within a graph represents a one-plant replication.

negative DIF, but it had a great influence on those grown under positive DIF: daily elongation was 90% greater under the 16-h photoperiod than under the 8-h photoperiod.

Daily elongation was separated into light and dark components. Elongation during the light span (E_L) increased as the light-span duration increased and decreased during the dark span (E_D) as the dark-span duration decreased (Fig. 4A and B). E_L increased less under negative DIF as photoperiod increased than under zero or positive DIF. DIF did not affect E_D.

Daily elongation was separated further into elongation percentage during the light and dark spans (PE_L and PE_D, respectively). The PE_L increased linearly as photoperiod and DIF increased, while PE_D decreased linearly as photoperiod and DIF increased (Fig. 4C and D).

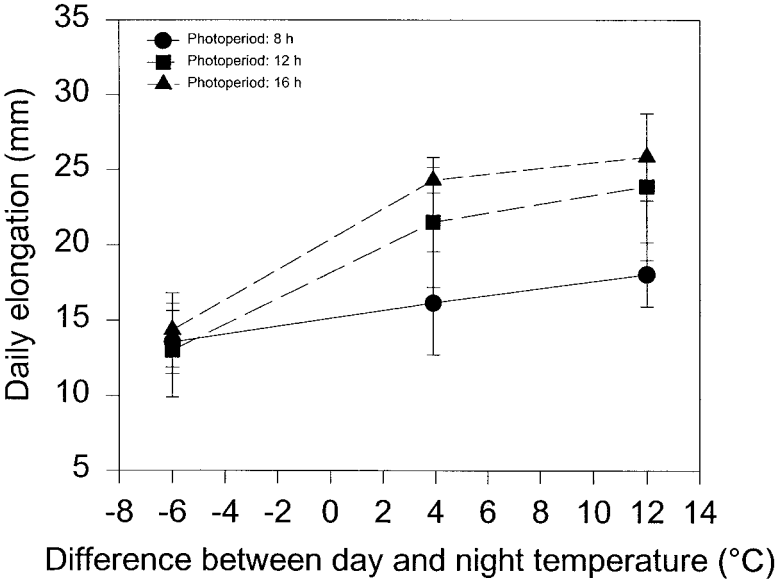
Photoperiod responses shown in Fig. 3 might be attributable to the length of the light and dark spans rather than actual differences in elongation rate during each span. Therefore, elongation was partitioned further based on elongation per hour within the light and dark spans (EH_L and EH_D, respectively) (Fig. 4E and F). According to this analysis, elongation was influenced significantly by DIF, not photoperiod.

Discussion

Typical stem elongation rate patterns in *Verbena bonariensis* under positive, zero, and negative DIF are shown in Fig. 2. SER under a 12-h photoperiod was similar during the dark under all DIF conditions but varied greatly during the light. It more than doubled after plants were transferred to light under positive DIF but decreased ≈50% under negative DIF. The observed increase in SER during the daily dark to light transition under positive DIF is similar to that observed by Tutty et al. (1994) and Erwin et al. (1992) in *Dendranthema ×grandiflora*. However, Tutty et al. (1994) observed a faster SER only on positive-DIF-grown *Dendranthema ×grandiflora* for 3 to 4 h before the SER decreased to a rate below that during the previous dark period. In contrast, SER of *Verbena bonariensis* plants grown in positive DIF was higher during the entire light span than at any time in the dark. Erwin et al. (1992) and Tutty et al. (1994) observed a large peak in SER immediately after the light–dark transition for negative-DIF-grown plants; however, we observed only a small increase in SER during this same period.

Erwin and Heins (1995) observed that the rate of plant stem elongation decreased during the light and increased during the dark under both positive and negative DIF in *Dendranthema ×grandiflora*.

Fig. 3. Influence of photoperiod and DIF on total daily stem elongation of *Verbena bonariensis* plants just after the first florets opened. Vertical bars indicate 95% confidence intervals of the means of 12 observations.



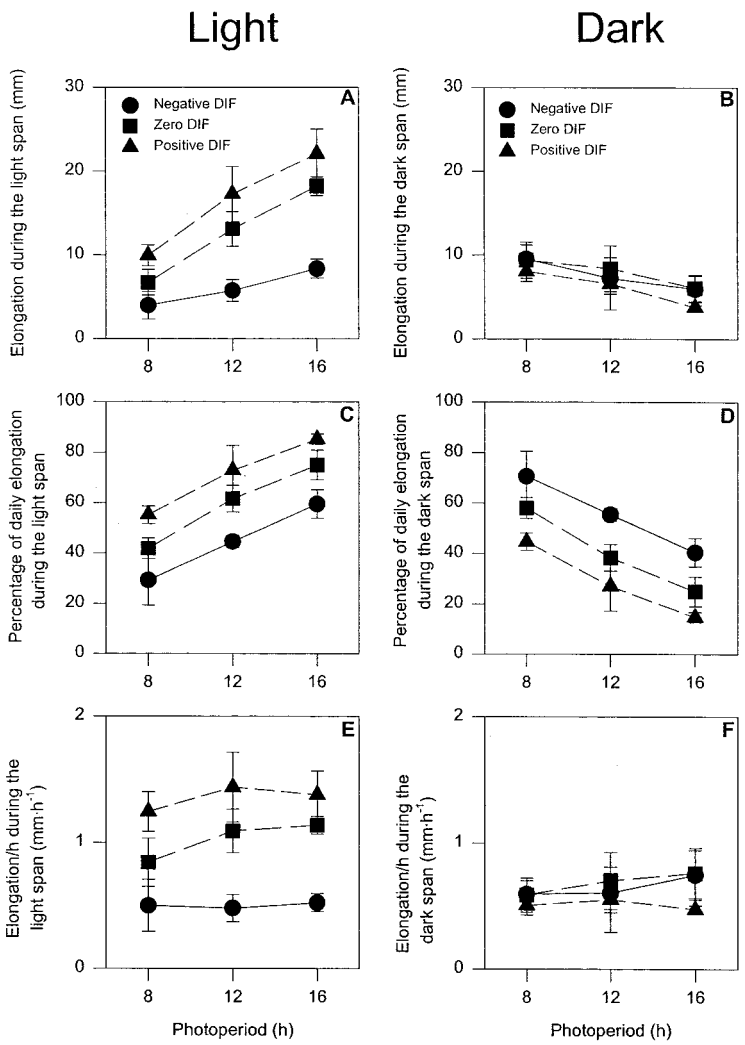


Fig. 4. Influence of photoperiod and DIF on daily stem elongation during the (**A**) light and (**B**) dark period of the day, percentage of daily elongation during the (**C**) light and (**D**) dark period of the day, and elongation per hour during the (**E**) light and (**F**) dark period of the day. Vertical bars indicate 95% confidence intervals of the means.

In contrast, we observed a sharp increase in SER in positive-DIF-grown plants immediately after the transition from night to day, followed by a slight rise until the maximum value occurred. After the peak, SER decreased gradually until the night period started. On the other hand, SER under negative DIF decreased slowly after the night–day transition until a low point was reached, and increased gradually thereafter. The SER's shape at zero DIF was similar to that at positive DIF, probably because the actual temperature yielded a slightly positive DIF. However, the magnitude of response was lower. The SER during the dark showed a similar pattern and value, and there were small oscillations in SER in all DIF treatments.

Positive DIF enhances internode elongation more than zero or negative DIF in many species, and this effect results in greater stem elongation. A quantitative response to DIF was shown in *Lilium longiflorum* (Erwin et al., 1989a), *Campanula isophylla* (Moe and Heins, 1990) and *Euphorbia pulcherrima* (Berghage and Heins, 1991). Internodes were shorter as DIF decreased from a positive to a negative number. The experiments in this study demonstrated similar phenomena. Plant stem elongation increased markedly with increasing DIF, irrespective of photoperiod duration (Fig. 2).

The effect of DIF or temperature on elongation during the day or night period has been investigated using transducers connected to plant shoots. According to Christ (1987), the total elongation rate of stems and leaves in *Triticum aestivum* L. 'Probus' ('Probus' wheat), which was measured as the upward fastened position of the leaf tip using an LVDT, was ≈60% to 70% lower during the night than during the day. His experiment was conducted in a growth chamber at 20 °C during the day and night with a 14-h photoperiod each day. Under field conditions, leaf extension rate of *Triticum aestivum* during the night was also less than that during the day (Gallagher et al., 1976). However, since the leaf-extension measurement was conducted in the field, there is no doubt that temperature during the day was higher than it was during the night and that DIF was positive. Likewise, positive DIF is possible on plants even when air temperatures are constant due to radiant heating of plant tissue under sunny conditions. Neily et al. (1997) reported the SER of *Zinna violacea* Cav. ('Pompon' zinnia) in visible bud and preanthesis stages was faster during the day than during the night under 0 DIF conditions, and found the magnitude of SER during the day depended on the developmental stage of plants. However, Erwin et al. (1992), using an angular-displacement transducer, found that elongation during the dark span was faster than that during the light span in *Dendranthema ×grandiflora*. A similar result was reported for *Dendranthema ×grandiflora* where elongation during the night was faster than that during the day in a constant 18.3 °C temperature regimen (Tutty et al., 1994). Bertram and Karlsen (1994) also noted that the SER of *Dendranthema ×grandiflora* and *Lycopersicon esculentum* Mill. (tomato) plants was greater during the night than during the day under a constant 20 °C. In the present study, E_L of *Verbena bonariensis* at zero or positive DIF was more pronounced than E_D under 12- and 16-h photoperiods; however, there was not as much E_L as E_D in an 8-h photoperiod. These results combined suggest that the magnitude of elongation during the day compared with that during the night is species-dependent.

Results herein indicate that DIF significantly affected E_L, and response to DIF increased as photoperiod increased. DIF had no statistically significant effect on E_D; the absolute values of E_D (mm) under all DIF treatments were similar (Fig. 4B). E_D decreased slightly as photoperiod increased from 8 to 16 h. PE_D was a direct consequence of changes in PE_L due to DIF and photoperiod (Fig. 4C and D).

Some but not all differences in daily elongation (Fig. 3) attributed to DIF and photoperiod may have been influenced by differences in average daily temperature. For example, temperature may have contributed to the greater daily elongation measured under positive DIF compared to negative DIF in the 16-h photoperiod because average daily temperature was 3.5 °C greater under positive DIF. However, average temperature cannot explain differences in elongation in the 12-h and 8-h photoperiods. In the 12-h photoperiod, average temperature was only 0.5 °C greater under positive DIF, while average temperature under positive DIF was actually 2.5 °C lower than under negative DIF in the 8-h photoperiod. Therefore, changes in daily elongation caused by DIF and observed in Fig. 3 were not due to differences in average daily temperature.

Neily et al. (1997) stated that, for *Zinnia violacea*, DIF influenced mainly the SER pattern during the light span. Our results show that more E_L was caused by more-positive DIF or a longer photoperiod, and less E_L occurred with a more-negative DIF or a shorter

photoperiod. The PE_L and PE_D obviously depended on DIF and the length of the photoperiod. Positive DIF and long photoperiods caused a high PE_L and low PE_D, and negative DIF and short photoperiods caused a low PE_L and a high PE_D. However, since actual changes in E_D were very small, daily plant elongation was determined mainly by E_L. Because we provided the same daily light integral in all treatments, *PPF* during the light span is confounded with photoperiod. It is not possible from this experiment to separate the effects of *PPF* and photoperiod.

Elongation per hour during the light and that during the dark were not significantly affected (Fig. 4E and F) by photoperiod duration, while elongation per hour in the light increased with more-positive DIF treatment. The EH_L undoubtedly was affected by DIF, but the differences in EH_D were not statistically significant (Fig. 4F). The response to DIF is quantitative (Erwin et al., 1987; Heins and Erwin, 1990; Moe and Heins, 1990). The quantitative relationship between elongation and DIF was shown clearly as EH_L and EH_D. Each DIF had inherent EH_L and EH_D, so E_L increased and E_D decreased as photoperiod extended.

We conclude that DIF primarily affects stem length of *Verbena bonariensis* by affecting the rate of elongation during the light period of the day, not the dark period. Final stem length will increase as photoperiod increases because the faster elongation rate occurs for a longer time each day. Longest plant stems occur under long photoperiods and positive DIF, while shortest stems occur under short photoperiods and negative DIF.

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