Temperature and Developmental Stage Influence Diurnal Rhythms of Stem Elongation in Snapdragon and Zinnia

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ABSTRACT. Stem elongation rates (SERs) of 'Giant Tetra' snapdragon (*Antirrhinum majus* L.) and 'Pompon' zinnia (*Zinnia violacea* Cav.) were determined in three temperature regimes in which differentials had been established between day and night temperature. The differentials [expressed as day temperature – night temperature (DIF)] were +5 DIF, 21 °C day/16 °C night; 0 DIF, 18.7 °C constant; and –5 DIF, 16.5 °C day/21.5 °C night; daily average 18.7 °C. In each regime SERs were determined for three developmental stages—vegetative, visible bud, and preanthesis. SER was measured in controlled-environment chambers under 13-hour day/11-hour night photoperiods using linear voltage displacement transducers. Snapdragon and zinnia displayed rhythmic patterns of growth with strikingly different characteristics. SER for snapdragon consisted of a large peak in growth at the day/night (D/N) transition followed by a minimum in SER at the night/day (N/D) transition. The pattern did not change through development. In contrast the SER pattern changed significantly in zinnia. At the vegetative stage, diurnal SER was dominated by a large peak after the N/D transition [an early morning peak (EMP)]. At the later growth stages, the EMP remained visible, but the proportion of growth occurring at night increased. SER was rhythmic in both species for a limited period in continuous light and constant temperature. Zinnia displayed a stronger endogenous rhythm of SER than snapdragon. In both species, only day period growth was affected by DIF. The size of EMPs in both species increased under positive DIF and decreased under negative DIF, resulting in the overall DIF effect on plant height (a progressive increase in total diurnal elongation as DIF increased from –5 to +5). Internode lengths for snapdragon and zinnia were similar for plants grown to full flower at constant 17, 20, or 23 °C (0 DIF), indicating that DIF—not average daily, night, or day temperature—is a major determinant of extension growth.

The effect of temperature on plant morphological development has been the subject of many studies. Most have focussed on the remarkably consistent findings that internode elongation increases as the value of day temperature – night temperature (DIF; Karlsson et al., 1989) increases (Erwin et al., 1989b; Erwin and Heins, 1995; Hendriks and Scharpf, 1985), whereas average daily temperature generally has little influence on elongation within a defined range. These observations have been put to practical use in the greenhouse industry where the reliance on chemical growth regulators to control stem elongation has been reduced. In some cases, however, elongation response to DIF is inconsistent: studies have shown that the effects of DIF depend on prevailing conditions such as light quality, photosynthetic photon flux (PPF), and photoperiod (Myster and Moe, 1995).

The effects of DIF are most pronounced when internodes are expanding rapidly (Heins and Erwin, 1990), but relatively little attention has been paid to the effects of DIF at different stages of crop development. Since height control using DIF and techniques

such as graphical tracking (Erwin, 1992; Karlsson and Heins, 1994) depend on a predictable response, it is essential to understand the relationship between DIF and crop growth stage to exploit the potential of these techniques fully.

We report the results of experiments conducted using high-resolution growth measurement techniques to investigate the effects of DIF on diurnal patterns of stem elongation rate (SER) in two bedding plant species at specific stages of plant development.

Materials and Methods

PLANT MATERIAL AND INITIAL CULTURAL CONDITIONS. Seedlings of 'Giant Tetra' snapdragon (*Antirrhinum majus*) and 'Pompon' zinnia (*Zinnia violacea*) were potted in 10-cm pots containing a peatlite growing medium (Pro-mix BX; Premier Brands Inc.). Controlled-release fertilizer (Nutricote type 100; 14N–6.2P₂O₅–11.3K₂O; Chisso-Ashai Fertilizer Co., Tokyo) was premixed into the medium at a rate of 2.0 g/pot. Plants were grown in controlled-environment (CE) chambers without humidity control. PPF was maintained at 350 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at the upper leaf surfaces for 13 h each day. The light source consisted of a mixture of cool-white fluorescent and incandescent lamps (75%:25% input wattage). Red:far red ratio was 2:1 (SKR 100, 660/730nm sensor; Skye Instruments, Wales). Chamber temperature was maintained at 18.7 $\pm$ 0.5 °C and monitored by shielded, aspirated copper-constantan thermocouples. Plants remained in the CE chamber under these conditions until they reached the appropriate stage of development for study.

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Three developmental stages were chosen. At stage 1 (vegetative), snapdragon and zinnia were 8 to 10 cm tall and showed no visible flower bud. Stage 2 (visible bud) was the period from when buds were first visible to when they reached ≈ 1.0 cm in diameter. Plant height was 18 to 21 cm in snapdragon and 12 to 14 cm in zinnia. Stage 3 (preanthesis) was just before flowering, with the first sign of color in the flower bud. Snapdragons were 25 to 30 cm tall and zinnias were 16 to 19 cm tall.

HIGH-RESOLUTION SER MEASUREMENT. SER was measured using linear voltage-displacement transducers (LVDTs) (models 200DC-D and 250 DC-E with small-diameter cores; Schaevitz Engineering, Pennsauken, N.J.) in an apparatus modified from Kristie and Jolliffe (1986) and previously described by Tutty et al. (1994). The core of the transducer was attached via a polyester thread just below the junction of the uppermost leaf and the stem. A datalogger (model CR7; Campbell Scientific, Logan, Utah) simultaneously recorded LVDT output voltages and CE chamber temperatures. Outputs were recorded each second and averaged for the last minute of a 5-min interval, once every 5 min. Stem position at successive 5-min intervals was calculated from the LVDT output voltages and differenced once to give the SER. Since the attachment point for the transducer core was the last visible node on the stem, data collected represented the integrated elongation rate of all internodes on the stem. The data displayed high frequency oscillations similar to those found in *Dendranthema grandiflorum* Tzvelev. (Tutty et al, 1994) and were therefore filtered using previously described methods so that the underlying rhythms would be displayed (Tutty et al., 1994). System stability to changes in temperature was verified by replacing the plant by various inert materials (wood and copper wire inserted in soil). Only slight changes in position were observed due to expansion or contraction of system components. Calculated rates of growth of the system subjected to temperature change never exceeded $\pm 15 \mu\text{m}\cdot\text{h}^{-1}$.

TEMPERATURE EFFECTS (EXPT. 1). Plants at the appropriate growth stage were moved to CE chambers and attached to LVDTs 24 h before initiating measurements. PPF, photoperiod, and red:far red ratio were unchanged from the premeasurement conditions. For each growth stage plants were subjected to three DIF regimes (+5 DIF, 21 °C day/16 °C night; 0 DIF, 18.7 °C constant; and -5 DIF, 16.5 °C day/21.5 °C night), each with a daily average temperature of 18.7 °C. At the day/night (D/N) and night/day (N/D) transitions, the new temperature was attained within 15 min of the light change. Each plant was measured for three consecutive diurnal cycles. The experiment was designed as a completely randomized factorial arrangement of treatments. Data for each species were analyzed separately, with developmental stage and DIF as factors. Individual plants were grown to the appropriate growth stage and assigned randomly to CE chambers equipped with LVDT systems. During measurements, there was a single plant in each chamber; a new plant was used for each growth stage and DIF treatment. Plants were subirrigated to ensure constant moisture levels in the medium and prevent disturbance to the shoot. For snapdragon, each growth

treatment was repeated three times and, for zinnia, five times. Total stem growth and growth during day and night periods were calculated by integrating the area under the SER traces.

GROWTH PATTERNS UNDER CONSTANT TEMPERATURE AND LIGHT (EXPT. 2). Stage 1 plants of zinnia and snapdragon were placed in chambers maintained at constant 18.7 °C and connected to LVDTs. Each plant was then subjected to 48 h under successive 11-h night/13-h day periods. Thereafter, continuous light conditions were maintained for an additional 72 h. The experiment was repeated three times.

LOW-RESOLUTION MEASUREMENT OF INTERNODE ELONGATION (EXPT. 3). Twenty-five newly potted plants of zinnia and snapdragon were placed in each of six CE chambers under similar light conditions to those described previously. Temperatures in each of two chambers were constant at either 17, 20, or 23 °C. Plants were grown to full flower, at which time the effects of constant temperature on elongation were assessed by measuring overall stem height from the soil surface at harvest and the length of individual internodes. Preliminary analysis revealed no significant differences between chambers at the same temperature, so data for all plants at each temperature were pooled for final analysis.

Results

The SERs of snapdragon and zinnia displayed a diurnal rhythmicity with a repeating pattern of stem elongation closely associated with changes in thermoperiod and photoperiod. For snapdragon, there was a tendency toward higher SER as plants matured, but patterns of stem elongation were similar irrespective of growth stage (Fig. 1). SER was rhythmic, declining during the night and increasing during the day. Under 0 DIF conditions, the rhythm

Fig. 1. Patterns of stem elongation rate (SER) for snapdragon at three stages of development and under three (DIF) regimes (+5, 21/16 °C; 0, constant 18.7 °C; -5, 16.5/21.5 °C). For the visible bud stage, arrows highlight early morning peaks, and shaded areas indicate day period growth. D = day, N = night. DT = day temperature, NT = night temperature, DIF = day temperature - night temperature. Traces are averages of three plants for each stage-DIF combination.

Fig. 2. Patterns of stem elongation rate (SER) for stage 1 (vegetative) snapdragon (A) and zinnia (B) plants subjected to continuous light following 48 h growth in 13-h light/11-h dark periods. Temperature was constant at 18.7 °C. Traces are averages of three plants.

consisted of a peak in SER centered at or slightly after the D/N transition [the early night peak (ENP)]. Thereafter, SER declined steadily through most of the night and then more rapidly ≈ 1 h before the N/D transition. Lowest SER values were recorded immediately after the N/D transition, but SER recovered quickly and a small peak occurred 3 to 4 h after the start of the day period (EMP). Under continuous light and constant temperature, the rhythm in stage 1 plants persisted for one complete diurnal cycle with a period of 28 h. Thereafter the previously established pattern was lost (Fig. 2A). SER, however, remained high for at least 72 h following the onset of continuous light.

Stem elongation patterns in zinnia were not consistent among growth stages. On the contrary, under 0 DIF conditions the stem elongation pattern changed progressively with each developmental stage (Fig. 3). Overall, SER increased as plants matured, as in snapdragon, but nighttime growth became prominent at the later growth stages. Early in development (stage 1; vegetative), most growth occurred as a broad peak in SER during the early day. By stage 3 (preanthesis), the main growth peak had shifted to the early part of the night and the transition between these two patterns was evident at stage 2 (visible bud). At stage 1 (vegetative), an EMP occurred at or shortly after the N/D transition, and a much smaller ENP occurred at the D/N transition. At visible bud, the EMP was still evident 4 to 5 h after the start of the day period, but by this stage two

distinct peaks were observed during the night: the first, as at stage 1 shortly after the D/N transition and the second just before the N/D transition. Elongation patterns of stage 3 (preanthesis) plants resembled those of plants at visible bud, although the EMP and overall daytime growth were reduced in comparison with the previous stage. Under continuous light and constant temperature, the SER rhythm of stage 1 (vegetative) plants persisted for 2 diurnal cycles with a period of ≈ 27 h (Fig. 2B).

DIF had little effect on the main features of the SER patterns in snapdragon (Fig. 1), but affected the size of the ENP, especially in vegetative plants, and the EMP. Under -5 DIF conditions the EMP was absent, but it became prominent as DIF increased (i.e., became more positive). In zinnia, at each stage of development DIF influenced mainly the daytime SER pattern (Fig. 3). The EMP was the feature most profoundly influenced by DIF and, as in snapdragon, the size of the EMP increased progressively as DIF increased from -5 to $+5$.

Dissimilarities in snapdragon and zinnia SER patterns were reflected in differences in diurnal growth distribution (Table 1). In snapdragon under 0 DIF conditions, more growth occurred at night than in the day and developmental stage had no significant effect on this distribution. However, DIF influenced growth distribution; the proportion of growth occurring during the night period increased under -5 DIF conditions and decreased at $+5$ DIF. In zinnia, stem growth distribution was significantly affected by developmental stage and DIF. Under all temperature regimes, growth shifted from predominately dur-

Fig. 3. Patterns of stem elongation rate (SER) for zinnia at three stages of development and under three (DIF) regimes ($+5$, 21/16 °C; 0, constant 18.7 °C; -5 , 16.5/21.5 °C). For the visible bud stage, arrows highlight early morning peaks, and shaded areas indicate day period growth. D = day, N = night. DT = day temperature, NT = night temperature, DIF = day temperature – night temperature. Traces are averages of five plants for each stage–DIF combination.

Table 1. Percentage of stem elongation in snapdragon and zinnia occurring during the day period.

DIF ^y	Day period elongation (%) ^z					
	Snapdragon			Zinnia		
	Vegetative	Visible bud	Preanthesis	Vegetative	Visible bud	Preanthesis
+5	46.6	51.7	49.2	64.1	51.7	42.6
0	39.2	36.9	36.3	60.5	47.5	37.2
-5	34.0	29.9	26.5	49.6	41.4	27.5
Statistical analysis						
	Overall SEM ^x (n = 3; df = 18): 2.2			Overall SEM ^x (n = 5; df = 36): 2.90		
DIF			**			**
Linear			**			**
Stage			NS			**
DIF × stage			NS			NS

^zAverage of day growth/total growth × 100% for three consecutive diurnal cycles.^yDifference between day temperature (DT) and night temperature (NT); +5 DIF, 21 °C DT/16 °C NT; 0 DIF, 18.7 °C constant; -5 DIF, 16.5 °C DT/21.5 °C NT. Daily average temperature, 18.7 °C; Photoperiod, 13 h.^xSEM = standard error of the mean.NS, **Nonsignificant or significant at *P* = 0.01, respectively.

ing the day period during the vegetative stage to predominately during darkness at preanthesis. At each stage, the contribution of daytime growth to the diurnal total increased as DIF increased. DIF had significant effects on total diurnal stem elongation in snapdragon and zinnia (Table 2). Growth increased as DIF increased, but the effect of increasing DIF from 0 to +5 was, on average, greater than an increase from -5 to 0. In both species, the magnitude of the DIF response increased at later growth stages; maximum response occurred at stage 3 (preanthesis) when total elongation rate was highest. In vegetative snapdragon, for example, growth increased 38% as DIF increased from -5 to +5, whereas at preanthesis the same change resulted in a 77% increase.

Snapdragon and zinnia showed similar relationships between DIF and day period growth (Table 3) and DIF and night period growth (Table 4). In both species, growth during the day was strongly affected by DIF and the magnitude of the effect increased with developmental stage. In contrast, nighttime growth was unaffected by DIF at any stage.

Under alternating 13-h light/11-h dark periods, there was no significant difference in final stem height or average internode length in snapdragon when plants were grown at 17, 20, or 23 °C

(data not shown). Zinnia showed a linear increase in final stem height as temperature increased, but average internode length was not significantly affected by growing temperature.

Discussion

Stem elongation in snapdragon and zinnia follows a rhythmic diurnal pattern that is strongly influenced by temperature and light. The patterns appear to have an endogenous component, since each is recognizable in the absence of regularly changing external stimuli and shows a periodicity for slightly longer than 24 h. Similar, but often much more persistent, endogenous rhythms of stem and internode elongation have been described for several other species including *Lycopersicon esculentum* L. (Bertram and Karlsen, 1995; Ibrahim et al., 1981), *Chenopodium rubrum* L. (Lechamy et al., 1985), and *Dendranthema grandiflorum* (Tutty et al., 1994). In some cases, circadian rhythms are evident for many days following the imposition of continuous light or darkness, but others, as in this case, disappear after a few days and appear to depend much more on the primary environmental signals of light and temperature (Bünning, 1973).

Table 2. Total growth over 3 d in snapdragon and zinnia at three growth stages and in three DIF regimes. Data obtained by integrating the area under the stem elongation rate (SER) patterns in Figs. 1 and 3.

DIF ^y	SER (mm) ^z					
	Snapdragon			Zinnia		
	Vegetative	Visible bud	Preanthesis	Vegetative	Visible bud	Preanthesis
+5	26.09	55.34	57.24	18.81	40.43	50.63
0	21.73	40.50	40.04	18.22	36.62	37.68
-5	18.97	33.14	32.40	16.65	28.83	35.22
Statistical analysis						
	Overall SEM ^x (n = 3; df = 18): 2.85			Overall SEM ^x (n = 5; df = 36): 2.45		
DIF			**			**
Linear			**			**
Stage			NS			**
DIF × stage			NS			NS

^zValues are the total growth for three diurnal periods.^yDifference between day temperature (DT) and night temperature (NT); +5 DIF, 21 °C DT/16 °C NT; 0 DIF, 18.7 °C constant; -5 DIF, 16.5 °C DT/21.5 °C NT. Daily average temperature: 18.7 °C; photoperiod, 13 h.^xSEM = standard error of the mean.NS, **Nonsignificant or significant at *P* = 0.01, respectively.

Table 3. Day period growth over 3 d in snapdragon at three growth stages and in three DIF regimes. Data obtained by integrating the area under the stem elongation rate (SER) traces for three day periods.

DIF ^y	SER (mm) ^z					
	Snapdragon			Zinnia		
	Vegetative	Visible bud	Preanthesis	Vegetative	Visible bud	Preanthesis
+5	12.17	28.71	28.17	12.13	20.25	21.26
0	8.56	14.99	14.46	11.01	17.56	13.84
-5	6.49	9.81	8.87	8.23	11.73	9.72
Statistical analysis	Overall SEM ^x (n = 3; df = 18): 1.51			Overall SEM ^x (n = 5; df = 36): 1.85		
DIF			**			**
Linear			**			**
Stage			**			**
DIF × stage			**			*

^zValues are the total growth for three day periods

^yDifference between day temperature (DT) and night temperature (NT); +5 DIF, 21 °C DT/16 °C NT; 0 DIF, 18.7 °C constant; -5 DIF, 16.5 °C DT/21.5 °C NT. Daily average temperature, 18.7 °C; photoperiod, 13 h.

^xSEM = standard error of the mean.

*,** Significant at *P* = 0.05 or 0.01, respectively.

Stem elongation responses of a very wide range of plant species are similarly influenced by DIF (Erwin and Heins, 1995), and snapdragon and zinnia share some of the characteristics associated with the DIF response in other species. For example, the DIF effect increases as total SER increases (Heins and Erwin, 1990), and increasing DIF above 0 has a relatively greater effect than a decrease from 0 to negative values (Berghage and Heins, 1991; Karlsson et al., 1989; Moe, 1990). It is clear that these similarities exist despite widely divergent diurnal patterns of stem elongation and diurnal growth distribution not only between species (Bertram and Karlsen, 1994a, 1994b) but, as in the case of zinnia, within one species at different growth stages. The progressive increase in absolute SER with increasing maturity in snapdragon and zinnia is likely due to an increase in the number of actively elongating internodes. Berghage and Heins (1991) showed that, although internodes lower on the stem of poinsettia plants elongated more rapidly than those formed later in development, they also matured (i.e., ceased to elongate) sooner. At later stages of development, several internodes may be elongating simultaneously, resulting in an overall increase in total stem elongation rate. This does not

explain the relative changes in diurnal growth distribution, although we may hypothesize that, in zinnia, later-formed internodes have a different elongation response to photoperiod than those formed earlier in development.

Several species show sensitivity to DIF during day and night periods (Bertram and Karlsen, 1994a; Tutty et al, 1994), but in others, including those in the present study, day period growth is predominately affected and is the major determinant of the total DIF effect on stem elongation (Erwin and Heins, 1988). In zinnia, the predominance of the day period effect persists despite significant changes in the overall contribution of nighttime growth to total diurnal elongation through development. The question arises as to whether stem elongation in snapdragon or zinnia is, in fact, responding to DIF or whether nighttime growth is simply insensitive to changes in temperature, which elicit a strong response during the day period. Our results suggest that this is not the case, since internode length was unaffected by constant temperatures of 17 to 23 °C in both species. If simple differential D/N sensitivity to temperature were involved, we would expect a strong influence of increasing temperature at 0 DIF. While total stem height of

Table 4. Night period growth over 3 d in snapdragon at three growth stages and in three DIF regimes. Data obtained by integrating the area under the stem elongation rate (SER) traces for three day periods.

DIF ^y	SER (mm) ^z					
	Snapdragon			Zinnia		
	Vegetative	Visible bud	Preanthesis	Vegetative	Visible bud	Preanthesis
+5	13.92	26.63	29.07	6.67	20.18	29.37
0	13.18	25.51	25.58	7.17	19.06	23.84
-5	12.48	23.33	23.52	8.30	17.10	25.51
Statistical analysis	Overall SEM ^x (n = 3; df = 18): 1.71			Overall SEM ^x (n = 5; df = 36): 2.79		
DIF			NS			NS
Stage			**			**
DIF × stage			NS			NS

^zValues are the total growth for three night periods

^yDifference between day temperature (DT) and night temperature (NT); +5 DIF, 21 °C DT/16 °C NT; 0 DIF, 18.7 °C constant; -5 DIF, 16.5 °C DT/21.5 °C NT. Daily average temperature, 18.7 °C; photoperiod, 13 h.

^xSEM = standard error of the mean.

NS,** Nonsignificant or significant at *P* = 0.01, respectively.

zinnia was affected by increasing temperature (possibly as a result of delay in flower initiation at higher temperatures), average internode length was not.

Despite widely divergent patterns of stem elongation in snapdragon and zinnia, the principle effects of DIF on day period growth appear to be closely correlated with the amplitude of the EMP in SER. In each case, the size of the EMP increased with increasing DIF just as observed previously in *Dendranthema grandiflorum* (Bertram and Karlsen 1994a; Tutty et al., 1994). The position of the EMP in the diurnal cycle corresponds with the time of maximum sensitivity to temperature in several species (Erwin et al., 1989a; Grindal and Moe, 1994; Heins and Erwin 1990) and it is tempting to generalize that DIF preferentially affects internode elongation during this time. However, while the EMP always seems to be influenced by DIF, the effects may sometimes be reversed (i.e., decreased amplitude with increased DIF in *Lycopersicon esculentum*; Bertram and Karlsen, 1994a).

The precise nature and underlying mechanisms of the DIF response in snapdragon, zinnia, and many other species remain unclear. The evident importance of early photoperiod growth and the fact that absolute values of day or night temperature do not control SER, however, point to a possible role for the change of temperature at the N/D transition. Much attention has been focussed on the possible interaction of DIF and gibberellin (GA) synthesis or activity in influencing stem elongation (Erwin et al., 1989b; Moe, 1990; Erwin and Pierson, 1992; Zieslin and Tsujita, 1988). The influence of a temperature change at the N/D transition is consistent with the involvement of GA in the DIF response since GA synthesis and transport are temperature dependent (Menhennett and Waring, 1975; Tagliavini and Looney, 1991). Furthermore, GA synthesis follows a circadian rhythm in some plants, with higher levels produced during the day period (Foster and Morgan, 1995; Talon et al., 1991). Further investigation of the influence of temperature differences on these rhythms and in particular their relationship to SER rhythms could shed further light on the mechanisms underlying plant response to DIF.

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