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The Influence of Photoperiod and Temperature on the Kinetics of Stem Elongation in *Dendranthema grandiflorum*

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Abstract. **Stem elongation rate (SER) in *Dendranthema grandiflorum* (Ramat.) Kitamura was determined in light and in darkness under various temperature regimes. Stem growth as measured with linear voltage displacement transducers on plants in growth chambers. Under alternating 11-hour days and 13-hour nights, SER was strongly temperature dependent and showed patterns that were characteristic of the particular photoperiod–temperature regime under which the plants were grown. Total daily elongation was similar at constant 18.3C and at 11.5C days and 24C nights, but was much greater at 25.7C days and 12C nights. SER was rhythmic in continuous light with a period of slightly less than 24 hours. In continuous darkness, however, SER declined rapidly and the rhythm disappeared within 11 hours. Low-temperature pulses (a rapid decline from 18.3C to 8.3C) applied for 2, 4, 6, 8, or 11 hours during the day induced an immediate decline in SER followed by a slow recovery and peak shortly after the end of the pulse. Total diurnal stem growth declined with increasing pulse length, although short (2-hour) duration pulses apparently had little effect on growth. The results are discussed in relation to the influence of day and night temperature differentials (DIF) on stem growth in *Dendranthema*.**

Stem elongation in many plants is influenced by the relationship between day and night temperature (Erwin et al., 1989a; Karlsson et al., 1989). In *Dendranthema*, stem elongation increases when day temperature increases or when night temperature decreases (Erwin, 1992). The temperature differential (DIF) (Erwin and Heins, 1988a) that is maintained between day and night temperatures determines the stem height at harvest; a large positive DIF results in greater stem elongation than a negative or zero DIF with the same daily mean temperature (Erwin and Heins, 1988a, Erwin et al., 1989a). Plants respond rapidly to a change in DIF, allowing greenhouse growers to manipulate plant height by appropriately adjusting day and night temperatures (Erwin, 1992)

Stem elongation in some species shows a diurnal rhythm that can be modified by temperature (Lecharny and Wagner, 1984; Lecharny et al., 1985). Preliminary studies (Erwin and Heins, 1988b; Tutty and Hicklenton, 1990; Tutty et al., 1992) using high-resolution growth-measurement techniques have indicated that *Dendranthema* stem elongation is rhythmic, but these authors have not discussed the nature of this diurnal rhythm. Characterizing the response should lead to an understanding of how temperature affects stem growth and how stem elongation can be controlled by short-term manipulation of greenhouse temperature. In this paper, we describe some of the stem elongation patterns in *Dendranthema* and report the influence of photoperiod and temperature on these patterns.

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Materials and Methods

Plant material and cultural conditions

Rooted cuttings of *Dendranthema grandiflorum* 'Envy' were potted in 0.5-liter (10-cm-diameter) pots containing a peatlite growing medium (Nova Mix; Annapolis Valley Peat Moss, Aylesford, N.S.). Controlled-release fertilizer (Nutricote Type 100; Chisso-Ashai Fertilizer Co., Tokyo) was premixed into the medium at a rate of 5 $kg \cdot m^{-3}$. Plants were pretreated according to two protocols. In the first protocol, plants were grown in a greenhouse under 24-h high-pressure sodium lighting that provided a supplemental photosynthetic photon flux (PPF) of 170 $\mu mol \cdot s^{-1} \cdot m^{-2}$ on the upper leaves. The lamps were raised as required to maintain supplemental PPF conditions. The greenhouse was maintained at 16C night and 25C day, with venting at 26C. In the second protocol, plants were grown in a controlled-environment (CE) chamber in which PPF at the uppermost leaves was maintained at 170 $\mu mol \cdot s^{-1} \cdot m^{-2}$ for 11 h each day. Chamber temperature was maintained at 18.3 ± 0.5C. At the end of the pretreatment period, greenhouse-grown plants had between 8 and 10 leaves, whereas those grown in CE chambers had between 12 and 14.

Stem elongation rate measurement

Stem elongation rate (SER) was measured using linear voltage displacement transducers (LVDTs) (models 200 DC-D and 250 DC-E with small diameter cores; Schaevitz Engineering, Pennsauken, N.J.). Each LVDT consists of a cylindrical transformer coil and a free-moving metal core that travels vertically within the coil. Under the influence of an excitation voltage, the transducer produces an electrical signal that is linearly related to the core position. In our experiments, the coil was mounted on the mechanical stage of a modified microscope body (Kristie and Jolliffe, 1986) that allowed optimum positioning of the coil and core. The apparatus was shielded from chamber air currents and mounted on a concrete base that was buffered from CE chamber vibrations by foam pads.

The core was attached to a plant at the intersection of the stem and the base of the uppermost petiole by a threaded alloy extension rod, hook, and polyester thread. The core, extension rod, and hook were counterbalanced using a pulley and a 2.0-g weight. Transducer output voltage was monitored and recorded at 5-min intervals using a datalogger (model CR7; Campbell Scientific, Logan, Utah), which simultaneously recorded CE chamber temperatures sensed by shielded copper-constantan thermocouples.

A series of transducer output voltages was converted to 5-min linear displacements (representative of stem growth) and then differenced once to produce a new series that gave the change in length for each 5-min interval. These data were compromised by a high frequency rate oscillation that underlay the lower frequency diurnal pattern. Since diurnal rhythmicity was of prime interest in this work the high-frequency oscillation was removed by digital filtering.

Filtering algorithm. A symmetric exponentially weighted moving average (EWMA) filter was constructed by combining left and right-handed EWMAs. The left-handed EWMA averaged the k previous values in the input series x_t, with weights $\lambda(1-\lambda)^k$ to produce a smoothed output series y_t: $y_t = (1-\lambda)y_{t-1} + \lambda x_t \approx \lambda\{x_t + (1-\lambda)x_{t-1} + (1-\lambda)^2 x_{t-2} + \ldots + (1-\lambda)^k x_{t-k}\}$ for large t and $k \leq t$.

Using the backward shift operator (Jenkins and Watts, 1968) the smoothed series can be written as a transfer function applied to x_t: $y_t = [(1-\lambda)/(1-\lambda B)]x_t$, where $0 < \lambda < 1$.

For this study, the value for $(1-\lambda)$ was chosen empirically as 0.9 to filter out frequencies >21.25 cycles/h. Transients at the endpoints of the series were reduced by using the autoregressive integrated moving average to back-forecast the input series values before x_0, with the EWMA fitted as a transfer function model.

Reversing the x_t series and applying the same procedure resulted in an output series weighted by the values to the right of and including x_t. The two output series y_t consisted of an exponentially weighted average of the values to the left of (and including) x_t and one to the right. The resulting symmetric EWMA filter was obtained by averaging the left and the right filtered series, which was corrected for the common use of x_t in both series. All time-series models were calculated as procedures in the Genstat 5 statistical programming language (Payne, 1987).

A sample of raw data and equivalent filtered trace is compared (Fig. 1) Fig. 1B illustrates the nature of the underlying high-frequency oscillation evident in all traces. The origin of this oscillation is unknown; it may be an artifact related to electrical noise, vibration, or nutation of the shoot. Alternatively, it may reflect genuine changes in SER of the plant shoot similar to the short period oscillations observed in etiolated stems (Kristie and Jolliffe, 1986) and some green plants (Cosgrove, 1992).

Temperature treatments and SER measurement protocol. Plants were moved to a CE chamber and connected to a LVDT-measurement system 24 h before beginning measurement. PPF (170 $\mu mol \cdot s^{-1} \cdot m^{-2}$) was supplied by high-pressure sodium lamps for 11 h each day. The first experiment involved measuring SER in three temperature regimes: 25.7 day/12C night, constant 18.3C, and 11.5C day/24C night. The regimes were chosen to provide equivalent average daily mean temperatures and to compare differences in SER patterns under positive, zero, and negative DIF conditions.

The second experiment was conducted to determine 1) whether the growth patterns evident under the three basic temperature regimes included endogenous circadian rhythms and 2) whether temperature cycling alone could entrain a rhythm in SER. Plants were subjected to three treatments: continuous lighting for up to 90 h at constant 18.3C; continuous darkness (also at 18.3C); continuous lighting with temperature cycling (25.7C for 11 h/12C for 13 h).

The third experiment investigated the effects of temperature change (pulse) applied for different periods on SER. Plants growing at 18.3C were subjected to 8.3C for 2, 4, 6, 8, or 11 h beginning at the start of the day, or for 2 h beginning 2 h after the start of the day. To describe the effect of low-temperature pulses on day, night, and total diurnal growth, the percentage change in plant growth under the various low-temperature treatments was calculated for each period and regressed against pulse duration.

The number of sample plants used in these studies varied, and is given in the figure legends.

Results

Kinetics of stem elongation under three temperature regimes. SER patterns were similar for plants pretreated in the greenhouse and CE chamber. The averaged SER response (Fig. 2A) fairly represented typical individual plant traces (Fig. 2B). Plants grown at 25.7/12C had a higher mean SER than those grown at constant 18.3C or at 11.5/24C (Fig. 2). SER peaked immediately following the start of the day at 25.7/12C and constant 18.3C regimes, although the peak was of greater amplitude at 25.7/12C. A mini-

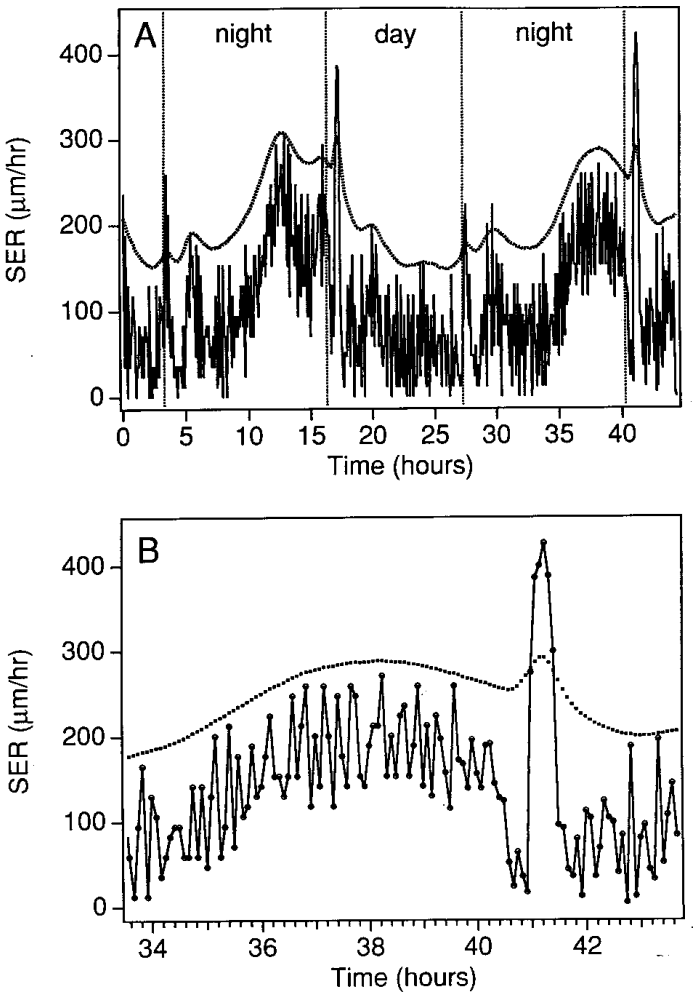

Fig. 1. (**A**) Representative raw (solid line) and time-series filtered data (broken line) showing stem elongation rate in one *Dendranthema grandiflorum* plant. For clarity, the filtered data are offset by a constant of 100 $\mu m \cdot h^{-1}$. (**B**) Expanded portion of the trace showing short-period oscillations in apparent stem elongation rate (lines as in A).

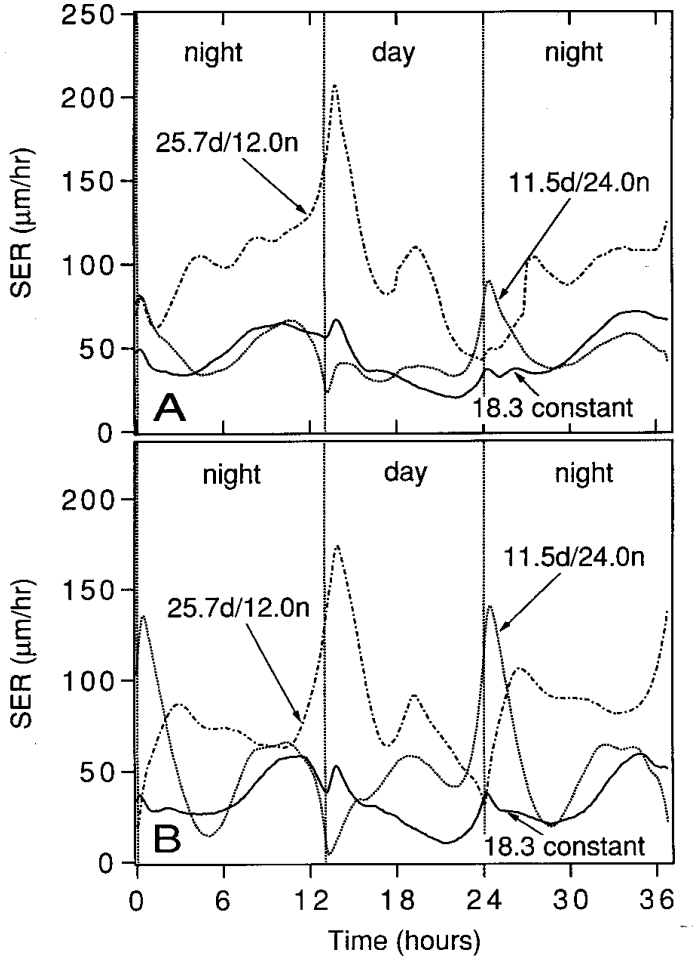

Fig. 2. (**A**) Mean stem elongation rates in *Dendranthema grandiflorum* 'Envy' under constant 18.3C (s = 12), 25.7/12C (s = 8), and 11.5/24C (s = 9) regimes; (**B**) Representative traces showing stem elongation rates in the three regimes; s = number of samples, d = day, n = night.

mum in SER occurred shortly after the start of the day in the 11.5/24C regime. Plants grown at 18.3 and at 11.5/24C showed an early night peak in SER, immediately after the day–night transition; the peak was pronounced at 11.5/24C but was absent in plants grown at 25.7/12C.

In each regime, growth during the night was greater than that during the day (Table 1). However, in the 25.7/12C regime, the difference was small, and, on an average hourly basis, rates for these plants were virtually identical during the day and night (96 and 95 $\mu m \cdot h^{-1}$, respectively). Total diurnal growth was similar in the constant 18.3C and 11.5/24C regimes but was over twice as great in plants grown at 25.7/12C. The percentage of total growth

Table 1. Mean growth during day, night, and full diurnal periods for *Dendranthema grandiflorum* 'Envy' under three temperature regimes.

	Mean total growth during period (µm)		
Temp (°C)	Night	Day	Full diurnal
18.3	663 b (66.0)[z]	383 b (34.0)	1003 b
25.7/12	1232 a (53.3)	1057 a (46.7)	2310 a
11.5/24	670 b (61.1)	426 b (38.9)	1096 b

[z]Mean separation within columns at $P \leq 0.05$ according to Waller–Duncan K ratio *t* test. Numbers in parentheses indicate percentage of total growth in either days or nights.

that occurred during the day and night periods was similar for plants pretreated in the greenhouse and CE chamber, although total diurnal growth was, on average, greater for the younger (eight- to 10-leaf) plants (comparative data not shown). Even among plants of uniform age, rates varied considerably. However, diurnal patterns of stem elongation were consistent for plants treated alike.

Stem elongation rhythms and temperature entrainment. Under continuous lighting and constant 18.3C, rhythmic patterns of stem elongation rate were maintained for periods ranging from 1.5 to 4 days (Fig. 3B). The period of the free-running rhythm was slightly less than 24 h. The rhythm dampened with increasing time under constant conditions, but SER remained high. Under continuous darkness and constant temperature, SER showed a familiar pattern of increase (through the first 13-h night) and decrease (through the subsequent 11-h day; Fig. 3A). However, rates did not recover thereafter. When plants were placed under continuous lighting, but at 25.7/12C (Fig. 3C), the characteristic rhythm, with a period of exactly 24 h, was maintained.

Effect of low temperature for part of the day period. SER declined when temperature decreased to 8.3 from 18.3C for 2 h at the start of the day. SER began to recover within 1 h and peaked ≈1 h after the end of the pulse (Fig. 4A). Increasing pulse length to 4, 6, 8, and 11 h also resulted in initial declines in SER followed by

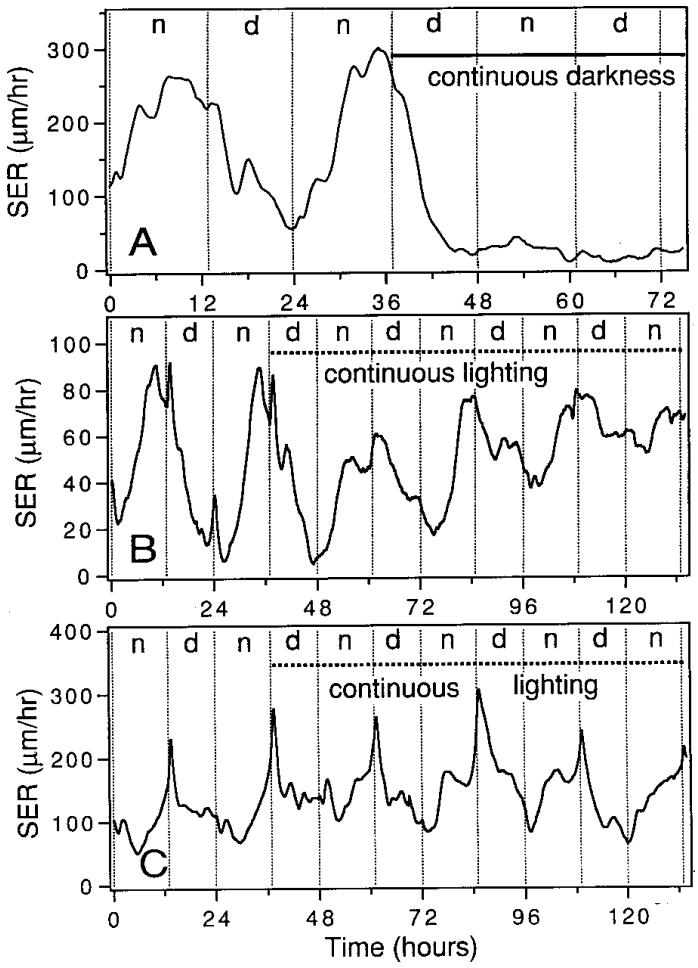

Fig. 3. Representative traces showing stem elongation rates in *Dendranthema grandiflorum* 'Envy' under (**A**) continuous darkness and constant 18.3C (s = 2); (**B**) continuous lighting and constant 18.3C (s = 5); and (**C**) continuous lighting and 25.7/12C (11 h and 13 h, respectively) alternations (s = 2). In each case, standard conditions (11-h days/13-h nights; constant 18.3C) were maintained for 37 h before other conditions were imposed; s = number of samples, d = day, n = night.

recovery and peak between 0.25 and 1 h after the end of the pulse. Small fluctuations in SER were often observed during the low-temperature period (e.g., 6-h pulse; Fig. 4A). In the case of the 11-h pulse, the peak occurred during the first hour of the night. After each pulse, the typical SER pattern, established under constant temperature, resumed with no change in phase. Low-temperature pulses applied 2 h after the start of the day caused a similar decline to that observed under the same conditions at the dark–light transition (Fig. 5).

Linear regression analysis revealed a weak inverse relationship between percentage change in height and low-temperature pulse duration for plants subjected first to constant temperature conditions (18.3C) and then to a low-temperature pulse (Fig. 6A). However, very little of the overall variation in percentage change in height was explained by the regression equation ($r^2 = 0.18$). The relationship was much stronger when the night and total diurnal periods were considered (Fig. 6 B and C), but even then only pulses of 4 h or longer showed a consistent reduction in stem elongation.

Discussion

The stem elongation rate of *Dendranthema* grown under regular 11-h light/13-h dark constant temperature cycles follows a rhythmic pattern. The pattern, consisting of a general decrease in rate during the first 11 h (day period) and an increase during the following 13 h (night period), was similar in plants of different ages preconditioned in either greenhouses or growth chambers. This pattern apparently is endogenous, since it continues under constant environmental conditions of light and temperature and shows a free-running period that is slightly shorter than 24 h (Wilkins, 1969). The decline to a constant, low SER in continuous darkness suggests a requirement for recent photosynthate, or some light dependent factor or signal. Similar endogenous stem elongation patterns have been observed in *Chenopodium rubrum* L. (Lecharny and Wagner, 1984; Lecharny et al., 1985); in both cases, the rhythm was significantly modified by temperature (e.g., Fig. 3C) and photoperiod (Fig. 2), which both act as entraining factors (Bunning, 1967).

Light–dark and dark–light transitions had marked effects on SER, but the nature of the changes that occurred at these transitions were temperature dependent. These results indicate an interaction of light and temperature in producing specific and unique patterns of SER that show several similarities with those previously described for *C. rubrum* (Lecharny and Wagner, 1984; Lecharny et al., 1985). For example, in both taxa, when temperatures immediately preceding the dark–light transition are lower than those during the subsequent day period (the 25.7/12C regime), the amplitude of the early day peak in SER is increased. This effect cannot be explained by a burst of growth after low-temperature inhibition, since SER was higher at low night temperatures in *Dendranthema*. However, since a peak in SER occurs after a low- to high-temperature shift at either the dark–light or light–dark transition (i.e., at 25.7/12C and 11.5/24C), we suggest that it may have a common basis. Previous work has indicated a direct relationship between tissue gibberellin content and SER in some plants (Jones and Phillips, 1966). Gibberellin synthesis, transport, or both is sensitive to plant temperature (Menhennett and Waring, 1975; Tagliavini and Looney, 1991), a result suggesting that a shift to higher temperature may gradually increase shoot gibberellin content and SER. However, the peak in growth rate occurs soon after the low- to high-temperature shift in *Dendranthema*, a result implying that other factors, such as changes in gibberellin activity (Vogelzang, 1992) or a temperature influence on hydration changes

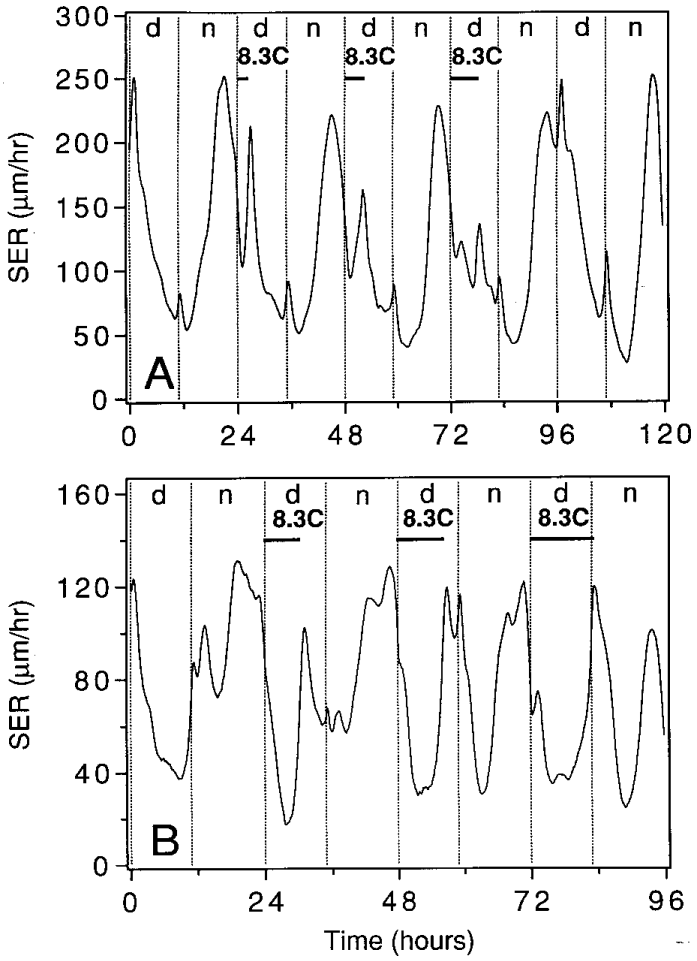

Fig. 4. Representative traces showing stem elongation rates in *Dendranthema grandiflorum* 'Envy' for (**A**) 37 h at 18.3C under 11-h days/13-h nights followed by 2 h (s = 22), 4 h (s = 15), or 6 h (s = 14) at 8.3C at the start of successive day periods; (**B**) 24 h at 18.3C under 11-h days/13-h nights followed by 6 h (s = 22), 8 h (s = 6), or 11 h (s = 8) at 8.3C at the start of successive days. Temperature was restored to 18.3C following each low-temperature pulse; s = number of samples, d = day, n = night.

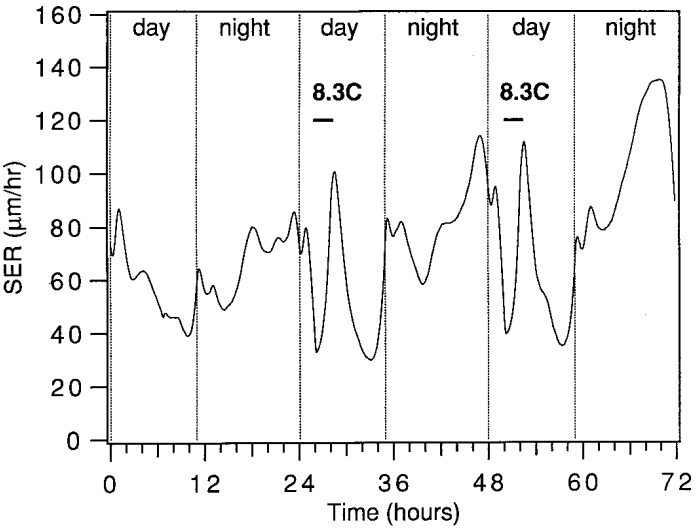

Fig. 5. Representative trace showing stem elongation rates in *Dendranthema grandiflorum* 'Envy' subjected to 2-h low-temperature pulses (decrease from 18.3C to 8.3C) beginning 2 h after the start of the day. The first low-temperature pulse was preceded by 24 h under standard conditions (11-h days/13-h nights; constant 18.3C) (s = 8); s = number of samples, d = day, n = night.

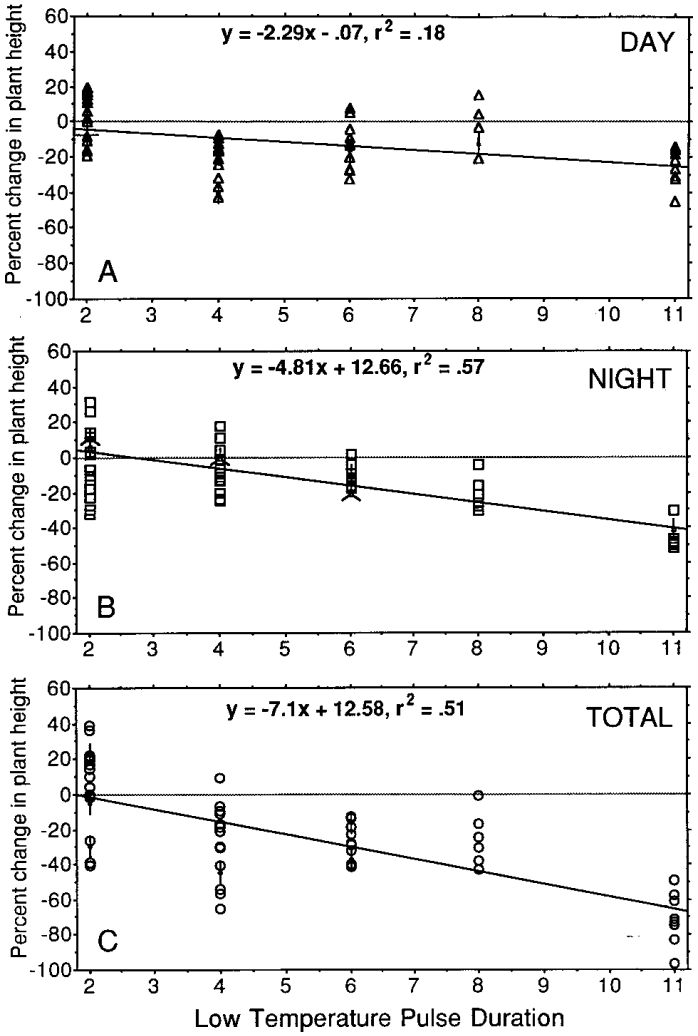

Fig. 6. Relationship between start-of-day low-temperature pulse duration (decrease from 18.3 to 8.3C) and percent change in stem growth of *Dendranthema grandiflorum* 'Envy' plants transferred from standard conditions (11-h days/13-h nights; constant 18.3C) to pulse treatments. (**A**) Days only (11 h); (**B**) nights only (13 h); (**C**) total diurnal period (24 h). All regression lines were significant at $P \leq 0.01$. Coincidence of points is indicated by rays.

within the plant that occur at light–dark–light transitions (Christ, 1978), may be involved.

The amplitude of the rhythm in *Dendranthema* was changed by diurnal temperature conditions. Increased SER during days and nights at 25.7/12C compared with constant 18.3C is consistent with the effect of wide positive DIF on increasing internode growth in *Dendranthema* (Karlsson et al., 1989). Under negative DIF (11.5/24C), however, when SER patterns differ from those observed under the 25.7/12C and constant 18.3C regimes, internodal growth is not significantly different from that at constant temperature. A recent study with *Dendranthema* 'Bright Golden Anne' (Erwin et al., 1992) has also shown very little difference between integrated daily internode elongation in zero DIF and –6C DIF regimes, despite a pronounced effect on final internode length of similar treatments (Karlsson et al, 1989). Taken together, these results suggest that reduced stem growth under negative DIF regimes is due to effects other than reduced daily SER. A possible explanation is a shorter period of elongation for individual internodes under negative DIF regimes.

Low temperatures, whether imposed at the dark–light transition or 2 h after the start of the day period, had similar effects on SER. Previous studies have indicated a close link between changes in SER and the start and end of a low-temperature pulse (Lecharny et al., 1985), but our results indicate a recovery of SER before a return to higher temperatures. It is plausible that the high- to low-temperature shift initiates a timing process of SER restoration, which depends on ambient temperature conditions; the timer is reset if cool conditions persist. This response could explain the small transient increases in SER part of the way through the low-temperature period (e.g., 6-h pulse; Fig. 4A). The effects of low-temperature pulses (<11 h) are transient, since the subsequent phase or amplitude of the rhythm is unaffected by pulse length. This result is consistent with previous ones with *C. rubrum* in which short-duration low-temperature pulses did not result in a phase change in the SER rhythm (Lecharny et al., 1985). Temperature pulses that are shorter than the photoperiod are capable of modifying, but not changing, the course of the basic photoperiod-controlled rhythm. However, extending the pulse through the day can permanently change rhythm and pattern (e.g., Fig. 2 and Fig. 4B)

Low-temperature pulses applied at the start of the day affect growth during days and nights (Fig. 6). Thus, while short-term temperature changes do not rephase the rhythm, the perturbation affects the amplitude for the remainder of the diurnal cycle. There was considerable variation in the response to particular pulse lengths; 2-h pulses, whether applied at the dark–light transition or later during the day period, showed no consistent growth suppression or enhancement during the day or night. But, as pulse length increased, the growth suppression effect predominated. The inconsistent effect of 2-h pulses was surprising in light of the observed effects of similar treatments in reducing total stem growth in *Dendranthema* (Erwin et al., 1989b). The results suggest that even short-duration low-temperature pulses may have other effects, such as a reduction in the total duration of internode expansion, as discussed above.

We conclude that SER in *Dendranthema* is governed by an endogenous circadian rhythm, entrained by photoperiod and modified by diurnal temperature conditions. Some previously observed effects of DIF on *Dendranthema* (notably stem growth enhancement at positive DIF; Karlsson et al., 1989) can be explained based on SER patterns developed under specific temperature and photoperiodic conditions. Others, such as the growth-suppressing effects of negative DIF regimes and short-duration low-temperature pulses, are not satisfactorily explained by resultant SER patterns.

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