Influence of Day and Night Temperature Differentials on Root Elongation Rate, Root Hydraulic Properties, and Shoot Water Relations in Chrysanthemum

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ABSTRACT. The difference between night and day temperature (DIF = day – night temperature) has been shown to affect plant height. A positive DIF (+DIF), cooler night than day temperature, increases stem elongation while a negative DIF (–DIF), warmer night than day temperature, decreases stem elongation. The physiological mechanism underlying the growth response to DIF is not understood, however, and the effects of day/night temperature differentials on root permeability to water and root elongation rate have not been studied. The objective of this study was to describe how +DIF and –DIF temperature regimes affect leaf water relations, root water flux (J_r), root hydraulic conductivity (L_p), and root elongation rates of ‘Boaldi’ chrysanthemum [*Dendranthema ×grandiflora* Kitam. ‘Boaldi’ (syn. *Chrysanthemum ×morifolium* Ramat.)] plants over time. Leaf turgor pressure (ψ_p) was 0.1 to 0.2 MPa higher in plants grown in a +6 °C DIF environment throughout both the light and dark periods, relative to those in a –6 °C DIF environment. J_r differed markedly in roots of plants grown in +DIF vs. –DIF environments. Rhythmic diurnal patterns of J_r were observed in all DIF treatments, but the relative timing of flux minima and maxima differed among treatments. Plants grown in positive DIF regimes exhibited maximum root flux at the beginning of the light period, while those in negative DIF environments had maximum root flux during the first few hours of the dark period. Plants grown in +DIF had significantly higher L_p than –DIF plants. Plants grown in +DIF and –DIF environments showed differences in the diurnal rhythm of root elongation. During the dark period, +DIF plants exhibited minimal root elongation rates, while –DIF plants exhibited maximal rates. During the light period, the converse was observed. In –DIF temperature regimes, periods of rapid root elongation coincided with periods of high J_r . Results of this study suggest that negative DIF environments lead to leaf turgor reductions and markedly alter diurnal patterns of root elongation. These changes may, in turn, act to reduce stem elongation.

The floriculture market requires many crops with specific harvest date and height specifications. Until recently, chemical plant growth retardants were the major tools available for controlling stem elongation. Interest in nonchemical plant height control has increased appreciably recently because of the risk of chemical pollution of the environment and the negative public response to products treated with chemicals.

Went (1944) first described the effects of temperature differentials between light and dark periods on plant morphology and development, a phenomenon he termed thermoperiodicity. More recently, research has shown that stem elongation is highly correlated with the difference between day temperature (DT) and night temperature (NT), rather than with the actual DT and NT environments under which plants are grown (Erwin et al., 1989). Erwin et al. (1989) defined the day/night temperature differential as DIF (DIF = DT – NT), and they reported that stem elongation can be reduced by growing plants in negative DIF (–DIF) temperature regimes, where night temperatures are higher than day temperatures (Erwin and Heins, 1990; Erwin et al., 1989). The imposition of negative DIF environments subsequently has been

adopted as a nonchemical means of plant height control in many commercial greenhouses in the northern United States; the approach has reduced substantially the number of treatments with chemical plant growth retardants (Erwin and Heins, 1995).

The physiological mechanism underlying the growth response to DIF is still not understood, although numerous hypotheses have been advanced. Some evidence suggests that DIF can bring about changes in the levels of endogenous bioactive gibberellins (Erwin et al., 1989; Moe et al., 1991; Zieslin and Tsujita, 1988). Phytochrome also has been associated with the DIF response (Erwin et al., 1989; Moe and Heins, 1990), and interactions between DIF and far red light have been suggested (Moe et al., 1991). Whether DIF acts directly to control stem elongation via specific regulatory processes or indirectly by providing a more favorable or less favorable growth environment is unknown.

Renewed interest in plant thermoperiodism and thermomorphogenic responses recently has led to numerous investigations of DIF effects on stem and leaf development. Few studies have quantified the influence of DIF on root growth, however, and there are no published reports, to our knowledge, that test the effect of DIF temperature environment on root elongation rate. Whether root growth is a continuous process or shows periodic alternation with shoot growth is not known for chrysanthemum [*Dendranthema ×grandiflora* ‘Boaldi’ (syn. *Chrysanthemum ×morifolium*)]. If, for example, shoot and root elongation occur in alternating rhythms, this may suggest that shifting competition between these two sinks for available assimilates may be involved in the response to DIF. Furthermore, little is known about how shoot water status or root hydraulic properties are affected by

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DIF. Considering their critical roles in cell enlargement, it is of interest to quantify how these variables are affected by day and night temperature differentials. Finally, understanding how DIF temperature regimes influence root elongation and shoot water relations may suggest alternative strategies for the control of stem elongation.

The general objective of this study was to determine how day/night temperature differentials influence root elongation and shoot water relations in chrysanthemum and to evaluate those responses in light of the known effects of DIF on stem elongation. The specific objectives were to describe how growth of plants in +DIF and -DIF temperature regimes affects leaf water potential and its osmotic and pressure components, pressure-induced root water flux, root hydraulic conductivity, and root elongation rates over time.

Materials and Methods

PLANT MATERIAL AND INITIAL CULTURAL CONDITIONS. Three separate studies were conducted from Dec. 1997 through Apr. 1998. Rooted stem cuttings of chrysanthemum were potted into 7.6-cm² pots (T.O. Plastics Inc., Minneapolis, Minn.) using Fafard P-2 growing medium (Conrad Fafard Inc., Agawam, Maine). Plants were transferred to 0.15-m³ reach-in growth chambers (model AR-75LX; Percival, Boone, Iowa) and grown for 2 to 6 weeks at the given DIF treatment. Light was supplied by cool-white fluorescent and incandescent lamps. Photosynthetic photon flux (PPF) in the region of the growing apices was maintained at $160 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ as measured with a quantum sensor (LI-COR Inc., Lincoln, Nebr.). Plants were exposed to 16-h photoperiods, starting at 5:00 AM and ending at 9:00 PM. The fluorescent lamps provided 80% of the total PPF. The DIF treatments were +8, +6, -6, and -8 °C with 16 h day/8 h night air temperatures of 25/17, 24/18, 20/26, and 19/27 °C ± 1 °C, respectively. The same average daily temperature of 22 °C was maintained in each DIF treatment. Vapor pressure deficits (VPD) for +8, +6, -6, and -8 °C DIF were $0.2379 \pm 0.0660/0.1671 \pm 0.0569$, $0.2028 \pm 0.0673/0.2014 \pm 0.0670$, $0.2019 \pm 0.0670/0.1021 \pm 0.0653$, and $0.1439 \pm 0.0578/0.0680 \pm 0.0679$ kPa (day/night), respectively. Vapor pressure deficit was measured with an aspirated psychrometer (Cole-Parmer Instrument Co., Vernon Hills, Ill.). Plants were placed in the chamber in a randomized block arrangement and irrigated daily at 10:00 AM to container capacity. The plants were fertilized at each watering with a 20N-4.4P-16.6K water soluble fertilizer (Scotts, Marysville, Ohio) which provided N at 225 mg·L⁻¹, P at 49 mg·L⁻¹, K at 187 mg·L⁻¹, and micronutrients.

LEAF WATER POTENTIAL MEASUREMENTS. Rooted stem cuttings were potted 4 Dec. 1997. The potted cuttings were placed directly into the growth chambers at a DIF temperature treatment of +6 or -6 °C. Plants were pinched 13 d after potting on 17 Dec. Leaf water potential (ψ_w) was measured every 3 h over 24 h starting at 12:00 PM on 24 Jan. 1998 using a pressure chamber (PMS Instruments Co., Corvallis, Ore.). Only new, fully expanded leaves from the middle of the plant were sampled. One leaf sample was taken per plant; five plants were sampled from each temperature treatment during each sampling time period. Once a leaf was severed from a plant in the growth chamber, it was immediately sealed in the pressure chamber for measurement. After leaf ψ_w of the sample was determined, the leaf was sealed immediately in a labeled zip lock polyethylene freezer bag and placed in a freezer at -10 °C for subsequent determination of osmotic potential (ψ_π).

The ψ_π of each leaf sample was determined using a Wescor 5500XR vapor pressure osmometer (Wescor Inc., Logan, Utah). The leaf samples were removed from the freezer and thawed at 21 °C for 10 min. The leaf tissue was macerated quickly inside the bag using a weighted ball bearing race, and a 5- μL sap sample was collected for determination of sap osmolarity. Osmotic potential was calculated as described by Saneoka et al. (1995). Leaf turgor (ψ_p) was calculated for each sample by subtracting ψ_π from ψ_w . Means and SE values for ψ_w , ψ_π , and ψ_p were calculated for each time period sampled in each temperature treatment. The experiment was replicated three times with similar results.

ROOT WATER FLUX (J_v) AND HYDRAULIC CONDUCTIVITY (L_p) MEASUREMENTS. For three replications of the study, rooted cuttings were potted in July and Aug. 1997 and in Apr. 1998. Plants were transferred to the growth chambers as described above and grown for 2 weeks at the given DIF treatment. Treatments were randomized among growth chambers over time. Plants harvested were selected at random from ≈ 15 plants in each treatment. The volume flow of water (J_v) and root hydraulic conductivity (L_p) of six plants within a single chamber were measured at a time; three plants each from +6 and -6 °C DIF were measured concurrently or three plants each from +8 and -8 °C DIF were measured concurrently.

Root systems were gently separated from the growing medium, and the stems were severed ≈ 3 cm above the soil level. Tissues peripheral to the vascular cambium were peeled from the upper portion of the stump of each root system to prevent axial water flow through cortical cells. Each root system was mounted singly in the lid of a stainless steel chamber filled with aerated half-strength Hoagland's solution (Hoagland and Arnon, 1950) maintained at 25 °C. Stems were first inserted through a parafilm-wrapped brass tube before they were sealed into the lid of the chamber though a rubber gasket to avoid compression injury to soft tissue. The measurement system and procedures followed were as described by Joly (1989) and Maggio and Joly (1995).

After root systems were sealed in the lid, chamber pressure was increased gradually to 0.21 MPa and held constant during measurement of flow rate, Q . Water expressed from each cut stump was delivered via tygon tubing to a system of computer-controlled valves and partitioned such that the exudate from one root system at a time was weighed by an electronic balance. Q was computed every 30 min, and valves were automatically switched to allow sequential data collection from each of six root systems (three +DIF and three -DIF plants). Average root flux curves for each treatment were constructed by plotting mean root flux at 30-min intervals over an 18 to 24 h time period.

Root hydraulic conductivity (L_p) of these root systems was then measured after 18 to 24 h, using methods described by Graves et al. (1991) and Maggio and Joly (1995). Four pressures were applied in ascending order (0.21, 0.28, 0.35, and 0.42 MPa). Flow rate was recorded for 1 h at each pressure, allowing a 5-min equilibration period between pressures. L_p was estimated after making the assumption that the root can be considered, to a first approximation, a cylindrical membrane system with a radius r (Fiscus and Kramer, 1975). The total length, l , of each root system was measured upon completion of the exudation measurements. Root diameter was obtained by sampling root cross-sections, measured to the outside of the epidermis, and an average surface area was calculated as πdl . J_v was computed by transforming Q to reflect flux on the basis of the root surface area, and L_p was estimated as the slope of the regression of J_v on applied hydrostatic pressure (Dalton et al., 1975; Fiscus, 1977). Root hydraulic

conductivity data were subjected to an analysis of variance.

ROOT ELONGATION RATE. Root growth of plants grown in +8, +6, -6, and -8 °C DIF regimes was measured from Nov. 1997 through Mar. 1998. Rooted cuttings having three to six roots of 1 to 3 cm length were used. The plants were potted into a rhizotron composed of two glass plates (31 × 46 cm) set in a wooden frame. One plate was vertical while the other was angled at 15° from vertical. A piece of black cotton cloth was placed on the inside of the angled glass plate. Three rooted cuttings were then attached to the angled plate, with the base of the cutting directly above the top of the black cloth, thus allowing new roots to form between the glass and the cotton cloth. Half of the roots were placed between the glass and the cotton cloth. The rhizotron contained growing medium composed of 1 medium vermiculite : 1 Fafard P-2 growing medium (v/v). The rhizotron was transferred to a 0.15-m³ reach-in growth chamber (Percival, Boone, Iowa) and grown for 4 d under a given DIF treatment before root measurements began.

A millimeter ruler was placed adjacent to an elongating root, and a VideoLabs FlexCam (VideoLabs, Inc., Minneapolis, Minn.) was positioned directly in front of the root and ruler. The camera was connected to a Power Macintosh 8500/120 PowerPC computer (Apple Computer Inc, Cupertino, Calif.), and the computer program 'Adobe Premiere' (Adobe Systems Inc., Mountain View, Calif.) was used to record root elongation over time. The rhizotron and camera were covered with a heavy black cloth to keep the root systems in darkness. A 30-W green light bulb was placed under the cloth in order to view root extension. Frames were recorded hourly throughout a 24 to 48-h period using the stop-motion program option, and a time-lapse video was created for each root recorded. Root elongation was measured directly off the computer screen, and a root elongation rate (mm·h⁻¹) was calculated for each root. Two roots from each plant in the rhizotron were recorded in each replication, and each DIF treatment was replicated three times with runs over time and randomized among chambers. Day/night root medium temperatures measured within 1 mm of the glass surface were 26/24, 26/24, 25/27, and 26/27 °C in the +8, +6, -6, and -8 °C DIF treatments, respectively, ±1 °C.

Results

LEAF WATER POTENTIAL AND COMPONENTS. 'Boaldi' chrysanthemum plants exhibited significant treatment differences for ψ_w , ψ_π , and ψ_p when grown in +6 °C and -6 °C DIF environments. Leaf ψ_w ranged between -0.35 and -0.45 MPa during the dark period in both DIF treatments (Fig. 1A). During the light period, ψ_w was lower in -6 °C DIF plants than +6 DIF plants, with an average difference of ≈0.15 MPa occurring between 12:00 and 4:00 PM.

The ψ_π of leaf sap was higher during both the light and dark periods in plants grown in a -6 °C DIF environment, relative to those grown at +6 °C DIF (Fig. 1B). In both positive and negative DIF treatments, ψ_π was lowest at the end of the light period, reaching a value of -1.09 MPa for +6 °C DIF and -1.33 MPa for -6 °C DIF. ψ_π increased during the dark period in +6 and -6 °C DIF treatments, reaching its highest values near the end of the dark period or the beginning of the subsequent light period.

ψ_p was generally higher in plants grown in the +6 °C DIF environment throughout both the light and dark periods (Fig. 1C). Further, for both DIF treatments, ψ_p was higher during the dark than during the light period. During the first 3 h of the dark period, ψ_p in leaves of +6 DIF plants was ≈0.2 MPa higher than that measured in -6 DIF plants.

ROOT WATER FLUX (J_r) AND HYDRAULIC CONDUCTIVITY (L_p) MEASUREMENTS. Pressure-induced root water flux differed markedly in roots of chrysanthemum plants grown in +DIF vs. -DIF environments. Rhythmic diurnal patterns of root water flux were observed in all four DIF treatments, but the relative timing of flux minima and maxima differed among those treatments. Plants grown at +6 or +8 °C DIF regimes exhibited minimum or near minimum root flux at the beginning of the dark period and near maximum root flux in the light period (Figs. 2A and 3A). In contrast, plants grown at -6 or -8 °C DIF regimes exhibited near minimum root flux near the midpoint of the light period and near maximum root flux during the first few hours of the dark period (Figs. 2B and 3B). The diurnal patterns of root water flux observed for plants grown in +DIF and -DIF environments appear to be shifted from each other by ≈8 h.

The mean root L_p values of plants grown at +6 and -6 °C DIF regimes were greater than those of plants grown at +8 and -8 °C DIF regimes (Table 1). Furthermore, +DIF plants had roots with significantly higher L_p than roots of -DIF plants (Table 2).

ROOT ELONGATION RATE. The timing of root elongation differed markedly for chrysanthemum plants grown in +DIF vs. -DIF environments. A diurnal pattern of root elongation rate was

Fig. 1. (A) Leaf water potential, (B) solute potential, and (C) leaf turgor potential of 'Boaldi' chrysanthemum grown at +6 and -6 °C DIF temperature regimes. Five plants were sampled once every 2 h over 24 h. Means and SE values (vertical bars) were calculated at each sampling period. Shaded area represents the 8-h night period; DT/NT = 24/18 °C at +6 °C DIF and 20/26 °C at -6 °C DIF.

Fig. 2. Effect of (A) +6 and (B) –6 °C DIF temperature treatment on pressure-induced root water flux in 'Boaldi' chrysanthemum. Root water flux of three root systems per run were measured hourly over 18 to 24 h. Shaded area represents the 8-h night period; DT/NT = 24/18 °C at +6 °C DIF and 20/26 °C at –6 °C DIF. Run represents the replication of the treatment. Vertical bars are SE values.

observed in all four DIF treatments. The minimum and maximum root elongation rates were ≈ 0.25 and $0.6 \text{ mm} \cdot \text{h}^{-1}$, respectively, regardless of the DIF environment. However, the timing of minimum and maximum root elongation differed greatly between +DIF and –DIF treatments. Plants grown in a +6 or +8 °C DIF environment exhibited minimum root elongation rates near the end of the dark period and maximum elongation rates near the end of the light period (Figs. 4A and 5A). In contrast, plants grown in a –6 or –8 °C DIF environment exhibited minimum root elongation rates during the middle of the light period and maximum elongation rates during the dark period.

The relative timing of maximum root elongation rate varied between the two –DIF treatments (Figs. 4B and 5B). Plants grown in the –6 °C DIF environment had maximum elongation rates during the final half of the dark period, while those in the –8 °C DIF environment had maximum rates during the first half of the dark period.

Discussion

'Boaldi' chrysanthemum plants grown in +DIF vs. –DIF environments differed from each other for leaf turgor pressure (Fig. 1), diurnal patterns of root water flux (Figs. 2 and 3), root hydraulic conductivity (Table 2), and the relative timing of maximal and minimal root elongation rates (Figs. 4 and 5). A novel and remarkable outcome of these experiments is the effect of DIF temperature regime on root elongation rates throughout the light/dark cycle (Figs. 4 and 5). Plants grown in +DIF and –DIF environments show a reversal in the diurnal rhythm of root elongation. During the dark period, +DIF plants exhibited minimal root elongation rates, while –DIF plants exhibited maximal rates. During the light period, the converse was observed.

The underlying reason for the altered diurnal pattern of root elongation is unknown. No consistent relationship between pressure-induced root water flux and root elongation rate was evident across both positive and negative DIF treatments. However, two associations were apparent among plants grown in –DIF regimes. First, root water flux and root elongation rates both increased at the beginning of the dark period in plants grown in –DIF environments (Figs. 2–5). Second, plants grown

Fig. 3. Effect of (A) +8 and (B) –8 °C DIF temperature treatment on root water flux in 'Boaldi' chrysanthemum. Root water flux of three root systems per run were measured hourly over 18 to 24 h. Shaded area represents 8-h night period; DT/NT = 25/17 °C at +8 °C DIF and 19/27 °C at –8 °C DIF. Run represents the replication of the treatment. Vertical bars are SE values.

Table 1. Root hydraulic conductivity (L_p) of 'Boaldi' chrysanthemum grown at +6, -6, +8, and -8 °C DIF temperature regimes. Hydraulic conductivity of three root systems for each run was determined. Means and SEs were calculated for each run.

Treatment ^z	Run ^y	Mean L_p	
		($\text{m}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$) $\times 10^{-7}$	SE
+8 °C DIF	1	1.75	3.35×10^{-8}
	2	1.67	4.20×10^{-8}
	3	1.46	6.97×10^{-8}
+6 °C DIF	1	2.72	8.57×10^{-9}
	2	2.52	1.48×10^{-8}
	3	1.90	3.10×10^{-8}
-6 °C DIF	1	2.31	3.68×10^{-8}
	2	2.16	2.29×10^{-8}
	3	2.28	5.37×10^{-9}
-8 °C DIF	1	1.58	2.10×10^{-8}
	2	1.97	1.35×10^{-8}
	3	1.20	1.58×10^{-9}

^zDifference between day temperature and night temperature; +8, +6, -6, and -8 °C DIF = 25/17, 24/18, 20/26, and 19/27 °C (16 h day/8 h night temperature), respectively. Average daily temperature, 22 °C.

^yReplication of the treatment.

Table 2. Analysis of variance for root hydraulic conductivity (L_p) of 'Boaldi' chrysanthemum plants grown in +DIF and -DIF temperature regimes.

Parameter	df	ms	F	P
Treatments				
+DIF ^z vs. -DIF	1	3.458	17.13	0.01
+6 °C DIF vs. -6 °C DIF	1	0.082	0.47	NS
+8 °C DIF vs. -8 °C DIF	1	0.002	0.01	NS
Run ^y	2	0.537	2.66	NS
Run vs. treatment	6	0.174	0.86	NS
Error	24	0.202		

^zDifference between day temperature and night temperature; +8, +6, -6, and -8 °C DIF = 25/17, 24/18, 20/26, and 19/27 °C (16 h day/8 h night temperature), respectively. Average daily temperature, 22 °C.

^yReplication of the treatment.

^{NS}Nonsignificant.

in -DIF environments showed minimal root water flux and minimal root elongation during the light period. No consistent relationship between root water flux and root elongation rate was detected in plants grown in +DIF environments.

As noted above, the root elongation rate of plants grown in -DIF temperature regimes was associated with root water flux. Periods of rapid elongation coincided with periods of high root water flux, suggesting that elongation may have been facilitated by higher root permeability to water. However, our experiments cannot resolve cause and effect, and an alternative explanation that root water flux was itself affected by root growth cannot be excluded. Ivanov (1980), citing earlier work by Russian investigators, suggested that daily periodicity in root pressure exudation was related to daily cycles of cell division and root growth. This hypothesis appears to be supported by Bunce (1978) who reported that increased root hydraulic resistance was correlated with decreased root elongation.

Root temperature was not controlled in these studies. Although we did not observe large root medium temperature differences, these studies can not assess the effect of root temperature differences. Certainly the commercial application of DIF would be similar to our results as root temperature is generally not controlled.

Root hydraulic conductivity (L_p) was significantly lower in plants grown in -DIF environments than in +DIF environments (Tables 1 and 2). Because L_p defines the ability of the root system to supply water to growing cells, it could, in theory, affect stem elongation. Any reduction in L_p brought about by a -DIF environment would act to steepen the water potential gradient between growing and absorbing regions. The net effect would be a lower rate of water delivery to the shoot and a concomitant reduction in stem elongation. However, although analysis of variance showed that L_p values differed at $P < 0.01$ in +DIF and -DIF plants, it should be noted that L_p measured in root systems of -DIF plants was only $\approx 4\%$ lower than that in +DIF plants. It is unlikely that such a small difference in root permeability to water could result in appreciable differences in stem elongation.

Leaf turgor pressure of new fully expanded leaves differed in relative magnitude but not in periodicity for +DIF and -DIF plants (Fig. 1C). Leaf ψ_p was higher in +DIF plants at most times during the 24-h light/dark cycle, with the exception of the middle 6 h of the light period. During the dark period, ψ_p was ≈ 0.15 MPa higher, on average, in +DIF plants than in -DIF plants. The steady increase in leaf ψ_p observed in +DIF plants during the final 8 h of the light period was likely the result of the concomitant decline in ψ_π during this period (Fig. 1B). It is notable that although leaf ψ_p increased in +DIF plants to its highest level during the first 3 h of the dark period, root elongation rate actually decreased during this period. This suggests that high turgor pressure in the shoot is not associated with root elongation processes. We did not measure leaf turgor pressure of expanding leaves in this study. It would be interesting to study that tissue during the expansion phase in relation to DIF treatments.

Shoot elongation rates were not measured in this study, so the relative kinetics of root and shoot growth cannot be quantified. Nevertheless, numerous studies have shown maximum stem elongation occurs at sunrise in chrysanthemum plants grown in +DIF environments and at the beginning of the dark period in -DIF environments (Bertram and Karlsen, 1994; Erwin and Heins, 1990; Erwin et al., 1992; Tutty et al., 1994). The observation that maximum leaf ψ_p was reached during the first 3 h of the dark period in both +DIF and -DIF plants (Fig. 1C) suggests that a simple hypothesis invoking turgor-driven stem elongation cannot fully explain the reports of shoot growth differences in the +DIF and -DIF environments. Nevertheless, several observations point to at least a partial role for turgor in stem elongation. First, leaf ψ_p was nearly always higher in +DIF plants than in -DIF plants throughout the 24-h measurement period. Further, although ψ_p increased during the early hours of the dark period in both +DIF and -DIF plants, its rate of increase was greater in +DIF plants. Thus, although periods of maximal ψ_p do not coincide with periods of maximal stem elongation, greater stem elongation was, in general, associated with higher ψ_p .

Growth is controlled in a complex fashion by turgor, cell-wall extensibility, and membrane permeability to water. Pritchard (1994) and Wu et al. (1996) reported that cell expansion was controlled principally by cell-wall extensibility rather than by the prevailing turgor pressure in the elongating region, for example. Future studies where growth, wall extensibility, and turgor are

Fig. 4. Effect of (A) +6 and (B) -6 °C DIF temperature treatment on root elongation in 'Boaldi' chrysanthemum. Root elongation rates of six roots (two roots/plant) in each experiment were determined each hour over 24 h. Hourly means and SE values (vertical bars) were calculated for each run. Shaded area represents the 8-h night period; DT/NT = 24/18 °C at +6 °C DIF and 20/26 °C at -6 °C DIF. Run represents the replication of the treatment.

evaluated concurrently will be helpful in identifying those biophysical properties that change most rapidly in response to temperature reversals.

The physiological mechanism(s) underlying the effect of DIF environment on the diurnal pattern of root elongation remain to be elucidated. Neither leaf ψ_p nor root hydraulic properties appear to be directly related to the well-defined diurnal patterns of root elongation. It is interesting to note that the root elongation rate minima shown in Figs. 4 and 5 occur $\approx$ 4 to 6 h in advance of the widely reported stem elongation rate maxima, regardless of whether the DIF treatment is positive or negative. This suggests that root and shoot growth in chrysanthemum may occur in alternating pulses and that the DIF environment may influence metabolic processes governing carbon allocation and/or partitioning. The rate of root elongation in many species has been shown to vary in relation to shoot development (Reich et al., 1980; Thaler and Pages, 1996). Reich et al. (1980) reported that in a constant environment, seedlings of several oak (*Quercus L.*) species underwent a series of synchronous flushes of shoot growth alternating with periods of root growth. Appreciable root growth occurred only while leaves and shoots were not growing.

The well-described reduction in stem elongation induced by growing plants in a -DIF temperature regime (Erwin and Heins, 1990; Erwin et al., 1989) may be related to the apparent shift in the timing of root elongation reported herein. Mobilization of available photosynthate towards rapidly elongating roots during the midportion of the dark period in -DIF plants may decrease the supply of carbon available to support rapid stem elongation, which normally would occur at sunrise in +DIF environments. This hypothesis could be tested by measuring the effects of day and night temperature differentials on the kinetics of root and shoot growth and on the synchrony of movement of labeled carbon to these organs.

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Fig. 5. Effect of (A) +8 and (B) -8 °C DIF temperature treatment on root elongation in 'Boaldi' chrysanthemum. Root elongation rates of six roots (two roots/plant) in each experiment were determined each hour over 24 h. Hourly means and SE values (vertical bars) were calculated for each run. Shaded area represents the night period; DT/NT = 25/17 °C at +8 °C DIF and 19/27 °C at -8 °C DIF. Run represents the replication of the treatment.

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