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Day/night temperature environment affects cell elongation but not division in *Lilium longiflorum* Thunb.

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Abstract

Lilium longiflorum Thunb. cv. 'Nellie White' plants were grown in different day/night temperature (DT/NT) environments to determine the anatomical basis for differential responses of stem elongation to DT and NT. *Lilium* plants were forced in 1986 and 1987 under 25 and 12 different DT/NT environments, respectively, with temperatures ranging from 14 to 30 °C. Parenchyma and epidermal cell length and width were measured in stem tissue (1987) and epidermal cell length and width were measured in leaf tissue (1986). Total cell number per internode and vertical cell number per internode were calculated. Stem parenchyma and stem and leaf epidermal cell length increased linearly as the difference (DIF) between DT and NT increased (DIF = DT − NT), i.e. as DT increased relative to NT. DIF had no effect on stem parenchyma width, stem and leaf epidermal cell width, or cell number per internode. Data suggested that stem elongation responses to DIF are elicited primarily through effects on cell elongation and not division.

Key words: Thermoperiodism, thermomorphogenesis, stem elongation, DIF, cell division, cell elongation, leaf expansion.

Introduction

Early research by Went (1944, 1952) showed that day/night temperature (DT/NT) significantly affects plant height. Plant height increased as DT increased and NT decreased (Went, 1957). However, the way in which temperature affected plant height was unclear as Went did not determine internode number.

Tangeras (1979) and Karlsson (1988) reported that the effect of DT and NT on plant height was due to differences in internode elongation and not number, when DT/NT ranged from 10 to 20 °C and 10 to 26 °C on *Fuchsia × hybrida* Hort. ex Vilm. and *Dendranthema grandiflora* L., respectively. Both Tangeras and Karlsson demonstrated that internode elongation increased as DT increased and NT decreased.

Morphological development in some plants is highly correlated with the relationship between DT and NT rather than the actual DT/NT plants are grown at when DT/NT range from 10 to 25 °C (Erwin *et al.*, 1989, 1991; Karlsson *et al.*, 1989; Berghage and Heins, 1990; Moe *et al.*, 1991). Specifically, internode length in *Lilium* increased 482% as the difference (DIF) between DT and NT (DIF = DT − NT) increased from −16 to +16 °C (Erwin *et al.*, 1989). While Went (1957) suggested that plant stem elongation was primarily influenced by DT, our measurements of internode lengths from photographic plates of *Pisum sativum* L. plants in Went's (1957) original article (Plate IX) showed that internode length was highly correlated with DIF ($r^2 = 0.72$). The effect of temperature on plant morphology was referred to as 'thermomorphogenesis' (Erwin *et al.*, 1989).

Leaf expansion is also affected by temperature (Milthorpe, 1959; Dale, 1964, 1965). In *Fuchsia* cv. 'Dollar Princess', leaf expansion increased as DIF increased from −12 to +12 °C with DT/NT ranging from 12 to 24 °C (Erwin *et al.*, 1991). In *Phaseolus vulgaris* L., leaf expansion was greatest when DT and NT were equal, i.e. 0 °C DIF (Dale, 1965). Examination of Dale's data (1964) showed that conclusions on temperature effects on leaf expansion were based on a number of temperature regimes which contained either a 30 °C DT/NT. Based on Dale's data and conclusions, leaf

expansion was reduced with 30 °C DT compared to 25 °C. If data from environments with a 30 °C DT are excluded, leaf area increased linearly as DIF increased.

In contrast to *Fuchsia* and *Phaseolus*, leaf expansion of *Cucumis sativus* L. and *Lilium* did not increase as DIF increased. Instead, *Cucumis* leaf expansion increased when plants were grown at constant 20 °C (0 °C DIF) compared to fluctuating DT/NT (Erwin and Strefeler, unpublished data). *Lilium* leaf expansion was a function of NT only where leaf expansion decreased as NT increased (Erwin *et al.*, 1989).

The basis for temperature effects on plant stem elongation and leaf expansion are not understood. Indeed, the effect of DT/NT on cell dimensions in stems and leaves is unknown. The objective of our research was to determine how DT/NT affects cell elongation and division in elongating internodes and expanding leaves. In particular, we were interested in identifying whether DIF effects on stem elongation and leaf expansion are due to differences in cell elongation and/or division.

Materials and methods

Lilium longiflorum cv. 'Nellie White' bulbs 17.7–20.3 cm in circumference were planted in 15.2 cm plastic pots on 28 October, 1986 (Expt 1) and 1 November, 1987 (Expt 2) in a soilless medium consisting of equal parts of sphagnum peat, perlite and vermiculite (1:1:1). Base levels of phosphorus and micronutrients were added to the soilless medium when it was mixed. Potted bulbs were then placed in a controlled environment greenhouse for 2 weeks where air temperature was adjusted to maintain a medium temperature of 17 ± 1 °C to encourage root development. Plants were then vernalized in the dark for 6 weeks at 4 °C, after which plants were placed in a glasshouse under natural photoperiodic conditions with constant 20 °C DT and NT.

Upon shoot emergence, plants received a long day treatment for 7 d consisting of a night interruption (2μmol m^{-2} s^{-1} (400–700 nm wavelength)) from 2200–0200 h delivered with incandescent lamps. After the long-day treatment, plants were returned to natural photoperiodic conditions (*c.* 9 h 15 min photoperiod).

Time of flower initiation in Expts 1 and 2 was established by terminal shoot dissections on randomly selected plant samples starting 13 January, 1986 and 11 January, 1987, respectively. Plant samples were taken every 3 d. Flower initiation was defined as the first visible sign of a reproductive meristem (De Hertogh *et al.*, 1976). Flower initiation was observed on 100% of the plants sampled in Expts 1 and 2 on 22 January, 1986 and on 27 January, 1987, respectively.

Experiment 1 (1986)

One hundred and twenty five plants were selected for uniformity after flower initiation (22 January, 1986). Plants were then divided into 5 groups of 25 plants each and were moved to glasshouses maintained at constant 14, 18, 22, 26 or 30 ± 1.5 °C. Within each glasshouse, plants were further divided into 5 groups of 5 plants each. Each group of 5 plants constituted a DT/NT regime treatment group. DT/NT treatment groups were moved among greenhouse sections at 0800 and 1700 h each day

to yield a total of 25 different DT/NT regime treatments (5 plants per DT/NT regime group). Each treatment group received the same DT/NT regime from the initiation of the experiment until anthesis. Movement of plants at 0800 and 1700 h required approximately 30 min at each move period.

An opaque curtain was pulled over plants after they were moved at 1700 h and was retracted just prior to 0800 h to provide a 15 h nyctoperiod to parallel the NT treatment. Plants were spaced to provide 900 cm^2 per plant. The uppermost leaf of each plant was marked with a black dot when plants were moved into the glasshouse to indicate the stage of development of each plant at the inception of the temperature treatments.

Plants were watered as needed to ensure that the medium was always moist for each DT/NT regime. Fertilizer was composed of 14.3 mM calcium nitrate and 5.1 mM potassium nitrate at each watering. Phosphorus and micronutrients were added when soil was mixed and were retained in the medium throughout the experiment. Levels of nutrients were in the recommended ranges for production in soilless media as identified through Spurway analysis throughout the experiment. Electrical conductivity was maintained at 0.75 to 1.0 mS to maintain similar fertility across DT/NT regimes.

Experiment 2 (1987)

Seventy two plants were selected for uniformity after flower initiation (27 January, 1987). Plants were divided into 4 groups of 18 plants each and were moved to glasshouses maintained at 15, 20, 25, or 30 ± 1.8 °C. Within each glasshouse, plants were further divided into 3 groups of 6 plants each. Each group of 6 plants constituted a DT/NT regime treatment group. Plants were moved among glasshouse sections at 0800 and 1700 h each day but no plants were placed in the 30 °C glasshouse at night. Therefore, plants were exposed to 12 DT/NT regimes (6 plants per DT/NT regime). Other procedures were as discussed in Expt 1.

Tissue collection

Leaf and stem samples were collected at anthesis. A leaf was collected from 5 cm below the base of the inflorescence on 3 plants from each temperature regime treatment (3 of the 5 plants) in Expt 1, i.e. 3 leaves were collected from 3 different plants. A stem segment approximately 2 cm in length was collected between the 5th and 10th internodes below the base of the inflorescence on 4 plants from each treatment (4 of the 6 plants) in Expt 2, i.e. 4 stem segments were collected from 4 different plants. Tissue samples were placed in a formalin based fixative (formaldehyde, glacial acetic acid, and tertiary butyl alcohol) immediately after excision.

Leaf tissue measurements

Epidermal cell length and width data were collected on leaf tissue. Leaf tissue was blotted dry and a clear solution of nail polish (Mabelline—01 'crystal clear) was applied to the leaf surface with a brush. Clear plastic tape was placed on the dried nail polish. The tape was then removed along with a replica of the leaf surface on the nail polish. The tape and replica were then mounted on a slide for epidermal cell measurements.

Stem tissue measurements

Longitudinal sections were were cut using an Oxford Vibratone Model No. 501 for central stem parenchyma cell length and width determinations. Stem epidermal cell dimensions were determined as described above for leaf epidermal cell collection.

Data collection

A Zeiss microscope fitted with a Nikon FX-35A camera and a Nikon UFX exposure meter were used for brightfield observations and photography of all samples. Measurements of cell dimensions were made from photographs. An enlargement of the slide micrometer was used for cell dimension determinations. Measurements of cell dimensions were made with an accuracy of ± 10 microns.

As mentioned previously, 3 leaves and 4 stem segments were collected for sampling from each DT/NT regime treatment in Expt 1 and 2, respectively. A single photograph was taken from each leaf for leaf epidermal cell length and width determinations. Two photographs were taken from each stem segment: one to identify stem epidermal cell length and width; one to identify central parenchyma cell length and width. Ten measurements were taken at random from each photograph or slide.

Therefore, there were 30 leaf epidermal cell length and width determinations made for each DT/NT regime treatment (30 measurements from 3 photographs from 3 plants). There were 40 measurements each for stem epidermal cell length and width and parenchyma cell length and width taken from 4 plants (10 measurements per plant) from each DT/NT regime treatment.

Internode length was calculated by dividing leaf number above the leaf marked at the beginning of the treatment by the change in stem length from the beginning of the treatment. Internode width was measured using a digital micrometer when cell length and width measurements were made.

Cell number per internode and vertical cell number per internode were calculated from internode and cell dimension data (Table 1). Cell number per internode was calculated by dividing the calculated volume of an internode by average calculated parenchyma cell volume. Volumes were calculated using the formula for the volume of a cylinder. Vertical cell number in an internode was calculated by dividing internode length by parenchyma cell length.

Data analysis

The experiments were organized as a 5×5 and a 4×3 factorial, respectively, for Expt 1 and 2, with DT and NT as the main factors. There were 30 (10 measurements from 3 plants) and 40 measurements (10 measurements from 4 plants) for leaf and stem cell data, respectively. Analysis of variance was conducted for each dependent variable and are reported in each table.

Since the data was 'continuous', analysis using multilinear regression analysis was also appropriate. DT, NT, average temperature, and DIF were evaluated as independent variables to determine DT/NT effects on cell length and width. DIF levels were calculated for each DT/NT treatment. Polynomials and interactions between the before-mentioned terms were also evaluated. Selection of regression functions were based on significance of the model and individual parameters, correlation (r^2), and visual inspection of the regression fit. Analysis of variance and regression analysis were conducted using the Systat statistical analysis program (Systat Inc., Exanston, IL, USA).

Results

Internode length increased as DT increased and NT decreased (Table 1). For instance, internode length increased from 20 to 36 mm as DT increased from 15 to 25 °C when NT was held at 15 °C. In contrast, internode

Table 1. *The effect of day (DT) and night temperature (NT) on* Lilium longiflorum *Thunb. cv. 'Nellie White' internode length and width*

Data values represent means calculated from four sample plants. DT ranged from 15 to 25 ± 2 °C. NT ranged from 15 to 30 ± 1 °C. Plants were grown under a 9 h photoperiod. Thermoperiod parallelled the photoperiod.

NT (°C)	DT (°C)		
	15	20	25
	Mean internode length (mm)		
15	20	31	36
20	15	23	24
25	11	17	32
30	13	12	18
	Mean internode width (mm)		
15	15	12	11
20	14	11	10
25	12	12	10
30	12	8	10

Parameter	Internode length	Internode width
DT	****a	*
NT	***	**
DT × NT	***	n.s.

a Significance of terms as determined in an analysis of variance (alpha = 0.05). Significance of terms where * = 0.05, ** = 0.01, and *** = 0.001 significance of *F* parameter.

length decreased from 36 to 18 mm as NT increased from 15 to 30 °C when DT was held at 25 °C.

The effect of DT and NT on internode length could best be described quantitatively as a function of DIF rather than by DT or NT independently. Internode length increased linearly as DIF increased from -10 to $+10$ °C (Fig. 1).

Internode width decreased slightly as DT increased and NT decreased (Table 1). For instance, internode width decreased from 15 to 11 mm as DT increased from 15 to 25 °C when NT was held at 15 °C. Conversely, internode width decreased slightly from 11 to 10 mm as NT increased from 15 to 30 °C when DT was held at 25 °C.

Stem parenchyma and epidermal cell length increased as DT increased (Table 2). For instance, stem parenchyma cell length increased from 158 to 295 μm as DT increased from 15 to 25 °C when NT was held at 15 °C. Stem epidermal cell length increased from 172 to 388 μm as DT increased from 15 to 25 °C when NT was held at 15 °C.

Stem parenchyma and epidermal cell length decreased as NT increased (Table 2). For instance, stem parenchyma cell length decreased from 295 to 173 μm as NT increased from 15 to 30 °C when DT was held at 25 °C. Stem epidermal cell length decreased from 388 to 219 μm as NT increased from 15 to 30 °C when DT was held at 25 °C.

Leaf cell elongation responded similarly to DT and NT as stem cell elongation (Table 2). Leaf epidermal cell length increased from 354 to 464 μm as DT increased from 14 to 26 °C when NT was held at 14 °C. In general,
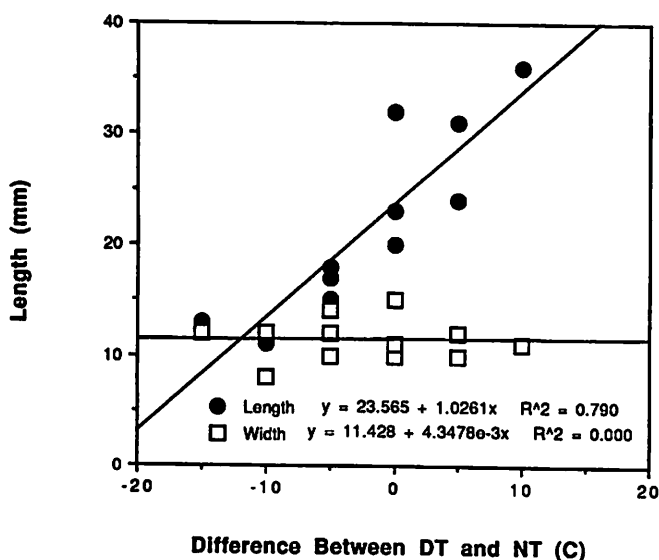
Fig. 1. The effect of the difference (DIF) between day (DT) and night temperature (NT) (DIF=DT−NT) on *Lilium longiflorum* 'Nellie White' internode length (●) and width (□). Symbols represent 12 treatment means from 12 DIF regimes calculated from each DT/NT regime (Table 1). The model significance for the length and width equations were <0.001 and n.s., respectively.

leaf epidermal cell length decreased if DT was increased further from 26 to 30 °C. Leaf epidermal cell length decreased from 464 to 331 μm as NT increased from 15 to 30 °C when DT was held at 26 °C.

The effect of temperature on cell elongation in *Lilium* could best be described quantitatively as a function of DIF rather than DT and/or NT. Cell elongation increased linearly as DIF increased, i.e. as DT increased relative to NT. Stem parenchyma and epidermal cell length increased from 95 to 295 μm and from 200 to 388 μm, respectively, as DIF increased from −15 to +10 °C (Fig. 2a). Similarly, leaf epidermal cell length increased from 300 to 464 μm as DIF increased from −16 to +16 °C (Fig. 3).

Stem parenchyma and stem epidermal cell width were unaffected by DT, NT, or DIF within the temperature range studied (Table 2; Fig. 2b). Leaf epidermal cell width was also unaffected by DIF (Fig. 3).

Calculated cell number per internode was not affected by DT or NT and was not correlated with DIF (Table 3). Similarly, the calculated vertical cell number per internode was not affected by DT, NT, or DIF (Table 3).

Discussion

Results presented in this paper suggest that DT/NT or DIF effects on stem elongation and leaf expansion in *Lilium* are elicited primarily through effects on cell elongation and not division. The bases for this conclusion are (1) cell length is strongly correlated with DIF, (2) cell width was not strongly correlated with DIF, and (3) cal-

Table 2. *The effect of day (DT) and night temperature (NT) on* Lilium longiflorum *Thunb. cv. 'Nellie White' stem parenchyma and epidermal cell length and width*

DT and NT ranged from 15 to 25±2 °C and from 15 to 30±1 °C, respectively, in Expt 2 when stem data were collected. DT and NT ranged from 14 to 30±1.5 °C in Expt 1 when data on leaf tissue were collected. Plants were grown under a 9 h photoperiod. Thermoperiod parallelled the photoperiod.

NT (°C)		DT (°C) 15	20	25
		Stem parenchyma (μm)		
15	Length	158ᵃ	234	295
	Width	146	120	108
20	Length	187	185	249
	Width	124	110	104
25	Length	145	153	177
	Width	128	130	114
30	Length	95	147	173
	Width	114	93	109

Parameter	Length	Width
DT	**ᵇ	n.s.
NT	**	n.s.
DT×NT	**	n.s.

		Stem epidermal		
15	Length	172	318	388
	Width	33	29	26
20	Length	345	447	413
	Width	39	30	28
25	Length	155	196	224
	Width	47	34	29
30	Length	200	236	219
	Width	30	26	32

Parameter	Length	Width
DT	*	n.s.
NT	**	n.s.
DT×NT	***	n.s.

		Leaf epidermal				
		14°C	18°C	22°C	26°C	30°C
14	Length	354ᶜ	340	409	464	367
	Width	75	80	80	85	88
18	Length	304	298	356	356	378
	Width	76	76	83	72	79
22	Length	304	316	374	379	303
	Width	85	78	79	80	83
26	Length	296	277	337	336	299
	Width	80	83	71	85	78
30	Length	300	263	362	331	382
	Width	81	79	79	77	79

Parameter	Length	Width
DT	***	n.s.
NT	**	n.s.
DT×NT	**	n.s.

ᵃ Numerals represent treatment means based on 40 measurements taken from 4 plants per DT/NT regime.
ᵇ Significance of terms as determined in an analysis of variance (alpha=0.05). Significance of terms where *=0.05, **=0.01, and ***=0.001 significance of *F* parameter.
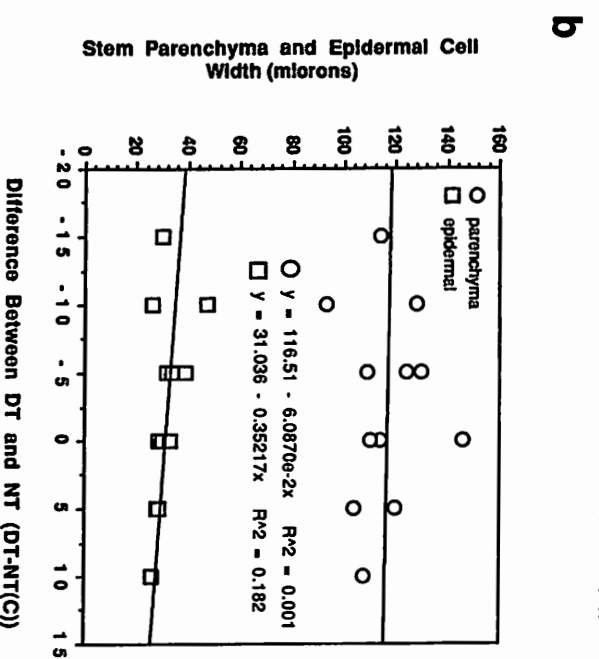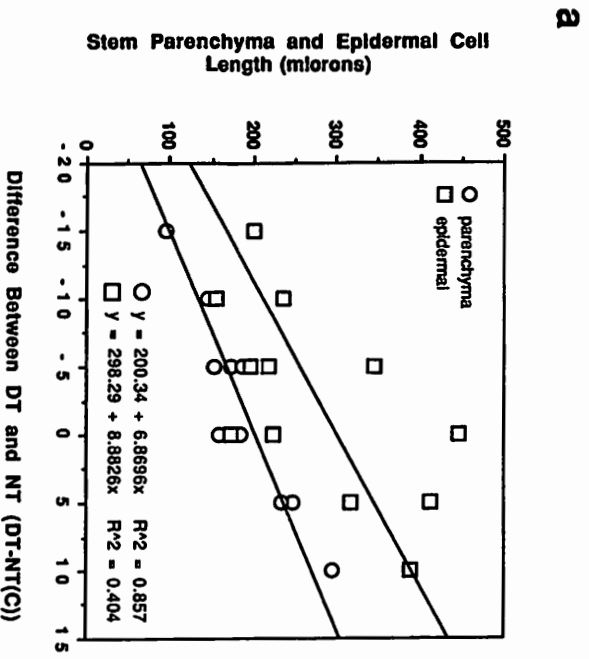ᶜ Numerals represent treatment means based on 30 measurements taken from 3 plants per DT/NT regime.

culated cell number per internode was not correlated with DIF. The basis for differential effects of DIF on cell elongation but not division is unclear.

Stem elongation responses to DIF are believed to be associated with alterations in bioactive gibberellin (GA) levels (Zieslin and Tsujita, 1988; Erwin et al., 1989, 1992; Moe et al., 1991). Application of GA_{4+7} to Lilium bulbs before planting overcame subsequent inhibition of stem elongation by a negative DIF environment (Zieslin and

Fig. 2. The effect of the difference (DIF) between day (DT) and night temperature (NT) (DIF=DT−NT) on Lilium longiflorum 'Nellie White' stem central parenchyma (○) and epidermal cell (□) length (a) and stem central parenchyma and epidermal cell width (b). Symbols represent 12 treatment means from 12 DIF values calculated from 12 DT/NT regimes (Table 2). Regression model significance (P) for parenchyma and epidermal cell means was <0.01 and <0.001, respectively. Regression model significance (P) was n.s. for both parenchyma and epidermal cell width.

Stem Parenchyma and Epidermal Cell Length (microns)

○ parenchyma
□ epidermal

y = 200.34 + 6.8696x R^2 = 0.857
y = 298.29 + 8.882x R^2 = 0.404

Difference Between DT and NT (DT-NT(C))

Stem Parenchyma and Epidermal Cell Width (microns)

○ parenchyma
□ epidermal

○ y = 116.51 - 6.08706e-2x R^2 = 0.001
□ y = 31.036 - 0.35217x R^2 = 0.182
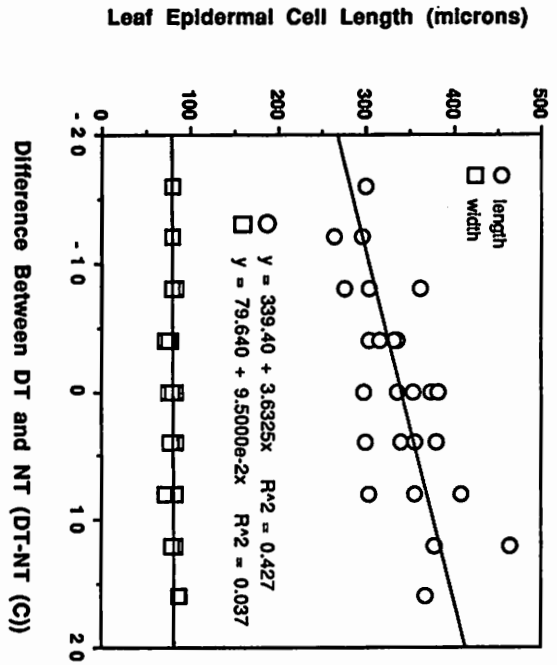
Difference Between DT and NT (DT-NT(C))

Fig. 3. The effect of the difference (DIF) between day (DT) and night temperature (NT) (DIF=DT−NT) on Lilium longiflorum 'Nellie White' leaf epidermal cell length (○) and width (□). Symbols represent 25 different DT/NT treatment regimes (Table 2). Regression model significance (P) was <0.01 and n.s., respectively, for leaf epidermal cell length and width, respectively.

Leaf Epidermal Cell Length (microns)

○ length
□ width

○ y = 339.40 + 3.6325x R^2 = 0.427
□ y = 79.640 + 9.5000e-2x R^2 = 0.037

Difference Between DT and NT (DT-NT (C))

Table 3. The influence of day (DT) and night temperature (NT) on Lilium longiflorum cv. 'Nellie White' calculated total cell number per internode and vertical cell number per internode

Calculated amounts are determined by dividing mean calculated total internode volume by mean calculated individual cell volume (original data from Tables 1 and 2). Vertical cell number was calculated by dividing mean internode length by mean individual parenchyma cell length.

NT (°C)	Cell number/internode DT (°C) 15	20	25	Vertical cell number/internode DT (°C) 15	20	25
15	1327[a]	1358	1265	12.7	13.2	12.2
20	873	1265	927	8.0	12.4	9.6
25	711	1051	1585	7.6	11.1	18.0
30	1416	667	916	13.7	8.2	10.0

Parameter	Cell number/internode	Vertical cell number/internode
DT	n.s.[b]	n.s.
NT	n.s.[b]	n.s.
DT×NT	n.s.	n.s.
r^2 (correlation with DIF plus constant model)	0.12	0.09

[a] Numerals represent treatment values calculated from calculations based on data presented in Tables 1 and 2.

[b] Significance of terms where * =0.05, ** =0.01, and *** =0.001 significance of F parameter.

Tsujita, 1988). Similarly, exogenous applications of GA_3 overcame inhibition of *Campanula isophylla* Morettii. and *Lycopersicon esculentum* L. internode elongation, respectively, when plants were grown in a negative DIF environment (Moe *et al.*, 1991; Erwin and Pierson, 1992). In contrast, application of a GA biosynthesis inhibitor, ancymidol, resulted in a greater percentage decrease on internode elongation of positive-DIF-grown plants than negative-DIF-grown *Lilium* plants (Erwin *et al.*, 1989).

Temperature influences both the levels of bioactive GA levels and the ability of tissue to respond to GA. Endogenous levels of GA_1 increased 1.6-fold when *Triticum aestivum* L. plants were grown at constant 25 versus 10 °C (Pinthus *et al.*, 1989). No data were found which resolved the effect of fluctuating temperatures on endogenous GA levels.

Both light and temperature affect the ability of tissue to respond to GA. Lockhart (1958) demonstrated that dwarfism in *Phaseolus* occurred only in light-grown plants. Pinthus *et al.* (1989) demonstrated that genotypic differences were conspicuous among genetic dwarf *Rht* mutants of *Triticum* when plants were grown at constant 25 °C, but were only slight or inconspicuous when plants were grown at constant 11 °C. Interestingly, the increase in the endogenous GA_1 level was much greater, i.e. 3-fold, 6-fold, and 9-fold on the *Rht1*, *Rht2*, and *Rht1 + 2* genotypes, respectively, than the 1.6-fold increase in GA_1 in the wild-type when temperature was increased from 10 to 25 °C. Apparently, the response of *Triticum* tissue to endogenous or applied GA is restricted by the upper limits set by the different *Rht* alleles.

Whether GA effects on stem elongation are mediated through effects on cell elongation and/or division is unclear. GA application has been shown to affect both cell elongation and division (Kaufmann, 1965; Raskin and Kende, 1984; Katsumi and Ishida, 1991). Greulach and Haesloop (1958) reported that dwarfism in *Phaseolus* could be overcome with exogenous GA application and that the increase in internode elongation on dwarf *Phaseolus* was due to an increase in cell number per internode. However, Skjedstad (1960) determined that similar application of GA to overcome dwarfism in *Zea mays* L. resulted in an increase in cell number and size. More recently, Keyes *et al.* (1989) showed that dwarfism induced by the GA response *Rht* alleles in *Triticum* was a result of a reduction in cell length and not number in leaf blades.

Lastly, data (J.E. Erwin, unpublished) suggested that the temperature of the elongating region of a stem and not the roots was critical in eliciting DIF effects on stem elongation. The independence of the shoot tip temperature relative to the root temperature suggested that turgor pressure was not the primary factor through which DIF affects stem elongation. In contrast, *Chenopodium album* L. stem elongation was affected when shoot temper-

ature was altered independently of root temperature (Lecharny *et al.*, 1985). Lecharny *et al*'s data (1985) suggested that turgor (associated with root temperature) may play a partial role in eliciting temperature effects on stem elongation. Hence, turgor may play some role in elicitation of DIF effects on stem elongation.

The response of stem elongation and/or cell elongation to DIF is an observation which leads to questions concerning the ecological or evolutionary basis for DIF responses. The dependence of stem *elongation on* DIF has been demonstrated across a variety of plant species and is not exclusive to *Lilium* (Erwin, 1991). It could be hypothesized that plant stem elongation responses to DIF may be a mechanism by which plants can direct elongation growth during different periods of a year to maximize stem elongation at critical times to compete effectively in a plant community. Such a mechanism would be of significance for temporal orientation during the year as well. Experiments are currently underway to determine the potential ecological significance of stem elongation responses to DIF.

Acknowledgements

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