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ABSTRACT

THERMOMORPHOGENESIS

By

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Plant stem elongation, leaf expansion, and leaf orientation were influenced more by the difference (DIF) between day (DT) temperature and night (NT) temperature (DT-NT) than absolute temperature between 10 and 30°C in a wide range of plant species. Stem elongation, leaf orientation, and leaf expansion increased as DIF increased. Light quality (R/FR), DIF, and application of GA_{4+7} or ancymidol interacted to affect stem elongation. The percentage stimulation of internode elongation by far red light and GA_{4+7} decreased as DIF increased. In contrast, inhibition of stem elongation by ancymidol increased as DIF increased. The ratio of *Cucurbitaceae* male/female flower number increased as DIF increased. The increase in male flowers relative to female flowers and the interaction between light quality, DIF and exogenous applications of GA_{4+7} and ancymidol suggested that the transduction pathway for temperature effects on stem elongation may involve endogenous gibberellin levels. A system using angular displacement transducers was developed to measure the kinetics of plant stem elongation. Stem elongation rate varied during a 24 hr period. Maximum

response to DIF occurred during the last 2 hours of the night period and the first 2 hours of the day period. The basis for the differential sensitivity of stem elongation to temperature is discussed with respect to the effect of DIF on circadian stem elongation rhythms.

Dedication

This thesis is dedicated to my friends. Without them this thesis would not have been possible. Each of them is special in their own way. I love them all very much.

Timothy R. Cefai

Royal D. Heins

Desmond R. Layne

Robert J. Lechnar

Brian J. Kovanda

Mark V. Yelanich

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The process of initiating and completing a doctorate thesis can be grueling. Although it was difficult, I never regretted undertaking the task. Receiving my doctorate is a dream which has been dear to me for some time.

Upon finishing this dissertation the thought has occurred to me that I have never learned quite so much in so short a period of time. The experience has been invaluable to me. Interestingly, the greatest benefit of the dissertation process to me has not been the gaining of scientific knowledge but rather personal growth. Fortunately, I had a major professor, friends, and family who appreciated this process and tolerated my 'growing pains'.

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Section I

Thermomorphogenesis

In *Lilium longiflorum* Thunb.

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THERMOMORPHOGENESIS IN LILIUM LONGIFLORUM[1]

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ABSTRACT

Stem elongation and leaf orientation in *Lilium longiflorum* Thunb. were influenced more by the difference (DIF) between day temperature (DT) and night temperature (NT) than absolute DT or NT from 14 to 30 C. Plant height and internode length increased 129 and 382%, respectively, as DIF (DT-NT) increased from −16 to 16 C as compared to only 15 and 58% when either DT or NT was increased from 14 to 30 C, respectively. Leaf orientation, defined as the angle between a line perpendicular to the stem and the line from the leaf base to the leaf tip, increased 43° (leaves became more upright) as DIF increased from −16 to 16 C. In contrast to plant height, internode length, and leaf orientation, leaf and flower length were influenced more by absolute temperature than DIF. Leaf and flower length decreased 32 and 14%, respectively, as NT increased from 14 to 30 C. DT had little effect on either leaf or flower length. The influence of DIF on stem elongation suggested that thermomorphogenesis was not a function of total plant carbohydrate or carbohydrate translocation. Instead, DIF appeared to influence the endogenous gibberellin content or the response of plant tissue to gibberellin. Similarities between thermomorphogenic plant responses and photomorphogenic plant responses suggested that these two processes may be related with respect to their perception and/or transduction.

GROWTH is thermoperiodic in many plant species (Dorland and Went, 1947; Went, 1953; Viglierchio and Went, 1957; Hellmers and Sundahl, 1959; Groves and Lang, 1970; Erwin and Heins, 1985; Karlsson and Heins, 1986). For instance, plant height is greater when plants are grown with day temperatures (DT) warmer than night temperatures (NT) in a wide range of plant species including *Lycopersicon* (Went, 1944; 1945), *Phaseolus* (Viglierchio and Went, 1957), *Chrysanthemum* (Karlsson and Heins, 1986), and *Capsicum* (Dorland and Went, 1947). Other plant characteristics which respond to diurnal changes in temperature are flower size (Karlsson and Heins, 1986), leaf shape (Fischer, 1954; Njoku, 1957), and leaf orientation (Erwin and Heins, 1985).

Plant height in *L. longiflorum* Thunb. cv. Ace was influenced by DT and NT (Wilkins, 1973). Lily plants grown with a 32 C DT and 16 C NT from the visible bud stage to anthesis were 149% taller than plants grown with a 16 C DT and 32 C NT (Wilkins, 1973). The cv. Nellie White responded similarly to temperature, with respect to plant height as cv. Ace (Erwin and Heins, 1985). In addition, leaf size, flower size, and leaf orientation were also influenced by DT and NT with cv. Nellie White (Erwin and Heins, 1985). In contrast, plant height of *Lilium longiflorum* Thunb. cv. Croft was not greatly influenced by DT or NT between 10 and 27 C (Smith and Langhans, 1961).

Morphological responses to temperature will be referred to as *thermomorphogenic* in this paper. The term is derived from the Greek derivatives *therme*, meaning heat; *morphos*, the quality of having form; and *gignesthai*, to be born. Hence, *thermomorphogenesis*, the effect of temperature on plant morphogenesis. The term thermomorphogenesis is consistent with the term photomorphogenesis which describes the effect of light on plant morphogenesis.

The objective of this study was to quantify thermomorphogenic responses in *Lilium longiflorum*. In the process of determining morphogenic responses to temperature, we wished to gain some insight into what processes may control thermomorphogenic responses.

MATERIALS AND METHODS—*Lilium longiflorum* Thunb. cv. Nellie White bulbs 17.7–20.3 cm in circumference were planted in 15.2 cm plastic pots on 28 October 1985 in soilless medium consisting of equal parts of sphagnum peat, perlite, and vermiculite (1:1:1). Potted bulbs were placed in a controlled environment greenhouse for two weeks where air temperature was adjusted to maintain a medium temperature of 17 C ± 1 C to encourage root development. Plants were then vernalized in the dark for 6 wk at 5 C. Following vernalization,

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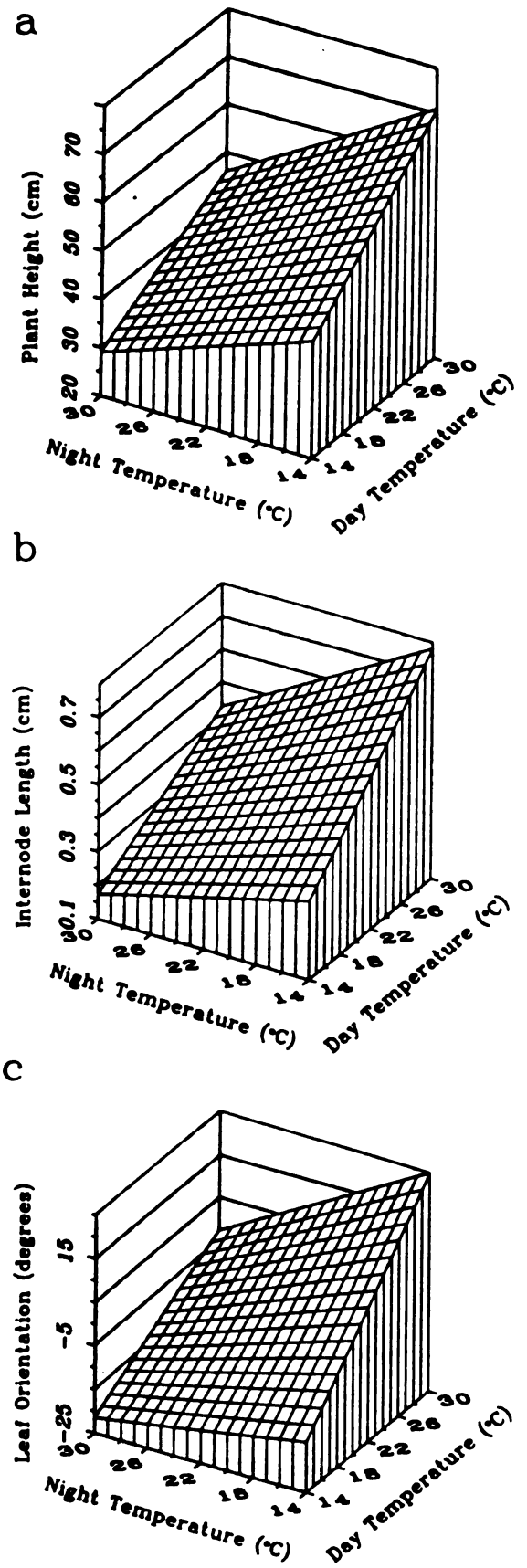

all plants were placed in a greenhouse under natural photoperiodic conditions with constant 20 C DT and NT. Upon shoot emergence, plants received a long day treatment for 7 days consisting of night interruption lighting from 2200 to 0200 hr delivered with incandescent lamps at 2 micromol sec^{-1} m^{-2} (400–700 nm wavelength). After the long day treatment, plants were returned to natural photoperiodic conditions (ca. 9 hr, 15 min light span).

Time of flower initiation was established by terminal shoot dissections on randomly selected plant samples starting 13 January 1986. Plant samples were taken every 3 days. Flower initiation was defined as the first visible sign of a reproductive meristem (De Hertogh, 1976, figure 2c). Flower initiation was observed on 100% of the sample on 22 January. One hundred twenty-five plants were then selected for uniformity based on plant height and leaf number and moved to greenhouses with temperature setpoints of 14, 18, 22, 26, or 30 C. Actual average temperatures during the experiment did not vary by more than 1.8 C from the desired temperature setpoints. Plants were moved among greenhouse sections at 0800 and 1800 hr each day to yield a total of 25 DT/NT treatment combinations. Movement of plants required approximately 30 min. An opaque curtain was pulled over the plants after the plants were moved at 1800 and was retracted just prior to 0800 to provide a 14-hr scotoperiod to parallel the night temperature treatment. Plants were spaced to provide 900 cm^2 per plant.

During 1987, a group of *Lilium longiflorum* Thunb. cv. Nellie White plants were grown as specified above. At flower initiation, 6 groups of 10 plants each were placed in controlled environment greenhouses maintained at 15, 20, and 25 C. Each group of plants was rotated among greenhouses to yield a total of 9 DT/NT temperature treatments. Within each temperature treatment the plants were divided into 2 groups of 5 plants each. One group was grown as a control. The other group received two applications of 0.25 mg ancymidol (alpha-cyclopropyl-alpha-(4-methoxyphenyl)-5-pyrim-

←

Fig. 1. Response surface plots generated from predicted final plant height (a), internode length (b), and leaf orientation (c) on *Lilium longiflorum* Thunb. cv. Nellie White as influenced by day and night temperature. Surfaces were based on the regression functions: (a) 1.48602•DIF + −0.0416•DT•NT + 1.91394•AVG TEMP + 25.661 (r^2 = 0.84), (b) 0.0223117•DIF + − 0.000752•DT•NT + 0.0390916•AVG TEMP − 0.0652671 (r^2 = 0.82), and (c) 1.80309•DIF + −0.07495•DT•NT + 4.02815•AVG TEMP − 55.18 (r^2 = 0.68), respectively.

idinemethanol) 7 and 14 days after flower initiation to the plant apex. Ancymidol was applied using a Labsystems Finnpipette Dispenser (20–200 μl) as ten 100 μl droplets.

Data were collected at anthesis (terminal flower) on total plant height, leaf number, aborted and non aborted flower number, flower length, leaf length, and leaf orientation. Plant height was defined as the height of the plant from the soil line to the tip of the uppermost pedicel. Internode length was calculated by dividing stem length by leaf number. Leaf number was constant, since plants had initiated flowers prior to placement in the experimental environments. Leaf orientation was defined as the angle between a line perpendicular to the stem and a line from the leaf base to the leaf tip. A 0° leaf orientation indicated a horizontal leaf orientation. Similarly, a positive angle of leaf orientation indicated hyponastic, or upward leaf orientation, and a negative angle of leaf orientation indicated an epinastic, or downward leaf orientation.

Data were statistically analyzed as a 5 × 5 factorial design with DT and NT as the main factors for the 1986 data. Data were statistically analyzed as a split plot design with DT and NT as the main factors and ancymidol concentration as the subplots in the 1987 data. The ANOVA subroutine of the "Statistical Package of the Social Sciences" (Nie, 1975) was used for analysis of variance. The "All Possible Subsets Regression (P9R)" and the "Stepwise Regression (P2R)" subroutines of the "Biomedical Statistical Software Package" (Dixon, 1983) were used for multilinear regression analysis.

RESULTS AND DISCUSSION—DT and NT influenced plant height in opposite ways. Plant height increased 64% as DT increased from 14 to 30 C with NT held at 14 C. Plant height decreased 29% as NT increased from 14 to 30 C with DT held at 14 C. (Fig. 1a; Table 1).

DT and NT also interacted to influence plant height. The influence of NT on final plant height increased as DT increased. Increasing NT from 14 to 30 C decreased plant height 12.5 cm (29%) when the DT was 14 C and 21.1 cm (30%) when the DT was 30 C. In contrast, the influence of DT on final plant height decreased as NT increased. Increasing DT from 14 C to 30 C increased plant height 27.8 cm (64%) when the NT was 14 C and 19.2 cm (61%) when the NT was 30 C. The percent increase in plant height due to increasing DT was not influenced by NT and vice versa.

The relationship between DT and NT influenced final plant height to a greater extent than DT, NT, or average temperature. Plants grown with a NT warmer than DT were consistently shorter than plants grown with equal DT and NT while plants grown with the NT cooler than the DT were taller (Table 1). Plant heights were similar when the relationship between DT and NT was the same (Table 1). For example, the plants shown in Fig. 2 were all grown with a NT 4 C warmer than the DT. All the plants had similar plant heights at anthesis (40.5, 42.4, 41.2, and 42.2 cm, respectively) despite the very different average temperatures associated with each temperature treatment. Similar final heights occurred on other plants with similar relationships between DT and NT. Plant height increased as DT increased relative to NT. Plants grown with a 14 C DT/30 C NT were 40.3 cm shorter than plants grown with a 30 C DT/14 C NT temperature regime. The importance of the relationship between DT and NT on plant height is consistent with results of Lecharny, Schwall, and Wagner (1985) who suggested that the difference in temperature between the day and night was critical in determining the rate of stem elongation and/or phase resetting of the stem elongation circadian rhythm in *Chenopodium rubrum*.

The relationship between DT and NT was

TABLE 1. *Influence of day and night temperature on* Lilium longiflorum *cv. Nellie White plant height, internode length, and leaf orientation*

Night temperature (C)	Day temperature (C)				
	14	18	22	26	30
	Plant height (cm)				
14	43.8	54.6	62.2	68.4	71.6[a]
18	40.5	45.8	57.0	60.8	63.5
22	31.8	42.4	44.4	50.8	50.8
26	30.2	39.0	41.2	43.6	51.2
30	31.3	33.8	41.0	42.2	50.5
	Internode length (cm)				
14	0.31	0.48	0.60	0.68	0.82
18	0.25	0.38	0.56	0.64	—
22	0.23	0.31	0.46	0.48	0.54
26	0.22	0.27	0.41	0.45	0.46
30	0.17	0.20	0.36	0.38	0.49
	Leaf orientation (degrees)[b]				
14	−5.9	−5.0	11.6	18.9	26.3
18	−10.0	−17.9	5.8	11.9	14.7
22	−24.2	−10.2	−<>> V	2.7	6.1
26	−20.7	−13.3	−1.4	−2.6	8.3
30	−16.7	−13.7	−12.5	−7.3	1.7

[a] Values represent the experimental means. The greatest SD was 7.2 cm, 0.1 cm, and 15.2 degrees for plant height, internode length, and leaf orientation, respectively.

[b] Angle of the leaf, in degrees, between a line perpendicular to the stem and a line connecting the leaf tip to the leaf base.

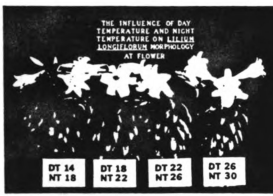

Fig. 2. Appearance of *Lilium longiflorum* Thunb. cv. Nellie White at anthesis when grown under four temperature regimes with day temperatures (DT) 4 C cooler than night temperatures (NT). Plants grown at higher average temperatures flowered earlier than plants grown at cooler average temperatures. As plants grown at higher temperatures reached anthesis, they were placed in a cooler (4 C) until plants grown at cooler temperatures reached anthesis. Stem elongation did not occur in the cooler. When all plants had reached anthesis, the photograph was taken.

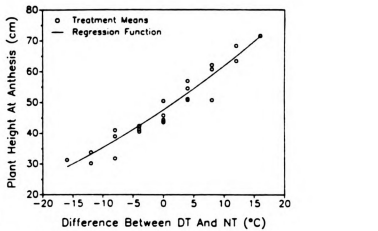

Fig. 3. Relationship between *Lilium longiflorum* Thunb. cv. Nellie White plant height at anthesis and the difference (DIF) between the day temperature (DT) and night temperature (NT). Squares represent mean plant heights for each temperature treatment. The solid line represents the regression function 1.4860•DIF − 0.0416•DT•NT + 1.9139•AVG TEMP + 25.661 (r^2 = 0.84). The regression line also represents the effect of both the day temperature by night temperature interaction and the effect of average temperature on final plant height.

described in regression analysis as the difference in temperature between DT and NT, i.e., DT minus NT (DIF). The DIF term was useful in that it described the difference between DT and NT and carried a sign to indicate whether DT or NT was greater. The importance of DIF in determining plant height was shown when it was evaluated independently as a linear function of plant height; DIF accounted for 78% of the variability in plant height among treatment plants.

TABLE 2. *Influence of day and night temperature on* Lilium longiflorum *cv. Nellie White leaf and flower length*

Night temperatures (C)	Day temperature (C)			
	14	18	22	26	30
	Leaf length (cm)[a]				
14	18.2[b]	21.0	20.8	20.2	19.6
18	17.0	18.0	19.5	18.4	19.1
22	16.6	16.7	16.7	17.8	16.8
26	15.6	14.7	15.7	15.3	15.0
30	12.4	13.3	13.8	14.0	13.6
	Flower length (cm)[c]				
14	17.7	17.8	17.9	18.4	16.5
18	17.5	18.6	17.7	17.2	17.2
22	17.6	17.4	17.7	16.9	16.5
26	16.5	16.8	16.7	16.7	16.4
30	15.3	15.8	16.8	16.3	16.0

[a] Length from the point of attachment of the leaf to the leaf tip.

[b] Values represent the experimental means. The greatest SD was 1.1 cm for both leaf and flower length.

[c] Length from the point of attachment of the petal to the pedicel to the petal tip.

Internode length responded to DT and NT in a similar fashion as plant height (Fig. 1b; Table 1). As DIF increased from −16 to 16 C, internode length increased 382% (0.65 cm). No difference in internode length was observed between internodes which matured early in plant development as opposed to late in plant development.

As with plant height and internode length, the relationship between DT and NT influenced leaf orientation of *Lilium longiflorum* (Table 1) to a greater extent than absolute DT and NT. An increase in DIF from −16 to 16 C increased leaf orientation 43°.

Leaf and flower length were influenced more by absolute DT and NT than DIF. Leaf length was primarily influenced by NT (Fig. 4). As NT increased from 14 to 30 C with a 14 C DT, leaf length decreased 32% (5.8 cm) (Table 2). DT had little influence on leaf length. These results contrast results of Friend and Pomeroy (1970) on *Triticum* where leaf length first increased as temperature increased from 10 to 25 C then decreased with temperatures above 25 C. The differences in response of *Lilium* and *Triticum* leaf length to temperatures above 25 C may be due to different temperature optima for leaf growth in these two species.

Both DT and NT influenced flower length (Table 2). NT had a greater effect on flower length than DT. As NT increased from 14 to 30 C with DT held at 14 C, flower length de-

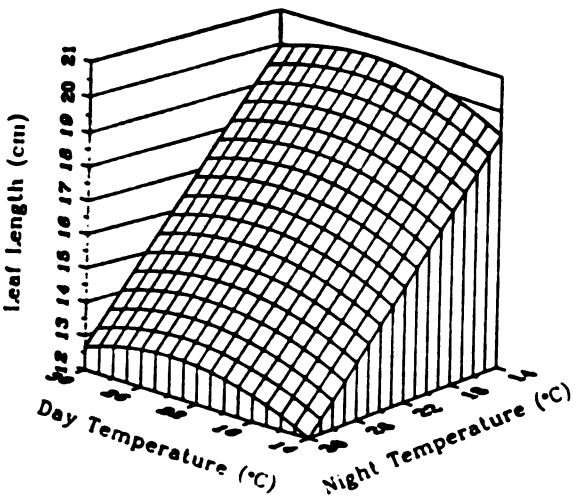

Fig. 4. Response surface generated from predicted final leaf length of *Lilium longiflorum* cm. Nellie White as influenced by day and night temperature. Predicted leaf length was based on the regression function 0.581132•DT + −0.012254•DT² + −0.425519•NT + 19.49 (r^2 = 0.72).

TABLE 3. *The effect of ancymidol and the day/night temperature regime on* Lilium longiflorum *Thunb. plant height at anthesis*

Temperature regime (C)	DIF	Plant height (cm)	Plant height 0.50 mg ancymidol spray	Percent reduction
25/15	10[a]	48.2[b]	39.1[c]	19[*d]
20/15	5	46.5	36.5	22[**]
15/15	0	36.0	30.4	16[**]
20/20	0	35.8	31.2	13[*]
15/20	−5	29.3	29.7	0 ns
15/25	−10	29.1	30.1	−3 ns

[a] Numerals represent day temperature minus night temperature.
[b] Numerals represent the treatment mean.
[c] Ancymidol was applied as two spray applications of 0.25 mg each. Applications were made 7 and 14 days after flower initiation.
[d] Significant at $P = 0.05$(*); $P = 0.01$(**); not significant (ns).

creased 39% (2.4 cm). In contrast, as DT increased from 14 to 30 C with NT held at 14 C, flower length decreased 15% (1.2 cm).

The results presented in this paper define thermomorphogenic responses in *L. longiflorum*. Went and Bonner (1943) suggested that thermomorphogenic stem elongation in *Lycopersicon esculentum* resulted from an alteration in the carbohydrate status in the elongating region of the stem. Thermomorphogenic stem elongation responses of *Dendrothema grandiflora* (Chrysanthemum) (Karlsson and Heins, 1986) and *Lilium* are similar. The similar thermomorphogenic responses of these two species showed that a supplemental carbohydrate source such as the *Lilium* bulb does not influence stem elongation. The effect of temperature on *Lilium* stem elongation was not affected by increasing or decreasing the irradiance which plants were grown under between 50 and 400 μmol s^{-1} m^{-2} (Erwin and Heins, unpublished data). The lack of differential thermomorphogenic responses of *L. longiflorum* to irradiance and the lack of a differential response to temperature between *Dendrothema* and *Lilium* suggested that total carbohydrate availability within the plant is not the primary factor responsible for the stem elongation response to temperature as Went and Bonner (1943) had suggested.

Our results would be compatible with Went and Bonner's (1943) work if carbohydrate availability were limited by translocation. Translocation has been shown to increase exponentially in *Glycine* as temperature increased from 5 to 40 C (Marowich, Richter, and Hoddinoly, 1986), i.e., translocation responds to absolute temperature. If carbohydrate translocation were the limiting factor in determining the stem elongation response to temperature in *Lilium*, stem elongation should have increased or decreased as DT and NT increased with a constant DIF. As is seen in Fig. 2, this was not the case. In addition, flower bud abortion should have been negatively correlated with plant height since flower bud abortion is sensitive to carbohydrate depletion (Einert and Box, 1967). This was not the case (r^2 = 0.03). It is, therefore, unlikely that thermomorphogenic stem elongation responses are a result of carbohydrate availability and/or carbohydrate translocation.

It is more likely that the effect of DT and NT (DIF) on *Lilium* stem elongation is mediated through differences in hormone synthesis or action, probably gibberellin. Preliminary results of experimentation studying the effect of temperature on stem elongation responses to a gibberellin biosynthesis inhibitor, ancymidol (Moore, 1979), suggested that there is a strong interaction between DIF and the endogenous levels of gibberellin within *Lilium* (Table 3). The effect of the ancymidol application on stem elongation decreased as DIF decreased. In addition, application of GA_{4+7} can overcome the inhibition of stem elongation induced by a negative DIF (N. Zieslin, personal communication).

Morphological characteristics of *Lilium* grown with a large positive DIF were similar to morphological characteristics of plants with low phytochrome photoequilibria, i.e., grown

under far-red light (Holmes and Smith, 1977). Similarly, the morphology of *Lilium* grown with a negative DIF were similar to morphological characteristics of plants with high phytochrome photoequilibria, i.e., grown under red light. Also, thermomorphogenic behavior appears to be much greater in plants which are highly photoperiodic (e.g., *L. longiflorum, Dendrothema grandiflora, Euphorbia pulcherrima, Fucshia hybrida*) than plants which are "day neutral" (e.g., *Tulipa hybrida, Narcissus pseudonarcissus, Cucumis sativa*) (Erwin and Heins, unpublished data). The similarity in thermomorphogenic and photomorphogenic responses suggested that these two processes may be related with respect to their perception and/or transduction. Investigations have been initiated to determine the possible interactions between phytochrome and thermomorphogenic behavior in plants.

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Section II

Temperature Effects On Lily Development Rate And Morphology From The Visible Bud Stage Until Anthesis

Temperature Effects On Lily Development Rate And Morphology From The Visible Bud Stage Until Anthesis

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Abstract

Day temperature (DT) and night temperature (NT) influenced *Lilium longiflorum* Thunb. 'Nellie White' stem elongation and development rate from the visible bud stage (VB) until anthesis (ANT). Plant height increase after VB was a function of the difference (DIF) between DT and NT (DT-NT). Plant height increased 90% as DIF increased from -16 to 16 C. A cubic model described bud development rate as a function of temperature from 14 to 30 C. A linear model adequately described bud development rate as a function of average daily temperature (ADT) from 14 to 21 C. Based on the linear model, bud development rate increased .05 per day for each 1°C increase in ADT. The base temperature for bud development, i.e. the temperature at which bud development rate was 0, was calculated as 3.5 C.

Introduction

Greenhouse forcing of vernalized Easter lilies, Lilium longiflorum Thunb., is commonly divided into 3 phases. These phases are: I) placement of vernalized bulbs in the greenhouse to flower initiation, II) flower initiation to the visible bud stage (VB), and III) VB to anthesis (AH) (DeHertogh and Wilkins, 1971). Plant morphological development differs during each of the forcing phases (DeHertogh and Wilkins, 1971). Growth during phase I is vegetative and consists of stem elongation and leaf expansion. Flower initiation, leaf expansion, and stem elongation occur during phase II. Inflorescence expansion and stem elongation occur during phase III.

Lily responses to temperature during phase III differed from those during Phase I and II (Wang and Roberts, 1983). Lily development rate, quantified as days to unfold a leaf, is a decreasing linear function of average daily temperature between 14 and 30 C during phase I and II (Karlsson et al, 1988). Lily development rate during phase III is a nonlinear function of temperature (Healy and Wilkins, 1984). The effect of temperature on the rate of lily development decreases as DT and/or NT increase during phase III (Roh and Wilkins, 1973; Healy and Wilkins, 1984).

Easter lily morphological development is thermomorphogenic. For instance, internode length increases as the difference (DIF) between day (DT) and night temperature

(NT), i.e. day temperature - night temperature, increases (Erwin et al, 1989). In addition, leaf orientation, leaf length, and flower length are also influenced by diurnal changes in temperature.

Quantification of Easter lily responses to temperature is useful to Easter lily growers. Selection of the proper average daily temperature is critical to achieve a desired rate of plant development so plants flower for a desired marketing date. Improper selection of temperatures during phases II and III may result in incorrect crop timing, flower bud abortion (Roh and Wilkins, 1973) and/or excessively tall or short plants at anthesis (Erwin et. al., 1989). Karlsson et. al. (1988) developed a mathematical function relating the rate of lily leaf unfolding to average daily temperature during phase II. Similarly, Erwin et. al. (1989) determined the functional relationships for the effects of DT and NT on stem elongation and leaf orientation during phase II. Healy and Wilkins (1984) developed functional relationships between lily bud length and the time to flower of plants grown with constant DT and NT during phase III. The functional relationships describing the rate of lily development and stem elongation for lily plants grown at different DT and NT during phase III have not been determined.

The objective of this research was to develop mathematical functions relating the rate of Easter lily development and stem elongation to DT and NT during phase III.

Materials And Methods

Easter lily bulbs 17.7-20.3 cm in circumference were planted in 15.2 cm (pot volume = 2,570 ml) plastic pots on 28 October, 1985, in a soilless medium consisting of equal parts of sphagnum peat, perlite, and vermiculite. Potted bulbs were placed in a greenhouse for two weeks where air temperature was adjusted to maintain a medium temperature of 17 $\pm$ 1 C to encourage root development. Plants were then vernalized for 6 weeks at 5 C after which all plants were placed in a glasshouse under natural photoperiodic conditions with constant 20 C DT and NT temperature setpoints. Upon shoot emergence, plants received a long day treatment for 7 days consisting of the natural photoperiod (ca. 9 hr 15 min.) plus a night interruption lighting from 2200 to 0200 hrs delivered with incandescent lamps at a 2 umol s^{-1} m^{-2} (400-700 nm wavelength). Plants were returned to natural photoperiodic conditions after the long day treatment.

Time of flower initiation was established by terminal shoot dissections every 3 days on 5 randomly selected plants starting 13 January, 1986. Flower initiation was defined as the first visible differentiation of the vegetative meristem into a reproductive meristem (DeHertogh et al, 1976, Figure 2c). Flower initiation was observed on 100 % of the sample on 22 Jan.

Plants were then selected for uniformity based on plant height and leaf number and moved to greenhouses with

maintained at 14, 18, 22, 26, or 30 C. Actual average temperatures during the experiment did not vary by more than 1.8 C from the desired temperature setpoints. Plants were moved among greenhouses at 0800 and 1800 hr each day to yield a total of 25 DT/NT treatment combinations. Each temperature treatment had 5 single plant replicates (total of 125 plants).

Movement of plants required approximately 30 min. An opaque curtain was pulled over the plants at 1800 and was retracted just prior to 0800 to provide a 14 hr scotoperiod to parallel the night temperature treatment. Plants were spaced at 11 plants m^{-2}.

Data were collected on the date and plant height at visible bud and anthesis. Plant height was defined as the height of the plant from the soil line to the tip of the uppermost bud.

Analysis of variance was conducted using the ANOVA procedure of The Statistical Package Of The Social Sciences (SPSS) (Nie, 1975). Regression analysis of the data were conducted using the 'All Possible Subsets Regression (P9R)' and the 'Stepwise Regression (P2R)' subroutines of the 'Biomedical Statistical Software Package' (Dixon, 1983). Models were selected based on evaluation of residuals, r^2, and Mallow's C_p (Draper and Smith, 1981). All parameters selected in the models were significant at the P=0.05 level.

Results

Change in height from VB until anthesis: Change in plant height after VB was a function of DIF between DT and NT (DT-NT). Plant elongation after VB increased from 14.2 to 27.0 cm as DIF increased from -16 to 16 C (Figure 1). The relationship between DIF and stem elongation after VB is consistent with previous lily research which showed a greater effect of DIF on internode elongation during stage II than absolute DT and/or NT (Erwin et. al., 1989). Kohl et. al. (1958) showed that plant heights were similar on lilies grown at constant 21.1, 15.5, or 10 C (0 DIF) temperatures, as expected if DIF controls elongation and not absolute temperatures between 10 and 30 C. Roh and Wilkins (1973) reported that stem elongation after VB was only affected by DT above 21.1 C. Regression of treatment means reported by Roh and Wilkins with DIF as the independent variable and plant height at anthesis as the dependent variable resulted in a model with an r^2 of 0.63. This model would likely have had a higher r^2 if the regression was based the change in height after VB only as treatments were only initiated following VB and a significant amount of stem elongation had occurred prior to VB. These data, however, are not reported. Our results contradict the results of Smith and Langhans (1962) who stated that DT and NT did not affect plant height during developmental stages II and III.

Development Rate From VB Until Anthesis: The time from VB to anthesis decreased as either DT or NT increased from 14 to 26 C (Table 1). The minimum time from VB to anthesis was 26 days when plants were grown at constant 26°C. These data are comparable to results of Roh and Wilkins (1973) who reported a minimum time of 24 days with Easter lily cv Ace grown at constant 32 C.

Lily flower bud development rate was a quadratic function of temperature when DT and NT were held constant (Figure 2). Maximum flower development rate was observed near 26 C. The maximum near 26 C is similar to that of wheat and maize where the maximum leaf unfolding rate occurred between 25 and 30 C (Alm et. al., 1988; Tollenaar et. al., 1979; Warrington and Karemasu, 1983). The temperature optimum for flower bud development is lower, however, than for lily leaf unfolding which is above 30 C (Karlsson et. al., 1988).

When DT and NT were not identical, daily flower bud development rate was the mathematical sum of the hourly flower bud development rates at the temperatures which plants were grown under. Figure 2 shows straight lines connecting to 30 DT/30NT treatment development rate with the 14 DT/14 NT, 18 DT/18 NT, 22 DT/22 NT, and the 26 DT/26 NT development rates. These lines represent the expected flower development rates for all average daily temperatures created by the DT and NT combinations of the temperatures connected by a line. Data points of actual development rates of plants from treatments

with temperature combinations associated with the lines show actual rates of development are close to predicted rates.

The prediction model for development rate was based on a 10-hr day and a 14-hr night period. This model can be modified for any length of day;

Daily Rate =

$$b_1 + \frac{b_2*((HDT*DT)+(HNT*NT))}{24} + \frac{b_3*HDT*DT^3}{10} + \frac{b_4*HNT*NT^3}{14} \quad (1)$$

where b_1, b_2, b_3, and b_4 are parameter coefficients. HDT and HNT are hours of day and night, respectively.

The model can be further modified to directly calculate hourly development rate at a specific temperature;

Hourly rate =

$$\frac{b_1}{24} + \frac{b_2 * T^3}{24} + \frac{(b_3 + b_4) * T^3}{24} \quad (2)$$

where T is the hourly temperature.

When either DT or NT do not exceed 22 C, daily flower development rate can be approximated by a linear function based on average daily temperature (ADT);

daily rate = -0.740904E-02 + (0.209036E-02 * ADT) . (3)

A linear ADT model can be used because development rate is nearly linear in the 14 to 22 C temperature range (Figure

2). When development rate is a linear function of ADT, a degree day model can be used (Karlsson et al, 1988). From function (3), 478 degree days are required above a base temperature of 3.5 C for lily flower bud development from VB to FLW. This base temperature calculated for flower bud development is comparable to the base temperature for lily leaf unfolding, 1 C (Karlsson et al., 1988).

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Table 1. The influence of day and night temperature on the number of days from visible bud to open flower in *Lilium longiflorum* cv 'Nellie White'.

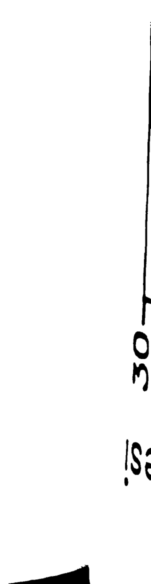
Night Temperature (°C)	Day Temperature (°C) 14	18	22	26	30
14	41.5 [z]	38.4	31.0	31.2	32.0
18	38.6	33.2	31.0	29.8	29.3
22	34.8	30.8	27.5	26.8	26.4
26	32.8	30.8	27.2	25.6	25.6
30	31.2	28.8	26.4	26.2	25.7

Day Temperature		Night Temperature	
Linear	*** [y]	Linear	***
Quadratic	***	Quadratic	***
Cubic	n.s.	Cubic	n.s.

[z] Numerals represent treatment means.

[y] Significance of data at P = .001 (***), not significant (n.s.)

Figure 1. Relationship between *Lilium longiflorum* cv 'Nellie White' height increase during phase III and the difference between the day and night temperature (DT-NT). Squares represent the mean change in plant height after visible bud for each temperature treatment as determined from 5 plants. The solid line represents the function Height increase after visible bud = (0.496946*DIF) + (0.150561*DIF^2) + 18.01 (r^2 = 0.77).



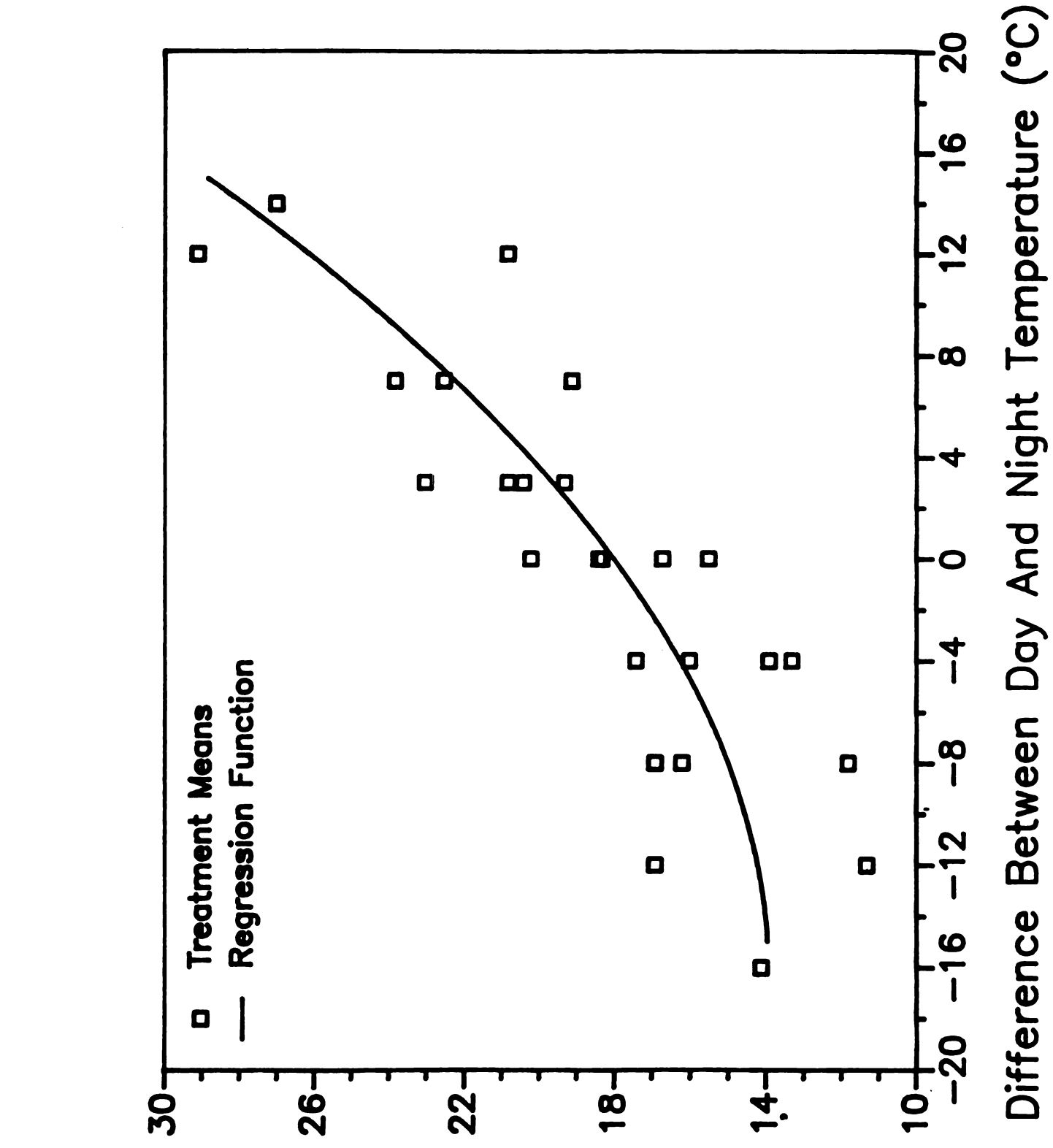
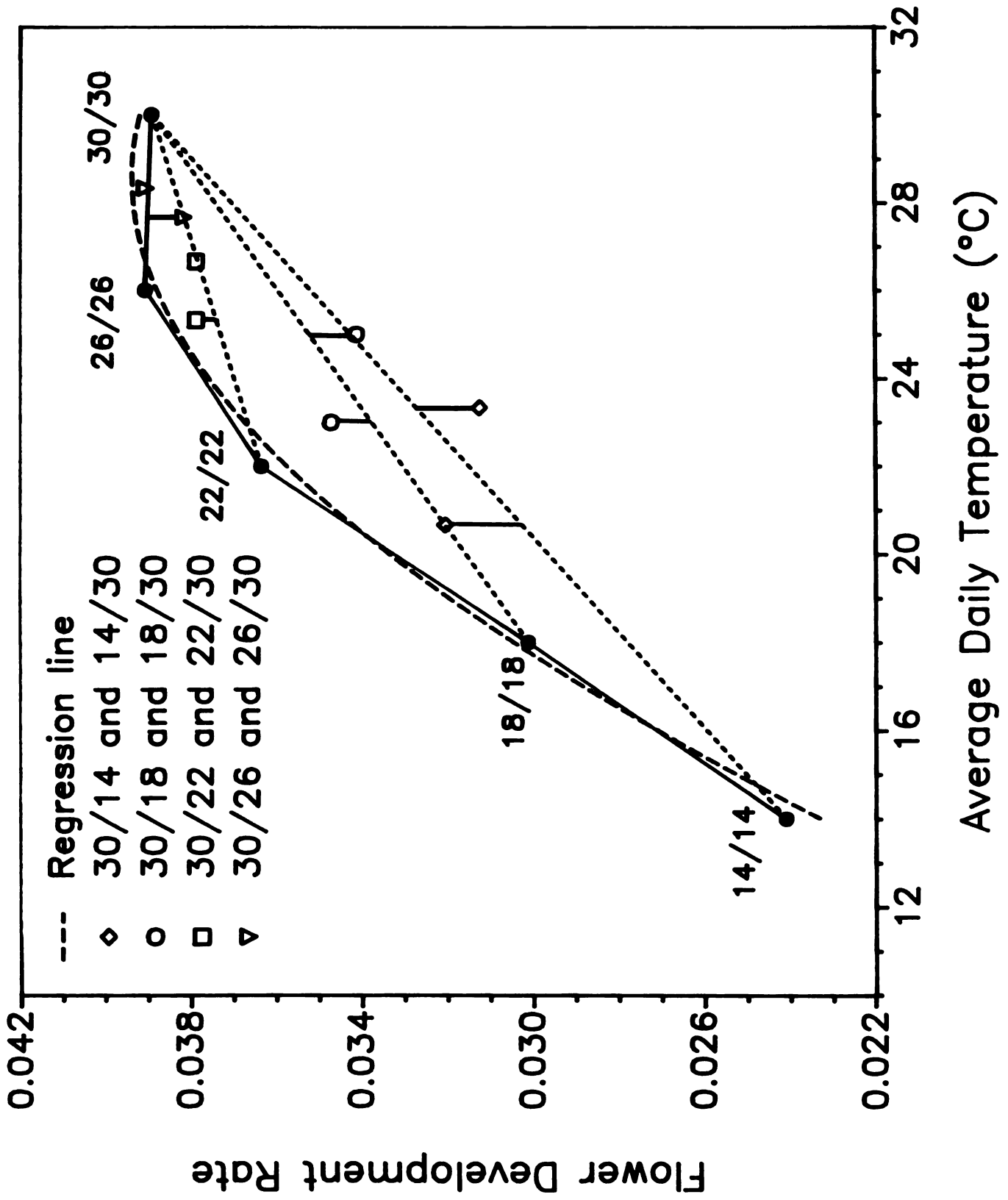

Change In Height From VB To Anthesis (cm)
30
26
22
18
14
10
Treatment Means
Regression Function
−20
−16
−12
−8
−4
0
4
8
12
16
20
Difference Between Day And Night Temperature (°C)

Figure 2. *Lilium longiflorum* 'Nellie White' bud development rate per hour as a function of temperature. The regression model is based on the function, Daily rate = $b_1 + b_2 * ((HDT * DT) + (HNT * NT))/24 + b_3/10 * HDT * DT^3 + b_4/14 * HNT * NT^3$ ($r^2 = .96$). B_1, b_2, b_3, and b_4 are parameter coefficients. HDT and HNT are hours of day and night temperature, respectively. The bars associated with the data points represent deviation between observed and expected flower development rate.


Flower Development Rate
0.042
0.038
0.034
0.030
0.026
0.022
12
16
20
24
28
32
Average Daily Temperature (°C)
Regression line
30/14 and 14/30
30/18 and 18/30
30/22 and 22/30
30/26 and 26/30
30/30
26/26
22/22
18/18
14/14

Section III.

Temperature And Photoperiod Effects On *Fuchsia x hybrida* Morphological Development

Temperature And Photoperiod Effects on *Fuchsia x hybrida* Morphology

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Abstract

Fuchsia x hybrida 'Dollar Princess' plants were grown under 41 different day/night temperature (DT/NT) environments over a 2 year period with temperatures ranging from 10 to 30 C. Plants were grown under short days (9-hr photoperiod) or long days (9-hr photoperiod plus a 4-hr night interruption) within each environment. The relationship or difference (DIF) between DT and NT (DT - NT) influenced Fuchsia stem elongation and leaf expansion more than absolute DT and NT between 10 and 24 C. Both internode length and leaf area increased linearly as DIF increased from -14 to +14 C with DT and NT between 10 and 24 C. Internode length increased an average of 0.071 cm and leaf area increased an average of 400 cm^2 per leaf per 1 C increase in DIF. DT or NT above 24 C reduced stem elongation and leaf expansion, regardless of DIF. The response of stem elongation and leaf expansion to DIF was greater on a percent basis when plants were grown under short days and long days, respectively. On an absolute basis, both internode length and leaf area were greater on long day grown plants. Branching increased as average daily temperature decreased from 30 to 10 C. Photoperiod did not affect branching.

Introduction

Plant morphology is thermomorphogenic in many plant species (Erwin et al., 1989; Erwin, 1990a). The effects of temperature on plant growth have historically been ascribed solely to absolute temperature (Went, 1952). Recent experimentation showed that morphological development of some plants is influenced primarily by the relationship between day (DT) and night temperature (NT), i.e. independent of absolute temperature within a limited temperature range (Erwin et al., 1989; Moe and Heins, 1990). For instance, Lilium longiflorum stem elongation and leaf orientation were best described by the difference (DIF) between DT and NT (DT - NT) rather than absolute DT and NT between 10 and 30 C (Erwin et al., 1989; Erwin and Heins, 1990b). As DT increased relative to NT, i.e. as DIF increased, Lilium stem elongation increased and leaf orientation became more upright. Similarly, Streptocarpus nobilis, Xanthium stromium, Lycopersicum esculentum, Zea maize, Salvia splendens, Impatiens walleriana, Nephrolepis exaltata (Erwin, 1990a; Erwin et al., 1990c), Euphorbia pulcherrima (Berghage, 1989), Dendranthema (Karlsson et al., 1989), and Campanula isophylla (Moe and Heins, 1990) stem elongation were best described by DIF, and increased as DIF increased within the 10 - 30 C temperature range.

Correlative evidence suggests that thermomorphogenic responses may be mediated by or interact with phytochrome to elicit growth responses (Erwin et al., 1989; Erwin, 1990a;

Moe and Heins, 1990). Plants grown under positive DIF environments (higher DT than NT) appear morphologically similar to plants irradiated with lighting consisting of a low red (660 nm):far-red (720 nm) ratio; plants have long internodes and an upright leaf orientation. Conversely, plants grown under negative DIF environments (higher NT than DT) appear similar to plants irradiated with lighting with a high red:far-red ratio; plants have short internodes and a horizontal leaf orientation.

In addition to indirect evidence for phytochrome involvement, there is an interaction between DIF and light quality (Erwin, 1990a; Moe and Heins, 1990). Incandescent lighting (low R:FR ratio) during the night period can overcome inhibition of stem elongation by a negative DIF environment in Campanula isophylla (Moe and Heins, 1990). In contrast, fluorescent lighting (high R:FR ratio) during the night period enhanced the inhibition of Campanula elongation which resulted from growing plants in a negative DIF environment. An interaction between light quality and DIF suggests that phytochrome is involved in perceiving and/or interacting with DIF to affect plant growth.

An understanding of how photoperiod and DIF interact to affect plant stem elongation may result in alternative methods of plant height control in controlled environments which utilize both light and temperature to control plant growth. The objective of the research conducted in this study

was to determine if DIF and photoperiod extension through night interruption lighting interact to affect plant morphology. Fuchsia was chosen for these studies because Fuchsia exhibits a strong stem elongation response to DT and NT (Tageras, 1979), and the effect of photoperiod on Fuchsia stem elongation has been studied extensively (Vince-Prue, 1977).

Materials And Methods

1988 Experiment: Fuchsia x hybrida 'Dollar Princess' (fuchsia) rooted cuttings were planted in 12.7 cm (volume = 390 cm^3) plastic pots on 2 Jan., 1988, in a soilless medium consisting of equal parts of sphagnum peat, perlite, and vermiculite. Plants were grown for 2 weeks in a glasshouse under natural photoperiodic conditions and maintained at 20 $\pm$ 2 C air temperature. Plants were then selected for uniformity based on leaf number, plant height, and lateral shoot number, and moved to glasshouses maintained at 12, 16, 20, and 24 C. Half of the plants within each glasshouse, 24 plants, were grown under short days (SD) which consisted of a 9 hour photoperiod. The other half of the plants received a long day treatment (LD) which consisted of a 9-hr photoperiod plus night interruption lighting from 2200 to 0200 hr delivered with incandescent lamps at an irradiance of 2 umol m^{-2} s^{-1}.

Plants were moved among the 4 glasshouses at 0800 and 1700 hr each day to yield a total of 16 DT/NT environments

within each photoperiod. Each environmental treatment contained 6 samples. Movement of plants required 15 min. An opaque curtain was pulled over the plants at 1715 hr after they were moved at 1700 hr and was retracted at 0800 to provide a photoperiod paralleling the thermoperiod. Light pollution between LD and SD plants within a glasshouse section was eliminated by pulling an opaque curtain between plants at 1715 hr and retracting the curtain at 0800 hr. The uppermost unfolded leaf pair on each plant was marked with black ink to identify the developmental stage of each plant when the experiment was initiated.

Glasshouse temperatures were controlled using a glasshouse climate control computer and monitored by a datalogger using iron/constantan thermocouples. Actual glasshouse section temperatures were determined by thermocouple readings taken every 10 sec by a datalogger which then calculated mean glasshouse temperatures every 2-hr. Average DT and NT were calculated for each environmental treatment based on bihourly temperature means and the length of time which plants were grown within an environment. Average DT and NT did not vary by more than 2 C from the temperature setpoints over the course of the experiment (Table 1). All plants were within 2 m of thermocouples during the experiment Treatments are described by treatment setpoints throughout the paper. Actual temperatures were used in regression analysis.

Internode length, leaf length and width, and lateral shoot number were collected at anthesis on plants grown under LD, and after 78 days on plants grown under SD. Internode length was collected from the second internode above the marked leaf pair. Leaf length and width were collected from a leaf at the base of the second internode above the marked leaf pair. Since leaves were elliptic in shape, leaf area was estimated by the formula for the surface area of a standard ellipse: leaf area = (leaf length/2) * (leaf width/2) * 3.718.

1989 Experiment: The 1988 experiment was replicated with the following changes:

1) Temperature treatments were started on 22 Oct., 1988.
2) Terminal shoots were removed twice prior to the start of treatments.
3) Glasshouse sections were maintained at 10, 15, 20, and 25 C.
4) Three addition temperature environments were added; 10 C DT/30 C NT, 30 DT/10 C NT, and constant 30 C.
5) Data were collected after 74 days on plants grown under SD.

Data were analyzed for both experiments by analysis of variance (ANOVA) using a 4 x 4 x 2 factorial model with DT,

NT, and photoperiod as the main factors. Interaction terms could not be evaluated through ANOVA as each temperature treatment constituted a single replicate. The relative importance of individual environmental parameters in affecting morphological development was evaluated through multilinear regression analysis. Selection of functions was based on r^2, Mallow's C_p (Draper and Smith, 1981), significance of parameters, and visual inspection of the fit of the regression function with the data.

The functional relationships between DIF and internode length and leaf area were best described with linear regression analysis. Interactions between DIF and photoperiod were evaluated by analyzing differences between slopes of the regression functions. Statistical analysis of differences between slopes and elevations among regression functions followed the procedure reported by Snedecor and Cochran (1967).

Results

I. Internode Length: Fuchsia internode length was affected by photoperiod and temperature. Internode length, averaged over all treatments, was 142% greater on plants grown under LD than plants grown under SD (Table 2). Absolute differences ranged from 0 to 3.4 cm.

Internode length increased as DT increased and/or NT decreased (Table 2) but was best described by DIF (Figure 1). Internode length increased as DIF increased when absolute

temperatures ranged from 10 to 26 C (Figure 1). Internode length increased from 2.5 to 6.2 cm as DIF increased from -15 to 16 C on LD grown plants in the 1989 experiment. Increasing DT above 24 C reduced fuchsia internode length, regardless of DIF (Table 2). For example, internode length decreased from 6.2 to 4.1 cm as DT increased from 24 to 30 C with a 10 C NT on LD grown plants in the 1989 experiment even though DIF increased from 15 to 20 C.

Slopes of regression functions (b_1) representing the effect of DIF on internode length when temperatures ranged from 10 and 24 C were not significantly different between the 1988 and 1989 experiments (Table 3). Therefore, data from each photoperiod were combined across years by normalizing data based on the difference in elevation (b_0) between the functions (Figure 2). This was done by adding 0.266 (1.861-1.595) to 1988 SD means and -0.447 (4.281-4.728) to 1988 LD means.

DIF and photoperiod interacted to affect stem elongation as shown by a significant difference between slopes (b_1) of the functions in Figure 2, i.e. between LD and SD plants (Table 3). Plants grown under SD showed a lesser response to DIF on an absolute basis but a greater response to DIF on a percent basis than plants grown under LD. For instance, internode length increased 326% and 224% as DIF increased from -14 to 14°C when plants were grown under SD and LD, respectively.

II. Leaf Size: Leaf size was affected by photoperiod and temperature. Leaf area, averaged over all treatments, was 22% greater on plants grown under LD than plants grown under SD (Table 4). Absolute differences ranged from 0.1 to 7.0 cm^2 per leaf.

As with stem elongation, leaf area increased as DT increased and/or NT decreased (Table 4) but was best described by DIF (Figure 3). Leaf area increased from 7.3 to 15.4 cm^2 (+111%) as DIF increased from -15 to 16 C on LD grown plants in the 1989 experiment. As with stem elongation, DT above 24 C reduced leaf expansion (Table 4). Increasing DT from 24 to 30 C decreased leaf area from 15.4 to 7.9 cm^2 (-49%) on LD grown plants even though DIF increased from 14 to 20 C.

Slopes of regression functions (b_1) representing the response of leaf expansion to DIF were not significantly different between 1988 and 1989 within photoperiod treatments (Table 5). Therefore, data from each photoperiod were combined across years by normalizing data based on differences in elevation (b_0) between functions (Figure 3). This was done by adding 0.256 (12.949-10.390) to 1989 SD means and -0.447 (4.281-4.728) to 1988 LD means.

Slopes of functions representing the response of leaf expansion to DIF between LD and SD grown plants were significantly different indicating an interaction between DIF and photoperiod (Table 4). In contrast to stem elongation, plants grown under LD showed a greater response to DIF on a

percent basis (Table 4, Figure 3). Leaf area increased 249% and 289% as DIF increased from -15 to 16 C on SD and LD grown plants, respectively.

III. Branching:

Lateral shoot development was primarily influenced by ADT. Lateral branch number per plant decreased as ADT increased from 12 to 24 C, regardless of photoperiod (Table 6, Figure 4). For instance, the number of lateral branches per plant decreased from 11.5 to 4.5 branches (-61%) as ADT increased from 12 to 24 C on LD grown plants in the 1988 experiment. Photoperiod had no significant effect on lateral branching.

Discussion

Stem elongation on reproductive (LD) plants was greater than on vegetative (SD) plants. This was not unexpected as fuchsia internode elongation is affected by 3 photoperiod related factors: 1) fuchsia is a long day plant and stem elongation increases after flower induction (Wilkins, 1985), 2) internode length increases as photoperiod increases (Wilkins, 1985), and 3) internode length increases as the red/far red content of the last light exposure prior to darkness decreases (Vince-Prue, 1977). Irradiating plants with a night interruption (NI) of incandescent light (low R:FR), as in this experiment, increased stem elongation

through one or more of these three factors. Internode length was a function of the relationship between DT and NT within a limited temperature range. Internode length increased as DT increased and NT decreased as has been reported previously on other plant species (Tageras, 1979; Karlsson et al., 1989; Erwin et. al., 1989; Berghage et. al., 1989; Moe and Heins, 1990). The effect of temperature on stem elongation could be described more comprehensively with the term DIF than by absolute DT or NT as previously shown on Lilium (Erwin et. al., 1989; Erwin et. al., 1990) and Campanula isophylla (Moe and Heins, 1990). While original research by Went (1957) suggested that plant stem elongation was primarily influenced by DT, our measurements of internode lengths from photographic plates of Pisum sativum plants in his original article showed internode length was indeed strongly influenced by DIF.

The transduction pathway for the effects of DIF on stem elongation is believed to involve gibberellin (GA) synthesis (Zieslin and Tsujita, 1988, Erwin et al., 1989; Moe, personal observation). Application of gibberellins (GA_{4+7}) to Lilium bulbs prior to planting overcame subsequent inhibition of stem elongation by a negative DIF environment (Zieslin and Tsujita, 1988). Similarly, Moe and Heins (1990) showed that spray applications of GA_3 overcame inhibition of Campanula isophylla stem elongation when plants were grown in a negative DIF environment. In contrast, application of a GA synthesis

inhibitor, ancymidol (alpha-cyclopropyl-alpha-(4-methoxyphenyl)-5-pyrimidinemethanol), resulted in a greater percent decrease in stem elongation of positive DIF grown plants than negative DIF grown Lilium plants (Erwin et al, 1989). An interaction between DIF and GA action on stem elongation is, therefore, apparent.

Both gibberellins (Jones and Zeevaart, 1980; Pharis and King, 1985) and DIF (Erwin, 1990a) affect sex expression in the dioecious family Cucurbitaceae. Application of gibberellins to Agrostemma causes maleness (Jones and Zeevaart, 1980; Pharis and King, 1985). In contrast, application of GA synthesis inhibitors induces femaleness in muskmelon (Halevy and Rudich, 1967; Pharis and King, 1985). Plants grown in a positive DIF environment have more male flowers than female flowers. Conversely, plants grown under a 0 or a negative DIF environment have equal or more female flowers than male flowers (Erwin, 1990a). Although other factors can influence sex expression in Cucurbitaceae, such as ethylene, these results combined with previous data provide additional evidence that a positive DIF environment may promote GA synthesis and/or that a 0 or negative DIF environment may reduce GA synthesis. DIF, therefore, appears to influence the endogenous levels of biologically active gibberellins. Alternatively, a 0 or negative DIF environment may stimulate synthesis of an elongation inhibitor or promote GA degradation.

DIF and photoperiod interacted to affect stem elongation in this study where night interruption lighting with incandescent lamps was used. The question arises as to whether the interaction between temperature and photoperiod is due to a response to light quality or light duration. Berghage (1989, personal observation) showed that increasing photoperiod via a day extension treatment using white light also resulted in a photoperiod x DIF interaction. Therefore, a DIF x photoperiod interaction is present independent of a light quality effect. The data presented in the current research and that of Berghage (1989, personal observation) both showed a greater response of stem elongation to DIF on a percent basis on SD grown plants than LD grown plants.

DIF strongly influenced leaf expansion. The effect of DIF on fuchsia leaf expansion contrasts previous research on Lilium longiflorum where leaf expansion was a function of NT only (Erwin et. al., 1989). Earlier work by Dale (1964) suggested that Phaseolus vulgaris leaf expansion was greatest when DT and NT were constant, i.e. a 0°C DIF. Our reexamination of Dale's data (1964) showed this conclusion was based on a number of treatments which contained either a 30 C DT or NT. Based on Dale's own data and conclusion's (1964), leaf expansion was reduced at 30 C. Therefore, conclusions relating temperature effects and leaf expansion based on 30 C temperature treatments may be misleading. If Dale's data (1964) from environments not containing a 30 C DT and/or NT

are eliminated, leaf area increased as DIF increased. The greatest leaf area occurred in the environment with the highest DIF which did not contain a 30 DT or NT (20 C DT/10 C NT). In contrast, recent research by Erwin and Strefeler (1990, personal observation) showed that Cucumis leaf expansion was greater when plant were grown with constant temperatures versus fluctuating temperatures. Greater leaf expansion in a positive DIF environment or a constant temperature environment is probably species dependent.

Leaf expansion is often influenced by ADT as has been shown in Phaseolus (Dale, 1964), Cucumis (Milthorpe, 1959), and Euphorbia (Berghage, 1989). No response of fuchsia leaf expansion to ADT was observed in the current study.

Branching in Fuchsia decreased as ADT increased. A decrease in lateral branching as ADT increased had also been reported on Petunia (Kaczperski et. al., 1989) and Dianthus (Moe, 1983).

Night interruption lighting using incandescent lighting has been shown to reduce lateral branching on Dendranthema (Heins and Wilkins, 1979a), Campanula (Moe and Heins, 1990), and Dianthus (Heins and Wilkins, 1979b) when compared to plants which received no NI or received a day extension treatment. Heins and Wilkins (1979a, 1979b) suggested that the reduction in lateral shoot number was due to inhibition of lateral shoot breaking by far red light and/or induction of flowering, as was the case with Dianthus. Flower induction of

fuchsia did not significantly affect branching in the current study.

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Table 1. Temperature setpoints and actual average day (DT) and night (NT) temperatures (DT/NT) for all environmental treatments for 1988 and 1989.

NT Setpoint (°C)	DT Setpoint (°C) 12	16	20	24
	1988 Actual Temperature (DT/NT)			
12	14/12	18/12	21/12	25/12
16	14/17	17/17	21/16	25/17
20	14/20	17/20	21/20	25/20
24	14/24	17/24	21/24	26/24

	10	15	20	25	30
	1989 Actual Temperatures				
10	11/10	15/10	19/10	24/10	30/10
15	11/15	15/15	19/15	24/15	-
20	11/20	15/20	19/20	24/20	-
25	11/25	15/25	19/25	24/25	-
30	11/31	-	-	-	30/31

Table 2. The effect of DT, NT and photoperiod on *Fuchsia x hybrida* 'Dollar Princess' internode length at anthesis. LD were delivered as a 9-hr photoperiod plus a 4-hr night interruption using incandescent lamps at an irradiance of 10 umol s^{-1} m^{-2}. SD were delivered as a 9-hr photoperiod only.

NT (°C) Treatment	DT (°C) Treatment				
	10	15	20	25	30
10					
LD	- [z]	4.8	5.6	6.2	4.1
SD	1.0	1.4	2.2	3.4	2.9
15					
LD	3.3	4.7	5.1	5.2	-
SD	0.9	1.4	2.3	3.2	-
20					
LD	3.3	3.7	4.3	4.7	-
SD	0.6	1.1	2.0	2.7	-
25					
LD	2.5	2.9	3.5	3.8	-
SD	0.9	1.3	1.8	2.6	-
30					
LD	1.6	-	-	-	1.8
SD	1.0	-	-	-	1.9

Table 2 - continued

Day Temperature	*** [y]
Linear	***
Quadratic	n.s.
Cubic	n.s.
Night Temperature	***
Linear	***
Quadratic	n.s.
Cubic	n.s.
Photoperiod	***

[z] Numerals represent treatment means from 1989 experiment.

[y] Significance of both 1988 and 1989 experiments combined at P = .001 (***), not significant (n.s.).

Table 3. Regression coefficients calculated to predict internode length of *Fuchsia x hybrida* 'Dollar Princess' plants from experiments conducted during 1988 and 1989 studying the effect of DT, NT, and photoperiod on plant morphology. Comparison of slopes and intercepts were evaluated using the technique outlined by Snedicor and Cochran (1967).

	Raw Data					
	SD		LD		Normalized Data Regression	
Coefficients	88	89	88	89	SD	LD
b_0	1.595	1.861	4.728	4.281	1.871	4.727
b_1	0.067	0.073	0.124	0.132	0.071	0.129
r^2	0.884	0.572	0.696	0.964	0.644	0.867

Comparison Of Slopes

Raw data 88 SD versus 89 SD	F = 1.5	(df=1,31)	n.s.
Raw data 88 LD versus 89 LD	F = 3.6	(df=1,30)	n.s.
Normalized data SD versus LD	F = 36.9	(df=1,61)	***

Comparison Of Intercepts

Raw data 88 SD versus 89 SD	F = 9.2	(df=1,33)	***
Raw data 88 LD versus 89 LD	F = 12.3	(df=1,32)	***
Normalized data SD versus LD	F = 441.8	(df=1,65)	***

Table 4. The effect of DT, NT and photoperiod on *Fuchsia x hybrida* 'Dollar Princess' single leaf area at anthesis. LD were delivered as a 9 hour photoperiod plus a 4 hour night interruption delivered using incandescent lamps at an irradiance of 2 umol s^{-1} m^{-2}. SD were delivered as a 9 hour photoperiod only. Leaf area was calculated by measuring leaf length and width and calculating the area of an ellipse, i.e. leaf area = (width/2) * (length/2) * 3.78.

		DT (°C) Treatment				
NT (°C) Treatment		10	15	20	25	30
10						
	LD	- [z]	18.4	16.6	15.4	7.9
	SD	8.9	11.4	10.9	12.1	7.1
15						
	LD	10.3	13.5	18.5	15.5	-
	SD	8.8	9.4	14.8	12.8	-
20						
	LD	7.4	10.1	13.7	12.7	-
	SD	6.8	9.4	12.0	10.8	-
25						
	LD	7.3	8.5	10.0	10.8	-
	SD	5.9	7.4	8.7	9.0	-
30						
	LD	4.3	-	-	-	3.4
	SD	3.9	-	-	-	3.5

Day Temperature	*** [y]
Linear	***
Quadratic	n.s.

Table 4 - continued

	Cubic	n.s.
Night Temperature		***
	Linear	***
	Quadratic	n.s.
	Cubic	n.s.
Photoperiod		***

[z] Missing treatment mean. Numerals represent treatment means from 1989 experiment.

[y] Significance of both 1988 and 1989 experiments combined at P = .001 (***), not significant (n.s.).

Table 5. Regression coefficients calculated to predict single leaf area of *Fuchsia x hybrida* 'Dollar Princess' plants from experiments conducted during 1988 and 1989 studying the effect of DT, NT, and photoperiod on *Fuchsia* morphology. Comparison of slopes and intercepts were evaluated using the technique outlined by Snedicor and Cochran (1967).

	Raw Data					
	SD		LD		Normalized Data Regression	
Coefficients	88	89	88	89	SD	LD
b_o	12.95	10.39	14.54	12.68	13.10	14.99
b_1	0.48	0.33	0.58	0.42	0.40	0.52
r^2	0.62	0.75	0.76	0.80	0.66	0.81

Comparison Of Slopes

Raw data 88 SD versus 89 SD	F = 3.6	(df=1,31)	n.s.
Raw data 88 LD versus 89 LD	F = 2.7	(df=1,30)	n.s.
Normalized data SD versus LD	F = 121.5	(df = 1,61)	***

Comparison Of Intercepts

Raw data 88 SD versus 89 SD	F = 20.9	(df=1,31)	***
Raw data 88 LD versus 89 LD	F = 6.6	(df=1,30)	***
Normalized data SD versus LD	F = 12.43	(df = 1,61)	***

Table 6. The effect of DT, NT and photoperiod on *Fuchsia x hybrida* 'Dollar Princess' branch number at anthesis. LD were delivered as a 9-hr photoperiod plus a 4-hr night interruption delivered using incandescent lamps. SD were delivered as a 9-hr photoperiod only. A branch was defined as any axillary break which has 2 or more nodes.

NT (°C) Treatment	DT (°C) Treatment			
	12	16	20	24
12				
LD	11.5 [z]	9.0	8.0	6.8
SD	12.8	10.3	10.2	8.0
16				
LD	8.8	7.2	6.2	6.0
SD	9.0	9.2	9.2	7.0
20				
LD	9.0	8.3	6.2	5.7
SD	7.8	6.0	6.6	5.8
24				
LD	6.2	5.8	6.0	4.5
SD	5.8	7.8	7.2	6.6

Day Temperature	*** [y]
Night Temperature	***
Photoperiod	n.s.

[z] Numerals represent treatment means from 1989 experiment.

Table 6 - continued

[y] Significance of both 1988 and 1989 experiments combined at P = .001 (***), not significant (n.s.).

Figure 1. The effect of the difference between DT and NT (DT - NT) on Fuchsia x hybrida 'Dollar Princess' internode length on plants grown during the 1989 experiment. Plants were grown under long day conditions, i.e. a 9-hr photoperiod plus a 4-hr night interruption using incandescent lighting at an irradiance of 2 mol m^{-2} s^{-1}.

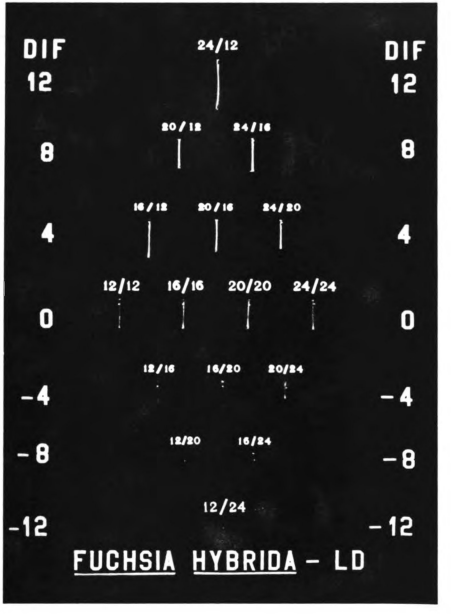

DIF
12
8
4
0
-4
-8
-12
DIF
12
8
4
0
-4
-8
-12
24/12
20/12
24/16
16/12
20/16
24/20
12/12
16/16
20/20
24/24
12/16
16/20
20/24
12/20
16/24
12/24
FUCHSIA HYBRIDA - LD

Figure 2. The effect of the difference between DT and NT (DT-NT) on Fuchsia x hybrida 'Dollar Princess' internode length on plants grown under LD (9-hr photoperiod plus 4-hour night interruption using incandescent lamps at an irradiance of 2 umol m^{-2} s^{-1}) and SD (9-hr photoperiod). Data were normalized across 1988 and 1989 experiments within photoperiod treatments. The regression function calculated from LD data was Internode Length (cm) = 4.727 + (0.129 * X) (r^2 = 0.87). The regression calculated from SD data was Internode Length (cm) = 1.871 + (0.071 * X) (r^2 = 0.64).

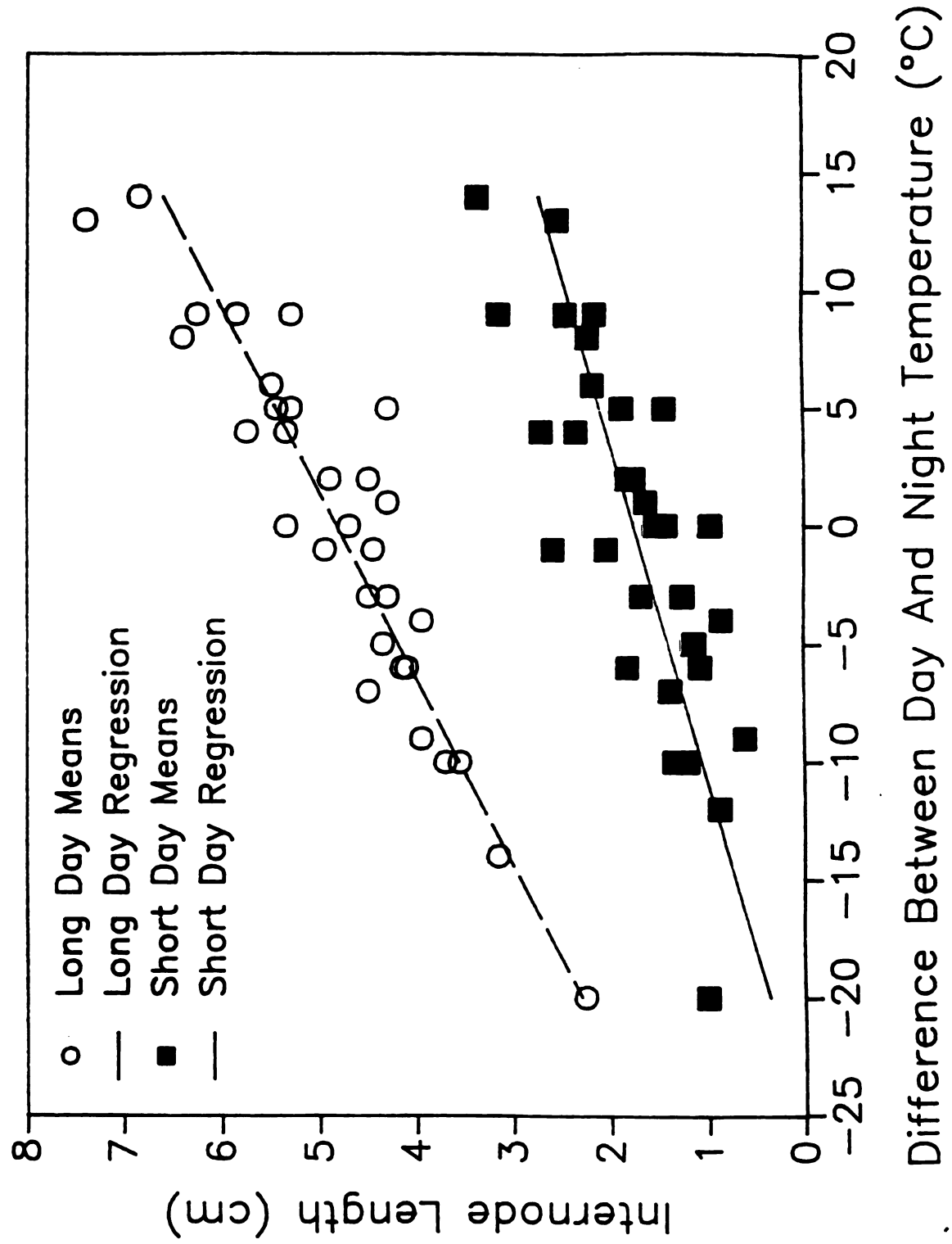

Internode Length (cm)
0
1
2
3
4
5
6
7
8
−25
−20
−15
−10
−5
0
5
10
15
20
Difference Between Day And Night Temperature (°C)
Long Day Means
Long Day Regression
Short Day Means
Short Day Regression

Figure 3. The effect of the difference between DT and NT and photoperiod on Fuchsia x hybrida 'Dollar Princess' leaf area on plants grown under LD (9-hr photoperiod plus 4-hr night interruption using incandescent lamps at an irradiance of 2 umol m^{-2} s^{-1}) and SD (9-hr photoperiod). Data were normalized across time within each photoperiod. The regression function calculated from LD data was Leaf area (cm^2) = 14.99 + (0.52 * X) (r^2 = 0.81). The regression function calculated from SD data was Leaf area (cm^2) = 13.10 + (0.40 * X) (r^2 = 0.66).

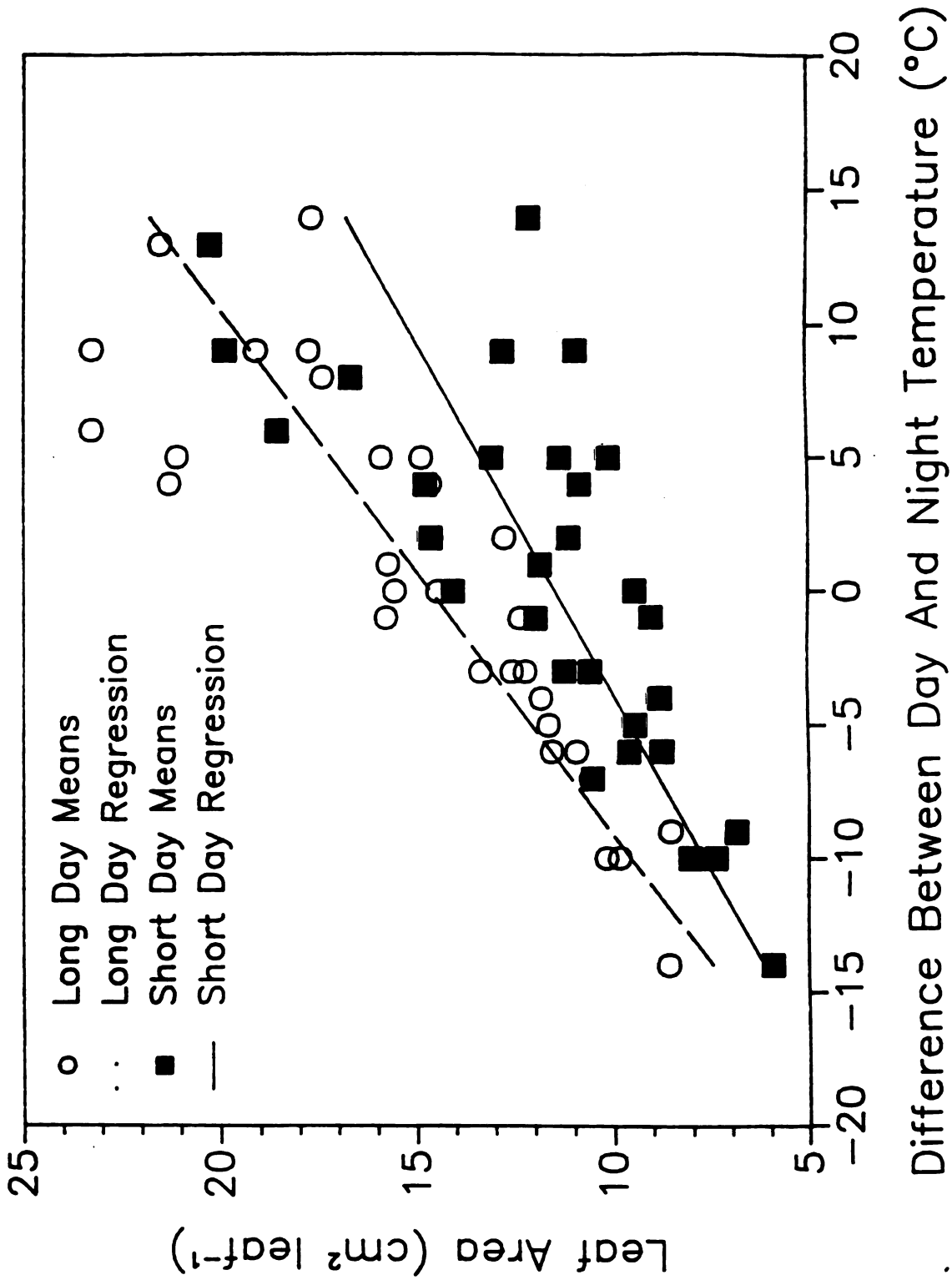
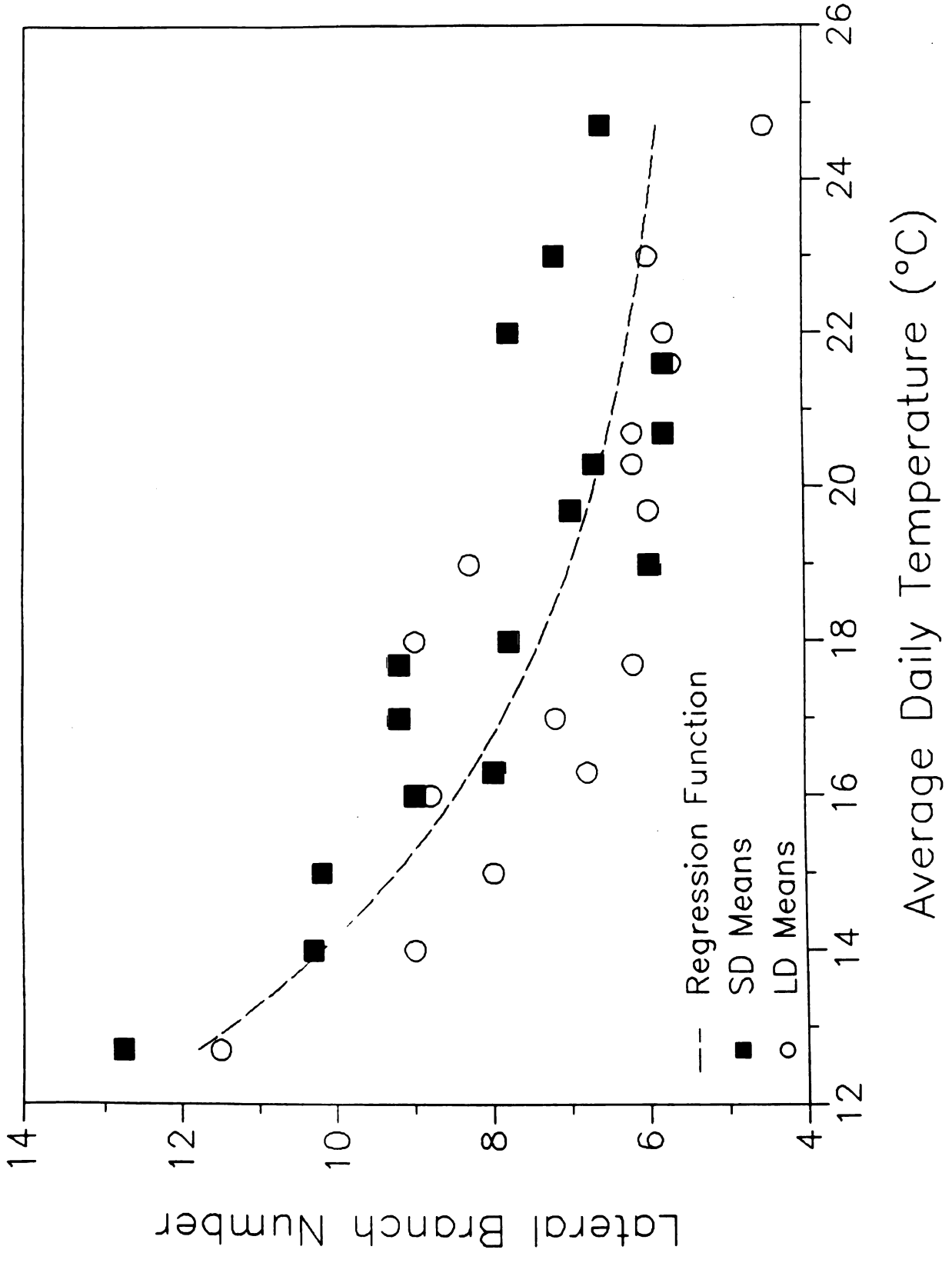

Leaf Area (cm² leaf⁻¹)
25
20
15
10
5
−20
−15
−10
−5
0
5
10
15
20
Difference Between Day And Night Temperature (°C)
Long Day Means
Long Day Regression
Short Day Means
Short Day Regression

Figure 4. The effect of ADT and photoperiod on Fuchsia x hybrida 'Dollar Princess' branch number at anthesis on plants grown under LD (9-hr photoperiod plus 4-hr night interruption using incandescent lamps at an irradiance of 2 umol s^{-1} m^{-2}) or after 78 days on plants grown under SD (9-hr photoperiod). Only data from the 1988 experiment is presented. The regression function calculated from the data is the exponential function Branch Number = 106.28 * EXP(-.22188 * X) + 5.43 (r^2 = 0.74).


Lateral Branch Number
14
12
10
8
6
4
12
14
16
18
20
22
24
26
Average Daily Temperature (°C)
Regression Function
SD Means
LD Means

Section IV.

Differential Sensitivity Of Plant Stem Elongation To Temperature Fluctuations During The Day

Differential Sensitivity Of Plant Stem Elongation To Temperature Fluctuations During The Day

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Abstract

Plant stem elongation is sensitive to temperature fluctuations during the day. *Lilium longiflorum* cv Nellie White, *Salvia splendens* cv Red Hot Sally, and *Impatiens walleriana* cv Blush were grown at constant 20 C. Each of the above plant species received either a 15 C or 25 C temperature pulse at different times and for varying durations during the day or the beginning or end of the night period. *Lilium* internode length was significantly reduced when plants received a 15 C pulse during the first 2 or 4 hr of the light period. *Lilium* internode length was also significantly reduced if plants received a 25 C pulse during the last 2 hr of the dark period. *Impatiens* and *Salvia* internode lengths were not significantly reduced by a cool temperature pulse during the day. However, *Impatiens* and *Salvia* internode elongation increased if plants received a warm temperature pulse during the day. Specifically, the earlier during the day that plants received a warm temperature pulse, the greater the stimulation of stem elongation.

Introduction

Research by Went (1944) showed that day (DT) and night temperature (NT) had different, but significant, effects on plant stem elongation. Specifically, stem elongation increased as DT increased and NT decreased. In contrast, Dale (1964) showed that *Phaseolus vulgaris* stem elongation was optimal when DT and NT were constant. Research by Smith and Langhans (1962) and Roh and Wilkins (1973) showed that stem elongation of *Lilium longiflorum* increased only when DT exceeded 21°C.

Recent research supports the conclusions of Went. Tageras (1979) showed that *Fuchsia x hybrida* stem elongation increased as DT increased and NT decreased. Karlsson et. al. (1989) and Berghage et. al. (1989) showed that DT and NT had similar effects on plant stem elongation of *Dendranthema grandiflora* (chrysanthemum) and *Euphorbia pulcherrima (poinsettia)*, as those seen by Tageras (1979) and Went (1944).

More recent research suggests that stem elongation may be influenced more by the relationship between DT and NT rather than absolute DT and/or NT within a limited temperature range. Research by Lecharny and Wagner (1985) suggested that *Chenopodium* stem elongation rate responded to the relationship between DT and NT. The significance of the relationship between DT and NT was confirmed by Erwin et al. (1989) on *Lilium longiflorum*. Stem elongation increased as the difference (DIF) between DT and NT (DT-NT) increased, i.e. as

DT increased relative to NT. Similar effects of DIF were found on *Fuchsia hybrida*, *Xanthium strumarium*, *Streptocarpus nobilis*, *Zea maize*, *Salvia splendens* (Erwin, personal observation), *Dendranthema grandiflora* (Karlsson et. al., 1989), *Euphorbia pulcherrima* (Berghage et al., 1989), and *Campanula isophylla* (Moe, personal communication).

In addition to DIF, average daily temperature (ADT) was also important in *Euphorbia* (Berghage 1989), and *Dendranthema* (Karlsson et al., 1989). An ADT effect on stem elongation was, however, not evident in *Fuchsia* or *Lilium* (Erwin, personal observation; Erwin et al., 1989a).

The effect of temperature on plant stem elongation is not uniform during a day or night thermoperiod. This was not unexpected since plant stem elongation is not uniform during a 24 hr period but follows a circadian rhythm (Went, 1944; Lecharny and Wagner, 1985; Erwin and Heins, 1988). Plant stem elongation is greater during the night than the day (Went, 1944; Erwin and Heins, 1988). Lecharny and Wagner (1985) showed that cool temperature pulses during the night period could rephase the circadian stem elongation rhythm. Preliminary research by Erwin et al. (1989) suggested that a cool pulse (-DIF) in temperature during the early part of the morning was more effective in inhibiting stem elongation than a cool pulse in the afternoon on *Lilium*.

The objective of the study presented in this paper was to determine the effects of temperature fluctuations during the

day on plant stem elongation. The effects of warm and cool temperature pulses immediately before and after the photoperiod were also evaluated.

Materials And Methods

Lilium longiflorum cv 'Nellie White', *Impatiens walleriana* cv 'Blush', and *Salvia splendens* cv 'Red Hot Sally' were studied in this experiment. Vernalized *Lilium longiflorum* plants in 15.2 cm plastic pots with a soil volume of 2,570 cm^3 were obtained after flower initiation, i.e. approximately 40 days after emergence. All remaining plant species were obtained as 10-day-old seedlings. All seedlings were transplanted 7 days before the initiation of the experiment into plastic containers composed of 6 individual cells per container with a medium volume of 50 cm^3 per cell 7 days before the initiation of the experiment. All plants were maintained in a glasshouse maintained at 20 C prior to the initiation of experimental treatments. Mean day and night temperatures did not vary by more than 2 C.

Plants were then placed in glasshouses maintained at 15, 20, or 25 C on 8, April, 1989. Average temperatures within the glasshouse sections did not vary by more than 2 C during a 24 hr period. Plants were moved from the 20 C glasshouse into either the 15 or 25 C glasshouses at different times and for different durations as shown below:

Experimental Treatments

0700-0900 hr
0900-1100 hr
1100-1300 hr
1300-1500 hr
1500-1700 hr
1700-1900 hr
0900-1300 hr
1300-1700 hr
constant 20°C

Transfer of plants among treatments required 10 min. An opaque curtain was pulled over the plants at 1710 hr after they were moved and was retracted at 0900 to provide an 8 hr 10 min photoperiod. The uppermost leaf pair on each plant was marked with a black ink dot to identify the developmental stage when each plant was first exposed to experimental treatments.

Greenhouse temperatures were controlled using a greenhouse climate control computer and monitored by a datalogger using iron/constantan thermocouples. Temperatures in each greenhouse section and light intensity were measured every 10 sec by the datalogger and were averaged to provide mean temperatures every 2 hr. All plants were within 2 m of temperatures sensors during the experiment.

Internode length was measured on the second internode above the marked leaf pair on *Salvia* and *Impatiens* after 30 days. Internode length data on *Lilium* were collected at anthesis. *Lilium* internode length was calculated by dividing the increase in stem length from the beginning of the experiment by the number of stem leaves which had unfolded

above the marked leaf.

Results And Discussion

The sensitivity of *Lilium* stem elongation to temperature fluctuations varied during the day (Figure 1). A cool temperature pulse (from 20 to 15 C) during the first 2 hr of the morning significantly reduced internode length from .27 to .20 cm. In addition, a 4 hr drop in temperature during the morning or the afternoon also significantly reduced internode length in *Lilium* (Figure 1). There was no significant difference in internode lengths of plants which had received cool temperatures from , 0900-1100, 0900-1300, and 1300-1700 hr and plants which received cool temperatures from 0900-1700 hr, i.e. all day.

The sensitivity of *Salvia splendens* and *Impatiens walleriana* stem elongation to a cool temperature pulse was similar to that seen in *Lilium* (Tables 1 and 2), i.e. stem elongation was reduced by cool temperatures early in the morning. However, the variation in internode lengths was so great that a significance between internode lengths from the cool temperature treatments and the constant 20 C could not be determined.

The sensitivity of a plant to a warm temperature pulse also varied during the day (Figures 1 and 2). *Lilium* internode length significantly increased when plants received a 4 hr increase in temperature from 20 to 25 C during the

morning or the afternoon (Figure 1). For example, *Lilium* internode length increased from .27 to .34 and .33 cm when plants received a warm temperature pulse from 0900-1300 or 1300-1700 hr, respectively (Figure 1). In contrast, stem elongation was significantly inhibited by a warm temperature pulse during the last 2 hr of the night (Figure 1).

As with a cool temperature pulse *Salvia* and *Impatiens* internode lengths varied to such an extent that significance of treatments was not determined using mean separation techniques. However, a significant trend was determined using linear regression analysis. Stimulation of stem elongation by a warm temperature pulse decreased as the temperature pulse occurred later during the day (Figure 2).

Interestingly, *Impatiens* internode length significantly increased when plants received a warm temperature pulse during the beginning of the night period. For example, mean internode length increased from 1.95 to 3.55 cm when plants received a warm pulse from 1700-1900 hr (Table 3).

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Table 1. The effect of warm and cool temperature fluctuations at different times of the day on *Salvia splendens* cv Red Hot Sally internode length (cm). All plants were grown at 20°C. Plants were moved to either 25°C or 15°C at the prescribed times. The photoperiod was initiated at 0900 and was terminated at 1700 hr.

Time Of Exposure	15°C	25°C
0700 to 0900 hr	2.17 ± 0.57 [z]	1.85 ± 0.13
0900 to 1100 hr	1.72 ± 0.18	2.45 ± 0.71
1100 to 1300 hr	1.67 ± 0.15	2.65 ± 0.74
1300 to 1500 hr	2.30 ± 0.72	2.22 ± 0.21
1500 to 1700 hr	1.95 ± 0.30	1.97 ± 0.21
1700 to 1900 hr	1.52 ± 0.32	1.72 ± 0.32
0900 to 1300 hr	1.43 ± 0.23	2.50 ± 0.16
1300 to 1700 hr	1.80 ± 0.47	2.52 ± 0.29
constant 20	2.10 ± 0.20	
0900 to 1700 hr	1.30 ± 0.00	3.60 ± 0.83

[z] Numerals represent treatment means and the standard deviation about the mean.

Table 2. The effect of warm and cool temperature fluctuations at different times of the day on *Impatiens walleriana* cv Blush internode length (cm). All plants were grown at 20°C. Plants were moved to either 25°C or 15°C at the prescribed times. The photoperiod was initiated at 0900 and was terminated at 1700 hr.

Time Of Exposure	15°C	25°C
0700 to 0900 hr	2.58 ± 0.59 [z]	1.78 ± 0.30
0900 to 1100 hr	1.97 ± 0.62	2.78 ± 0.41
1100 to 1300 hr	1.55 ± 0.39	2.48 ± 0.66
1300 to 1500 hr	0.95 ± 0.29	2.12 ± 0.09
1500 to 1700 hr	1.65 ± 0.17	1.80 ± 0.29
1700 to 1900 hr	1.85 ± 0.24	3.55 ± 0.66
0900 to 1300 hr	1.08 ± 0.15	2.12 ± 0.47
1300 to 1700 hr	1.48 ± 0.33	2.72 ± 0.74
constant 20	1.95 ± 0.77	
0900 to 1700 hr	1.18 ± 0.38	2.53 ± 0.45

[z] Numerals represent treatment means and the standard deviation about the mean.

Figure 1. The effect of the time and duration of a cool or warm temperature exposure on *Lilium longiflorum* cv Nellie White internode length. Plants were grown at constant 20 C accept when plants received the cool temperature pulse (15 C). The photoperiod was initiated at 0900 and was terminated at 1700 hr. Significance between treatment means was determined using Tukey's test for mean separation (H.S.D.). Treatment means which are above or below the lines are significantly different from plants grown at constant 20 C.

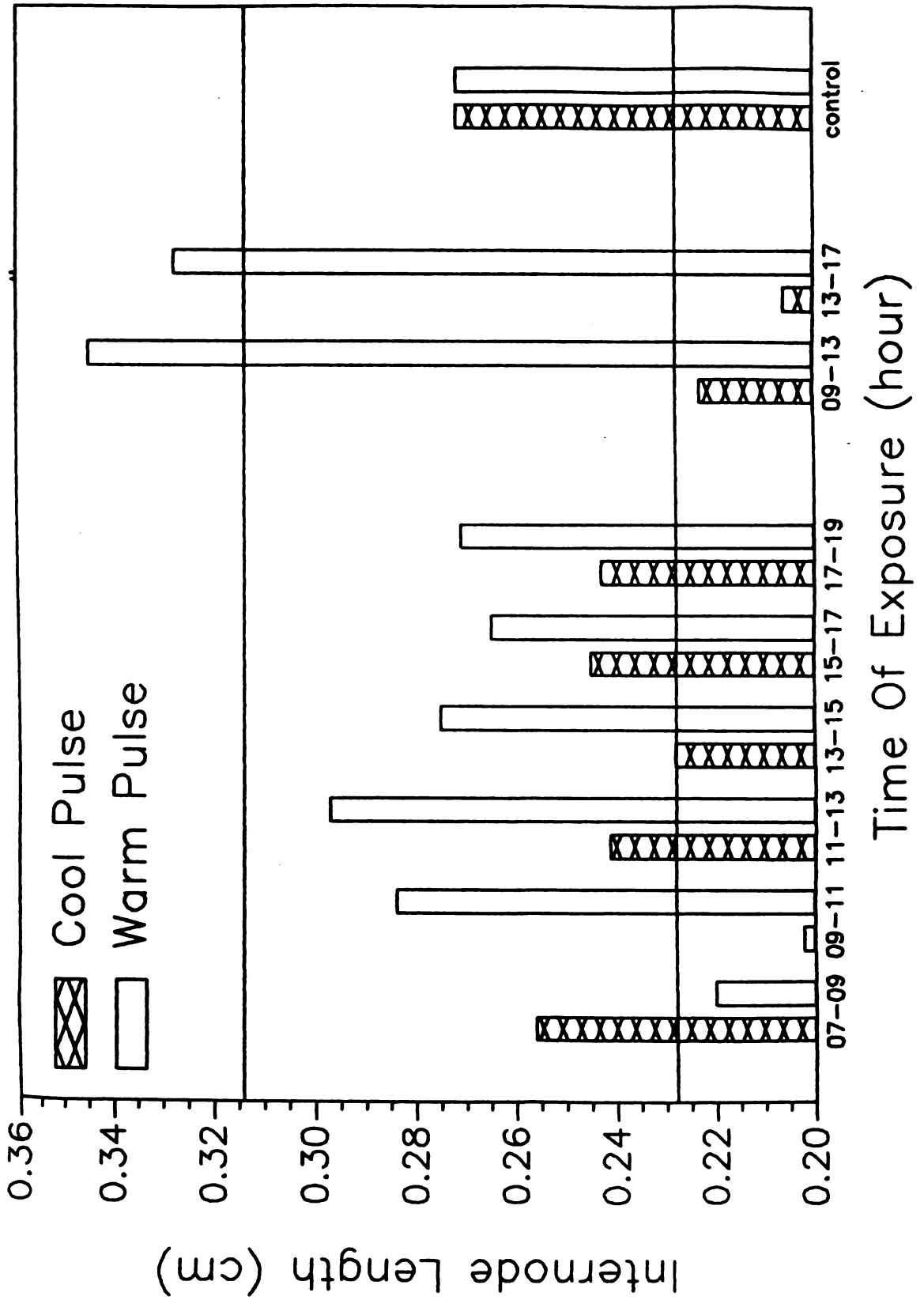
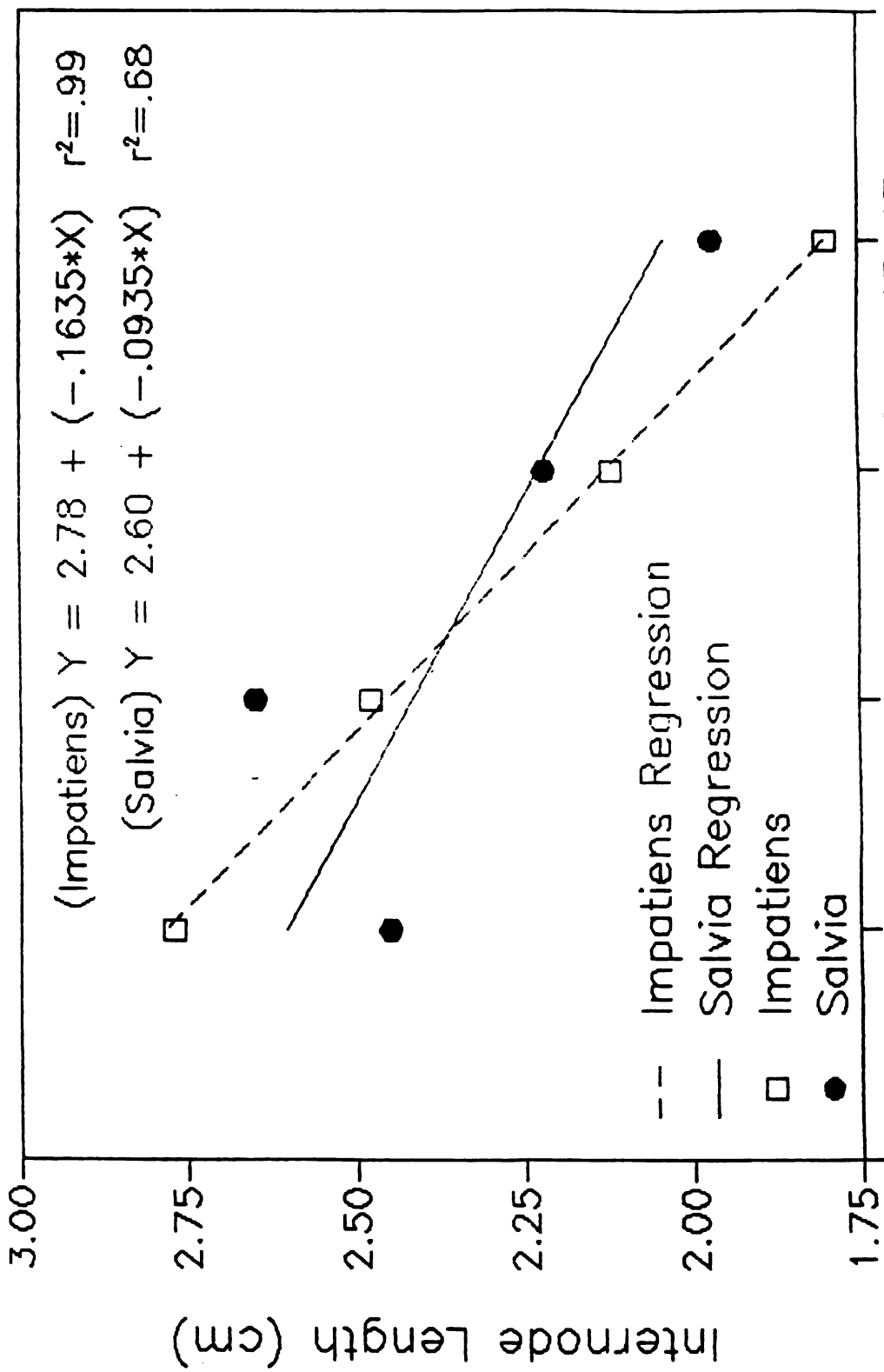

Internode Length (cm)
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
Cool Pulse
Warm Pulse
07-09
09-11
11-13
13-15
15-17
17-19
09-13
13-17
control
Time Of Exposure (hour)

Figure 2. The effect of the time and duration of a warm temperature exposure on *Salvia splendens* and *Impatiens walleriana* internode length. Plants were grown at constant 20 C except when plants received the warm temperature pulse (25 C). The photoperiod was initiated at 0900 and was terminated at 1700 hr.


(Impatiens) Y = 2.78 + (-.1635*X) r²=.99
(Salvia) Y = 2.60 + (-.0935*X) r²=.68
Impatiens Regression
Salvia Regression
Impatiens
Salvia
Internode Length (cm)
3.00
2.75
2.50
2.25
2.00
1.75
09-11
11-13
13-15
15-17
Time Of Exposure To 25°C

Section V.

Interaction Between Light Quality, Day/Night Temperature Environment And Temperature EnvironmentGrowth Regulators On *Fuchsia x hybrida* Stem Elongation

Interaction Between Light Quality, Day/Night Temperature Environment, And Growth Regulators On *Fuchsia x hybrida* Stem Elongation

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Abstract

The effect of light quality, day\night temperature environment, and growth regulators on Fuchsia x hybrida cv 'Dollar Princess' stem elongation was studied. Fuchsia stem elongation was influenced by the relationship between day and night temperature. Internode length increased as the difference (DIF) between day (DT) and night (NT) temperature (DT-NT) increased. Red lighting during the night period had no significant effect on stem elongation. Far red lighting during the night period increased Fuchsia stem elongation. Light quality interacted with DIF to affect stem elongation. The percentage increase in stem elongation from an expsoure to far red lighting during the night period decreased as DIF increased. The percentage increase in stem elongation from an application of GA_{4+7} decreased as DIF increased. In contrast, the percentage inhibition of stem elongation from an application of a gibberellin biosynthesis inhibitor (ancymidol) increased as DIF increased. The interaction between light quality, DIF and growth regulators suggests that light quality and DIF may elicit responses through affecting the concentration of endogenous gibberellins.

Introduction

Plant stem elongation is influenced by light quality (Jabben and Holmes, 1983) and temperature (Went, 1952). Stem elongation increases when plants are exposed to light high in the far red (FR) portion of the light spectra (Vince-Prue, 1977). The extent to which FR stimulates stem elongation decreases as the time of an exposure occurs later in the scotoperiod (Vince-Prue, 1977; Wilkins, 1985). Compared to FR, blue or R lighting typically reduces stem elongation when an exposure occurs during the scotoperiod (Jabben and Holmes, 1983). However, R has been shown to increase stem elongation in some species when given late in the scotoperiod with Dendranthema (Cathey, 1974) or continuously in Fuchsia (Vince-Prue, 1977).

Stimulation of stem elongation in Chenopodium album by FR during the scotoperiod is reversible by a subsequent exposure of a plant to R. In contrast, inhibition of stem elongation by R, compared to stem elongation in the dark only, is reversible by a subsequent exposure of plants to FR (Morgan and Smith, 1981; Vince-Prue, 1977). Photoreversability of a stem elongation response to R and FR is regarded as evidence for the involvement of phytochrome (Stolwijk, 1954; Downs et. al., 1957). R converts P_r to P_{fr}. FR converts P_{fr} to P_r (Borthwick et. al., 1952). Phytochrome in the P_{fr} form restricts stem elongation whereas phytochrome in the P_r form allows maximal elongation (Morgan and Smith, 1981; Smith and

Morgan, 1983).

Recent evidence suggests that morphological changes in plant growth which are typically ascribed as phytochrome mediated can be induced by temperature alone, i.e. plant growth is thermomorphogenic (Erwin et. al., 1989). In particular, Dendrathema (Karlsson et al, 1989), Lilium (Erwin et al., 1989), Campanula (Moe et al., 1990), and Euphorbia (Berghage et al, 1990), stem elongation is strongly dependent on the relationship between day and night temperature (DIF = day temperature - night temperature). Stem elongation increased as DIF increased, i.e. as day temperature increased relative to night temperature.

Light quality and DIF interact to affect plant stem elongation. DIF only affected Campanula isophylla stem elongation if plants received R or darkness during the scotoperiod (Moe et. al., 1990). Irradiation of plants with FR during the scotoperiod eliminated the response of stem elongation to DIF.

Evidence exists which suggests similar transduction pathways for both photomorphogenic and thermomorphogenic responses. The transduction pathway for light effects on plant stem elongation are unclear but suggest the involvement of gibberellins (Loveys and Wareing, 1971a and b). Recently, Erwin et al. (1989) and Moe et al. (1990) suggested that promotion of stem elongation by DIF was also mediated by gibberellins.

The objective of the current study was to determine whether thermomorphogenic and photomorphogenic effects on stem elongation act through similar or different causal pathways. The interaction between DIF, light quality and exogenous applications of both GA_{4+7} and ancymidol was studied to this end.

Materials And Methods

Rooted cuttings of Fuchsia x hybrida cv Dollar Princess were planted in 12.5 cm plastic pots in a soilless medium consisting of equal parts of sphagnum peat, perlite, and vermiculite on 6 April, 1989. Plants were then placed in a controlled environment glasshouse under natural photoperiod conditions maintained at 20 $\pm$ 2 C. The photoperiod was ca. 9 hr 15 min. in length which maintained plants in a vegetative state. After 2 wks plants with 5 nodes were selected and the uppermost leaf pair on each plant was marked with black ink. All plants were then moved into controlled environment chambers maintained at 24, 20, and 16 C. Mean temperatures within the chambers did not vary by more than 1 C.

Plants received a 12-hr photoperiod with an intensity of 125 umol s^{-1} m^{-2} (13 mol day^{-1}) from 2000 to 0800 hr. Lighting was delivered with high pressure sodium lamps and incandescent lamps. Irradiance delivered with incandescent lamps was 25% of the total wattage delivered with high pressure sodium lamps. The light spectra which plants received during the

photoperiod is shown in Figure 1a. The R/FR ratio of the artifical lamps versus day light were 2.77 and 1.32, respectively. R/FR ratio determinations were made using an Isco spectroradiometer.

Each chamber was divided into 3 lighting sections during the scotoperiod (0800 to 2000 hr): supplemental R, supplemental FR, and darkness (D). R and FR were delivered with fluorescent lamps developed by Sylvania to deliver lighting high in R and FR. The lights delivered an irradiance of 5 umoles s^{-1} m^{-2} at the top of the canopy. A filter was necessary to remove blue light from the FR source. The R/FR ratio of the red and far red lamps was 80 and .05, respectively. The spectra for the R and FR light sources are shown in Figure 1a. Light pollution between sections was eliminated by pulling an opaque plastic curtain between the plants at 0810 and retracting it at 2000 hr.

Plants were moved among chambers to deliver the temperature treatments and between lighting sources during the night period to complete the treatment combinations for each experiment shown in Table 1. Day/night (DT/NT) temperature environments were 24/16 (+ DIF), 20/20 (0 DIF), and 16/24 C (- DIF). Lighting treatments consisted of supplemental lighting for 30 min at the beginning of the night (EOD), continuous lighting (CONT), or darkness.

Exogenous applications of GA_{4+7} and a GA biosynthesis inhibitor were applied to study the interaction of both DIF

and light quality on endogenous gibberellin concentration. GA_{4+7} was applied as five 20 ul droplets of a 10 ppm concentration solution (1 ug GA_{4+7} $plant^{-1}$) to the uppermost leaf pair 5 days after the initiation of the experiment using a digital Finnipippette (Cole-Palmer). The GA synthesis inhibitor ancymidol (alpha-cyclopropyl-alpha-(4-methoxyphenyl)-5-pyrimidiemethanol) was applied as five 20 ul droplets of a 50 ppm concentration solution (5 ug ancymidol $plant^{-1}$) to the uppermost leaf pair 5 days after the initiation of the experiment. No plants received both GA_{4+7} and ancymidol.

Plants received temperature and lighting treatments for 21 days. At the termination of the experiment, data was collected on internode length of the second internode above the marked leaf pair. There were 4 replicates per treatment within each temperature environment. Lighting treatments were replicated twice over time.

Results

Fuchsia x hybrida cv Dollar Princess internode length increased from 3.2 to 4.4 cm as the difference (DIF) between day (DT) and night (NT) temperature (DT-NT) increased from -8 to +8 C when plants received no lighting during the night period.

The increase in internode length as DIF increased from a 0 to a +8 DIF was not as great as was expected based on

previous research (Erwin, 1989). In some cases internode length was greater when plants were grown with a 0 DIF than a +8 DIF (Table 2). This was unexpected as internode length in Fuchsia was clearly shown to increase linearly as DIF increased within this temperature range when plants are grown under sunlight (Erwin, 1989). The greater stem elongation in the 20 DT/20 NT (0 C DIF) treatment may be attributed to less movement of plants than in the 24/16 C or 16/24 C environments. Movement of plants could potentially decrease stem elongation, i.e. stem elongation is thigmomorphogenic (Wareing, 1981). Plants in both the -DIF and +DIF environments were moved a minimum of 2 times every 24 hr. Plants in the 0 DIF environment were not moved among chambers but were only moved within a chamber. All plants within the 0 DIF environment were agitated at 0800 and 2000 hr to simulate diurnal movement in an effort to reduce potential thigmomorphogenic effects on stem elongation, however, the movement may not have been as vigorous as that which plants moved among chambers received. Due to the potential thigmomorphogenic effects on stem elongation, results were normalized by dividing internode lengths by the internode length of control plants within temperature and lighting environments for further data analysis (Figures 2, 3, and 4).

Light quality affected internode length in different ways. R did not affect internode length. In contrast, FR lighting given as an end-of-day (EOD) treatment or as

continuous irradiation (CONT) during the night period increased internode length (Table 2, Figure 2). Continuous FR resulted in greater elongation than an EOD FR exposure.

The question arises as to whether light quality and DIF interact to affect Fuchsia stem elongation. To analyze the simultaneous action of light quality and DIF on stem elongation, criteria developed by Lockhart (1965) were employed. If 2 factors act independently on the same causal sequence to elicit a response then a multiplicative behavior will be evident between those factors, a synergism may be apparent as the response to factor 1 will depend on the level of factor 2. In contrast if 2 factors act independently via different casual sequences to elicit a response then an additive behavior will be evident between those factors.

Clearly the temperature environment which plants were grown under had a significant impact on the response of Fuchsia stem elongation to lighting treatments. The effect of a lighting treatment on Fuchsia stem elongation decreased as DIF increased (Figure 2). Therefore, light quality and DIF did not act independently to control stem elongation in Fuchsia.

Moe et. al. (1990) also found an interaction between DIF and light quality on Campanula isophylla where only plants which received R or darkness during the night period responded to DIF. Irradiation of plants with FR eliminated the response of plant stem elongation to DIF. Therefore, Moe et al

suggested that phytochrome must be in the P_{fr} form for plant stem elongation to respond to DIF. Fuchsia stem elongation in this experiment responded to DIF after irradiation with either R or FR lighting (Table 2, Figure 2). Therefore, the necessity of phytochrome being present in the P_{fr} state as Moe et al. (1990) suggested was not apparent on Fuchsia in this experiment.

Application of GA_{4+7} increased stem elongation in all temperature environments and lighting treatments (Table 2, Figure 3). Percent increase in internode elongation resulting from an application of GA_{4+7} decreased as DIF increased (Figure 3). For example, as DIF increased from -DIF to + DIF when plants were not irradiated with light during the scotoperiod, stimulation of internode elongation by GA_{4+7} decreased from 133 to 89% (Figure 3).

Application of ancymidol to plants resulted in inhibition of internode elongation in plants which received no lighting during the scotoperiod or EOD R lighting (Table 1, Figure 4). The greatest inhibition of internode elongation occurred when plants received no lighting. Inhibition of internode elongation by ancymidol increased from 0 to 41% as DIF increased from a -DIF to a +DIF when plants received no lighting treatment during the scotoperiod (Figure 4). Interestingly, no inhibition of elongation was evident in the continuous FR treatment (Figure 4). Evidently, continuous FR lighting was able to overcome any inhibition of GA

biosynthesis which resulted from the ancymidol application.

The transduction pathways for phytochrome and temperature effects on plant stem elongation are unclear. Morgan and Smith (1983) showed that inhibition of Phaseolus stem elongation by R or white light was overcome by an exogenous application of GA_3. R followed by FR negated the GA_3 effect, i.e. light quality and GA_3 affected stem elongation in a multiplicative fashion. Similarly, Reid et. al. (1968 a and b) demonstrated that an exposure of etiolated leaves of Hordeum vulgare to R led to a rapid increase in endogenous gibberellin. Research by Loveys and Wareing (1971 a, b) demonstrated that some but not all of the increase in gibberellin following a R exposure was due to a release of gibberellin from a bound form. In addition to gibberellin, phytochrome has been shown to induce cytokinin biosynthesis (Wareing, 1981) and ethylene (Kang and Burg, 1973). The interaction between light quality and GA suggested that these 2 factors may have a similar transduction pathway with respect to stem elongation.

In contrast, data presented by Mohr (1972) suggested that light quality and exogenous applications of GA_3 acted in an additive fashion on mustard hypocotyl lengthening. Based on this information Mohr (1972) concluded that light quality and gibberellins act through different casual pathways to affect plant stem elongation.

Recently, Erwin et. al. (1989) and Moe et. al. (1990)

suggested that promotion of stem elongation by temperature may be mediated by GA. Inhibition of stem elongation by a negative DIF environment was overcome by an exogenous application of GA_{4+7} on Lilium longiflorum (Zieslin and Tsujita, 1988) and Campanula isophylla (Moe et. al., 1990). Little elongation resulted from an application of GA_{4+7} to Campanula isophylla grown in a +DIF environment.

Promotion of stem elongation by a +DIF environment was eliminated by an application of a GA biosynthesis inhibitor (ancymidol). Ancymidol had little or no effect on stem elongation of plants grown under a -DIF environment (Erwin et al., 1989). The question arises as to whether DIF and phytochrome interact to mediate GA synthesis and/or the response of plant tissues to GA?

Results shown in the current experiment suggested that DIF, light quality, and gibberellins may act through similar causal pathways. Percent promotion of Fuchsia internode elongation which received R or GA_{4+7} alone was significantly less than that of plants which received R plus GA^{4+7} (Table 2, Figure 5). The apparent synergism between R and GA_{4+7} on Fuchsia internode elongation suggested that this response was multilicative in nature and not additive (Lockhart, 1965). These data suggest that DIF and light quality may interact to affect Fuchsia stem elongation through the same casual sequence which involve gibberellin.

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Table 1. Experimental treatments designed to study the interaction between light quality and day/night temperature environments on Fuchsia x hybrida cv Dollar Princess internode elongation. Plants were moved among chambers to deliver the temperature treatments and between lighting sources during the night period to complete the treatment combinations. Lighting treatments consisted of supplemental lighting from red (R) or far red (FR) light sources for 30 minutes at the beginning of the night (EOD), continuous lighting (CONT), or darkness (DARK) during the scotoperiod. GA_{4+7} was applied as five 20 ul droplets of a 10 ppm concentration solution to the uppermost leaf pair 5 days after the initiation of the experiment using a digital Finnipippette (Cole-Palmer). Ancyimidol was applied as five 20 ul droplets of a 50 ppm concentration solution to the uppermost leaf pair 5 days after the initiation of the experiment.

	Day/Night Temperature Environment (°C)		
Lighting Treatment	24/16 (+DIF)	20/20 (0 DIF)	16/24 (- DIF)
DARK	X	X	X
EOD R	X	X	X

Table 1 - continued

EOD FR	X	X	X
CONT R	X	X	X
CONT FR	X	X	X
DARK + GA_{4+7}	X	X	X
EOD R + GA_{4+7}	X	X	X
CONT R + GA_{4+7}	X	X	X
DARK + ancymidol	X	X	X
EOD FR + ancymidol	X	X	X
CONT FR + ancymidol	X	X	X

Table 2. The effect of temperature, light quality, and growth regulators on Fuchsia x hybrida cv 'Dollar Princess' internode length. Temperature environments were 24 day (DT) temperature/16 night (NT) temperature (+ DIF), 20 DT/20 NT (0 DIF), and 16 DT/24 NT (- DIF). Lighting treatments were for 30 minutes at the end of the day (EOD), continuously (CONT), or not at all during the scotoperiod (DARK). Light sources were either red (R) or far red (FR). Growth regulator applications of five 20 ul droplets of either a 10 ppm solution (1 ug plant^{-1}) of GA_{4+7} (GA) or five 20 ul droplets of a 50 ppm solution (5 ug plant^{-1}) alpha-cyclopropyl-alpha-(4-methoxyphenyl)-5-pyrimidiemethanol (anc) were applied 5 days after the initiation of temperature and lighting treatments.

	Temperature Environment		
Lighting Treatment	- DIF	0 DIF	+ DIF
EOD R	3.3 ± 0.4 [z]	4.2 ± 0.4	4.1 ± 0.5
EOD R+GA	7.2 ± 1.2	7.7 ± 1.3	7.8 ± 0.6
CONT R	3.6 ± 0.9	4.8 ± 0.3	4.4 ± 0.5
CONT R+GA	8.4 ± 0.5	8.5 ± 1.1	8.3 ± 0.4
EOD FR	4.3 ± 0.4	5.3 ± 0.4	4.7 ± 0.1

Table 2 - continued

EOD FR+anc	3.8 ± 0.3	4.5 ± 0.6	3.7 ± 0.4
CONT FR	4.7 ± 0.5	6.4 ± 0.9	5.6 ± 0.9
CONT FR+anc	4.8 ± 0.2	6.5 ± 0.5	5.9 ± 0.5
DARK	3.2 ± 0.6	4.3 ± 0.6	4.4 ± 0.5
DARK+GA	4.6 ± 0.4	6.2 ± 0.1	5.5 ± 0.6
DARK+anc	3.2 ± 0.5	3.6 ± 0.5	2.6 ± 0.0
Light Quality		*** [y]	
Temperature Environment		***	
Light x Temperature		***	

[z] Numerals represent treatment means and standard deviation about the mean.

[y] Significance at P = 0.001 (***).

Figure 1a. Light spectra of daylight versus artificial lighting composed of high pressure sodium and incandescent lamps used in this experiment.

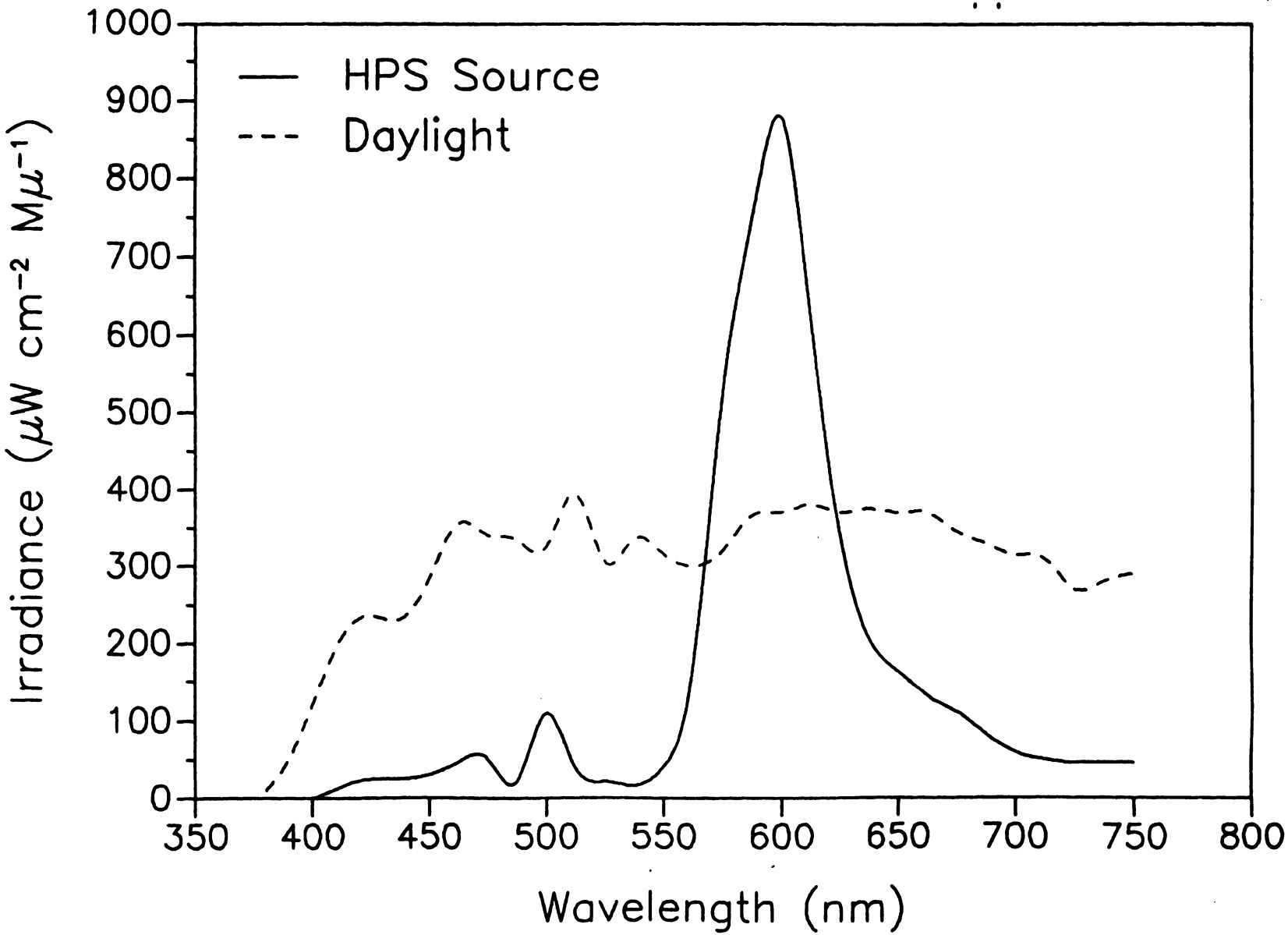

HPS Source
Daylight
Irradiance (μW cm⁻² Mμ⁻¹)
Wavelength (nm)
1000
900
800
700
600
500
400
300
200
100
0
350
400
450
500
550
600
650
700
750
800

Figure 1b. Light spectra of red and far red light sources used to deliver supplemental lighting during the scotoperiod.

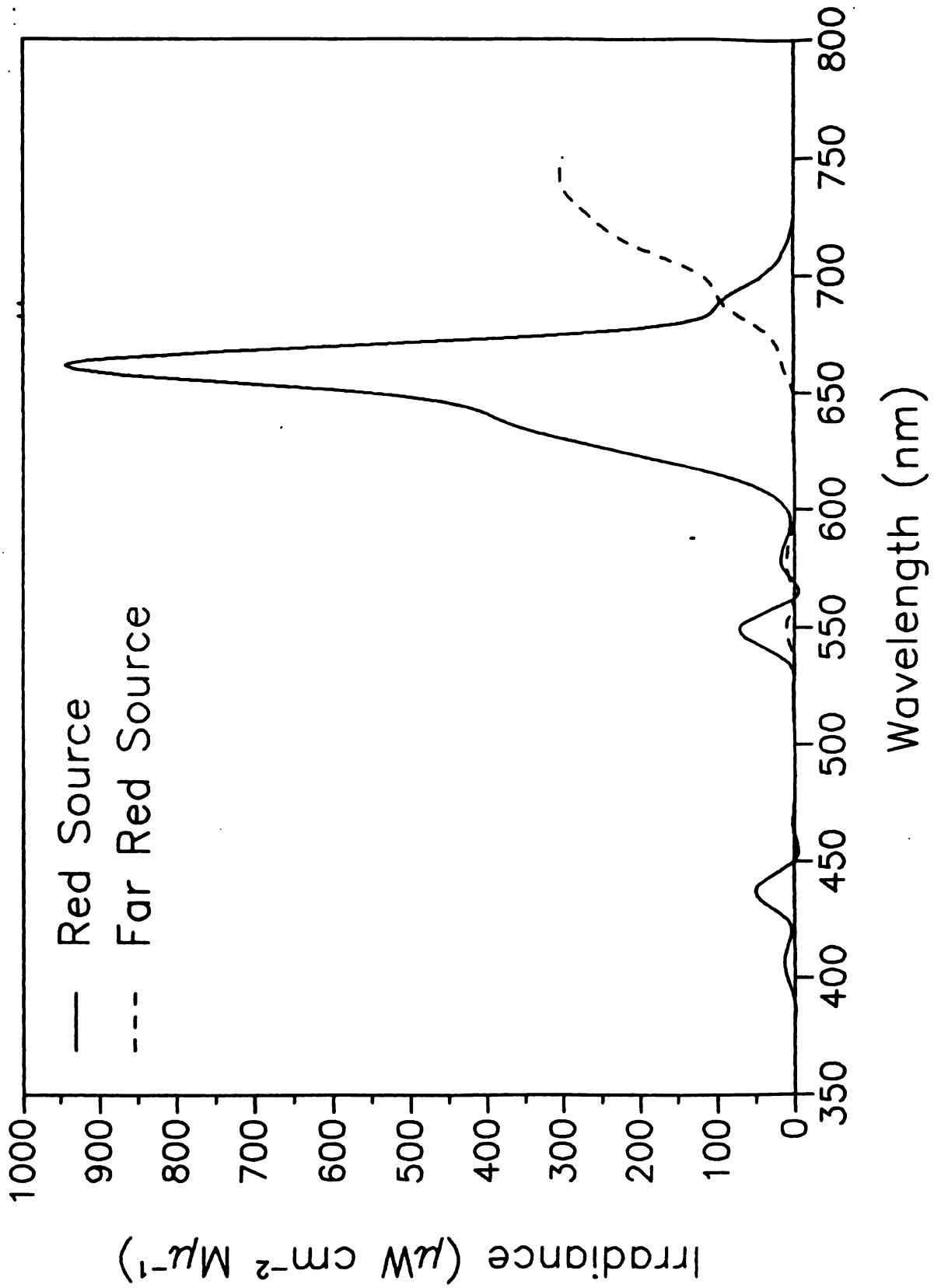

Irradiance (μW cm⁻² Mμ⁻¹)
1000
900
800
700
600
500
400
300
200
100
0
350
400
450
500
550
600
650
700
750
800
Wavelength (nm)
Red Source
Far Red Source

Figure 2. Percent stimulation of elongation of the second internode of Fuchsia x hybrida cv Dollar Princess when grown under different day/night temperature environments and light quality treatments. Light quality treatments were applied during the scotoperiod. Data is presented as the percent stimulation as compared to plants which received no lighting treatments.

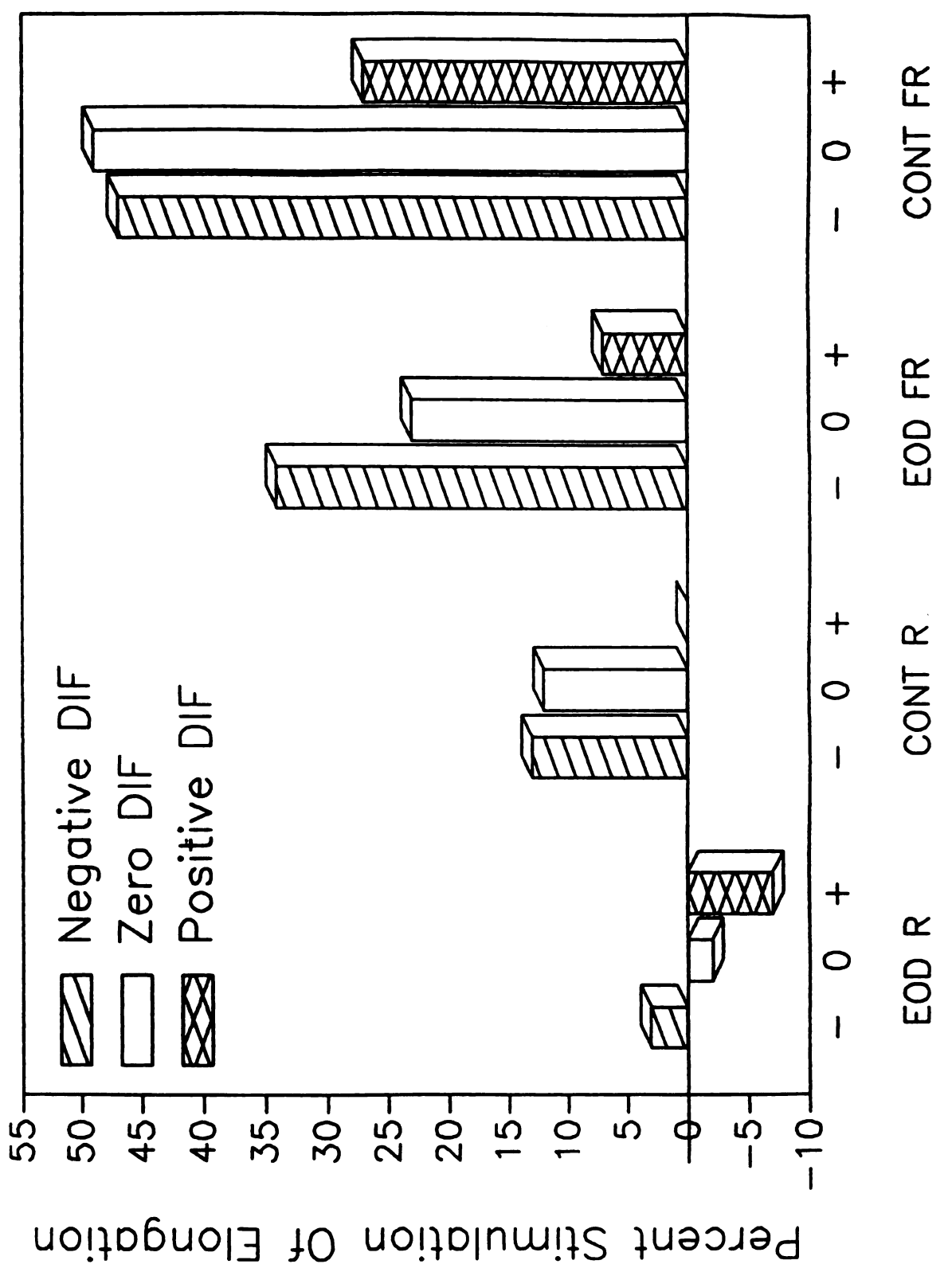

Percent Stimulation Of Elongation
55
50
45
40
35
30
25
20
15
10
5
0
−5
−10
Negative DIF
Zero DIF
Positive DIF
− 0 +
EOD R
CONT R
EOD FR
CONT FR

Figure 3. Percent stimulation of elongation of the second internode of Fuchsia x hybrida cv Dollar Princess following an application of GA_{4+7} when grown under different red lighting treatments. Red lighting treatments were applied during the scotoperiod. Data is presented as the percent stimulation compared to plants which received the red lighting treatments or darkness only.

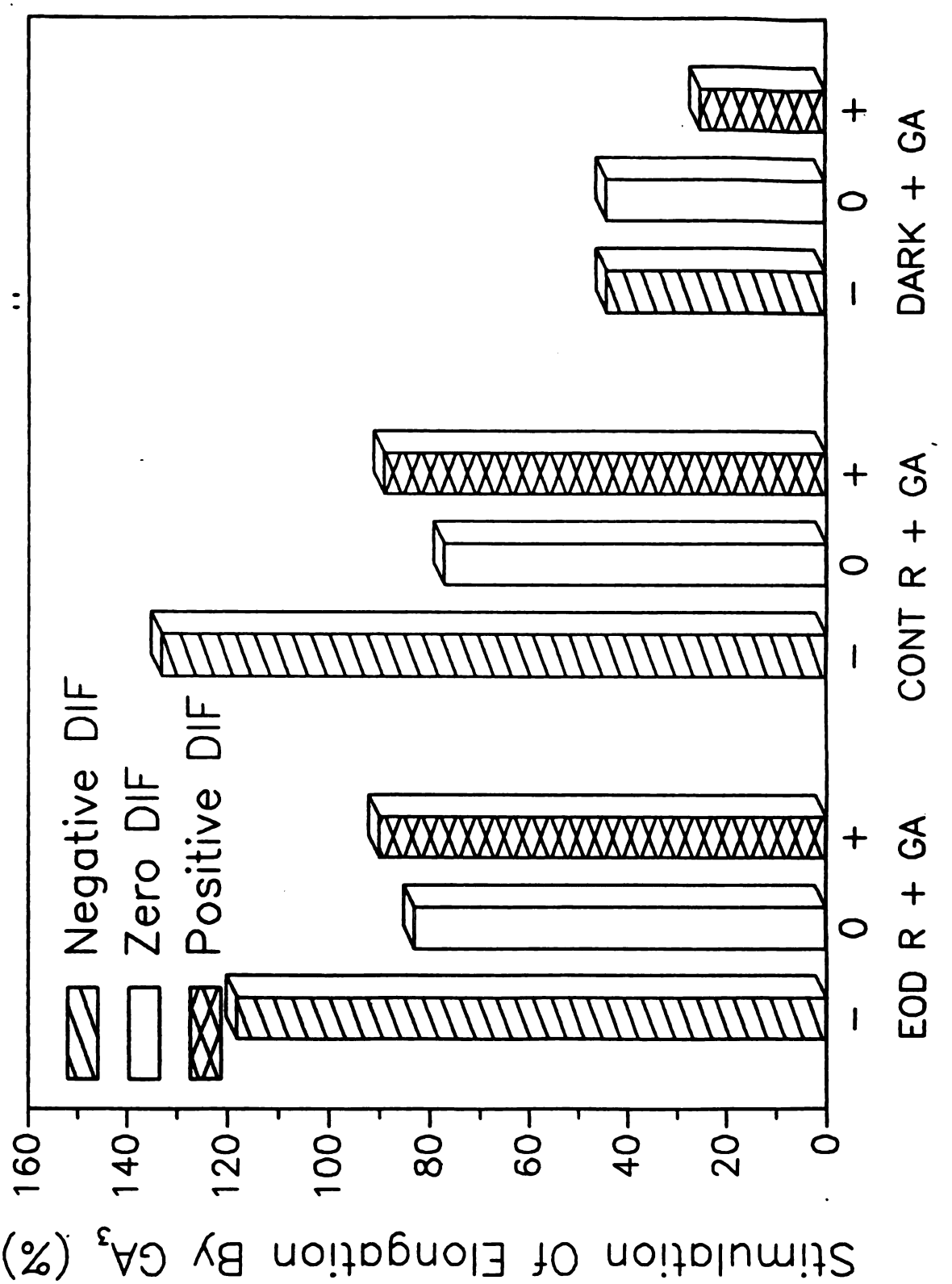

Stimulation Of Elongation By GA3 (%)
160
140
120
100
80
60
40
20
0
Negative DIF
Zero DIF
Positive DIF
- 0 +
EOD R + GA
CONT R + GA
DARK + GA

Figure 4. Percent inhibition of elongation of the second internode of Fuchsia x hybrida cv Dollar Princess following an application of ancymidol when grown under different far red lighting treatments. Far red lighting treatments were applied during the scotoperiod. Data is presented as the percent inhibition compared to plants which received the far red lighting treatments or darkness only.

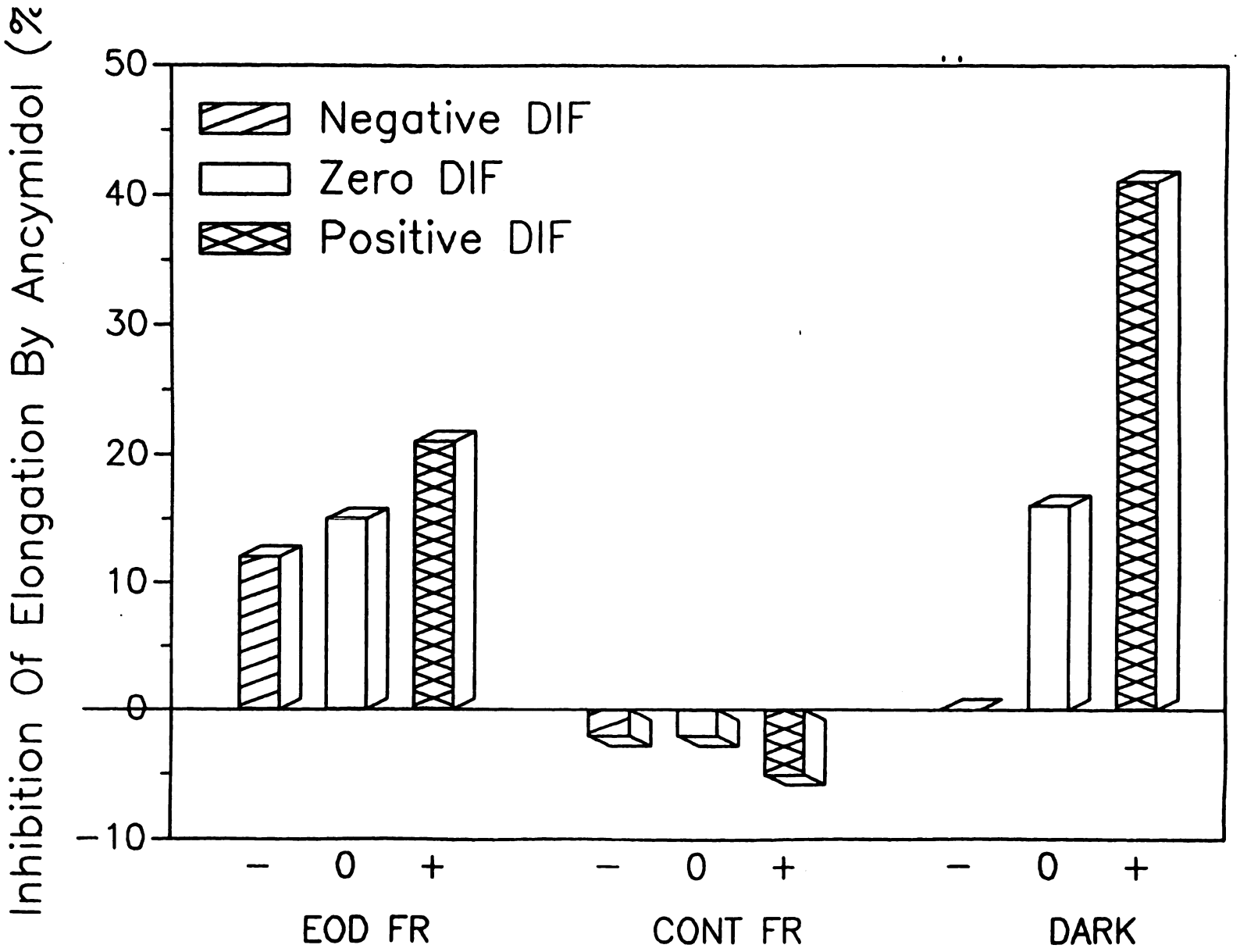
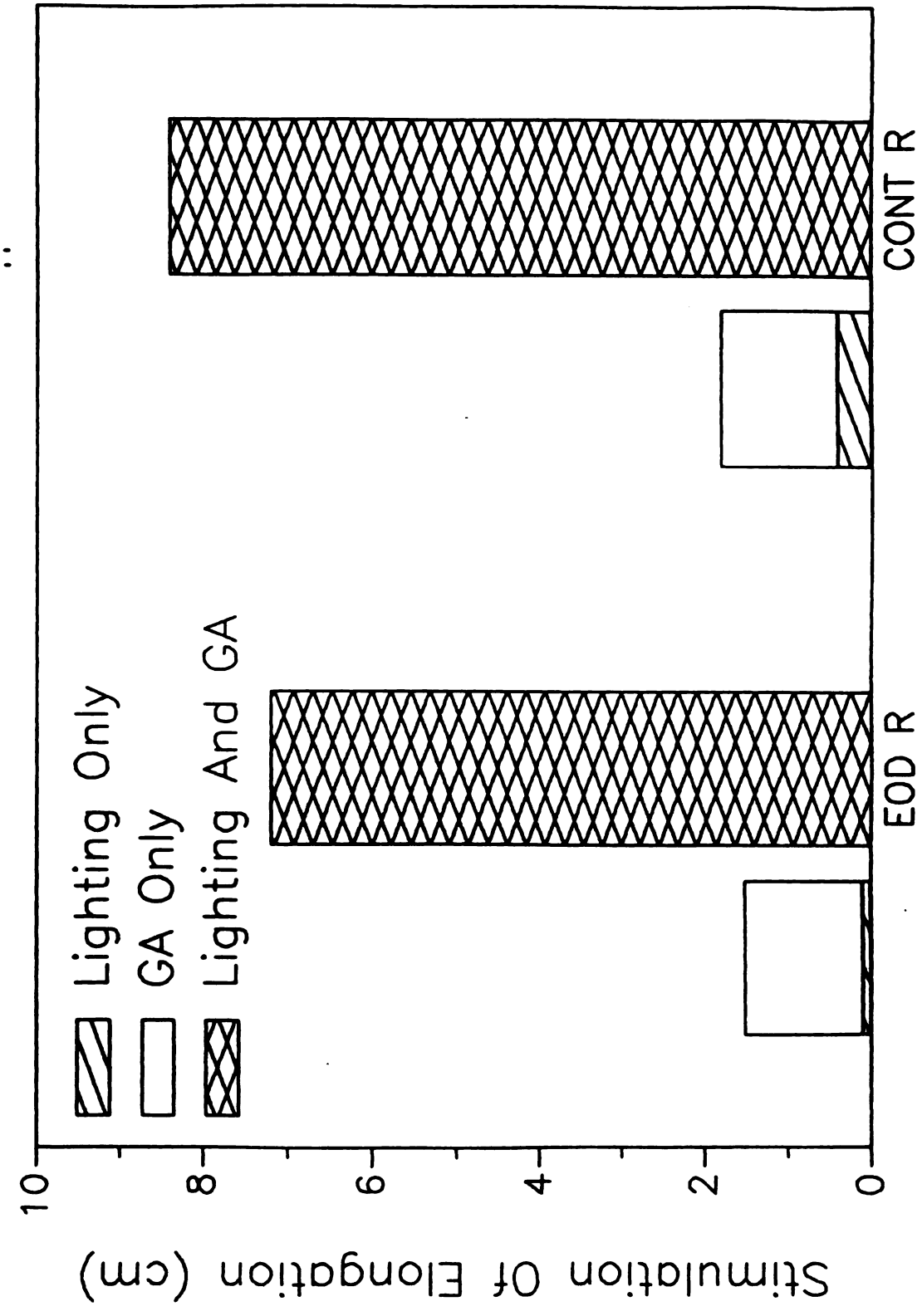

Inhibition Of Elongation By Ancymidol (%
50
40
30
20
10
0
−10
Negative DIF
Zero DIF
Positive DIF
−
0
+
EOD FR
CONT FR
DARK

Figure 5. Comparison of the increase in second internode length resulting from red lighting only, application of GA_{4+7} only, or red lighting plus application of GA_{4+7} on Fuchsia x hybrida cv Dollar Princess.


Stimulation Of Elongation (cm)
0
2
4
6
8
10
Lighting Only
GA Only
Lighting And GA
EOD R
CONT R

Section VI.

A System For Measuring Stem Elongation Kinetics

A System For Measuring Stem Elongation Kinetics

by

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Keywords: angular displacement transducer, linear displacement transducer, circadian rhythm.

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Abstract

A system was developed which utilizes angular displacement transducers to measure short term changes in stem elongation. The system has a resolution to 2 uM per 5 min period. An internal standard was used to account for changes in system output which result from changes in the temperature and air movement in differing environments. Advantages of this system are discussed.

Introduction

Methods for determining growth kinetics of plant stem elongation have been used since the early research of Sachs in 1874 (Penney et al., 1973; Sweeney, 1969). High resolution measurement of the rate of stem elongation is useful in that endogenous growth rhythms can be detected and studied more closely. In addition, the kinetics of growth regulator action and or other factors which affect stem elongation can be elucidated. Studies of plant growth kinetics are, however, often limited by the ability of a system to resolve changes in growth over relatively short periods of time (Penney et al., 1973).

Early research by Went (1944) utilized a simple pulley based system which was able to differentiate circadian rhythms in Lycopersicum stem elongation. Later, time-lapse photography was used to measure the rate of stem elongation of Avena coleoptiles (Ball and Dyke, 1954; Ball et al., 1957). Verbelen et al. (1981) have used direct measurements of hypocotyls to study circadian growth in Phaseolus vulgaris. Recently, methods for measuring growth rate based on changes in continuous voltage output produced by transducers have been developed.

A transducer is a differential capacitor with integral voltage regulation, oscillator, demodulator, and output buffer amplifier. A transducer is composed of a ferromagnetic core which gives a differential inductance as its position changes

relative to coils fixed in the outer part of the unit. The position of the shaft is converted into a direct current (DC) voltage proportional in amplitude and polarity to the displacement from the electrical null position of the transducer. A diagram of an ADT is presented in Figure 1. ADTs have traditionally been used for positioning optical devices, rotary actuators, servo position feedback, and robotic wrist and elbow control (Trans-tek).

Linear displacement transducers (LDT) have been used to measure the stem elongation rates of Cucumis (Addink and Meijer, 1972), Pisum (Warner and Leopold, 1971), Vigna (Lecharny and Jaques, 1982), Lycopersicum (Assaad Ibrahim et al., 1981), and Chenopodium (Lecharny et al., 1985). In addition, LDT have been used to study Maize (Hsiao et al., 1970) and Poa (Christ, 1978) leaf expansion. Gordon and Dobra (1972) developed a capacitance based system for growth measurement . A system developed by Evans and Ray (1969) was modified by De La Fuente and Leopold (1970) to utilize angular displacement transducers (ADT) to increase resolution in measurement of auxin stimulation of stem segment elongation.

This paper describes a system which utilizes ADT to measure stem elongation rates of intact plants. Benefits of this system compared to previously developed growth measuring devices will be discussed.

System Composition

A simplified diagram of the system is shown in Figure 2. A 'Mylar' filament was tied to an elongating internode on one end and a counterweight on the other. In between the plant and the counterweight the filament was wrapped twice around a pulley attached to an angular displacement transducer (ADT). The ADT was held above a plant with a ring stand. The voltage output from the ADT was used to measure stem elongation rate. The ADT used was model 604-0001 produced by Trans-Tek Inc, Ellington, Connecticut.

The transducer was powered by a ±15 volt DC power supply. The range in voltage which is acceptable to power the transducer is from ±14.5 to ±30 volts DC. The input voltage is unregulated and is input polarity protected. The maximum load when the current is less than ±5maDC is ±20maDC. The transducers are calibrated to deliver an output voltage of 100 mv DC per degree of rotation.

The monofilament between the pulley and the counterweight was surrounded by a hollow plastic tube held in position by a ring stand. The plastic tube reduced output 'noise' which resulted from swinging of the counterweight due to air movement.

Output from the transducers was processed by an 'Analog Connection Jr. Board' (Strawberry Tree Computers, Sunnyvale, California) which is an analog to digital (A/D) conversion board. The board was mounted in a Zenith personal computer and is connected to a terminal panel card which the

transducers are attached to. The terminal panels had cold junction compensation to accommodate direct thermocouple hook-up.

The complete system was composed of 8 transducers. Four transducers were placed in each of 2 growth chambers. A single A/D board and terminal panel is capable of having 8 independent transducers attached to it. However, only 4 terminals were used on a board for transducers. The other 4 terminals were utilized for measuring plant temperature, air temperature, soil temperature, and irradiance in each growth chamber. Therefore, 2 boards were required to run the 8 transducers which this system was composed of.

Software was provided with the A/D board which allowed easy programming of data conversion and logging. Each transducer is calibrated independently to give accurate conversion of voltage to a linear distance as each pulley had a slightly different diameter. Input voltage was converted to millimeters prior to logging data onto a hard disk.

Data from all 16 inputs was collected every 3 s and was placed in memory. After 5 min data from each terminal were averaged and were written to a file on the hard disk. The date and time is saved with the data.

Growth rate was determined by subtracting consecutive measurements. Data were smoothed by using a moving average technique (Penny et al., 1973; Lecharny and Wagner, 1984).

Discussion

Voltage Output: The output voltage from an ADT is sigmoidal in nature. A plot of the output voltage versus shaft position is shown in Figure 3. Because of the sigmoidal nature of the output voltage as the shaft rotates, the output is proportional to the position of the shaft only in certain ranges. Shaft rotation which includes an increase in position angle exceeding 90° will result in an output voltage which is not proportional to the change in position of the shaft. The typical linear range utilized is often 60° which ranges in voltage from -3 to +3 volts DC (Figure 3). If the output voltage exceeds +3 volts the shaft must be turned back to a position within the linear range. A conversion factor was calculated and utilized by the software to convert the output voltage of the transducer within the linear range as shown below:

$$\text{Conversion factor} = \frac{\text{Scale maximum - Scale minimum}}{\text{6 volts}}$$

The scale maximum and minimum was equal to 1/6 th of the diameter of the pulley, i.e. 60° of rotation. Six volts was the usable linear range of output voltage. With the system described in this paper the usable range after conversion was approximately 25 mm. In order for -3 volts to correspond to 0 mm an offset factor was calculated.

Offset factor = scale x (input minimum - scale minimum)

If the position of the transducer went below or above 0 to 25 mm, an audible alarm was activated.

Pulley Diameter: The resolution of an ADT system was influenced by the diameter of the transducer shaft. The system described utilizes a set of pulleys which increased the diameter of the shaft and therefore the distance which the shaft could rotate before the output voltage moved out of the linear range. Experiments which involve rapid stem elongation required larger pulleys as opposed to experiments which entail slower rates of stem elongation which could utilize smaller pulleys. The relationship between pulley diameter and usable distance of the pulley is shown in Figure 4. Pulleys were affixed to the transducer shaft using rubber cement. In this way pulleys are firmly attached to the shaft but could be removed easily.

Monofilament Composition: A plastic monofilament was used as opposed to a traditional cotton filament to eliminate changes in filament length associated with changes in the relative humidity of the environment (Penney et al., 1973). The monofilament was tied to an elongating internode using a slip knot.

Counterweight Mass: Because of the rather slow rate of rotation of the shaft, the torque necessary to start rotation of the shaft was considered as opposed to the torque necessary to move an already rotating pulley. The minimum torque necessary to turn the shaft is 5 g-cm. The relationship between the minimum force necessary to turn a pulley and pulley diameter is shown in Figure 4. The force which is employed to turn the pulley is gravity, i.e. a counterweight. A counterweight which is to light will fail to turn the shaft and register any stem elongation. If the counterweight necessary to turn the shaft was so heavy that the elongation of the plant was affected a count-counter weight can be attached to the monofilament between the plant and the pulley to reduce the tension.

Environmental Effects On Output: The system was subject to fluctuation in output voltage with changes in system temperature. Because of this and unknown factors which may affect the output of the transducer other than stem elongation, one transducer per chamber was employed as an internal standard. The internal standard was composed of a fixed weight, a monofilament, and a counterweight similar to the transducers measuring stem elongation. Internal standard output was subtracted from data collected from transducers measuring plant stem elongation to account for environmental effects on transducer output. Care was taken to make sure

that the length of the monofilament on the internal standard was similar to those attached to the experimental plants.

System Resolution: The system had a resolution to 2 uM per 5 min measurement period. This determination was made by determining the fluctuation in the readings of all transducers when they were connected to glass rods and temperatures were fluctuated between 10 and 30°C. The internal standard was used to smooth the data.

The pulleys to determine the resolution of the system were 4.0 $\pm$ 0.2 cm in diameter. As pulley size increased, the resolution of the system decreased. Conversely, a smaller pulley diameter increased the resolution of the system.

Advantages Of This System

The advantages of this system compared to other systems which have been developed are :

1) ADT apply less pressure to the elongating region of the meristem. LDT have both thread and core weight. The core weight is often at least 4 g. LDT which employ a spring, also have the pressure which is exerted by the spring potentially affecting elongation. In addition, if a spring is employed, the pressure on the meristem is variable. The basis for this is based on the equation: $F=kx$ where F=force, k=is a constant which is a measure of the stiffness of the spring, and x=the distance between full extension and contraction of

the spring (Sears et al., 1982). Since the force applied by a spring is directly proportional to x, the force which is placed on the meristem varies.

2) This system employs an internal standard. The internal standard accounts for all effects in transducer voltage output which may result from the environment on electrical and physical components of the system. Such variations in transducer output were found within this system and have been found in previously developed systems (Lecharny et al., 1985). No other systems using transducers have employed an internal standard to minimize such potential sources of error.

3) The software utilized by this system was advantageous in that:

a) Data was filtered to remove extraneous 'noise'.

b) Data were converted into meaningful units.

c) Data was collected every 3 seconds and is averaged every 5 minutes. Therefore, a considerable number of measurements were taken, thereby, increasing the reliability of the data.

d) A number of other useful parameters were able to be saved with the transducer data.

e) Data was written to the hard disk in a fashion which was directly readable by 'Lotus 1-2-3' for analysis.

f) The software was written in 'Basic' which allowed program modification by the researcher.

g) Often data files are so large that they could not fit on a standard floppy disk. The software included a program which broke files into usable sizes for combination after analysis.

4) The system employed simultaneous measurements on 3 transducers per chamber which were directly comparable to 3 transducers in an adjacent chamber. Therefore, data were compared across time which was the case with most studies which utilized transducers. The chambers themselves were synchronized and were run by internal computers which yielded precise environmental control.

5) The use of ADT offered a variable useful distance before the system had to be reset, i.e. the pulley size could be changed depending on the experiment length and the amount of elongation which was expected. For instance, etiolated seedling elongation may be so rapid that LDT systems may have to be reset more than once a day. LDT often have a maximum range of 20 mm $\pm$ 0.01 mm (Lecharny and Wagner, 1984). ADT offer more flexibility in this respect.

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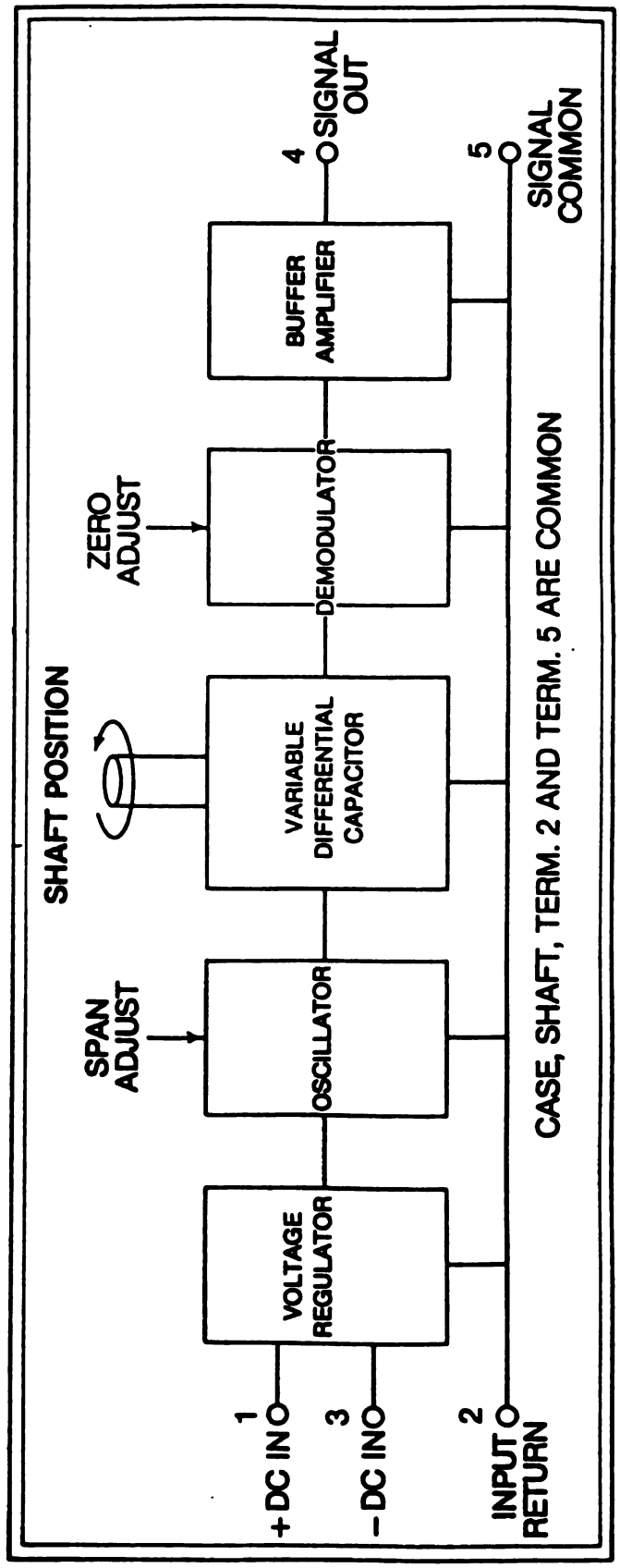
Figure 1. A schematic representation of the circuit block diagram of an angular displacement transducer.



CIRCUIT BLOCK DIAGRAM

Figure 2. Schematic diagram of a system developed to continuously measure plant stem elongation. Only one transducers is shown, however, a total of 8 transducers were employed in 2 growth chambers. All transducers were controlled by a single microcomputer.

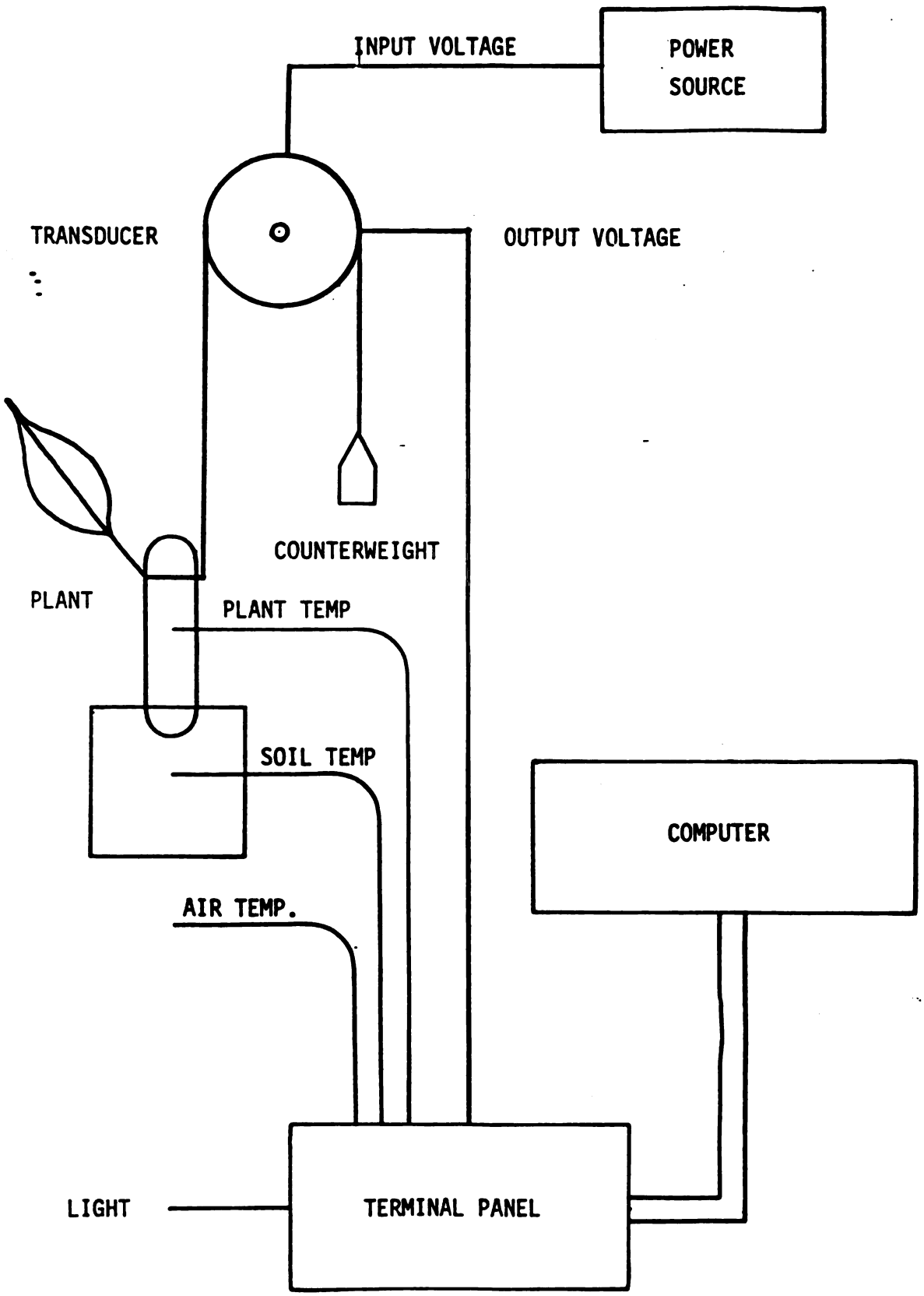
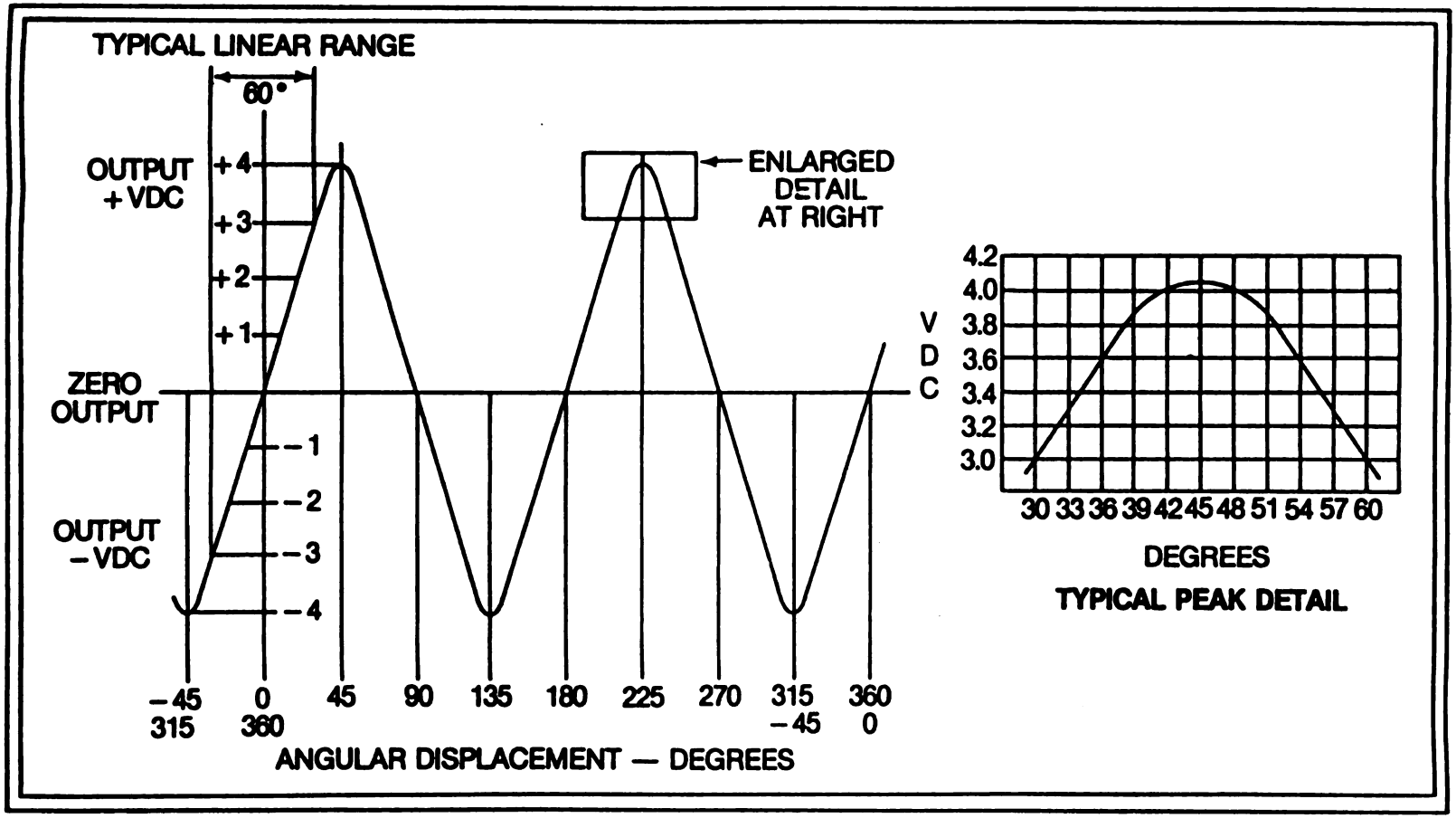

INPUT VOLTAGE
POWER SOURCE
TRANSDUCER
OUTPUT VOLTAGE
COUNTERWEIGHT
PLANT
PLANT TEMP
SOIL TEMP
COMPUTER
AIR TEMP.
LIGHT
TERMINAL PANEL

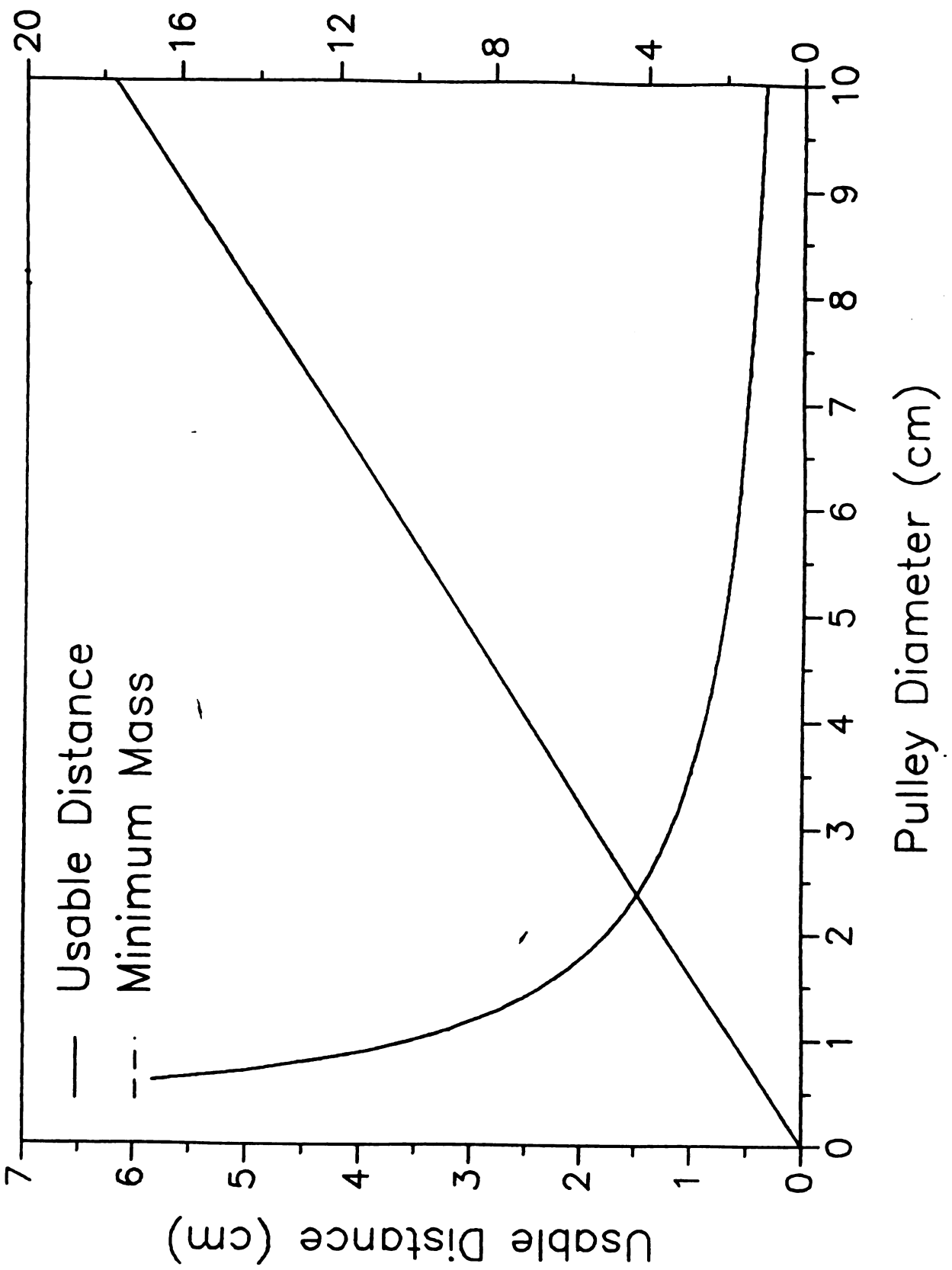
Figure 3. The output function of an angular displacement transducer. Note the typical linear range.



OUTPUT FUNCTION

The illustration above is a plot of output voltage versus shaft position for Model 0604-0000. By definition the output is 0 VDC at the zero position. Rotating the shaft CW provides a positive voltage proportional to the angular displacement from the zero position. CCW rotation from the zero position produces a negative voltage, again proportional to the shafts position in relation to 0°. The 0604-0001 is designed to provide a 0 to +6 VDC output proportional a 0° to 60° CW rotation, Model 0604-0002 gives a 0 to −6 VDC output proportional to a 0° to 60° CCW rotation.

Figure 4. The effect of increasing pulley diameter on the usable distance for direct linear measurement and the minimum mass required to turn the transducer shaft. The usable distance was calculated by dividing the circumference of the selected diameter pulley by 6 to yield the linear 60° distance. The maximum torque required to start rotation of the shaft is 5 g-cm. If this is held constant the minimum counterweight mass could be calculated from the equation: Torque (N-m) * Moment (m) = Mass (N) (Sears et al., 1982).


Usable Distance (cm)
Minimum Mass
Pulley Diameter (cm)
0
1
2
3
4
5
6
7
0
4
8
12
16
20
0
1
2
3
4
5
6
7
8
9
10

Section VII

Appendices

Appendix A

Temperature Effects

Schlumbergera truncata 'Madisto' Flower Initiation

Temperature Effects *Schlumbergera truncata* 'Madisto' Flower Initiation

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Abstract

Schlumbergera truncata 'Madisto' plants were grown under 19 different day/night temperature (DT/NT) environments ranging from 10°C to 30°C with a 9 hour photoperiod. Time from initiation of SD to anthesis varied from 50 days in the 20°C DT/ 25°C NT environment to 99 days in the 10°C DT/ 15°C NT environment. Flower initiation did not occur when plants were grown under the following DT/NT temperature environments, 10°/30°C, 30°/10°C, 25°/25°C, and 30°/30°C. Instead, only phylloclades developed. Plants grown in other environments had only flowers or both flowers and phylloclades. An optimal temperature for flower initiation, based on the ratio of flowers to phylloclades, existed at 20°C. Phylloclade number increased as DT increased and as DT increased relative to NT. Phylloclade number was greatest in the 30°C DT/10°C NT environment.

1. Introduction

Schlumbergera truncata Haw. plants are induced to flower by placing plants under short days (Roberts and Struckmeyer, 1939). Flower initiation is often incomplete, i.e. both flowers and phylloclades develop.

One environmental factor which influences *Schlumbergera truncata* flower initiation is temperature (Rünger and Führer, 1981). Roberts and Struckmeyer (1939) reported that flower initiation was inhibited under short days (SD) when day and night temperature exceeded 21-24°C, was promoted by SD between 17-18°C, and occurred under SD or long days (LD) at 13°C. Rünger and Führer (1981) reported that the higher the temperature, the shorter the photoperiod necessary to induce flowering. At 30°C, an 8-9 hour photoperiod was required to induce flowering. Yonemura (1979) determined the critical photoperiod for flower induction was 12 hr at 18-20°C.

Incomplete flower initiation, i.e. simultaneous development of phylloclades and flowers, is probably due to nonoptimal photoperiod/temperature conditions for maximal floral induction. The objective of the research presented in this paper was to determine the relationship between temperature and the degree of *Schlumbergera truncata* flower initiation under a 9 hr photoperiod.

2. Materials And Methods

Three *Schlumbergera truncata* Haw. 'Madisto' plants per 10.2 cm plastic pot were grown in a glasshouse with a 20° ± 2°C air temperature. Eighty pots were selected for plant uniformity, plants were pinched to 3 phylloclades (leveled), and pots were then moved to glasshouses with temperature setpoints of 10, 15, 20, and 25°C. Plants were moved among glasshouses at 0800 and 1700 hr each day to yield a total of 16 day/night (DT/NT) temperature combinations. In addition to the 16 DT/NT combinations, plants were placed in 10°/10°C, 10°/30°C, 30°/10°C, and 30°/30°C DT/NT environments. Each temperature treatment had 5 replicates.

Movement of plants required approximately 15 minutes. An opaque curtain was pulled over the plants after they were moved at 1700 hr and was retracted prior to 0800 hr to provide a 15 hr scotoperiod (9 hr photoperiod) paralleling

the NT treatment.

Date of anthesis, flower number, and phylloclade number were collected at anthesis on each pot. Data were statistically analyzed as a 4 x 4 factorial model with DT and NT as the main factors.

3. Results And Discussion

The time from induction (start of SD) to anthesis decreased nonlinearly from 100 to 52 days as the average daily temperature increased from 12°C to 20°C (Figure 1). Increasing ADT above 20°C did not hasten flowering.

Flower initiation did not occur when both DT and NT were warmer than 25°C. These results contrast research by Rünger and Führer (1981) which showed that flower initiation occurred at 30°C with an 8-9 hr photoperiod. Poole (1973) also showed that flowering could occur at temperatures above 23°C. Differences between this experiment and that of Rünger and Führer (1981) and Poole (1979) may be due to differences in the sensitivity of different cultivars to temperature and/or photoperiod.

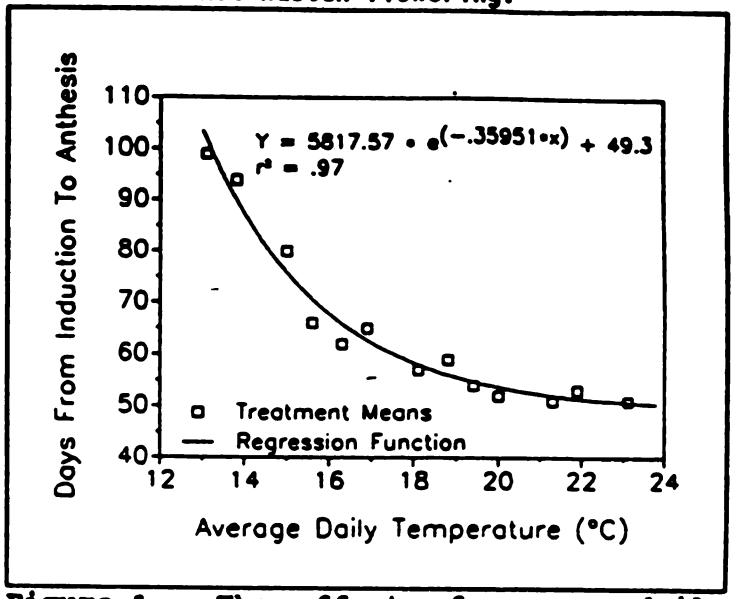

Figure 1. The effect of average daily temperature on the time from flower induction to anthesis on Schlumbergera truncata 'Madisto'.

Night temperature (NT) affected the degree of flower initiation. Day temperature (DT) had no significant effect on the degree of flower initiation. The optimal NT range for flower initiation, based on the ratio of flowers to phylloclades, was from 15 to 20°C (Figure 2). As NT increased above 20°C or decreased below 15°C, flower number decreased and/or phylloclade number increased. These data agree with research of Yonemura (1979) who suggested that the optimal temperature for flower initiation was 15-20°C when plants were grown with a 12 hr photoperiod; no distinction between day and night temperature was made. Similarly, Rünger and Führer (1981) suggested that the optimal temperature for

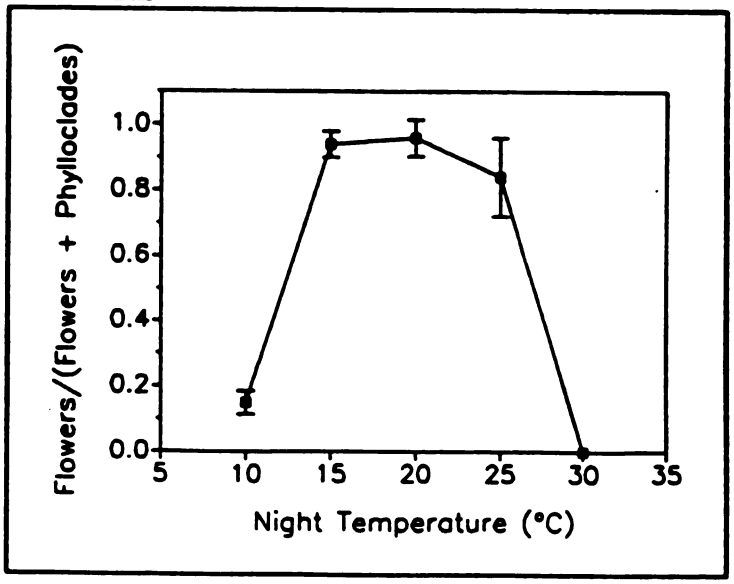

Figure 2. The effect of night temperature on the ratio of flowers to flowers plus phylloclades on Schlumbergera truncata 'Madisto'.

flower initiation was 15°C during the first week then increased to 18°C during the second week of induction.

Total break and phylloclade number per pot increased as DT increased (Tables 1 and 2). For instance, phylloclade number increased from 1.8 to 33.0 phylloclades per pot as DT increased from 10 to 30°C with a 10°C NT. Phylloclade number per pot was also greater when the DT was greater than the NT with DT over 25°C. For instance, phylloclade number was lower when plants were grown with a 30°C DT/ 30°C NT environment (19.4 phylloclades per pot) than when plants were grown with a 30°C DT/10°C NT environment (33.0 phylloclades per pot). The effect of DT on phylloclade number is in agreement with research by Runger (1979) which determined that phylloclade number increased with temperature up to 30°C.

4. Acknowledgement

The authors appreciate the technical assistance of Joy Hind, Wendy Cole, Mark Smith, and Martin Stockton. Plants were donated by Post Gardens of Battle Creek, Battle Creek, Michigan.

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Table 1. The effect of day and night temperature on total break number per pot of Schlumbergera truncata cv 'Madisto'.

Night Temperature (°C)	Day Temperature (°C) 10	15	20	25	30
10	2.4 [z]	11.0	18.6	19.4	33.0
15	6.6	8.8	11.5	13.2	-
20	10.2	11.8	13.4	12.4	-
25	9.8	9.6	10.8	19.6	-
30	4.6	-	-	-	19.4

Significance

Day Temperature	
Linear	*** [y]
Quadratic	n.s.
Night Temperature	
Linear	n.s.
Quadratic	n.s.

[z] Numerals represent treatment means.
[y] Significant at P = 0.001 (***): not significant (n.s.).

Table 2. The effect of day and night temperature on phylloclade number per pot of Schlumbergera truncata cv 'Madisto'.

Night Temperature (°C)	Day Temperature (°C) 10	15	20	25	30
10	1.8 [z]	11.0	15.2	17.0	33.0
15	0.7	0.8	0.5	0.0	-
20	0.2	0.0	0.0	1.1	-
25	1.0	0.8	3.2	18.2	-
30	4.6	-	-	-	19.4

Significance

Day Temperature	
Linear	*** [y]
Quadratic	n.s.
Night Temperature	
Linear	n.s.
Quadratic	n.s.

[z] Numerals represent treatment means.
[y] Significant at P = 0.001 (***); not significant (n.s.).

Appendix B

Thermomorphogenesis And Photoperiodic Responses Of *Nephrolepis exaltata* 'Dallas Jewel'

Thermomorphogenic And Photoperiodic Responses Of Nephrolepis exaltata 'Dallas Jewel'

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Abstract

Nephrolepis exaltata 'Dallas Jewel' plants were grown under 2 photoperiods for 92 days under 16 different day/night temperature environments with temperatures ranging from 15 to 30°C. Plant morphology was influenced by both temperature and photoperiod. Frond length increased from 9.8 to 17.8 cm on plants grown under short days (SD) and 9.3 to 21.9 cm on plants grown under long days (LD) as average daily temperature (ADT) increased from 15 to 30°C. Leaflet number per frond increased from 25 to 37 on plants grown under SD and 23 to 42 on plants grown under LD as ADT increased from 15 to 30°C. Stolon number was greatest on plants grown under SD and was greater when day temperature was less than the night temperature.

Plant development rate was also influenced by temperature and photoperiod. Frond unfolding rate increased from 0.14 to 0.38 fronds per day on plants grown under SD and 0.07 to 0.26 fronds per day on plants grown under LD as ADT increased from 15 to 30°C.

Therefore, SD grown plants had more fronds which were shorter in length and had fewer leaflets per frond than LD grown plants. Total leaf area per plant, calculated from leaflet area, leaflet number per frond, and frond number, was not significantly different between SD and LD grown plants.

1. Introduction

Plant morphology is influenced by day temperature, night temperature, and/or the relationship between day and night temperature, i.e. plant growth is thermomorphogenic (Erwin et. al., 1989). For instance, stem elongation is primarily dependent on the relationship between the day and night temperature (Erwin et. al., 1989; Karlsson et. al., 1989). In contrast, leaf area and shape are typically a function of absolute day and/or night temperature (Njoka, 1957; Erwin et. al., 1989).

Plant development rate is often a function of average daily temperature in a limited temperature range (Karlsson et. al., 1989; Alm et. al., 1988). The rate of leaf unfolding typically increases to a maximum rate then decreases as average daily temperature increases. For instance, poinsettia (Berghage et. al., 1989) and fuchsia (Erwin et. al., 1989) leaf unfolding rate increases to a maxima at an average daily temperature of approximately 25°C, then decreases as temperature increases above 25°C.

Little is known on the effect of temperature and photoperiod on fern development. The objective of this research was to determine how temperature and photoperiod influence Nephrolepis morphology and development rate.

2. Materials And Methods

Nephrolepis exaltata 'Dallas Jewel' plants were planted in 10.2 cm plastic pots on 8 October, 1988, in a medium consisting of equal parts of sphagnum peat, perlite, and vermiculite. Plants were growth for 2 weeks in a glasshouse maintained at a 20°C + 2°C air temperature. Plants were then selected for

uniformity based on frond number and size and moved to glasshouses with temperature setpoints of 15, 20, 25, and 30°C. Half of the plants within each glasshouse, 16 plants, received a long day treatment which consisted of night interruption lighting from 2200 to 0200 hr delivered with incandescent lamps at an intensity of 2 micromol s^{-1} m^{-2}.

Plants were moved among glasshouses at 0800 and 1700 hr each day to yield a total of 16 day/night temperature combinations within each photoperiod. Each treatment had 4 replicates. Movement of plants required 15 minutes. An opaque curtain was pulled over the plants after they were moved at 1700 hr and was retracted prior to 0800 to provide a 9 hour photoperiod paralleling the day temperature treatment. Light pollution between long and short days plants within a glasshouse was eliminated by pulling an opaque black curtain between the plants at 1700 and retracting the curtain at 0800 hr.

Frond number, frond length, leaflet number per frond, leaflet length and width, and stolon number were collected after 92 days on each plant. Frond length and leaflet number were collected on a fully expanded representative frond from each plant. Leaflet length and width were collected from a single leaflet on the representative frond from each plant.

Data were statistically analyzed as a 4 x 4 x 2 factorial model with day temperature, night temperature, and photoperiod as main factors. Significance of environmental parameters was determined using analysis of variance and multilinear regression analysis.

3. Results And Discussion

3.1. Morphology:

Frond length and leaflet number per frond were a function of average daily temperature (ADT) and photoperiod (Table 1). Frond length increased as ADT increased from 15 to 30°C regardless of photoperiod. In addition, frond length was longer when plants were grown under long days (LD) compared to plants grown under short days (SD). The increase in frond length due to LD may be a response to light quality or light duration. Further experimentation will address this question.

Leaflet number per frond increased as ADT increased from 15 to 30°C (Table 1). In addition, leaflet number per frond was greater when plants were grown under LD than when plants were grown under SD.

The minimum recommended night temperature (NT) for growth of Nephrolepis is 16°C (Joiner, 1981). One means to evaluate growth of foliage plants is by comparison of leaf area among plants. Research presented in this paper suggested that the optimal ADT for Nephrolepis exaltata 'Dallas Jewel' leaf area was 25°C (Table 1). Stolon number was influenced by DT and NT (Table 2). Stolon number decreased in a curvilinear fashion with significant linear and quadratic terms. In contrast, stolon number increased as NT increased. Photoperiod had no significant effect on stolon number.

3.2. Plant Development:

Frond unfolding rate increased as ADT increased from 15 to 25°C, then decreased as ADT increased above 25°C (Figure 1). A maximum frond unfolding rate at 25°C is similar to the response of leaf unfolding rate to temperature observed in Poinsettia pulcherrima (Berghage et al, 1989), Poa (Friend et al, 1962), and Fuchsia hybrida (Erwin, unpublished data) where leaf unfolding rate increased to 25°C then decreased as temperature increased above 25°C.

Frond unfolding rate was greater when plants were grown under SD than under LD at a common ADT. There was no significant difference between the leaf area of LD and SD grown plants (Table 1).

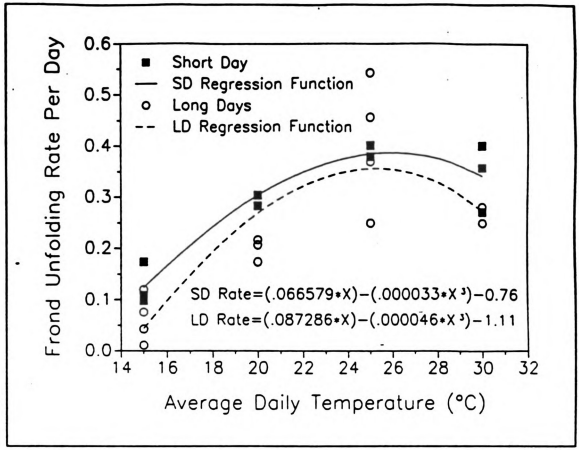

Figure 1. The effect of average daily temperature and photoperiod on frond unfolding rate of Nephrolepis exaltata 'Dallas Jewel'.

4. Acknowledgements

The authors appreciate the technical assistance of Joy Hind, Wendy Cole, Mark Smith, and Martin Stockton. Plants were donated by Green Circle Growers Inc. of Oberlin, Ohio.

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Table 1. Nephrolepis exaltata 'Dallas Jewel' frond length, leaflet number per frond and leaf area. Daylength was 9 hours. The long day treatment consisted of night interruption lighting from 2200 to 0200 hr delivered with incandescent lamps at an intensity of 2 umol s^{-1} m^{-2}. Frond length and leaflet number data were collected on a representative frond on each plant.

	Average Daily Temperature (°C)			
Characteristic	15	20	25	30
Frond Length (cm)				
Short Days	9.8 [z]	11.6	16.5	17.8
Long Days	9.3	17.3	20.3	21.9
Temperature				
Linear		*** [y]		
Quadratic		n.s.		
Photoperiod		***		
Leaflet Number Per Frond				
Short Days	25	27	34	37
Long Days	23	35	37	42
Temperature				
Linear		***		
Quadratic		n.s.		
Photoperiod		***		
Leaf Area Per Plant (cm^2) [x]				
Short Days	3,629	4,988	10,845	12,147
Long Days	1,720	9,121	14,648	13,091
Temperature				
Linear		***		
Quadratic		***		
Photoperiod		n.s.		

[z] Numerals represent treatment means.
[y] Significance at P=.001 (***), not significant (n.s.)
[x] Leaf area was calculated by multiplying leaflet area by leaflet number per frond by frond number.

Table 2. The effect of day temperature, night temperature and photoperiod on Kochroiopsis exaltata 'Dallas Jewel' stolen number.

Night Temperature (°C)	Day Temperature (°C) 15	20	25	30
15				
Short Days [z]	0.3	1.0	5.3	0.5
Long Days	0.0	0.5	0.8	0.3
20				
Short Days	5.0	7.3	3.0	0.0
Long Days	3.0	2.0	2.8	1.0
25				
Short Days	15.0	14.0	10.3	0.8
Long Days	6.0	8.0	7.5	1.3
30				
Short Days	10.0	18.8	13.8	3.0
Long Days	9.0	11.8	15.8	5.3

	[y]
Day Temperature	
Linear	*
Quadratic	**
Night Temperature	
Linear	***
Quadratic	n.s.
Photoperiod	n.s.

[z] Short days were based on a 9 hour photoperiod. Long days were delivered as a 9 hour photoperiod plus a 4 hr night interruption.

[y] Significant at P=0.05(*); P=0.01(**); P=0.001(***); not significant (n.s.).

Appendix C

Temperature Effects Sex Expression In *Cucurbitaceae*

Table 1. Effect of temperature and light fluctuations on Cucumis sativa cv Tay-Belle sex expression. Plants were grown for 60 days. Temperature and/or photoperiod length was 12 hours. Light intensity was 150 micro moles s^{-1} m^{-2}. In the 'constant light-fluctuating temperature' treatment, temperatures fluctuated between 23 and 17°C. Temperature was constant 20°C in the 'constant temperature-fluctuating light' treatment.

Environmental Treatments	Flower Number		
	Female	Male	Ratio
Constant Light Fluctuating Temperature	2.7 ± 2.1	5.6 ± 2.3	0.48 [z]
Constant Temperature Fluctuating Light	1.7 ± 0.5	1.3 ± 0.8	1.31
17°C Day Temperature 23°C Night Temperature	2.0 ± 0.7	2.0 ± 1.4	1.00
23°C Day Temperature 17°C Night Temperature	0.4 ± 0.5	5.6 ± 2.1	0.07

[z] Female Flower Number/ Male Flower Number

Appendix D

Temperature And Photoperiod Effects On Plant Chlorophyll Content

Table 1. The effect of daty temperature and night temperature on chlorophyll a, chlorophyll b and p chlorophyll content of Fuchsia x hybrida cv Dollar Princess grown under a 9 hour photoperiod.

Night Temperature (°C)	Day Temperature (°C) 12	16	20	24
	'chlorophyll a' [z]			
12	.073	.065	.078	.076
16	.077	.080	.069	.080
20	.070	.066	.065	.064
24	.060	.055	.067	.064
	'chlorophyll b'			
12	.021	.021	.026	.024
16	.023	.023	.021	.025
20	.018	.019	.020	.025
24	.015	.016	.019	.020
	'p chlorophyll'			
12	.008	.007	.009	.005
16	.008	.007	.007	.005
20	.004	.007	.006	.006
24	.005	.007	.006	.007

Table 1. - continued

	chlorophyll a/b ratio[z]			
12	3.41	3.18	3.04	3.13
16	3.40	3.47	3.29	3.24
20	3.96	3.38	3.22	2.60
24	3.90	3.35	3.57	3.26

[z] Chlorophyll content was expressed in ug cm^{-2}

Table 2. The effect of daty temperature and night temperature on chlorophyll a, chlorophyll b and p chlorophyll content of Fuchsia x hybrida cv Dollar Princess grown under a 12 hour photoperiod.

Night Temperature (°C)	Day Temperature (°C) 12	16	20	24
	'chlorophyll a' [z]			
12	.075	.067	.069	.071
16	.066	.058	.069	.060
20	.060	.059	.064	.055
24	.045	.046	.056	.054
	'chlorophyll b'			
12	.024	.021	.023	.024
16	.019	.019	.020	.020
20	.016	.018	.022	.019
24	.012	.013	.017	.017
	'p chlorophyll'			
12	.010	.007	.009	.007
16	.006	.006	.004	.006
20	.005	.006	.007	.006
24	.006	.004	.006	.005

Table 2. - continued

	chlorophyll a/b ratio[z]			
12	3.14	3.22	2.95	2.94
16	3.52	3.09	3.37	3.04
20	3.71	3.20	2.99	2.96
24	3.59	3.61	3.25	3.15

[z] Chlorophyll content was expressed in ug cm^{-2}

Table 3. The effect of daty temperature and night temperature on chlorophyll a, chlorophyll b and p chlorophyll content of Dendranthema grandiflora cv Bright Golden Anne grown under a 9 hour photoperiod.

Night Temperature (°C)	Day Temperature (°C) 12	16	20	24
	'chlorophyll a' [z]			
12	.081	.084	.082	.073
16	.071	.089	.088	.074
20	.057	.064	.064	.097
24	.086	.081	.079	.074
	'chlorophyll b'			
12	.026	.028	.025	.018
16	.021	.026	.024	.024
20	.013	.017	.017	.025
24	.027	.023	.024	.022
	'p chlorophyll'			
12	.003	.005	.002	.002
16	.002	.003	.002	.002
20	.001	.002	.002	.002
24	.002	.002	.002	.002

Table 3. - continued

	chlorophyll a/b ratio[z]			
12	3.13	3.04	3.23	4.05
16	3.45	3.42	3.67	3.11
20	4.39	3.74	3.75	3.83
24	3.24	3.56	3.31	3.27

[z] Chlorophyll content was expressed in ug cm^{-2}

Table 4. The effect of daty temperature and night temperature on chlorophyll a, chlorophyll b and p chlorophyll content of Pelargonium hortorum cv Red Elite grown under a 9 hour photoperiod.

Night Temperature (°C)	Day Temperature (°C) 12	16	20	24
	'chlorophyll a' [z]			
12	.047	.052	.043	.045
16	.045	.047	.047	.046
20	.050	.042	.049	.045
24	.038	.027	.036	.036
	'chlorophyll b'			
12	.014	.017	.013	.015
16	.013	.014	.015	.015
20	.014	.013	.017	.014
24	.009	.009	.012	.012
	'p chlorophyll'			
12	.003	.003	.002	.003
16	.003	.003	.002	.003
20	.002	.003	.003	.002
24	.002	.003	.002	.003

Table 4. - continued

	chlorophyll a/b ratio[z]			
12	3.42	3.14	3.21	3.12
16	3.41	3.22	3.04	3.05
20	3.62	3.25	2.95	3.22
24	4.13	2.91	3.04	2.86

[z] Chlorophyll content was expressed in ug cm^{-2}

Appendix E

The Effect Of Day And Night Temperature On Stem Elongation Of Micellaneous Species

Table 1. The effect of day temperature, night temperature, and photoperiod on Xanthium strumarium internode length (cm). Photoperiod was 9 hours long (short day) or 9 hours plus a 4 hour night interruption with incandescent lamps (long day).

Night Temperature (°C)	Day Temperature (°C) 16	20	24
		'Short Day'	
16	0.9 ± 0.1	1.4 ± 0.2	1.4 ± 0.1
20	0.6 ± 0.1	0.9 ± 0.1	1.0 ± 0.2
24	0.5 ± 0.1	0.7 ± 0.1	0.9 ± 0.1
		'Long Day'	
16	1.3 ± 0.2	1.9 ± 0.1	2.2 ± 0.1
20	1.2 ± 0.1	1.8 ± 0.2	1.9 ± 0.1
24	0.9 ± 0.1	1.6 ± 0.1	1.7 ± 0.2

Table 2. The effect of day temperature, night temperature, and photoperiod on Cucumis sativum internode length (cm). Photoperiod was 9 hours long (short day) or 9 hours plus a 4 hour night interruption with incandescent lamps (long day).

Night Temperature (°C)	Day Temperature (°C) 16	20	24
		'Short Day'	
16	0.8 ± 0.2	4.1 ± 0.6	6.8 ± 1.3
20	1.6 ± 0.5	3.6 ± 0.6	5.0 ± 0.9
24	1.1 ± 0.1	2.0 ± 1.2	3.8 ± 0.2
		'Long Day'	
16	1.4 ± 0.4	4.4 ± 1.0	9.3 ± 1.4
20	2.2 ± 0.5	5.0 ± 0.8	5.8 ± 1.0
24	1.5 ± 0.1	2.8 ± 0.1	5.2 ± 0.6

Table 3. The effect of day temperature, night temperature, and photoperiod on Streptocarpus nobilis internode length (cm). Photoperiod was 9 hours long (short day) or 9 hours plus a 4 hour night interruption with incandescent lamps (long day).

Night Temperature (°C)	Day Temperature (°C) 16	20	24
		'Short Day'	
16	3.1 ± 0.4	5.7 ± 0.8	7.1 ± 0.6
20	3.4 ± 0.4	5.9 ± 0.1	7.0 ± 0.7
24	3.1 ± 0.3	4.6 ± 0.4	6.4 ± 0.5
		'Long Day'	
16	3.3 ± 0.6	4.5 ± 0.4	5.1 ± 0.7
20	3.6 ± 0.2	5.7 ± 0.4	5.6 ± 0.8
24	3.0 ± 0.2	4.0 ± 0.2	5.5 ± 0.3