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Temperature and Light Effects on Stem Elongation

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Summary

Diurnal temperature fluctuation interacts with light quality and photoperiod to affect plant stem elongation. Stem cell elongation but not division increases as day temperature increases relative to night temperature and as day length increases for many species. The effect of diurnal temperature fluctuation and photoperiod on stem elongation are mediated via phytochrome where stem elongation increases as $\%P_{fr}$ decreases. The basis for diurnal temperature and photoperiod effects on stem elongation is associated with temperature fluctuation when stimuli occur during the period of most rapid stem elongation during a 24-hour cycle, i.e., the end of the scotoperiod and beginning of the photoperiod. The basis for thigmotropic inhibition of stem elongation is associated with endogenous stimulation of ethylene synthesis. Application of this information to commercial plant production and potential future research directions will be discussed.

Introduction

Stem elongation is commercially reduced to improve stem strength, decrease shipping costs, and/or to increase marketability. Often, stem elongation is reduced by applying chemical growth retardants that limit gibberellin biosynthesis. Concern over the impact of chemical growth retardants is limiting their use. Instead, there is renewed interest in developing effective non-chemical methods of height control and breeding crops to limit stem elongation. Environmental factors known to affect stem elongation include temperature, irradiance, and light quality. This paper summarizes temperature and light effects on stem elongation and our understanding of the basis of those effects.

When Do Plants Elongate?

Stem elongation is not constant during a 24-hr period (Tutty et al., 1994; Erwin et al., 1992a; Lecharny et al., 1985; Went, 1952). Stem elongation decreases from the beginning to the end of the photoperiod and increases from the beginning to the end of the scotoperiod (Fig. 1). Therefore, stem elongation rate is greatest at the end of the scotoperiod and beginning of the photoperiod. In some cases, there is a brief increase in stem elongation rate immediately after the transition from light to dark.

Temperature Effects

General responses

Went (1944, 1952, 1957) showed stem elongation was affected by day and night temperature (DT and NT) differently. *Lycopersicon esculentum* L. stem elongation increased as DT increased and NT decreased (Went, 1944). Similar stem elongation responses to DT and NT were observed on *Fuchsia* x *hybrida* Hort. ex Vilm. (Tageras, 1979), *Triticum aestivum* L. (Pinthus and Meiri, 1979), *Dendranthema grandiflora* Ramat. (Karls-

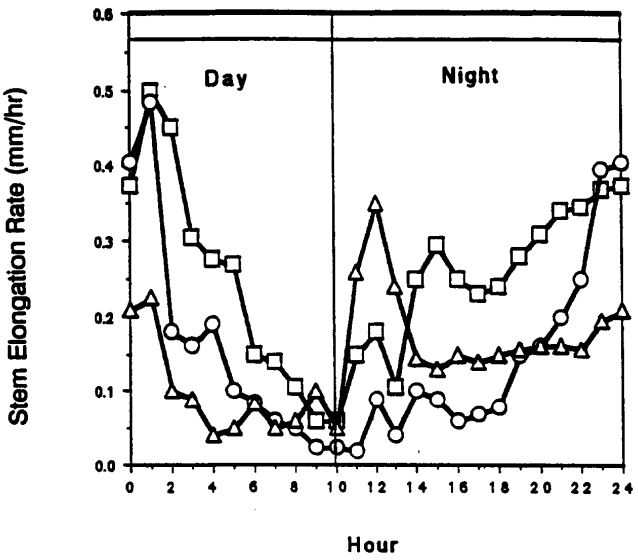

Fig.1. The effect of diurnal temperature fluctuations on the rate of *Dendranthema grandiflora* cv Bright Golden Anne stem elongation. Data presented were collected every five min over a three day period. Hourly means were then calculated. Data were collected with an angular displacement transducer (ADT) connected to a computer. The system had a resolution of two microns per five min period. Squares, circles, and triangles represent hourly treatment means of the stem elongation rate of plants grown with a higher day temperature than night temperature (23 ℃ day/17 ℃ night temperature), equal day and night temperature (20 ℃ day/20 ℃ night temperature), and cooler day than night temperatures (17 ℃ day/23 ℃ night temprature), respectively (Erwin et al., 1992a ; Erwin et al., 1990).

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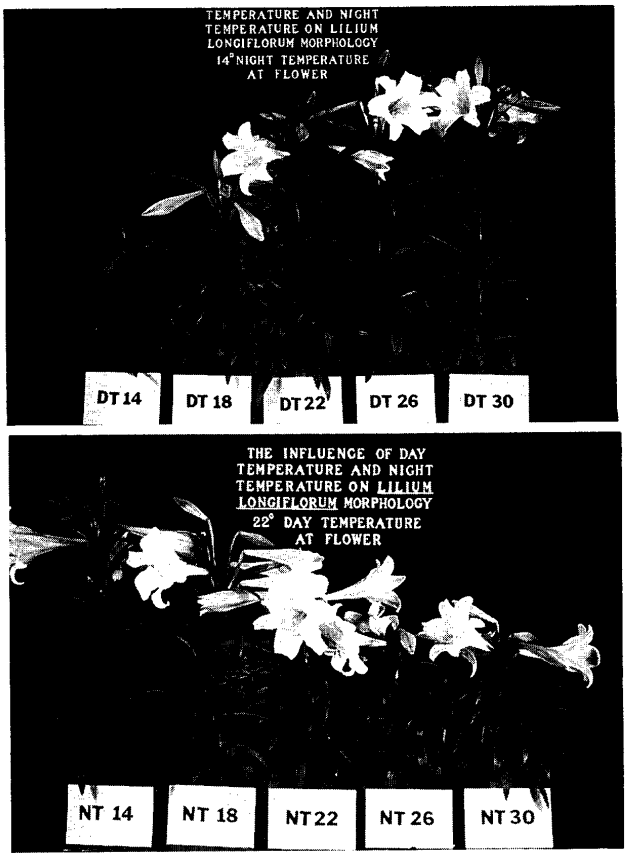

Fig. 2. The effect of increasing DT (top) and increasing NT (bottom) on the height of *Lilium longiflorum* Thunb. cv Nellie White at anthesis. Plants grown at higher average daily temperatures flowered earlier than plants grown at cooler average daily temperatures. As plants grown at higher average daily temperatures reached anthesis, they were placed in a cooler (4 ℃) 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. Internode number was not significantly different among plants (Erwin et al., 1989a ; Heins and Erwin, 1990).

son et al., 1989), *Campanula isophylla* Moretti. (Moe et al., 1991) and *Lilium longiflorum* Thunb. (Smith and Langhans; 1961, Erwin et al., 1989a) (Figure 2).

DT and NT effects on *L. longiflorum* internode elongation could best be described using the 'relationship' between DT and NT rather than by independent DT or NT effects when temperatures ranged from 10 to 26 ℃ (Fig. 3) (Erwin et al., 1989a). Internode elongation increased as the difference (DIF) between DT and NT (DIF=DT-NT) increased from -16 to +16 ℃ on *L. longiflorum* (Erwin et al., 1989a), *D. grandiflora* (Karlsson et al, 1989), *Euphorbia pulcherrima* Willd. ex Klotzsch (Berghage and Heins, 1990), *Xanthium pensylvanicum* L. (Erwin, 1991), *C. isophylla* (Moe et al., 1991), *F. hybrida* (Erwin et al., 1991a), *Begonia* x *tuberhybrida* Voss., *Kalanchoe blossifeldiana* Poelln. (Jacobsen et al., 1991), *Ribes sativum* Syme. (Hoover and Erwin, unpublished), and *Solanum tuberosum* L.

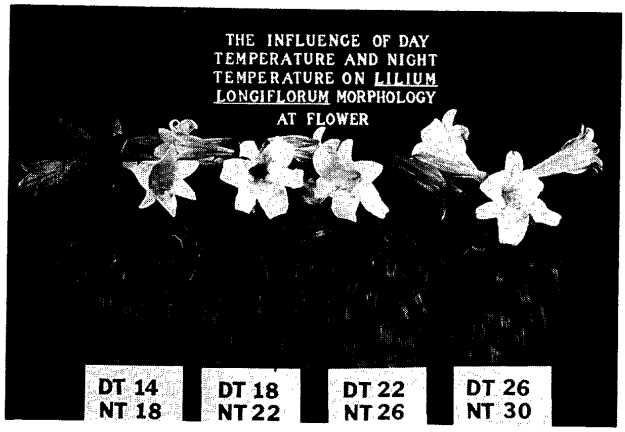

Fig. 3. Appearance of *Lilium longiflorum* Thunb. cv Nellie White at anthesis when grown under four difference DT/NT regimes with DT 4 ℃ warmer than NT across regimes, i.e. equal DT/NT relationship (+4 ℃ DIF). See Fig. 2.

(Kozai et al., 1992) (Fig. 4). While original reports by Went (1957) suggested stem elongation was primarily influenced by DT, measurement of internode lengths from his photographic plates (*Pisum sativum* L.; plate IX) showed internode length was strongly correlated with DIF (r^2 =0.72).

Variation in temperature sensitivity within the photoperiod

Stem elongation is most sensitive to temperature fluctuations during the beginning of the photoperiod and end of the scotoperiod when stem elongation rate is greatest (Erwin et al., 1989b; Heins and Erwin, 1990, 1991; Grindal and Moe, 1994). Reducing temperature during the beginning of the photoperiod is almost as effective in reducing stem elongation as reducing temperatures during the entire photoperiod. The greater and longer the reduction in temperature, the greater the inhibition of elongation (Ludolph, 1992; Ueber and Hendricks, 1992). In contrast to decreasing temperature, increasing temperature during the first 2-hours of the photoperiod was almost as effective in stimulating stem elongation as increasing DT the entire day (Erwin, 1991).

Variation among species

Responses to DT/NT vary across species. *Lycopersicon esculentum*, *Zea mays* L., *Cucumis sativus* L. and *Lilium longiflorum* exhibit a strong response to DIF, i.e., DT/NT greatly affected stem elongation. In contrast, *Pisum sativum* and *Phaseolus vulgaris* L. exhibit little response to DT/NT (Erwin et al., 1994b) (Table 1). *Cucurbita melopepo* var. *pepo* C. and *Citrullus lanatus* Thunb. exhibit an intermediate response to DT/NT. The only group of species that do not respond to DT/NT known are some ephemerals (*Tulipa* x *hybrida* L., *Narcissus pseudonarcissus* L., *Hyacinthus orientalis* L. (Heins and Erwin, 1990)), and species indigenous to

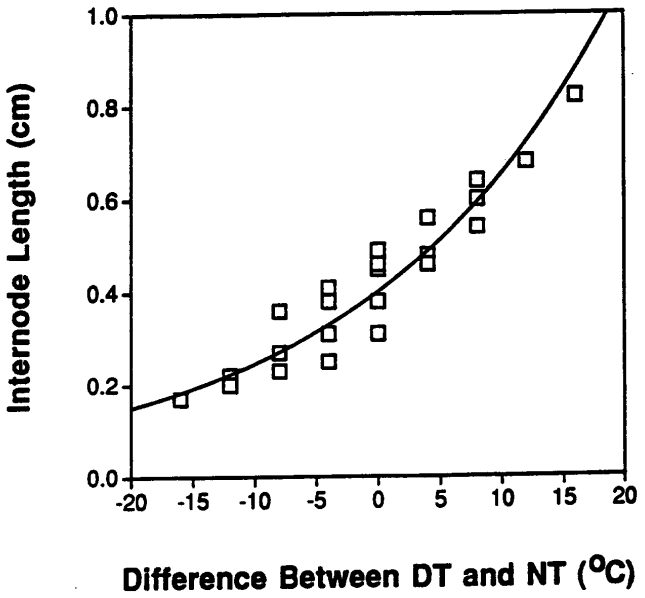

Fig. 4. Relationship between *Lilium longiflorum* Thunb. cv Nellie White plant height at anthesis and the difference (DIF) between the day temperature (DT) and the night temperature(NT). Squares represent mean plant heights for each treatment. The solid line represents the regression function 1.4860 *DIF- 0.0416*DT*NT + 1.9139* AVGTEMP + 25.661 (r^2 =0.84). The regression line also represents the effect of both day temperature and night temperature by night temperature interaction and the effect of average temperature on final height. Internode number was not significantly different among plants (Erwin et al., 1989a).

environments near the equator where DT/NT do not fluctuate greatly. Lastly, species indigenous to upper elevations where DT and NT vary considerably tend to be DT/NT sensitive.

Changes in temperature sensitivity during development

Stem elongation is most sensitive to temperature stimuli when a plant is elongating most rapidly. Therefore, elongation of determinate plants is most sensitive during the 'rapid elongation phase' of development compared to the beginning or end phase of development when plants are not elongating rapidly. For example, DT/NT effects on stem elongation are greatest when Euphorbia pulcherrima plants are elongating most rapidly during development, i.e., 2-6 weeks after 'pinching' on an 8-week cultivar (Heins and Erwin, 1990; Berghage, 1989). In contrast to determinant species, indeterminate species have equal sensitivity to DT/NT throughout development (Heins and Erwin, 1990).

Interaction between DT/NT effects and light

Photoperiod interacts with DIF to affect stem elongation (Erwin, 1991; Erwin et al., 1991a). Plant stem elongation responses to DIF decreased as photoperiod length increases on *F. hybrida* (Erwin et al., 1991a). Similarly, Myster et. al. (unpublished) showed that *Anthirrinum majus* L. 'Winchester Red' response to DIF decreased as photoperiod length decreased from 16 to 8 hr.

Irradiance interacts with DIF to affect stem elongation (Erwin et al., 1992a; Heins and Erwin, 1990; Ludolph, 1992). Stem elongation responses to DIF increase as irradiance levels increase (Erwin et al., 1992a; Erwin and Heins, 1995; Ludolph, 1992). Basis for differences in DT/NT effects on stem elongation based on location is likely due, in part, to variation in irradiance and/or photoperiod length. Irradiance effects on DT/NT effects on stem elongation are particularly interesting in that it suggests a possible phytochrome cycling role in DIF responses.

Light quality interacts with DT/NT to affect stem elongation (Erwin, 1991; Moe and Heins, 1990; Moe et al., 1991). Specifically, there are interactions between red/far red light, and blue light and DT/NT effects on stem elongation. Supplemental blue lighting (440-480

Table 1. Effect of DIF on *Zea mays* 'Snow Belle', *Pisum sativum* 'Mars', *Citrullus lanatus* 'Crimson Sweet', *Phaseolus vulgaris* 'Blue Lake', *Lycopersicon esculentum* 'Sunny', and *Cucumis sativus* internode length when grown under three different environments; 17℃ DT/23℃ NT (− 6℃ DIF); 20℃ DT/20℃ NT(0℃ DIF); 23℃ DT/17℃ NT(+6℃ DIF). The slope (b_0) was determined by regressing internode length against DIF in a linear equation $a + b_0 x = y$: where a=constant, b_0 =slope, x=DIF, and y=internode length. Significance of the differences in the response to DIF (slope) was determined using Tukey's test for mean separation (Erwin et al., 1994b.)

	Third internode length (cm)				
Crop	− 6℃ DIF	0℃ DIF	+6℃ DIF	b_0	Signif.
Zea mays	1.7 ± 0.4[z]	3.9 ± 1.5	5.5 ± 0.8	0.32	***[y]
Pisum sativum	2.4 ± 0.3	2.0 ± 0.3	2.3 ± 0.2	− 0.01	n.s.
Citrullus lanatus	0.4 ± 0.1	3.7 ± 1.0	2.5 ± 0.6	0.17	*
Phaseolus vulgaris	3.6 ± 0.6	4.2 ± 0.9	4.8 ± 0.8	0.10	*
Lycopersicon esculentum	2.0 ± 0.3	2.6 ± 0.3	4.6 ± 0.9	0.22	***
Cucumis sativus	4.7 ± 0.4	7.6 ± 1.1	7.7 ± 1.4	0.25	**

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

[y] n.s., *, **, ***; Nonsignificant, or significant at P=0.05, 0.01, or 0.001, respectively.

Table 2. Effects of day/night (DT/NT) fluctuations and different light quality exposures as day-extension lighting with incandescent lamps(INC) or fluorescent lamps(FL) on stem length and plant dry weight at visible bud(VB) and anthesis of Campanula isophylla Bla' Morettii. DT was applied during the 10-hr photoperiod at 89 μ mol m^{-2} s^{-1} supplied with fluorescent lamps(TL33). Nt was provided during the day-extension period of 14 hr. Irradiance during the day-extension period was 0.58 W m^{-2} (400-1000 nm) with each light source. Since day-extension lighting occurred during the entire night' period, plants were essentially grown under continuous lighting. Dry weight data was collected after 12 weeks from gemination (Moe et al., 1991).

DT/NT	Light source for day extension	Stem length (cm)		Dry weight (g)
		VB	Anthesis	
21/15℃ (+6 DIF)	INC	26.5a	43.1a	2.9b
21/15℃ (+6 DIF)	FL	20.5b	33.6b	2.4a
15/21℃ (−6 DIF)	INC	24.9a	39.6a	3.8c
15/21℃ (−6 DIF)	FL	14.4c	24.1c	3.0b

Letters represent mean differences identified through Tukey's test for mean separation across light source.

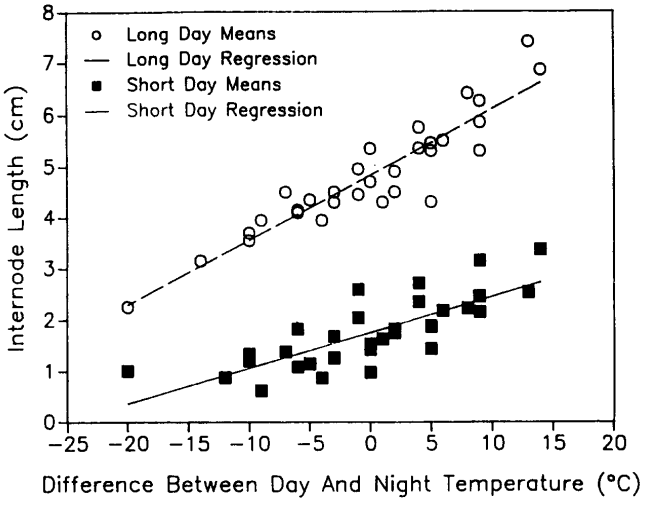

Fig. 5. Effect of DIF between DT and NT (DT-NT) on internode length of *Fuchsia* x *hybrida* 'Dollar Princess' plants grown under LD (9-h 15-min photoperiod plus 4-h NI using incandescent lamps at 2 μmol · m^{-2} · s^{-1})and SD(9-h 15-min photoperiod). Data were normalized across 1988 and 1989 experiments within photoperiod treatments. Regression function calculated from LD data was, internode length (cm) = 4.727 + (0.129 x DIF) (r^2=0.87) ; from SD data was, internode length (cm) = 1.871 + (0.071 x DIF)(r^2=0.64) (Erwin et al., 1991a).

nm) during the day reduced stem elongation but did not interact with DT/NT on *F. hybrida* (Erwin and Heins, unpublished). In contrast, stem elongation of plants grown in blue-deficient light did not respond to DT/NT (Maas and van Hattum, 1997). Continuous far-red (720-740 nm) light during the night overcomes cool DT/warm NT reduction in stem elongation on *Campanula isophylla* (Table 2) (Moe et al., 1991) and *Fuchsia hybrida* (Erwin, 1991). In contrast, continuous red light (660-680 nm) during the night increased cool DT/warm NT inhibition of elongation on *C. isophylla* (Moe et al., 1991). When daylight was supplemented with red light (5-10 μmol · m^{-2} · s^{-1}), reduction of *F. hybrida* elongation by cool DT/warm NT was enhanced/increased (Erwin and Heins, unpublished).

Anatomical Basis For DT/NT Responses

Basis for DT/NT effects on stem elongation are not clear. DT/NT effects on *L. longiflorum* stem elongation are due to differences in cell length (stem parenchyma and epidermal cells) and not division (Erwin et al., 1991b; Erwin et al., 1994a) (Figs. 6a and b). Cell elongation increased linearly as DIF increased, while cell width was unaffected by DIF. In contrast to *L. longiflorum*, DT/NT effects on *C. isophylla* 'Hvit' stem elongation resulted from effects on both cell length and number per internode (Strom and Moe, 1997).

Basis for DT/NT Responses

DT/NT effects on stem elongation are likely due to both physical and biochemical effects on stem elongation. For instance, DT/NT effects on stem elongation may be due, in part, to physical effects on shoot turgor. Lecharny et al. (1985) showed *Chenopodium rubrum* L. stem elongation was affected when root temperature was altered independently of shoot temperature. Their data suggested shoot turgor pressure may play some role in determining temperature effects on stem elongation.

Early evidence suggests gibberellin (GA) involvement in DT/NT effects on stem elongation (Erwin et al., 1989a; Moe et al., 1991; Pinthus and Meiri, 1979; Zieslin and Tsujita, 1988). Exogenous application of GA overcomes inhibition of stem elongation by a -DIF environment on *Triticum* (Pinthus and Meiri, 1979), *L. longiflorum* (Zieslin and Tsujita, 1988), *C. isophylla* (Moe et al., 1991), *L. esculentum* (Erwin and Pierson, 1992), and *A. majus* (Myster, unpublished). In contrast, ancymidol application (GA biosynthesis inhibitor) resulted in a greater percent decrease in internode elongation of +DIF-grown plants than -DIF-grown *L. longiflorum* plants (Erwin et al., 1989a).

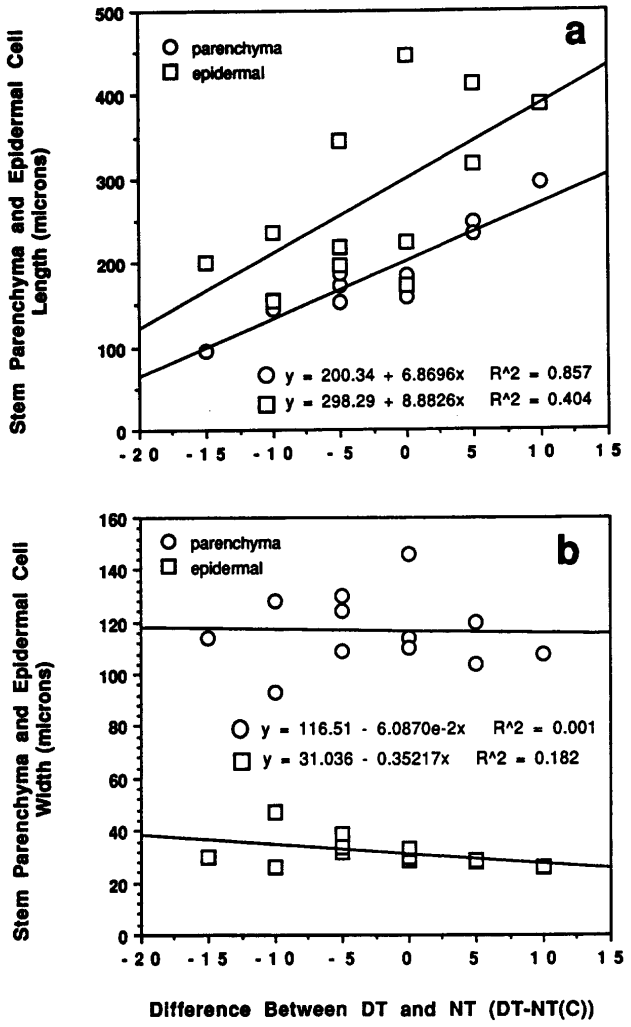

Fig. 6 a and b. The effect of the difference (DIF) between day (DT) and night (NT) temperature (DT-NT) on *Lilium longiflorum* cv Nellie White central parenchyma cell and stem epidermal cell length (a) and width (b). Equations are as follows : stem parenchyma cell length = 200 + 6.87 x DIF(r^2 = 0.86) ; stem epidermal cell length = 298 + 8.88 x DIF (r^2 = 0.40) ; stem parenchyma cell width=116 − 0.06 x DIF(r^2 =0.00) ; (stem epidermal cell width = 31.04 − 0.35 x DIF (r^2 =0.18) (Erwin et al., 1991b ; Erwin et al., 1994a).

In addition to data from exogenous application of GA, evidence suggests that DIF directly affects endogenous GA levels. Plants grown in a -DIF environment had reduced levels of GA1, GA19, GA44 and GA53 in *C. isophylla* compared to plants grown in a +DIF environment (Jensen et al., 1996).

Additional supportive evidence for GA involvement in DT/NT effects on stem elongation is evident in experiments utilizing genetic GA mutants. Work by Grindal and Moe (1997) showed that the dwarf *P. sativum na* mutant did not respond to DT/NT while the GA leaky synthesis mutants *ls* and *le* responded to DT/NT albeit in a reduced fashion. Further, the slender *P. sativum* mutant *la crys* (believed to be saturated in GA) showed little stem elongation response to DT/NT. Langton et al., (1997) showed that exogenous application of GA_{4+7} to the *gib*-1, *gib*-2, and *gib*-3 mutants of *L. esculentum* could completely overcome inhibition of stem elongation from growing plants in a cool DT/warm NT environment.

Data collectively, suggest that DT/NT effects on stem elongation are elicited primarily through effects on GA metabolism. Although there is a desire to develop a simplistic explanation for DT/NT effects on stem elongation, i.e. GA metabolism only, logic suggests that this response is likely an artifact of numerous points of regulation through effects on endogenous GA levels, changes in tissue responses to GA and physical effects on turgor. Both physical and biochemical effects on plant growth are both intrinsically involved in this process and can not be excluded.

Ecological Significance

What could be the ecological significance of DT/NT effects on stem elongation? Variation in DT/NT effects on stem elongation suggest species indigenous to tropical environments and woodland environments are less sensitive to DT/NT than species from temperate and prairie environments (Erwin et al., 1992a; Erwin et al., 1994b). Similarly, sensitivity to DT/NT appears to increase as the altitude of a species's indigenous environment increases. One hypothesis is that stem elongation responses to DT/NT are a mechanism by which plants direct growth towards elongation to maximize elongation at critical times to compete effectively in a community (Erwin et al., 1992a; Erwin and Heins, 1995). For instance, species native to temperate climates may direct growth towards elongation in spring (high DIF) when effective competition is critical. Genetic dependence of stem elongation on DIF is, therefore, probably based on the indigenous environment and the degree of competition among plants for a species in its community.

Light

Stem elongation responses to light are mediated through three classes of regulatory photoreceptors: 1) phytochromes, that respond mainly to red (660-680 nm) and far red (720-740 nm) light and secondarily to blue and UV-light, 2) photoreceptors that are specific to blue (often referred to as cryptochrome, 440-500 nm) and UV-A (320-400 nm) light and 3) UV-B (280-320 nm) receptors (Von Arnim and Deng, 1996). Each receptor system affects stem elongation to some degree. In general, plant stem elongation increases as P_{fr}/P_r decreases, and as the intensity of blue and UV-light decrease (Gaba and Black, 1979; Von Arnim and Deng, 1996).

Species differ in their relative responses to light quality. For instance, *Sinapis alba* hypocotyl elongation is most sensitive to red/far red light and *Arabidopsis* appears to be most sensitive to blue light. Regardless of species, data suggest there are multiple partially redun-

dant mechanisms controlling stem elongation since genetic mutants specific for a single receptor still showed responses, albeit diminished, to light quality (Casal, 1995; Quail et al., 1995).

The predominant photoreceptor affecting stem elongation on most crop plants is phytochrome. Stem elongation responses to phytochrome can be divided into 3 groups: very low fluence responses, low fluence responses and high irradiance responses (HIR). When we consider whole plant responses to light quality, we are considering primarily low fluence responses and high irradiance responses. Phytochrome exists in primarily two forms: phytochrome A (I) and B (II). Each phytochrome cycles between P_r and P_{fr}. Phytochrome A is the predominant phytochrome present in imbibed seed and dark-grown seedlings. In contrast, phytochrome B is the predominant phytochrome present in light-grown plants (Johnson et al., 1994; Reed et al., 1994).

In general, plant responses to light quality are directly affected by the relative amounts of red vs far red that a plant is exposed to. Plant leaves act as a filter that allow more far red than red light to pass through (Morgan and Smith, 1981). Therefore, light quality below a canopy has an elevated level of far red compared to red light. As the proportion of red : far red light decreases, stem elongation increases, branching decreases, leaf area increases, and flowering is reduced. The degree of red:far red filtering varies with species. The red:far ratio below a canopy varies from 0.5-0.75 (oak woodland) to 0.11-0.45 (sugar beet crop) (Morgan and Smith, 1981). In addition, the degree of response of a plant species to red:far red light varies (Morgan and Smith, 1981).

Species vary in the degree that their leaves filter light. Species such as *Petunia* x *hybrida* appear to decrease the red content of light significantly more than species such as fuchsia (*F. hybrida*) (Cutlan et al., 1997).

In addition to direct filtering of light by a canopy there is evidence of detection of adjacent plants via reflected a reduced red:far red light ratio. Ballare et al. (1987, 1990) demonstrated that *Datura ferox* stem elongation was stimulated by reflected light with a decreased phytochrome photoequilibria from adjacent plants. Not only can plants detect neighbors, but they can detect how far away they are (Smith et al., 1990). Therefore, shade avoidance responses can be induced before shading actually occurs.

High fluence responses are those that involve a high irradiance response (HIR). Earliest experiments showed that exposure of plants to an end-of-day (EOD) exposure to far red light dramatically increased elongation. This response is fully reversible by exposure to red light. Interestingly, EOD stimulation of elongation only occurred when a plant was simultaneously exposed to higher irradiance blue light (Casal and Smith, 1989). Therefore, canopy-shaded plants, plants exposed to twilight, or by reflected low red : far red light from neighboring plants (all have low blue component) would exhibit a reduced response to EOD far red lighting.

The physiological basis for phytochrome elicited stem elongation responses are not clear. Light quality effects on stem elongation act through both effects on phytochrome levels and/or changes in tissue sensitivity to hormones. Red-light inhibition of stem elongation can be overcome by application of GA's. Additionally, far-red grown plants exhibit a reduced response to exogenous GA application (Von Arnim and Deng, 1996). However, there is increasing evidence that P_r/P_{fr} levels affect tissue sensitivity to GA. For instance, depletion of P_{fr} (via FR exposure) in *Cucumis sativum* increased tissue responsiveness to exogenous gibberellin application (Lopez-Juez et al., 1995). Application of GA_1 to *Pisum* mutants deficient in GA (NGB1766, Potts and Reid, 1983) showed that either EOD far red lighting or 24-hr darkness increased the sensitivity of tissue to a GA_1 application (Reid, 1988; Reid et al, 1990). GA_1 levels in *Pisum* plants grown under short or short day + EOD far red exposure were similar even though elongation was markedly different suggesting that far red lighting was affecting tissue sensitivity to GA_1 (Ross and Reid, 1992). Additional evidence provided by Toyomasu et al. (1994) and Peng and Harberd (1997) shows a clear interaction between phytochrome photoequilibria and tissue sensitivity to GA.

It is likely that species, phytochrome type and GA levels act together to affect stem elongation. For instance, it is likely that different phytochromes perceive the same environmental signals, but act through the regulation of different partial processes in a cooperative manner to evoke the physiological responses that collectively confer ecological and adaptive value (Smith, 1994).

Irradiance

The response of stem elongation to increasing irradiance with constant light quality is not understood. It is known that the reduction in stem elongation to irradiance is proportional to the logarithm of irradiance. Such a simplistic response could arise if the concentration of a single component, directly proportional to pigment transformation, determined the rate of some subsequent first order reaction. Phytochrome could be that factor and be associated with irradiance-inhibition of stem elongation through effects on phytochrome cycling rate (Johnson and Tasker, 1979; Bartley and Frankland, 1982; Fukshansky and Schafer, 1983). Clear experimentation identifying effects of irradiance on phytochrome cycling and subsequent effects on elongation have not been completed.

Photoperiod

In general, stem elongation decreases as day length decreases. The response of stem elongation to photoperiod is dependent on the irradiance plants are grown under indicating that phytochrome cycling may also be

involved in photoperiod regulation of stem elongation. Alternatively, photoperiod effects on stem elongation could be due to a direct reduction in the light-dependent conversion of GA_{19} to GA_{20} controlled via GA_{19}-oxidase. Conversion of GA_{19} to GA_{20} is associated with long-day stimulation of stem elongation (Zeevaart et al., 1991).

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