Redistribution of growth during phototropism and nutation in the pea epicotyl

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Redistribution of growth during phototropism and nutation in the pea epicotyl*

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Abstract. First positive phototropism of the third internode of intact, 5-d-old pea (*Pisum sativum* L.) seedlings, grown under continuous, dim red light, showed maximal response following a photon fluence of 3 $\mu mol \cdot m^{-2}$ blue light. Greater or lesser fluences (with irradiation time 100 s or less) caused less bending, no response being detectable above 300 or below 0.03 $\mu mol \cdot m^{-2}$. Bilateral irradiation with blue light caused no detectable inhibition of growth rate over that range of fluences. The linear nutation of the pea third internode was shown to be driven by a balanced oscillation of growth rate such that the overall growth rate was little changed during the oscillation. Phototropic stimulation changed neither the amplitude nor the period of nutation. Nutation and phototropism probably regulate growth independently. Phototropism in response to the optimal blue light fluence was caused by concomitant depressed growth on the irradiated side and stimulated growth on the shaded side of the bending internode. These results are consistent with the Cholodny-Went hypothesis which states that unilateral blue light induces a lateral redistribution of a growth regulator.

Key words: Blue light – Growth redistribution – Nutation – Phototropism – *Pisum* (phototropism).

Introduction

Phototropism, the directed bending of plants in response to unilateral light, has been extensively studied in two grass species, oat and maize. In contrast, dicotyledons and other monocotyledons have received less attention. Characterization of the light dependence of the bending response in oat has shown the existence of two distinct response types (Went and Thimann 1937; Zimmerman and Briggs 1963). These are "first-positive" where the response is a function of light fluence only and irradiation duration is brief (less than 2 min); and "second-positive", for longer irradiations, where the response is a function of the length of irradiation (for reviews, see Dennison 1979; Pohl and Russo 1984). Steinitz and Poff (1986) have recently found for *Arabidopsis* hypocotyls that first and second positive phototropism may not be distinct types of response, despite their photobiological differences. Steyer (1967) compared the bending response of *Avena* to that of 13 species of dicotyledons as well as three other grass species, and made the discovery that the light dependence of the response in all of these species (save sunflower) was very similar, including both first and second positive bending. Thus, the mechanism for response to asymmetrical illumination may be shared widely in the plant kingdom.

To compare the phototropism of coleoptiles in greater detail to that of the stems of dicotyledons one should understand the growth reactions that drive the bending. Several investigations of the growth reactions during phototropic bending in *Avena* coleoptiles have been made and given complex and contradictory results (Macleod et al. 1986, and citations therein). *Avena* may possess several light-mediated growth responses and thus may be a poor choice for studying phototropic growth responses. Growth during first positive phototropism has been investigated in maize (Iino and Briggs 1984) and during second positive phototropism (i.e continuous irradiation) for a variety of dicotyledons (Franssen et al. 1981; Hart et al. 1982; Rich et al. 1985). The results in maize have shown a balanced redistribution of growth between the shaded and irradiated sides of the coleoptile, whereas the results with the dicotyledons have shown several different patterns. Because of the different experimental conditions, the results for

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Abbreviations: R = red light; BL = blue light the dicotyledons are not readily comparable to the ones for maize. To compare directly the results in maize to those in a dicotyledon, I have used conditions very similar to those used by Iino and Briggs (1984) and have investigated the growth changes during first positive phototropism in pea.

A problem with measuring elongation of dicotyledonous stems is circumnutation. This movement makes data from time-lapse photography misleading because the length of a marked stem zone recorded on the film will change as the stem changes its angle to the film plane. The linear form of nutation known to occur in pea (Britz and Galston 1982) means that meaningful elongation measurements can be made in this material, provided that the plane of linear oscillation is parallel to the film plane.

Time-lapse photography was used to measure the differential growth that occurred during nutation and phototropism in the third internode of pea seedlings grown under continuous red light (R). In addition, the fluence-response curve for first positive phototropism induced by blue light (BL) and the sensitivity of straight growth to BL applied bilaterally were characterized.

Material and methods

Plant material. Pea (*Pisum sativum* L. cv. Alaska) seeds were bought from W. Atlee Burpee Co. (Warminster, Pa., USA) and stored at 4°C in the dark. Seeds were imbibed for 4 h under running de-ionized water, and sown in clear, plastic boxes ($26 \cdot 36 \cdot 11$ cm^3) on two layers of bleached paper (No. 62360 Kimpack; Kimberly-Clark, Neenah, Wisc., USA) saturated with de-ionized water. The boxes had loosely-fitting, clear plastic lids. Seedlings were transplanted 2 d and experiments done 5 d after imbibition. From imbibition onward, the plants were kept under continuous dim R (0.2 μmol$\cdot$m$^{-2}\cdot$s^{-1}). Red light was obtained from red fluorescent lamps (F40/RED, Sylvania; GTE Products, Danvers, Mass., USA) filtered by one layer each of red and yellow plastic (Nos. 14 and 1 Cinemoid; Rank Strand Electrics, London, UK). All plants were grown and all experiments were done in the same room, where light other than R (and BL needed for experimentation) was excluded.

Experimental irradiation. Blue light was obtained with a slide projector (600 H; Eastman-Kodak, Rochester, N.Y., USA) from a 300-W projector lamp (ELH). Light passed through a broad-band, blue glass filter (B 5-60, 5 mm thick; Corning Glass Works, Corning, N.Y., USA). A light-tight box with a filter-port enclosed the projector. Fluence-rate was adjusted by neutral density filters (Balzers, Marlborough, Mass. USA). A tray of plants was placed perpendicular to the light beam, at a little over 2 m from the projector lamp. The hook and upper internodes were irradiated. For bilateral irradiations, a second, identical projector was placed at 180° to the first. Photon fluence rates were measured with a quantum photometer (Li 185-A; Lambda Instruments Corp., Lincoln, Neb., USA) before each series of irradiations. For bilateral irradiations, the fluence rate from each projector was matched to better than 5% by moving one projector. Red light was also provided during BL irradiation, from lamps placed above (approx. 1 m) the plants. The entire irradiation arrangement was enclosed by black cardboard and covered with black cloth so that BL penetration into the experiment room was undetectable.

Fluence-response studies: unilateral irradiation. Imbibition began in the morning. Two days after sowing, 10–20 seedlings were transplanted into plastic trays ($22.5 \cdot 7.2 \cdot 5$ cm^3; Instant Drawer Organizers; Rubbermaid Co., Chico, Cal., USA), filled with vermiculite and moistened with 400 ml of de-ionized water. A clear plexiglass cover ($22 \cdot 6.5 \cdot 9$ cm^3), with holes in the top, was placed over each tray, resting firmly on the vermiculite. These covers were removed only briefly for experimental treatment. On the third day following transplantation, the seedlings were 6–9 cm in height, with third internodes 0–2 cm long. To begin the experiment, plants without straight shoots were removed, as were those whose hook plane diverged more than 20° from that of the tray's long axis. From 6 to 14 plants would remain. After selection was completed for all trays, a short period (approx. 0.5 h) elapsed before unilateral irradiations, perpendicular to the hook plane, were begun.

At 120 min following BL irradiation, the hooks were cut off and plants excised above the root. The basal ends were stuck to a strip of masking tape affixed to a piece of plastic, such that the epicotyl curvature was coplanar with the plastic. This assembly was photocopied (3300 Bond Copier; Xerox Corp., Stamford, Conn., USA). Lines were drawn on the copies tangent to the first internode and to the apical-most region remaining (second or third internode). The angle between tangents was measured with a digitizer (9111 A; Hewlett-Packard, Palo Alto, Cal., USA), and used to quantify the phototropic response.

Fluence-response studies: bilateral irradiation. Plants were prepared as described above. After selection, they were marked with India ink applied with a fine brush. A pair of marks spanning approx. 1 cm was placed within the third internode (occasionally including part of the second), on the side that would face the camera (and a second pair on the opposite side, away from the camera). At 0.5 h after marking, the plants were photographed, given bilateral irradiation (perpendicular to the hook) and photographed again at 60 min after the first exposure. A fine-grained film (Kodak, Technical Pan Film 2415) was used for photography, exposed for 2 s under ambient light (R). Developed negatives were placed in a slide projector for analysis ($8 \times$ life size). From the enlarged image, the positions of marks, and the line joining them along the internode's central axis, were traced onto paper. The distance between marks, along the line, was measured with a digitizer (see above).

Time course: bilateral irradiation. Five beakers (30 ml) were placed in a plastic tray (same as above) and the whole assembly filled with vermiculite. Each beaker was given 20 ml and the surrounding vermiculite 300 ml of de-ionized water. Seedlings were transplanted one per beaker and the plexiglass covers (as above) put over the trays. Before experimentation, plants with straight shoots and of uniform size were selected. Third internodes were marked as described above, and the beakers were rotated so that the plane of the hook for each plant was parallel to the tray's long axis. Controls were treated exactly as experimentals except BL was not turned on. The zone's length at each time was obtained (as above) and the natural logarithm of the length taken. Logarithmic time-course data were normalized by subtracting the initial value from each subsequent one. For the phototropic time course shown (Fig. 5), plants were prepared and experiments carried out as above, except that after unilateral irradiation the plants were rotated by 90°, such that the plane of bending was parallel to the film.

Time course: distribution of growth and nutation. For these experiments, imbibition was started at night, but transplantation (into beakers as described above) and experimentation were done at the same time as for the morning-imbibed plants used for all of the above experiments; thus, the experimental plants were 5.5 d rather than 5 d old. Taller covers were placed over the seedlings ($22 \cdot 6.5 \cdot 13 \cdot cm^3$). After selection, third internodes were marked with two zones, as depicted in Fig. 1. These zones ranged in length between 0.8 and 1.4 cm (overall plant height between 8 and 11 cm). The beakers were then rotated so that the plane of the hook would be parallel to the BL beam. A half hour later, irradiation was given, the beakers were rotated by 90°, and time-lapse photography begun. Controls were handled identically except BL was not turned on.

A custom-built tripod pivot was used to photograph more than one tray of plants on the same occasion without moving the trays between photographic exposures. This pivot allowed the camera to be rotated in the horizontal plane between three set positions. In this way, three trays could be photographed indefinitely without moving them. Growth was measured as described above. Curvature was measured as the angular displacement from vertical of a line drawn tangent to the most apical region (below the hook) of the third internode (α in Fig. 1). A positive sign indicates a deviation away from the hook apex. Blue light was given with the apex away from the light (i.e. shaded by the internode); bending toward the light source would thus also be positive.

Statistical significance was assessed with paired t-tests unless stated otherwise.

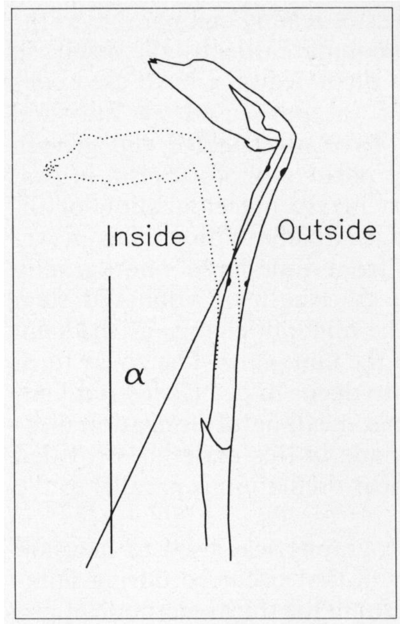

Fig. 1. Drawing of a pea third internode from nutation records. The hook is coplanar with the paper. The angle, α, used to quantify nutational movement, is shown by straight lines. Marked zones used to measure elongation are shown, as are the positions referred to as "inside" and "outside". Dotted image shows the opposite extreme of the nutational oscillation for this plant, 50 min later

Results

Nutation. To examine nutation, plants were grown in beakers and aligned as required for photographing movements parallel or perpendicular to the hook plane. Third internodes oscillated in the plane of the hook with an average amplitude of 15°, centered at 10° from the vertical, whereas in the plane perpendicular to the hook the average amplitude was 3° and was centered on the vertical. These magnitudes agree with those previously reported for R-treated pea by Galston et al. (1964) and Britz and Galston (1982). These results mean that projection error for length measurements of marked zones on the epicotyl can be minimized by placing the film parallel to the hook and the large-amplitude oscillations. (The reduction of that error is by more than the difference between amplitudes because the error varies as the cosine of the deviation from the vertical.)

To measure growth during nutation and phototropism, plants were irradiated in the hook plane (Fig. 1) and then rotated by 90° so that the plane of phototropic bending and of nutation were coplanar and parallel to the film. Figure 2 shows representative results from a single, control plant. The upper two lines show the growth of the internode towards (inside) and away from (outside) the hook (see Fig. 1). Periods of slow and rapid elongation alternated on the two sides of the internode.

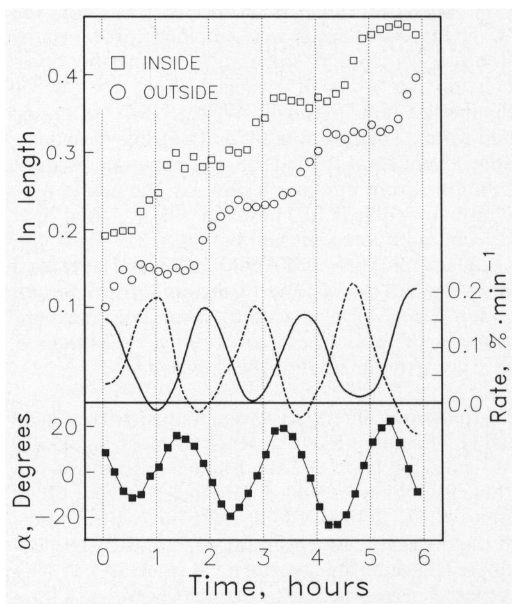

Fig. 2. Growth and nutation of a single pea seedling. For *upper two curves*, symbols show measurements made on inside (□) and outside (○) of a control plant (see Table 1). Initial length of each recorded zone was approx. 1.3 cm. Smoothed lines were drawn through the data by computer and differentiated numerically to give the rates plotted by the *middle two lines*. *Solid line* is for outside data. *Bottom curve* (■) shows angular displacement from vertical of the upper part of the third internode

This is more readily seen in the middle two lines in which growth rates derived from the length data are plotted. The oscillation in growth rate on either side of the internode was approximately sinusoidal, and the phase difference between the two sides was about 180°. Moreover, the mean growth rate (i.e., the growth rate of the central axis of the internode) was constant during the nutation.

The lowest curve plots nutation, the angular displacement from vertical of the upper part of the internode (α, Fig. 1). Comparison of this angle with the growth rates on either side of the stem shows that, as expected, when the growth rates were very different the angular deflection was changing rapidly; and when the rates were similar there was little angular change. The individual plant in Fig. 2 appears to have growth-rate minima that are negative (i.e. shrinking); but for most plants, growth-rate oscillations were not as large as those shown in Fig. 2, and minima were positive.

Interaction between unilateral BL and nutation. Records, similar to those in Fig. 2, were obtained for plants given the optimal BL fluence for phototropism (see below) and were analysed to detect interaction between unilateral BL and nutation. The results are presented in Table 1. The values found for period and amplitude agree with those reported before (Galston et al. 1964; Britz and Galston 1982). Neither the period of oscillation nor its amplitude was affected by the irradiation. The data on phase angle are presented for completeness, but their variability makes interpretation difficult. The phase angle for controls (both sets taken together) does equal 180°, as expected for randomly oscillating plants, whereas that for BL-treated plants is later, by about 50°. Such a delay is consistent with a linear (phototropic) displacement adding to a sinusoidal (nutational) displacement (see Heathcote and Aston 1970). Blue light only slightly synchronized the nutation (variance of the phase was significantly reduced in one experiment, Table 1). The clearest effect of BL on the oscillation was to increase the maximum value of the angular displacement (Table 1). This effect is highly significant, and persists over three cycles in the 6-h set with only slight decrease. The effect of BL was thus a net movement of the oscillating epicotyl toward the BL source, without change in the parameters of the oscillation. These results are most easily explained assuming nutation and phototropism are independent.

Growth during phototropism. The growth pattern observed following stimulation with the optimal BL fluence for first positive phototropism in pea (see below) is shown in Fig. 3. The curvature began at 10° from the vertical (the mean angular deflection of the third internode) and, with a lag of less than 20 min, rose to 30°. The growth rate for controls (Fig. 3, filled circles) has been obtained by averaging data from inside and outside, but taking

Table 1. Analysis of nutation in pea seedlings following a pulse of BL optimal for phototropism. Plants irradiated parallel to the hook plane with 3 $\mu mol \cdot m^{-2}$ in 17 s, or controls, were photographed at 10-min intervals for 2 h (Expt. 1) or for 6 h (Expt. 2). Maximum and minimum observed values of angular displacement were taken as peak and trough values. Period gives the average peak-to-peak and trough-to-trough time; phase (expressed as an angle between 0° and 360°) is the relative time in the cycle when the first peak occurred; magnitude is the average angular displacement from peak to trough; and peak is the average maximum angular displacement from the vertical. Means ± SE are presented. Sample size is given in parentheses beside treatment listing

Treatment	Period (min)	Phase (°)	Magnitude (°)	Peak (°)
Expt. 1				
Blue (15)	92.0 ± 3	215 ± 14[a]	29.6 ± 2.9	43.0[b] ± 3.3
Control (14)	91.4 ± 2	202 ± 32[a]	31.2 ± 3.1	26.5[b] ± 2.1
Expt. 2				
Blue (13)	100.5 ± 2	240[c] ± 16	32.2 ± 2.6	41.6[b] ± 2.2
Control (15)	102.0 ± 2	146[c] ± 23	28.3 ± 2.1	21.3[b] ± 1.6

[a] Equivalence of variances rejected at $P < 0.005$ (F test of variances)
[b] Equivalence of means rejected at $P < 0.001$
[c] Equivalence of means rejected at $P < 0.005$

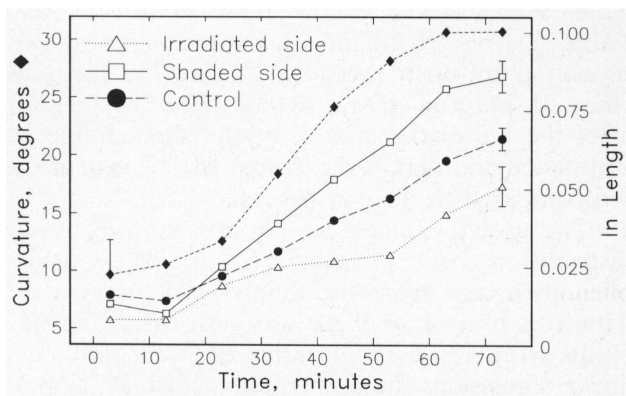

Fig. 3. Redistribution of growth in pea seedlings following a BL pulse, parallel to the hook plane, optimal for phototropism. Data taken from one of the experiments used to quantify nutation (Expt. 2 in Table 1). The average angular displacement from vertical (◆) is plotted as curvature, with a typical SE indicated at one time. Mean relative length is plotted for 15 control plants (●), and shaded (□) and irradiated (△) sides of 15 BL-treated plants. Typical SEs are shown at a single time

Table 2. Distribution of growth in pea seedlings following a BL pulse optimal for phototropism. From the same experiments described in Table 1, growth rates were found for each plant from slope of a linear regression line fit to six consecutive points (from 13 to 63 min after BL) in the elongation record. For control plants, rates obtained for the inside ("shaded") and outside ("irradiated") were averaged for analysis. Change gives the difference between the BL-treated and control rate as a percentage of the control rate. Means are presented ± SE; n = 15 throughout

	Rate ($10^{-4} \cdot min^{-1}$)		Change (%)
	Blue	Control	
Expt. 1			
Shaded side	$14.1^{a} \pm 1.2$	(8.8)	+ 57
Irradiated side	$5.2^{b} \pm 1.3$	(9.1)	− 42
Mean	9.7	$9.0^{c} \pm 0.8$	+ 7
Expt. 2			
Shaded side	$14.3^{d} \pm 1.2$	(8.2)	+ 54
Irradiated side	$4.7^{e} \pm 1.2$	(10.3)	− 49
Mean	9.5	$9.3^{f} \pm 0.8$	+ 3

a = b, d = e, rejected at $P < 0.001$
a = c, d = f, e = f, rejected at $P < 0.005$
b = c, rejected at $P < 0.025$

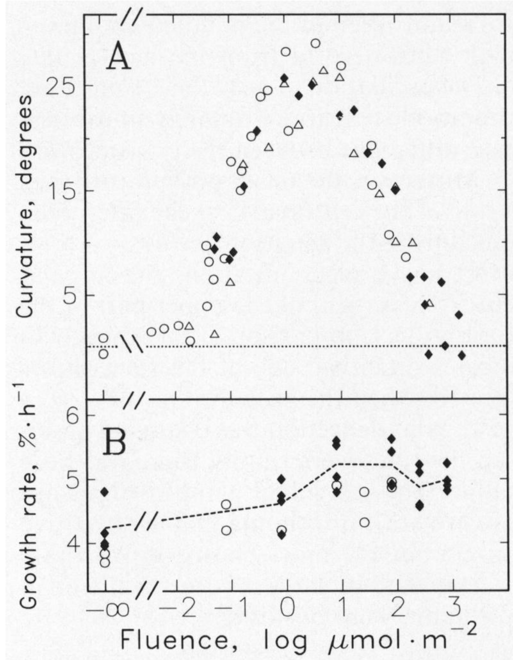

Fig. 4 A, B. Fluence-response curves for phototropism and straight-growth in pea seedlings. Minus infinity on the abscissa indicates unirradiated control. **A.** Phototropism. Unilateral BL given (perpendicular to the hook plane) in 10 s (○), 30 s (△) or 100 s (◆). Curvature was measured 2 h following irradiation. Each point shows mean curvature obtained from 2 to 5 trays of plants (total sample size between 15 and 30, SEs were around 2°). **B** Straight growth. Bilateral BL given in 10 s (○) or in 100 s (◆). Abscissa indicates total fluence given. Growth rate was computed as the natural logarithm of the ratio of initial to final length of the marked zone, divided by the time interval (1 h) between initial and final exposures. Points show mean growth rate for 9–15 plants, SEs ranged from 2 to 6% of the mean value. *Dashed line* passes through the mean of the replicates for 100-s irradiation

either side alone gives about the same rate (see Table 2). The growth of BL-treated plants is represented by open symbols. During the interval when BL-induced curvature took place (20–60 min after the pulse) the growth of the shaded side is stimulated and that of the irradiated side is depressed compared to the control rate.

The growth pattern in Fig. 3 is one of a redistribution of growth. To quantify this phenomenon, a regression analysis of the growth data from individual plants was performed. The six points from 13 to 63 min after BL were used for linear regression: the regression coefficient (slope) gave average growth rates for the interval, and these were treated as variates for each group in question (Table 2). The growth rate of the shaded side was stimulated by about 55% of the control rate, and that of the irradiated side was depressed by slightly less. The net result is but a small increase in growth (5%) for the central axis during the response. Thus, as for maize coleoptiles grown under R (Iino and Briggs 1984), a redistribution of growth appears to account for the first-positive phototropic bending of the pea epicotyl.

Sensitivity of pea to unilateral and bilateral BL. The sensitivity of pea epicotyls to single pulses of unilateral and bilateral BL was investigated over a range of fluences. For these investigations, plants were irradiated perpendicular to the hook plane, at right angles to the nutation. For measurements of phototropic bending in such orientation, the initial curvature (toward the light source) is essentially zero.

The light-dependence of the bending response of pea epicotyls to a unilateral pulse of BL is shown in Fig. 4A. The curve for the magnitude of bending on fluence is bell-shaped. This is the typical appearance of the first positive phototropic response in several higher-plant species (Steyer 1967), in the alga *Vaucheria* (Kataoka 1977) and in the fungus *Phycomyces* (Iino and Schäfer 1984). The optimal BL fluence for bending in peas, approx. 3 μmol·m^{-2} (Fig. 4A), is the same as that observed for maize coleoptiles grown under virtually identical conditions (Iino and Briggs 1984) and similar to that for etiolated oat coleoptiles pretreated with R (Zimmerman and Briggs 1963) and for dark-grown

Arabidopsis hypocotyls (Steinitz and Poff 1986). For the experiments of Fig. 4A, irradiations were given in 10, 30 of 100 s without appreciable difference in response; thus, over the limited time span tested, reciprocity holds, as it does for this response in coleoptiles of maize (Iino and Briggs 1984) and oat (Zimmerman and Briggs 1963), provided that the duration of irradiation be sufficiently brief (i.e. < 5 min).

Growth inhibition of dicotyledonous stems following prolonged irradiation with BL is well known (Gaba and Black 1979) and has been seen also for pulse irradiations (Cosgrove 1981). One possible mechanism for phototropic bending is the establishment of a transverse gradient of growth inhibition following the gradient of fluence rate established by unilateral irradiation (Blaauw 1918; Firn and Digby 1980). To ascertain whether the growth inhibition seen on the irradiated side of the pea epicotyl (Fig. 3) resulted from an inhibitory effect of BL on elongation, the sensitivity of epicotyls to bilateral BL irradiation was examined. Figure 4B shows the average growth rate over 1 h directly following bilateral irradiation. No growth inhibition was observed over the range of fluences for which the tropic response occurs. Instead, a tendency to promote growth was observed at the higher fluences. This is a small effect, and goes in the "wrong" direction to explain tropism: if it were induced asymmetrically with unilateral irradiation, the plants would bend away from the light source.

The small growth promotion by BL seen in Fig. 4B could arise from a strong growth inhibition followed by a rapid recovery and overshoot. It was thus necessary to measure the growth during the hour following irradiation. Results are shown in Fig. 5 for stimulation with the optimal BL fluence for bending. The curvature response to unilateral irradiation (perpendicular to the hook plane) proceded linearly after a lag of less than 20 min. An inhibition of growth was apparent over the first 10 min, but it occurred in the control plants as well as the BL treated ones. Such brief inhibitions of growth have been observed following experimental manipulation (Cosgrove 1981; Gordon et al. 1982) and may be here a response to movement to and from the irradiation chamber. After 10 min, the control and BL-treated plants grew at a similar, rapid rate, with no indication of any BL-induced growth inhibition. Interestingly, a stimulation of growth by BL appeared to occur in the last 20 min of the experiment. The slopes of regression lines drawn through growth data of individual plants were on the average greater for BL treatment than for controls, 7.0 ± 0.2 versus $5.6 \pm 0.2\% \cdot h^{-1}$, respectively (mean ± SE; equivalence of means rejected at $P < 0.001$).

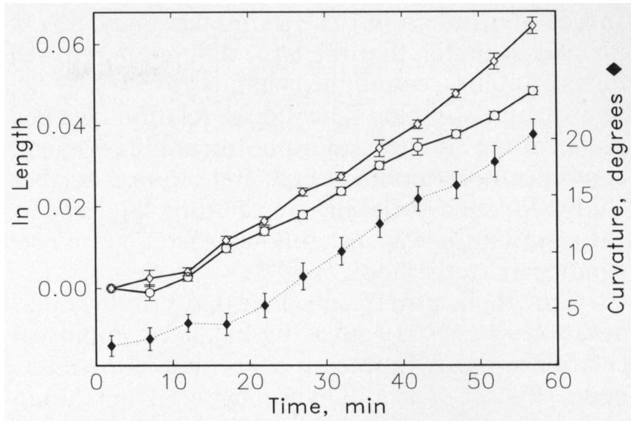

Fig. 5. Time course of curvature development and growth in pea seedlings following a pulse of BL. Starting at time zero, 25 s BL was given (perpendicular to the hook plane), unilaterally for curvature measurement (3 $\mu mol \cdot m^{-2}$) or bilaterally for growth measurement (total = 6 $\mu mol \cdot m^{-2}$). *Open symbols* plot mean normalized length ± SE (○) for control and (◇) for bilateral BL treatment. Diamonds (◆) plot mean curvature (in degrees) ± SE for unilateral BL treatment. Results from three experiments were pooled. Total sample size = 15 throughout

The time lag and the initial rate of curvature development observed here are similar to those shown in Fig. 3 for irradiation parallel to the hook. The time lag for curvature development in either plane (Figs. 3, 5) is an upper limit because of the transient growth inhibition happening after irradiation.

Discussion

The independence of phototropism and nutation. The linear nutation of the pea epicotyl has been shown to be independent of gravitropism (Britz and Galston 1982) and thus may represent the class of nutation driven by endogenous rhythms, for which the mechanism is unknown (see review by Johnsson 1979). In this study, the nutational movement of pea epicotyls grown under continuous R was apparently independent of phototropic movement (Table 1); the same conclusion was reached for second positive phototropism (Britz and Galston 1983). This independence implies that each type of movement uses a separate growth-controlling mechanism. However, the phase of nutation did exert some influence on the time course of phototropic bending. For plants irradiated parallel to the hook, the time lag before the start of the phototropic response was very different among individuals, apparently dependent on whether the plants were moving toward of away from the BL source at irradiation. The variability may be explained assuming that the large differential growth during nutation cannot be instantly reversed by the phototropic stimulus. The precise relation between phase of the nutation and phototropic movement could not be determined here and requires further study. No such variability in the time lag for curvature initiation was seen following irradiation perpendicular to the hook (Fig. 5).

Growth measurements here have shown that nutation in peas is caused by balanced, rapid oscillations of growth rate on either side of the internode (Fig. 2). The difference between maximum and minimum growth rates was large ($0–12\% \cdot h^{-1}$) and the time elapsed between the occurrence of these extremes was small (40–50 min). Any mechanism of growth control proposed for nutation must account for these large and rapid transitions. In peas, these oscillations are confined to the plane of the hook; however, in plants where circumnutation occurs, it is possible that zones of growth rate maximum and minimum move circularly (or helically) around the stem. Mayer et al. (1985) have shown that balanced oscillations of turgor pressure in cells of the laminar pulvinus cause the sun-tracking movements of bean leaves; however, those leaf movements have a circadian period and involve reversible volume changes, not growth, and any mechanistic connection to nutation they may have remains to be shown.

The linear nutation of the pea internode makes it a good system for studying the movement. Measurement of local elongation during the more usual circumnutation is difficult, requiring two cameras and stereoscopic processing (Mueller et al. 1984). Better-resolved measurements of localized growth could further characterize the shape of the oscillation in growth rate and could ascertain whether it propagated along the axis; such findings would deepen understanding of nutation.

Redistribution of growth during phototropism. The redistribution of growth found for first-positive tropism of pea (Fig. 3) probably underestimates the amount by which BL changes growth rates. To ensure visibility, the marks were placed a little off from the extreme edges of the internode (toward the camera) so the growth differential measured was not the maximum that occurred. The greatest source of error comes from the lack of synchrony among plants. The increased displacement towards the light source takes place on average as shown by the filled diamonds in Fig. 3; but many plants react sooner and others later. For a better estimate of the amount of BL-induced growth change, the data were aligned such that the first peak of angular displacement toward the light source coincided for all individuals; and six consecutive time points on the ascending side of that peak were then taken, and linear regression lines fit to the length data to get growth-rate values (same method as for Table 2). The growth rate found for the shaded side was $17 \cdot 10^{-4}\ min^{-1}$ and on the irradiated side it was $2 \cdot 10^{-4}\ min^{-1}$. These each represent a difference with respect to the control growth rate of approx. 80%, which is larger than the 50% change presented in Table 2.

Despite the uncertainty introduced by the lack of synchronized bending among BL-treated plants, the conclusion remains that both stimulation and depression of growth occurred along the pea internode during bending (Table 2, Fig. 3). The concomitant stimulation and depression of growth resembles what has been shown to occur with first positive phototropism for coleoptiles of R-pretreated oat (Blauuw-Jansen 1958) and for R-grown maize (Iino and Briggs 1984). Redistribution of growth has also been found for second positive phototropism in light-grown cress (Hart et al. 1982), mustard (Rich et al. 1985) and even for *Phycomyces* (Castle 1961). However, Macleod et al. (1986), investigating phototropism in *Avena* coleoptiles under a variety of conditions, have found that stimulation of growth does not always accompany inhibition of growth. Franssen et al. (1981) found inhibition of growth on the irradiated side to be the only consistently occurring growth change for a variety of dicotyledonous plants that had been continuously irradiated with unilateral white light.

For phototropism in maize, a lateral redistribution of auxin has been strongly implicated as the link between unilateral BL perception and altered growth rates (Briggs 1963; Baskin et al. 1985, 1986). The finding in pea of growth redistribution predicted by the Cholodny-Went hypothesis indicates that investigating endogenous auxin levels during pea phototropism would be fruitful. It would also be of interest to determine, if auxin redistribution does occur, whether it happens at the apical part of the third internode and moves basipetally, as in coleoptiles; or whether the redistribution is between epidermis and cortex all along the internode's axis, as has been seen for gravitropically responding pea internodes (Iwami and Masuda 1976).

Blue-light inhibition of straight growth occurs in many plants, including etiolated Alaska pea (Cosgrove 1981), and at fluences comparable to the larger of those used here (Fig. 4B). The absence of inhibition seen in Figs. 4B and 5 is surprising. It may be that growth under continuous R causes a loss of sensitivity for this light-growth response. Alternatively, were the rapid inhibitory effect of BL to be under phytochrome control in pea (unlike in many plants; Gaba and Black 1979), then, for phytochrome-saturating conditions, the inhibitory effect of BL would disappear. Hypocotyl growth in mustard has been shown to be under phytochrome control only, and growth inhibition from continuous, bilateral BL is not observed when mustard is grown under phytochrome-saturating conditions (Rich et al. 1985). Nevertheless, in pea, the growth stimulation induced by bilateral BL irradiation is probably real (Figs. 4B, 5), and if so, indicates that a BL-sensitive photosystem which influences elongation can still work.

First positive phototropic sensitivity in dicotyledons. Conflicting statements exist in the literature about first positive, BL-induced phototropism of etiolated, Alaska pea. Britz and Galston (1983) state that the response is undetectable. In contrast, Kang and Burg (1974) maintain that the fluence-response curve for first positive phototropism is not shifted to higher fluences by R-pretreatment. I show here (Fig. 4A) that the response exists in plants grown under continuous R. It may be that first positive phototropism is absent in truly dark-grown material and the green safelight used by Kang and Burg was able to induce sensitivity to a single BL-pulse. It is noteworthy that in the experiments of Steyer (1967), where first positive phototropic responses were found in a number of etiolated dicotyledons, the plants used were manipulated under (unspecified) red safelight. The fluence-response curve reported by Everett (1974) for R-treated radish matches that observed by Steyer (1967). Steinitz and Poff (1986) found first positive sensitivity in dark-grown *Arabidopsis* that had received 30 h of white light 3 d prior to BL irradiation. Whether the white treatment influenced subsequent sensitivity to BL was not determined. Thus, in dicotyledons, R-pretreatment may induce sensitivity to first positive phototropism; and this possibility merits critical investigation. If so, it is different from oat and maize, the coleoptiles of which do respond when etiolated, and in which R treatment lessens the sensitivity to a pulse of BL (Schäfer et al. 1984).

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