Growth Distribution during Phototropism of *Arabidopsis thaliana* Seedlings[1]

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The elongation rates of two opposite sides of hypocotyls of *Arabidopsis thaliana* seedlings were measured during phototropism by using an infrared imaging system. In first positive phototropism, second positive phototropism, and red light-enhanced first positive phototropism, curvature toward the light source was the result of an increase in the rate of elongation of the shaded side and a decrease in the rate of elongation of the lighted side of the seedlings. The phase of straightening that followed maximum curvature resulted from a decrease in the elongation rate of the shaded side and an increase in the elongation rate of the lighted side. These data for the three types of blue light-induced phototropism tested in this study and for the phase of straightening are all clearly consistent with the growth rate changes predicted by the Cholodny-Went theory.

It has been known for over a century that phototropism by a higher plant seedling results from different rates of elongation by the two sides of the shoot (Darwin, 1896). Blaauw (1909, 1915, 1918) postulated that the gradient of light induced different growth rates in the cells by which it was absorbed. Because the light was attenuated as it passed through the shoot, growth of the cells was inhibited more on the lighted side than on the shaded side (Blaauw, 1918). However, this localized light effect was not consistent with the demonstration of Boysen Jensen that there is stimulus transmission down the shoot (Went and Thimann, 1937). Three major theories consistent with the stimulus transmission were advanced to explain the differential growth during phototropism. These theories, those of Cholodny and Went (Cholodny, 1927; Went, 1928), Boysen Jensen (1928), and Paál (1919) suggested that unequal quantities of GF on opposite sides of the seedling are responsible for the changes in growth rates that result in curvature. The history of this aspect of phototropism is covered by Went and Thimann (1937) and Pohl and Russo (1984).

A controversy persists in the literature over the validity of the Cholodny-Went theory (Trewavas, 1992). Much of this controversy has resulted from a concentration on the identification and role of the GF. However, it is possible to study directly the applicability of the generalized Cholodny-Went theory without studying auxin distribution. As has been noted by Pohl and Russo (1984), the Cholodny-Went theory predicts an increase in growth rate on the shaded side and concomitant decrease in growth rate on the lighted side of the seedling as the result of a lateral movement of GF from the lighted to the shaded side (Cholodny, 1927; Went, 1928; Went and Thimann, 1937). In direct contrast, the Boysen Jensen theory predicts an increase in growth rate on the shaded side but no change in growth rate on the lighted side (Boysen Jensen, 1928). Finally, Paál's theory predicts a general inhibition of growth rate by light and a greater inhibition on the lighted side than on the shaded side (Paál, 1919). It is interesting that the prediction of Paál's theory is much the same as the prediction of Blaauw's hypothesis for differential growth, although the basic premise is different for the two. Paál's theory is predicated on the inhibition by light of a transmissible substance, whereas Blaauw's hypothesis is predicated on direct photoinhibition of growth of the individual cells. It follows that one should be able to distinguish between these possibilities (Cholodny-Went, Boysen Jensen, and Paál/Blaauw) with careful measurements of growth rates on the two sides of the tropistic organ.

As has been noted in the Cholodny-Went Forum (Trewavas, 1992), if the Cholodny-Went theory is to be generally accepted, the conditions for its validity must be carefully characterized. Since the study of tropisms has been refined, their complexities have come to be recognized. For example, multiple photoreceptor pigments are involved in the induction of phototropism (Galland and Lipson, 1987; Konjević et al., 1989). The amplitude of phototropic curvature is increased by the process of adaptation (Janoudi and Poff, 1991), and the kinetics of phototropic curvature may be quite complex (Orbović and Poff, 1991). This places increased importance on the careful characterization of the conditions for which the Cholodny-Went theory is valid.

Because of the emergence of *Arabidopsis thaliana* as a model system for the study of tropisms and because of difficulties of characterizing growth regulator(s) gradients across the extremely small *Arabidopsis* hypocotyls, we have measured growth rates of the hypocotyls during phototropism. Here we report growth rate changes on opposite sides of the hypocotyl during first and second positive phototropism and during the straightening following phototropism for both dark-grown and red light-preirradiated seedlings. These

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Abbreviation: GF, growth factor.

growth rate changes are all clearly consistent with the Cholodny-Went theory.

MATERIALS AND METHODS

Growth Conditions

Arabidopsis thaliana seedlings were grown as described previously (Orbović and Poff, 1991) with slight modifications. Two seeds of the Estland ecotype were sown per well of microassay strips containing 0.7% (w/v) agar supplemented with 1 mM KNO_3. The strips were placed in Parafilm-sealed plastic boxes, and germination was potentiated by chilling for 3 d at 4 ± 1°C in darkness followed by exposure to white light for 20 h at 25 ± 1°C. Following the white light treatment, the boxes containing the strips were placed in darkness for 42 h until the start of the experiment. Just before the beginning of each experiment, strips with the seedlings were removed from the boxes and positioned such that the seedlings could be imaged by the video camera. All manipulations of the seedlings were performed at 25 ± 1°C and RH >90% in complete darkness except for those experiments in which the seedlings were preirradiated with red light.

Light Sources

White light (65 μmol m^{-2} s^{-1}) for the potentiation of germination was provided by General Electric (Cleveland, OH) DeLux Cool-white fluorescent tubes. The blue light source consisted of a projector equipped with a Sylvania (GTE Products, Danvers, MA) 300-W ELH tungsten halogen lamp and a 450-nm interference filter (PTR Optics, Waltham, MA) with a half-bandwidth of 10 nm. First positive phototropism was induced by a 0.9-s pulse of blue light at 0.34 μmol m^{-2} s^{-1} to give a fluence of 0.3 μmol m^{-2}. This is the fluence required to induce the peak in first positive phototropism for *A. thaliana* (Steinitz and Poff, 1986). The red light that was used for the 1-h irradiation of seedlings from above (0.5 μmol m^{-2} s^{-1}) was obtained from a single gold fluorescent tube (GTE, Sylvania) wrapped with red cellophane (Highland Supply Corp., Highland, IL). This source provides radiation from 560 to 720 nm with a maximum output at 620 nm. The IR light source for the imaging system consisted of a Leitz Prado-Universal (Ernst Leitz GmBH, Wetzlar, Germany) projector with a 250-W tungsten halogen lamp and a Kodak Wratten 87c gelatin filter (Eastman Kodak, Rochester, NY) with <1.5% transmission at wavelengths lower than 800 nm (measured using a Perkin-Elmer Lambda 7 spectrophotometer). The IR source supplied radiation at 10 W m^2.

Fluence rates were measured with a Li-Cor (Lincoln, NE) Li-190 SA quantum sensor in combination with an Li 1000 Data Logger, or with a model 68 Kettering radiometer (Laboratory Data Control, Riviera Beach, FL). The duration of blue light irradiation was controlled with a Uniblitz shutter (Vincent Associates, Rochester, NY).

Data Collection

The IR imaging system described previously (Orbović and Poff, 1991) was used to record images of seedlings in the absence of visible radiation. Images were recorded every 10 min for 2 to 3 h and subsequently played back from the video tape for analysis using the Java (Jandel Scientific, Corte Madera, CA) video analysis program. Single-frame images of each seedling were displayed on the screen and the lengths of the two sides measured. The tip of the seedling was not used in the measurements because of the difficulty of finding a single point on the hook from which to measure. The lowest portion of the seedling (approximately one-eighth of the total length) was not used in the length measurement because it does not contribute to the elongation of the entire seedling (data not shown). Instead, the length of the hypocotyl was measured from a point approximately 0.5 mm above the well. The top of the hypocotyl was operationally defined as the apex of the hypocotyl on the inside of the hook (Fig. 1). Because the seedling and camera were fixed in place and magnification was held constant, this measurement was quite reproducible (see below).

The length of unirradiated seedlings and seedlings given blue or red light from above was measured along the central axis of the image of seedlings (Fig. 1, dotted line). For these three treatments, the average length of the opposite sides of a single plant for any particular time point was not significantly different from the length measured along the central axis. For this reason, the length of these seedlings was measured along the central axis. For all treatments, the initial length was subtracted from the lengths measured subsequently. This increment from the initial length was used for subsequent analysis.

The angle of curvature was measured from the frozen image of the seedling on the screen as previously described (Orbović and Poff, 1991), and any change from the initial
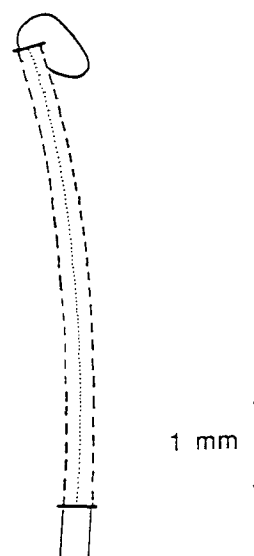

Figure 1. The image of a representative seedling "frozen" on the monitor screen. Dashed lines represent the length measured along opposite sides of the seedling. The dotted line represents the length measured along the central axis.

curvature was recorded as the increment or decrement in curvature.

The repeatability of length and angle measurements was assessed by 10 repetitions of length and curvature measurement for several seedlings. The repeatability error for length measurements of the 4.6-mm-long representative seedling ranged from 0.02% to 1.4% of total length. The repeatability error for angle measurements ranged from ±2° for 5° angles to ±5° for 40° angles. Sigma plot software (Jandel Scientific, Corte Madera, CA) was used for fitting curves to the data.

RESULTS

First Positive Phototropism

The elongation rate of unirradiated seedlings was approximately 50 μm 10 min^{-1} over the 3-h measurement period (Fig. 2A). These unirradiated seedlings showed no significant curvature over the 3-h monitoring period (Fig. 2B).

Seedlings that received a 0.3 μmol m^{-2} blue-light pulse from above showed no significant curvature over the 3-h period (Fig. 3B). Following the blue-light pulse, the growth rate of the seedlings was similar to that of the unirradiated seedlings (Figs. 2A and 3A). Throughout the 3-h monitoring period, the elongation rate of seedlings given the blue-light pulse from above was about 50 μm 10 min^{-1} (Fig. 3A).

For the first 80 min following a unilateral blue-light pulse, the shaded side of the seedlings elongated more rapidly than

Figure 3. The elongation rate (A) and the time course for development of average curvature (B) of seedlings irradiated with a blue-light pulse (0.3 μmol m^{-2}) from above at time zero. A, Elongation measured along the central axis, n = 18–34; vertical bars represent ± 1 SE. B, n = 18–34; vertical bars represent ± 1 SE.
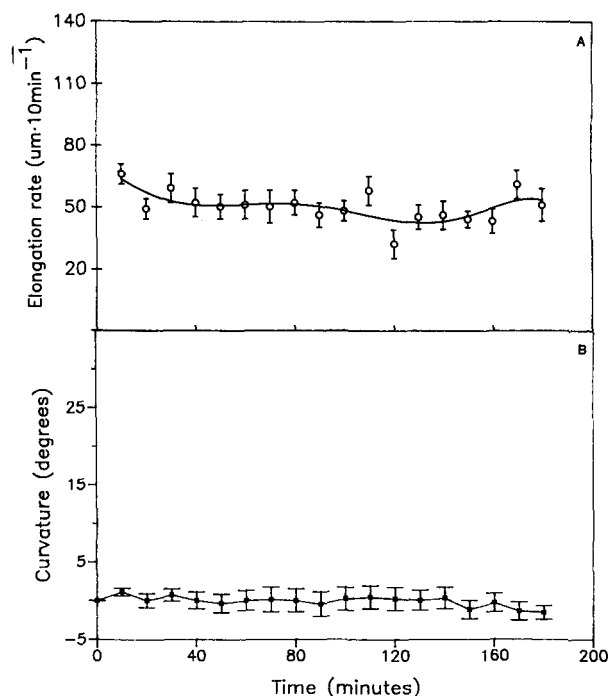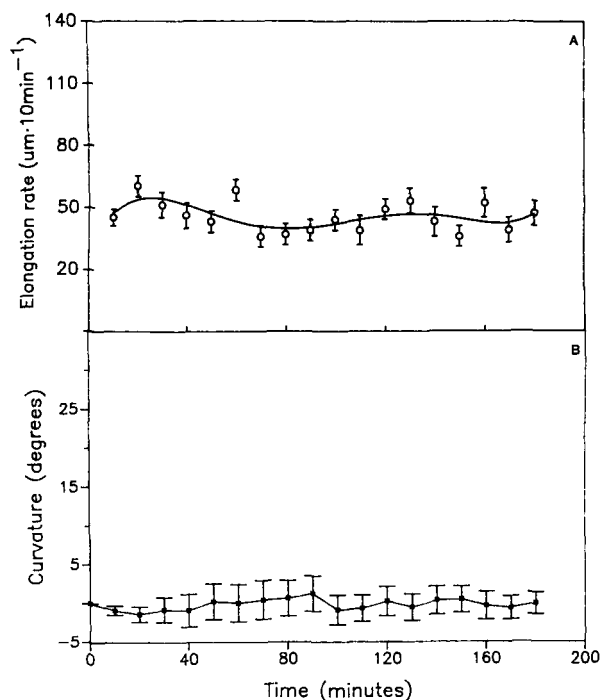

Figure 2. The elongation rate (A) and the time course for development of average curvature (B) of unirradiated seedlings. A, Elongation measured along the central axis; n = 25–30; vertical bars represent ± 1 SE. B, n = 25–30; vertical bars represent ± 1 SE.

the lighted side (Fig. 4A). During this time, the curvature of the seedlings steadily increased (Fig. 4B). About 30 min following the unilateral irradiation, the elongation rate of the shaded side reached its highest value while the elongation rate of the lighted side started decreasing. The elongation rate of the shaded side subsequently decreased and reached its lowest value about 150 min following the blue-light pulse. By 80 min after the blue-light pulse, the elongation rates of the two sides of the seedlings were approximately equal again. The elongation rate of the lighted side of the seedlings then exceeded the elongation rate of the shaded side. This corresponds very well with the point of maximum curvature at 80 min following the blue-light pulse and subsequent straightening (Fig. 4B).

Because the elongation rate of the lighted side of the seedlings during straightening did not reach a level as high as the elongation rate of the shaded side during bending (Fig. 4A), the seedlings retained a degree of curvature at the end of the experiment (Fig. 4B).

Second Positive Phototropism

Second positive phototropism was induced by 30 min of blue light at 4 × 10^{-4} μmol m^{-2} s^{-1} for a fluence of 0.72 μmol m^{-2}. Curvature and the elongation rates of the lighted and shaded side were measured for 120 min beginning with the initiation of the unilateral irradiation. The elongation rate of
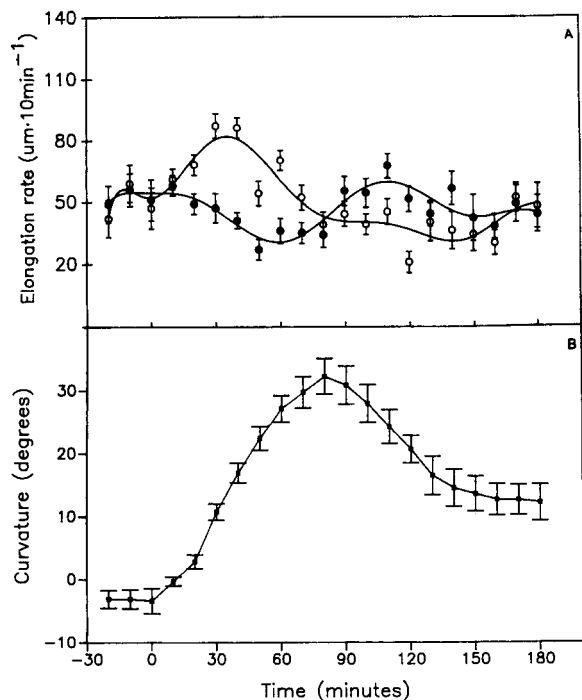
Figure 4. The elongation rate of lighted and shaded side (A) and the time course for development of average curvature (B) of seedlings during first positive phototropism (unilateral blue-light pulse, 0.3 μmol m^{-2}). A, O, Shaded side, n = 12–39; ●, lighted side, n = 12–39; vertical bars represent $\pm$ 1 SE. B, n = 12–39; vertical bars represent $\pm$ 1 SE.

the shaded side of the seedlings increased rapidly to a maximum about 30 min following the start of the irradiation and subsequently decreased (Fig. 5A). In contrast, the elongation rate of the lighted side decreased below the control level to a minimum at about 50 to 80 min and subsequently increased (Fig. 5A). At about 100 min following the initiation of the irradiation, the elongation rate of the lighted side became greater than that of the shaded side (Fig. 5A).

Second positive curvature was evident 20 min after the beginning of the irradiation. From 20 to 70 min, curvature of seedlings increased linearly; it reached its maximum at about 90 min, and then decreased until the end of the experiment (Fig. 5B).

Red Light-Enhanced First Positive Phototropism

Elongation of the red light-preirradiated seedlings was similar to but slightly higher than that of the unirradiated plants (Fig. 6A). The red-light preirradiation by itself induced no significant curvature in these seedlings (Fig. 6B).

When first positive phototropism was induced by a blue-light irradiation of 0.3 μmol m^{-2} in the red light-preirradiated seedlings, the growth rates on both sides of the seedlings rapidly changed (Fig. 7A). Within 10 min following the blue-light pulse, the shaded side of the seedlings elongated more rapidly than the lighted side. The elongation rate of the shaded side reached its maximum 20 min after the blue-light

pulse and subsequently started decreasing. The elongation rate of the lighted side decreased steadily following the blue-light irradiation, reached a minimum 40 min after the blue-light pulse, and subsequently increased. The elongation rate of the lighted side became higher than that of the shaded side by 80 to 90 min following the blue-light pulse and remained so until the end of the 2-h monitoring period (Fig. 7A).

Curvature to the blue-light pulse by the red light-preirradiated seedlings was evident within 10 min following the blue-light irradiation (Fig. 7B). Curvature increased to a plateau by about 70 min following the blue-light irradiation. Approximately 90 min after the blue-light irradiation, the seedlings began to straighten and continued to do so for the remaining 30 min in which they were monitored (Fig. 7B).

DISCUSSION

These data, taken together, show growth patterns that are predicted by the Cholodny-Went theory and not those predicted by either the Boysen Jensen theory or the Paál/Blaauw theories. The Boysen Jensen theory specifically addressed second positive phototropism and suggested that there is acceleration of growth on the shaded side with no effect on growth rate of the lighted side (Boysen Jensen, 1928). We observed an inhibition of growth on the lighted side (Figs.
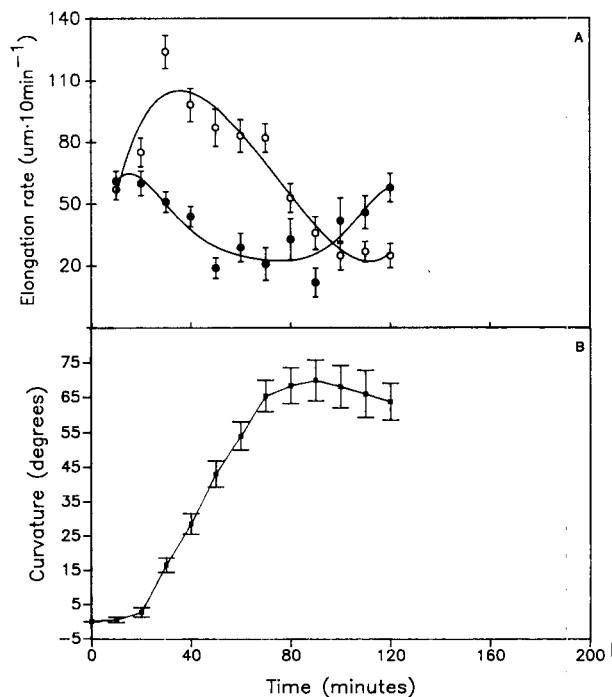

Figure 5. The elongation rate of the lighted and shaded side (A) and the time course for development of average curvature (B) of seedlings during second positive phototropism (unilateral blue light for 30 min, 0.72 μmol m^{-2}); A, O, shaded side, n = 19–26; ●, lighted side, n = 19–26; vertical bars represent $\pm$ 1 SE. B, n = 19–26; vertical bars represent $\pm$ 1 SE.
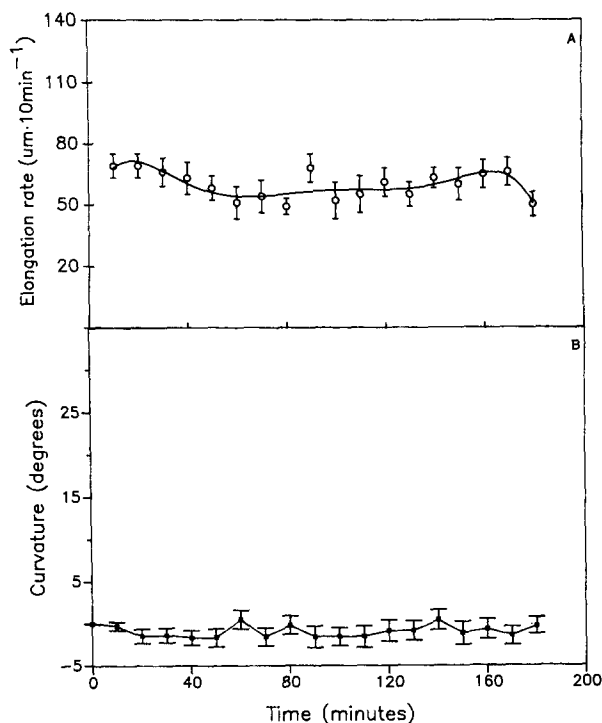
Figure 6. The elongation rate (A) and the time course for development of average curvature (B) of seedlings irradiated with red light for 1 h from above. A, Elongation measured along the central axis, $n = 21\text{--}26$; vertical bars represent $\pm$ 1 SE. B, $n = 21\text{--}26$; vertical bars represent $\pm$ 1 SE.

sides to reach their maximum and minimum, respectively, earlier than in the seedlings not preirradiated with red light (Fig. 7A).

The same growth rate changes that we see during phototropic curvature are also seen in reverse during the straightening phase, in which the seedling loses a portion of this curvature toward the light. The mechanism of straightening is unknown but it clearly results from a decrease in growth rate on the shaded side and an increase in growth rate on the lighted side. This is opposite to the changes in growth rate that were responsible for the curvature toward the light.

It is interesting to note that our conclusions might have been different had we measured growth at only one time or under only a single condition of phototropism. Under some conditions, the kinetics of growth rate changes appear to be different on the shaded and lighted sides of the seedlings. Because of this, individual time points can be found for which growth rate is increased on the shaded side and unchanged on the lighted side. Other individual time points can be found for which growth rate is unchanged on the shaded side and decreased on the lighted side. Thus, these time points, if taken individually, appear to be consistent with the Boysen Jensen or Paál/Blaauw theories. However, all of the data together are consistent only with the predictions of the Cholodny-Went theory.
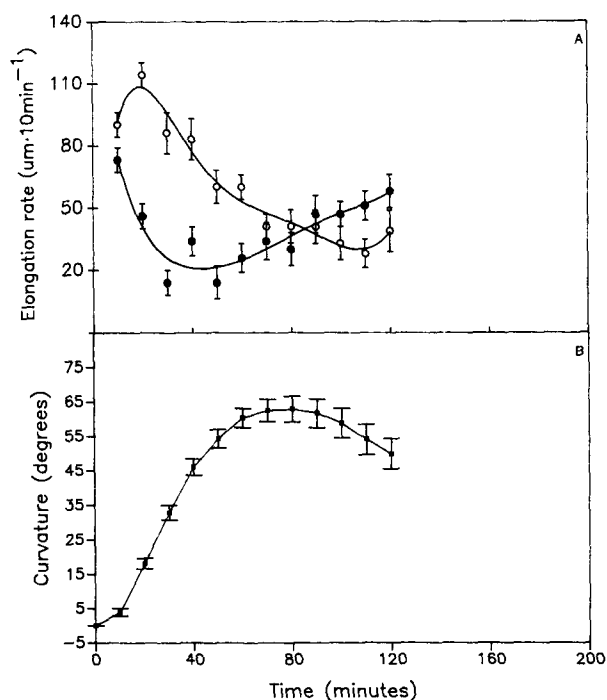
4A, 5A, and 7A) of *Arabidopsis* seedlings irrespective of the duration of blue-light photostimulation (0.9 s or 30 min) or pretreatment of seedlings (minus red light or plus red light). Similarly, the accelerated growth of the shaded side of the *Arabidopsis* seedlings following the beginning of unilateral blue-light irradiation (Figs. 4A, 5A, and 7A) is inconsistent with both the Paál (1919) and Blaauw (1918) theories. Our measurements show a significant increase in growth rate of the shaded side and a decrease in growth rate of the lighted side of the seedlings during the development of curvature under all conditions of phototropism: first positive, second positive, and red light-enhanced first positive. Thus, these data are in agreement with the predictions of the Cholodny-Went theory (Cholodny, 1927; Went, 1928).

The patterns of distribution of growth reported here for first and second positive phototropism are very similar (Figs. 4A and 5A). This similarity is consistent with a single mechanism controlling the two responses. However, a red light-preirradiation of the seedlings changes the pattern of growth distribution during the response to a subsequent blue-light pulse (Fig. 7A) in comparison with that of etiolated seedlings (Figs. 4A and 5A). The effect of the red-light preirradiation, probably acting through phytochrome (Janoudi and Poff, 1992), is to shorten the lag phase of the response, thereby permitting the elongation rates of the shaded and lighted

Figure 7. The elongation rate of lighted and shaded side (A) and the time course for development of curvature (B) of seedlings during red light-enhanced first positive phototropism (1 h of red light followed by a blue-light pulse, 0.3 μmol m^{-2}). A, O, Shaded side, $n = 18\text{--}25$; $\bullet$, lighted side, $n = 18\text{--}25$; vertical bars represent $\pm$ 1 SE. B, $n = 18\text{--}25$; vertical bars represent $\pm$ 1 SE.

Measurements of growth rates during phototropism have been reported for both monocotyledonous and dicotyledonous species. It was shown for maize coleoptiles that there is a redistribution of growth following unilateral irradiation with blue light such that the shaded side started elongating while the lighted side slowed down simultaneously (Iino and Briggs, 1984; Baskin et al., 1985). Similar findings have been reported for pea epicotyls for both first and second positive phototropism (Baskin, 1986; Briggs and Baskin, 1988). In contrast, Bruinsma and Hasegawa (1989) reported inhibition of growth on the lighted side of the sunflower and radish seedlings in response to unilateral irradiation while the shaded side maintained a constant growth rate. Hart et al. (1982) have worked with deetiolated seedlings of cress and concluded that, although growth was inhibited on the lighted side following unilateral irradiation, this inhibition was not always the major factor mediating phototropic curvature. Finally, Macleod et al. (1984) suggested that a complex pattern of acceleration and inhibition of growth in different zones of the coleptile is responsible for bending to unilateral light. Moreover, they reported that this pattern was dependent on the light pretreatment of the coleoptiles as well as on the point of administration of the actinic light pulse (Macleod et al., 1984).

To our knowledge this is the first report of a systematic measurement of growth rates under many of the different conditions of phototropism. In all of these conditions, curvature was the consequence of an increase in growth rate on one side and a decrease in growth rate on the other side, although the kinetics of these changes appeared not to be simultaneous.

The apparent difference in the kinetics of growth rate changes on the lighted and shaded side of the seedlings (Figs. 4A, 5A, and 7A) could result from any one or a combination of a number of factors. For example, a GF may be redistributed within the seedling (Iino, 1991) and the tissue may respond more slowly to withdrawal than to addition of that factor (Evans and Hokanson, 1969; dela Fuente and Leopold, 1970). Alternatively, the different kinetics could be a consequence of, or could be complicated by, changed tissue sensitivity to the GF (Ishikawa et al., 1991). However, if there is a chemical message transported across the bending organ, there should be a time delay before the response (Macleod et al., 1986). It should be noted that a red light-preirradiation decreases the delay time for the response such that the increased growth rate on the shaded side appears concomitantly with the growth rate decrease on the lighted side (Fig. 7A). However, we have no data that would permit us to identify the source of the difference in kinetics or the removal of that difference by the red light-preirradiation.

A growth response that is separate from the tropic response is induced in dark-adapted sporangiophores of *Phycomyces* (Galland et al., 1985). Could the blue-light irradiation itself introduce a transient growth response in *Arabidopsis* seedlings? To answer that question, seedlings were irradiated from above with blue light at the same fluence as that administered unilaterally to induce first positive phototropism. The results (Fig. 3A) show a growth rate comparable with that measured

for unirradiated seedlings (Fig. 2A). Therefore, blue light given from above to the seedlings in our experiment did not induce a growth response. It should be noted, however, that Rich et al. (1987) have shown that an irradiation from above may not be equivalent to a bilateral irradiation.

In summary, following a unilateral blue-light irradiation inducing phototropic curvature, the growth rate of the shaded side of an *A. thaliana* hypocotyl is increased while the growth rate of the lighted side is decreased. Regardless of the type of response being monitored, whether first or second positive phototropism, red light-enhanced first positive phototropism, or the phase of straightening following phototropic curvature, these results are consistent with predictions based on the Cholodny-Went theory and not with those based on either the Boysen Jensen or Paál/Blaauw theories.

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