

Phytochrome-Mediated Phototropism in De-Etiolated Seedlings¹

Occurrence and Ecological Significance

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ABSTRACT

Phototropic responses to broadband far red (FR) radiation were investigated in fully de-etiolated seedlings of a long-hypocotyl mutant (*lh*) of cucumber (*Cucumis sativus* L.), which is deficient in phytochrome-B, and its near isogenic wild type (WT). Continuous unilateral FR light provided against a background of white light induced negative curvatures (i.e. bending away from the FR light source) in hypocotyls of WT seedlings. This response was fluence-rate dependent and was absent in the *lh* mutant, even at very high fluence rates of FR. The phototropic effect of FR light on WT seedlings was triggered in the hypocotyls and occurred over a range of fluence rates in which FR was very effective in promoting hypocotyl elongation. FR light had no effect on elongation of *lh*-mutant hypocotyls. Seedlings grown in the field showed negative phototropic responses to the proximity of neighboring plants that absorbed blue (B) and red light and back-reflected FR radiation. The bending response was significantly larger in WT than in *lh* seedlings. Responses of WT and *lh* seedlings to lateral B light were very similar; however, elimination of the lateral B light gradients created by the proximity of plant neighbors abolished the negative curvature only in the case of *lh* seedlings. More than 40% of the total hypocotyl curvature induced in WT seedlings by the presence of neighboring plants was present after equilibrating the fluence rates of B light received by opposite sides of the hypocotyl. These results suggest that: (a) phytochrome functions as a phototropic sensor in de-etiolated plants, and (b) in patchy canopy environments, young seedlings actively project new leaves into light gaps via stem bending responses elicited by the B-absorbing photoreceptor(s) and phytochrome.

Phototropism occurs when a lateral light stimulus induces a difference in extension rate between the two sides of an elongating organ. The difference in extension rate is a response to the internal light gradient created by light scattering and absorption between the “illuminated” and “shaded” flanks of the phototropic organ (reviews by Firn [14], Briggs

and Baskin [11], and Iino [18]). Action spectra for phototropism in a variety of plant systems show peaks of quantum effectiveness between 320 and 500 nm (refs. in Dennison [13] and Iino [18]), indicating that a B/UV-A² photoreceptor plays a key role in the detection of internal light gradients. The roles of phytochrome in phototropism are not completely clear. Studies with etiolated oats (10, 13) and etiolated dicotyledonous seedlings (30) suggested that phytochrome does not function as a detector of radial light gradients, and it has been proposed that its main function in phototropism is to modulate the response to B light mediated by another receptor (34).

However, recent work with dark-adapted maize (19, 21) and totally etiolated pea seedlings (26) indicated that the radial Pfr gradient formed upon exposing the shoots to short pulses of lateral light can explain observed curvature responses. The picture is more complex in the case of de-etiolated seedlings because detailed information on spectral sensitivity is scant. Iino (18) suggested that the R:FR gradient that exists across green organs exposed to unilateral polychromatic light (29, 33) should generate a radial gradient of Pfr/P. This radial Pfr/P gradient might, in turn, lead to a gradient of growth inhibition and eventually to phototropic bending. Rough action spectra obtained by Atkins (4) using broadband light sources for de-etiolated seedlings of two dicotyledonous species do, in fact, show a small peak in the R region.

Shuttleworth and Black (31) obtained positive curvatures in green cucumber seedlings using broadband R light; the response was not observed in sunflower seedlings, where only one fluence rate was tested. Bünning (12) reported a phototropic effect of R light in sunflower seedlings de-etiolated under reduced sunlight; the same treatment was ineffective in the case of *Sinapis alba*. Recent studies with cucumber indicated that the bending of hypocotyls toward direct sunlight under glasshouse conditions is mainly a response to the B component; experimental reversal of the natural B light

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² Abbreviations: B, blue; UV-A, ultraviolet-A (320–400 nm); FR, far red; R, red; P, total phytochrome; WT, wild type; *lh*, long-hypocotyl mutant; WL, white light.

gradient between opposite sides of the seedlings led to reversal of the direction of curvature, and the effect of this treatment was the same in seedlings of WT and the phytochrome-B-deficient (*lh*) mutant (6).

In parallel with the uncertainty about the role of phytochrome in the detection of radial light gradients, there is little information on the influence of the spectral distribution of natural radiation on phototropic movements of light-grown plants (24). Remarkably few studies on phototropism have been conducted in natural light environments, and the gaps in our understanding of the ecological aspects of phototropic responses have been discussed recently by Firm (15) and Iino (18). In this study, we set out to test the role of phytochrome in the detection of radial light gradients in de-etiolated seedlings exposed to continuous unilateral illumination. We also tested phototropic responses in plant canopies and evaluated the possibility that changes in the spectral composition of scattered radiation brought about by nearby plants may elicit phototropic responses in young seedlings. Our approach is based on physiological experiments with seedlings of the *lh* mutant of cucumber and its near isogenic WT. The *lh* mutant lacks a phytochrome-B polypeptide (23), shows reduced levels of spectrophotometrically detectable phytochrome after de-etiolation (2, 27), and lacks (or exhibits severely reduced) elongation responses to end-of-day (2, 22) and daytime (6) R:FR treatments.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Seeds of the *lh* mutant and the near isogenic WT of cucumber (*Cucumis sativus* L.) (3) were obtained from the Department of Genetics (Wageningen Agricultural University, The Netherlands). For the field experiments, cucumber seeds were germinated under WL as described previously (5). Two-day-old seedlings were transferred to a glasshouse, planted in 10-cm pots containing a standard soil-less mixture, and grown for an additional 4 d under natural radiation supplemented with light from high-pressure sodium vapor lamps (5). The pots were then transferred to the field and distributed among light treatments. Maize seeds (*Zea mays* L. cv Early Jubilee) were sown directly in the field in recently cultivated soil on May 15, 1991. Six plots (1.0 × 0.5 m; east-west orientated) were planted at a rate of about 4000 seeds m⁻² in order to produce dense, homogeneous canopies.

The experiments were carried out between early July and early September 1991; during this period, maize plants were periodically clipped to maintain canopy height at 50 + 5 cm. All field experiments were carried out at the Vegetable Research Farm, Department of Horticulture, Oregon State University, near Corvallis, OR. For the controlled environment experiments, cucumber seeds were sown in 2.5-cm pots at a depth of 0.5 cm. Pots were incubated in the same growth room where the phototropic experiments were carried out. The cotyledons began to emerge from the soil 7 d after sowing; after 2 more d of growth, seedlings were selected for uniformity and allocated to the different light treatments. The WL (Fig. 1) in the growth room was provided by a mixture of 110-W F96T12/CW/HO fluorescent tubes (Syl-

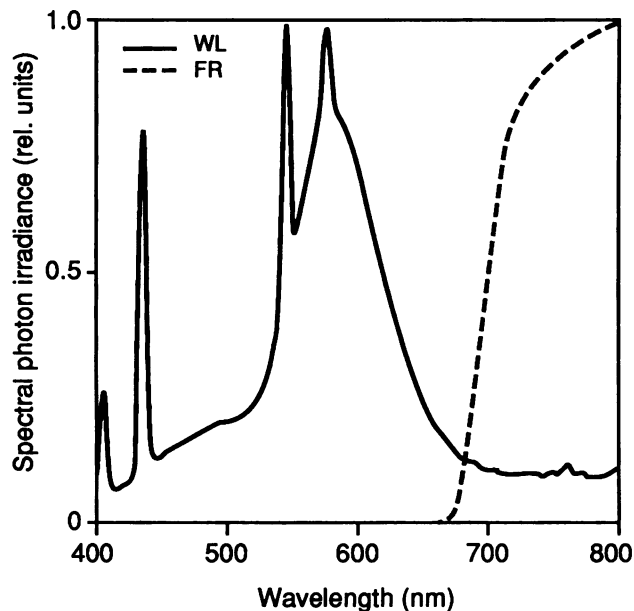


Figure 1. Spectral photon distributions of the light sources used in the controlled environment experiments. The quantum integral between 300 and 400 nm in the FR beam was < 0.01% of the output between 700 and 800 nm.

vania) and 300-W incandescent lamps (photoperiod = 12 h d⁻¹; PPFD [plant level] = 160 μmol m⁻² s⁻¹; day/night temperature = 22/16°C).

Light Treatments and Experimental Procedures

In the field experiments, potted cucumber seedlings were placed approximately 8 cm to the south of the directly sunlit edge of dense maize canopies or at the center of a 10 × 10 m plot where all weedy vegetation was removed periodically by soil cultivation. In the initial experiments, only WT seedlings were used. The pots were fitted inside 10 (i.d.) × 30 cm high clear-polyester open cylinders in order to prevent movement of the seedlings by wind. In experiments designed to test the role of phytochrome in natural phototropism, pots were fitted inside 10 (i.d.) × 30 cm (WT seedlings) or 40 cm high (*lh* seedlings) acetate cylinders that were prepared as follows. The hemi-cylinder that faced south (i.e. the one that received direct sunlight) was made of a sheet of Roscolux No. 21 (Golden Amber) acetate (Rosco Laboratories, Port Chester, NY) that absorbed most of the B/UV-A radiation with minimal effects on R-FR wavelengths, or a sheet of Roscolux No. 34 (Flesh Pink) acetate that reduced PPFD to a similar extent due to strong absorption in the green region (transmission of the pink film in the B and R-FR regions was 50 and >80%, respectively). This southern wall of the cylinder filtered all direct sunlight received by the seedlings. The hemi-cylinder that faced north (i.e. the one that received diffuse skylight or light scattered by the nearby canopy) was made of Roscolux No. 34. Seedlings were placed in front of the maize canopies or at the center of a clear plot as described above.

In the controlled environment experiments, continuous unilateral FR light (Fig. 1) was provided from the side against

a WL background (from above) by a bank of incandescent lamps. The light beam was filtered through 3 cm of water and one sheet of each of the following Roscolux filters: No. 83 (Medium Blue), No. 12 (Straw), and No. 42 (Deep Salmon). The resulting beam was a rectangle 60 cm wide and about 13 cm high that struck the entire shoot of the seedlings. Different fluence rates were obtained by inserting neutral density filters constructed of 1.1-mm mesh plastic netting between the light sources and the seedlings. A mock source covered with black plastic was used as a control. In preliminary experiments, we found that seedlings tended to bend away from the simulated and FR light sources even if the lights were off. This was remedied by placing a 30-cm high B-absorbing curtain (Roscolux No. 12) at a distance of 23 cm on the opposite side of the seedlings. In the experiments where FR light was applied bilaterally, the seedlings were positioned midway between the light source and a mirror; FR fluence rates were calculated by doubling the measured output of the lateral light source. In the experiments to determine the site of perception carried out with WT seedlings, a small, U-shaped aluminum piece (1×0.3 [lateral wings] $\times 2.5$ [height] cm) was used to prevent lateral FR from reaching the hypocotyl. The shield was positioned at a distance of 5 mm from the hypocotyl. Applications of GA_3 ($100 \mu M$) were carried out as described previously (5).

Phototropic responses were determined by measuring the angle between the vertical vector and the upper 1.5-cm section of the hypocotyl on the plane parallel to the lateral light beam (controlled environment experiments) or on the north-south plane (field experiments). The angle of curvature was measured 48 h after the beginning of treatments in the field experiments and at different intervals (see figures and figure legends) in the controlled environment. Hypocotyl length (defined as the distance between the rim of the pot and the base of the apex) was measured to the nearest 0.5 mm with a ruler. All light measurements were obtained by using a cosine-corrected receiver and a calibrated LI-COR 1800 spectroradiometer (Li-Cor).

Statistics

Individual plants (=pots) were assigned at random to each of the light treatments (i.e. light source or canopy \times filter combination). Each experiment was repeated at least three times with similar results; data from different experimental days were pooled for analysis. Results are presented as means \pm SE except where indicated otherwise.

RESULTS

Cucumber seedlings placed on the southern (sunlit) side of a green, dense maize crop bent toward the south (i.e. away from the neighboring crop) within 2 d of the beginning of the treatment. The hypocotyls of their isolated counterparts were almost vertical (Fig. 2). This neighbor-induced negative tropism could have been mediated by a B-absorbing photoreceptor or by phytochrome, because the proximity of green plants can change the horizontal component of radiation absorbed by these two photoreceptors due to absorption and reflection of sunlight (7, 9, 20, 32).

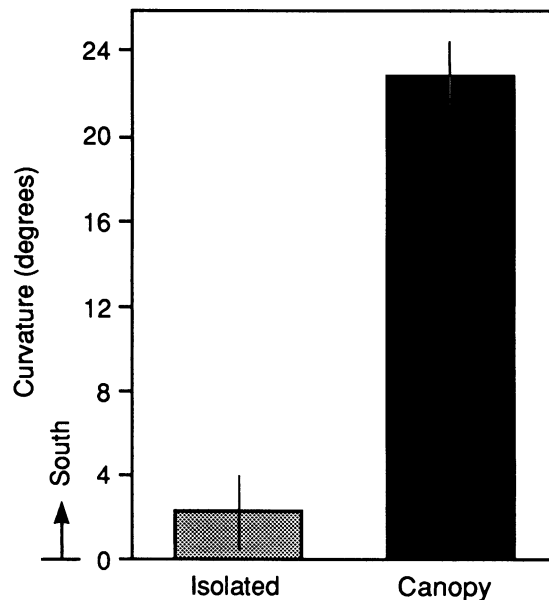


Figure 2. Effect of the proximity of a green canopy on the orientation of the hypocotyl of WT seedlings at solar noon. Seedlings were grown for 2 d at the center of a clear plot (isolated) or 8 cm to the southern (sunlit) side of a dense maize crop (canopy). Data are means of four independent experiments ($n = 12$ to 16).

Induction of hypocotyl curvature by lateral B light gradients is a well-documented phenomenon in de-etiolated dicotyledonous seedlings. A series of controlled environment experiments were carried out to test whether a phytochrome-mediated phototropism can be demonstrated in de-etiolated cucumbers. Seedlings de-etiolated for 2 d were given additional FR light from one side against a background of WL provided from above. In WT seedlings, continuous unilateral FR induced a negative phototropic bending that was statistically detectable after 2 h of treatment; curvature was about 90% of the maximal after 4 h. No curvature was detected in the *lh* mutant (Fig. 3). In WT seedlings, increasing the fluence rate of unilateral FR light between 17 and $122 \mu mol m^{-2} s^{-1}$ had a log-linear effect on hypocotyl curvature (Fig. 4). When WT seedlings were irradiated bilaterally, variation of FR fluence rate over such a range led to a 2-fold increase of hypocotyl elongation rate (Fig. 5). In seedlings of the *lh* mutant, additional FR light failed to promote elongation; however, applications of GA_3 were clearly effective in FR-treated and control seedlings (Fig. 5). This effect of GA_3 corroborates results obtained under a variety of other lighting conditions (1, 5, 6) showing that the potential for longitudinal growth promotion exists in *lh* seedlings.

In our experiments, the seedlings were positioned in front of the FR light source with the long axis of their cotyledons perpendicular to the lateral light beam. This positioning was done in order to minimize differences in light environment between cotyledons, which might have indirectly induced hypocotyl curvature (the so-called "simulated phototropism" [31]). Under these conditions, interposing an opaque barrier between the FR source and the hypocotyl without affecting

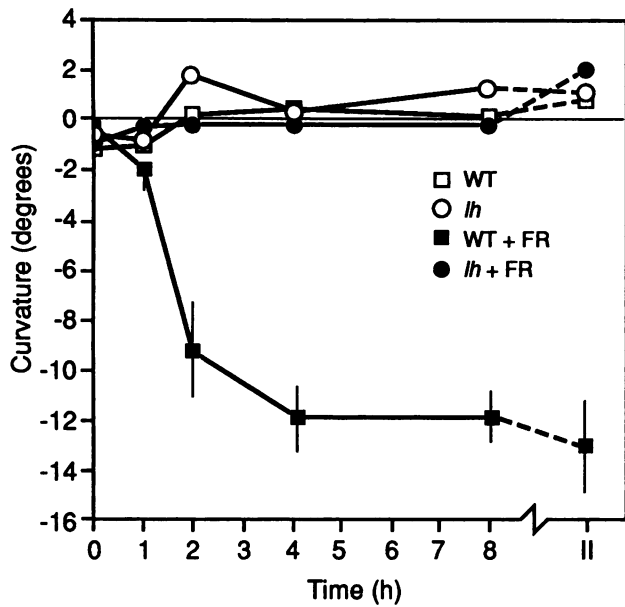


Figure 3. Time courses of hypocotyl bending in WT and *lh* seedlings growing under WL with or without exposure to unilateral FR light ($86.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). Time = 0 indicates the onset of FR irradiation; negative values on the y-axis indicate bending away from the FR source; 11 indicates the end of the 2nd d of treatment (i.e. two 8-h exposures to unilateral FR light). Data are means of four independent experiments ($n = 15$ to 28); for clarity of presentation, SE (all $< 1^\circ$) were omitted in the upper curves.

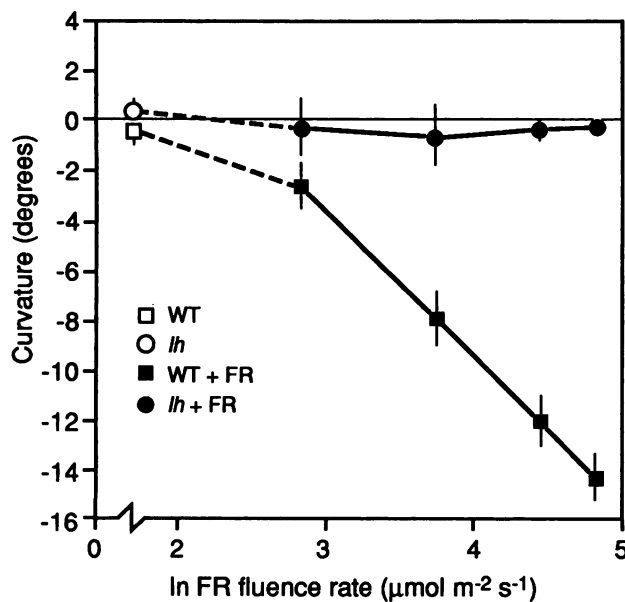


Figure 4. Effects of increasing the fluence rate of unilateral FR light on hypocotyl curvature in WT and *lh* seedlings. Curvatures were measured after 5 h of continuous FR light; negative values on the y-axis indicate bending away from the FR source. Data are means of four independent experiments ($n = 68$ to 80 , controls; $n = 8$ to 29 , intermediate fluences; or $n = 29$ to 37 , highest fluence).

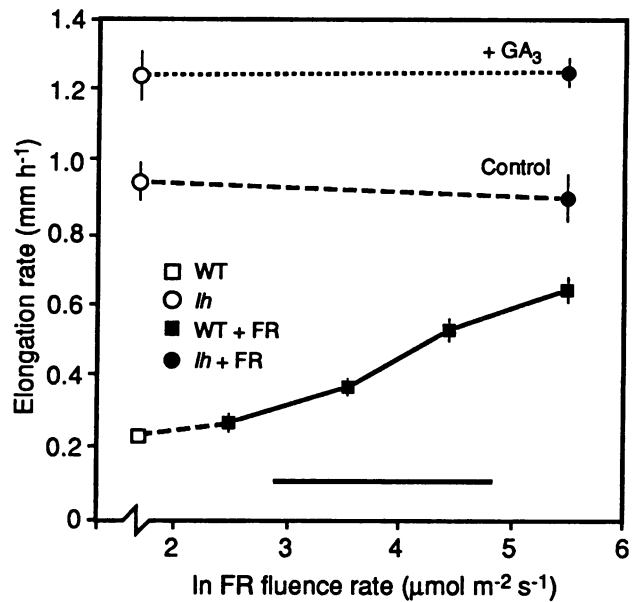


Figure 5. Effects of increasing the fluence rate of bilateral FR light on hypocotyl elongation in WT and *lh* seedlings (the latter with or without application of GA_3). Elongation rates were estimated from length measurements taken at the beginning of the experiment and after 5 h of continuous FR irradiation. The solid line parallel to the abscissa denotes the range of FR fluence rates used in the curvature experiments. Data are means of three independent experiments ($n = 13$ to 28).

the light environment of the cotyledons drastically reduced the negative phototropic response (Fig. 6).

Spectral scans of the light received by cucumber seedlings in the field showed that plants grown close to the sunlit edge of a maize canopy received less B and R light from the northern side and much more FR than isolated seedlings (Table I). To assess the relative contribution of each of these changes to the bending response shown in Figure 2, we (a) compared the curvature responses to green neighbors of WT and *lh* seedlings, and (b) tested the effect of eliminating the steep south-to-north B-light gradient created by the canopy by placing a B-absorbing filter on the southern side of the seedlings. To compensate for the reduction in PPFD caused by this treatment, control seedlings were shaded by a green-absorbing acetate (see "Materials and Methods"). The effects of the acetate filters and plant neighbors on the light received by the plant from the northern and southern sides are shown in Figure 7. Seedlings grown without neighbors (i.e. isolated seedlings) experienced a natural south-to-north gradient of B light (Fig. 7A), and their hypocotyls were slightly curved toward the south (Fig. 8, A and B). The B-absorbing filter placed on the southern side reversed the direction of the natural B-light gradient (Fig. 7B) and caused isolated seedlings to bend toward the north (Fig. 8, A and B). The response to the B barrier was of the same magnitude in isolated WT and *lh* seedlings. The presence of a green canopy on the northern side exaggerated the south-to-north B-light gradient and, in addition, created a steep R:FR gradient due to absorption of R light and back-reflection of FR radiation (Fig. 7C;

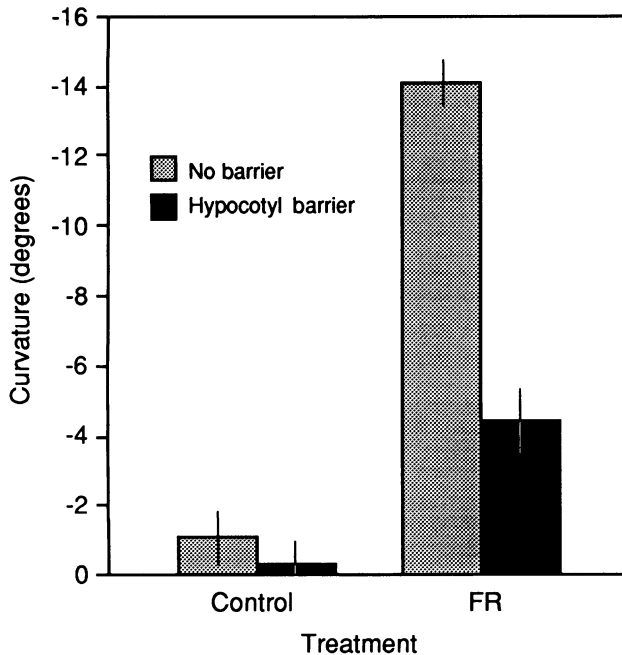


Figure 6. Effect of shading the hypocotyl during irradiation with unilateral FR light ($121.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) on hypocotyl curvature in WT seedlings. Curvatures were measured after 5 h of continuous FR irradiation; negative values on the y-axis indicate bending away from the FR source. Data are means of nine independent experiments ($n = 28$ to 37).

see also Fig. 7A and Table I). Plants grown in front of a green canopy were markedly curved toward the south (i.e. away from the canopy) (Fig. 8, C and D; see also Fig. 2). The bending response to the proximity of the canopy was significantly larger in WT than in *lh* seedlings (Fig. 8, C and D). Eliminating the B-light gradient induced by the canopy by means of a B-absorbing filter (Fig. 7D) abolished the negative

Table I. Effects of the Proximity of Green Plants on the Light Flux Measured Parallel to the Ground

Measurement	Photon Irradiance ^a			R:FR ^b
	B	R	FR	
	$\mu\text{mol m}^{-2} \text{s}^{-1}$			
Receiver pointed toward the south	137.5	223.7	238.3	1.00
Receiver pointed toward the north:				
No neighbors	36.3	42.8	72.6	0.63
In front of a green canopy	8.0	21.6	128.1	0.16

^a Measurements were taken near midday under clear sky on July 28, 1991. The surface of the light receiver was normal to the ground and received direct solar radiation when pointed toward the south. The receiver was positioned 8 cm to the south of the maize canopy to obtain the last row of data. B = 400 to 500 nm, R = 600 to 700 nm, FR = 700 to 800 nm. ^b (654–664/726–736) quantum flux ratio.

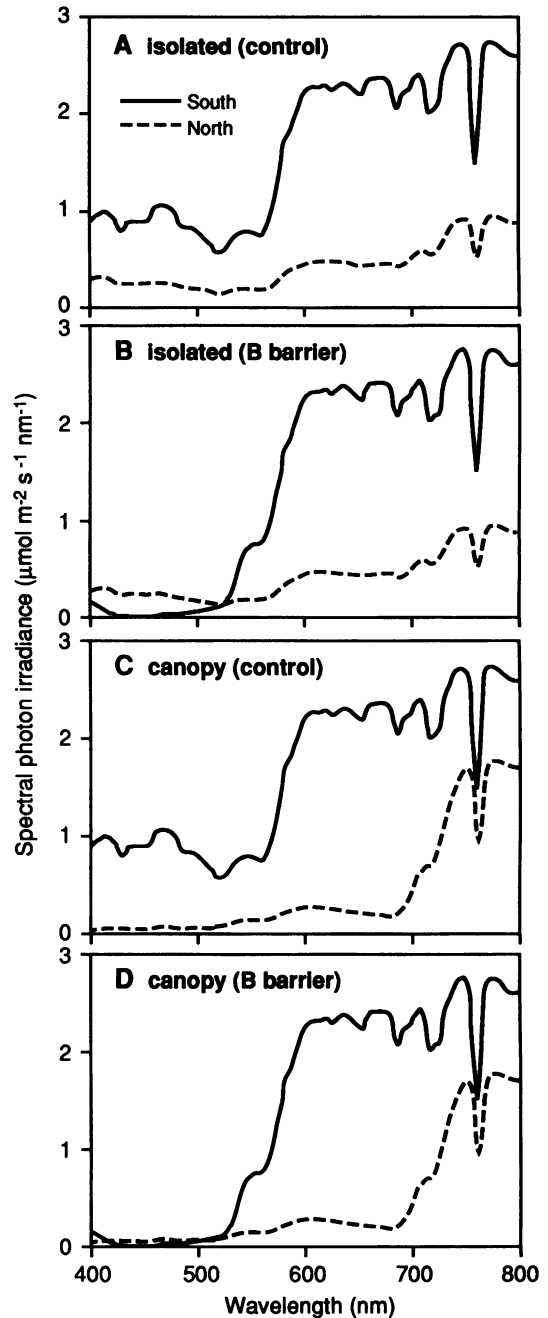


Figure 7. Effects of the proximity of a green maize canopy and B-absorbing acetate filters on the spectral photon distribution of the light flux measured parallel to the ground. Measurements were taken near midday under clear sky on July 28, 1991. The surface of the light sensor was normal to the ground and pointed toward the southern (solid line) or northern (dashed line) hemisphere. When pointed toward the south, the sensor received either direct sunlight filtered by a Roscolux No. 34 acetate (control) or direct sunlight filtered by a B-absorbing acetate No. 21 (B barrier). When pointed toward the north, the sensor was always shielded by the acetate No. 34 and received either diffuse skylight (isolated) or light back-scattered by an 8-cm distant maize canopy (canopy).

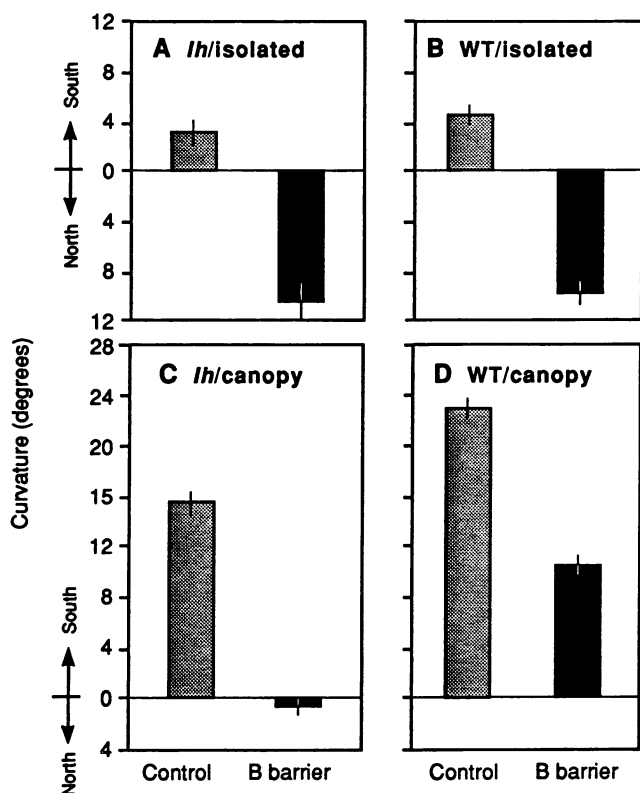


Figure 8. Effects of the proximity of a green maize canopy and B-absorbing acetate filters on the orientation of the hypocotyl of WT and *lh* seedlings at solar noon. Seedlings were grown for 2 d at the center of a clear plot (isolated) or 8 cm away from the southern edge of a dense maize crop (canopy). Data are means of 11 independent experiments ($n = 19$ to 26, isolated; $n = 42$ to 56, canopy).

tropic response in *lh* seedlings (Fig. 8C). In contrast, a residual curvature of approximately 11° (i.e. about 46% of the maximum response) remained in WT plants (Fig. 8D).

DISCUSSION

Our results strongly suggest that phytochrome functions as a detector of light gradients established across the hypocotyls of green cucumber seedlings and mediates phototropic responses to long-wavelength (>600 nm) radiation. Unilateral FR radiation administered against a background of WL provided from above induced a negative phototropic response in WT seedlings (Fig. 3). This response was (a) fluence rate dependent (Fig. 4), (b) not an indirect consequence of differential illumination of the cotyledons (Fig. 6; ref. 31), and (c) not observed in the phytochrome-B-deficient *lh* mutant (Fig. 3), even at very high fluence rates of FR light (Fig. 4). Comparison of these results with previous work is difficult because other authors used different species or experimental protocols. Atkins (4) obtained rough action spectra for the induction of phototropic responses to continuous irradiation using broadband light sources. The spectra for de-etiolated dicotyledonous seedlings (*Lepidium sativum* and *Celosia cristata*) showed a small (positive) peak in the R region in

addition to the peak in the B/UV-A. No data points were reported between 710 and 850 nm (*L. sativum*) or 650 and 850 nm (*C. cristata*). No such R peak was observed for etiolated oat coleoptiles, where the ineffectiveness of radiation above 500 nm has been documented extensively (e.g. refs. 10, 13).

Shropshire and Mohr (30) stated that continuous R or FR light did not induce hypocotyl curvature in etiolated seedlings of two dicotyledonous species, *Fagopyrum esculentum* and *Sinapis alba*. Continuous R light was also ineffective in de-etiolated sunflowers (12). Shuttleworth and Black (31) found that continuous unilateral R light induced positive curvature in hypocotyls of de-etiolated cucumbers. However, the authors were suspicious of the spectral purity of the R light source (i.e. B light contamination) and did not discuss that result further.

More recently, Parker et al. (26) interpreted the phototropic response of totally etiolated pea epicotyls to short B light pulses on the basis of phytochrome action. Based on previous results with dark-adapted maize mesocotyls (19, 21), they proposed that epicotyl curvature in their experimental conditions was induced by a Pfr gradient established across the epicotyls after illumination with unilateral B light. A related mechanism may account for the negative phototropism induced by continuous FR light in our experiments. Although fluence rate gradients for 660 and 730 nm have been measured in green hypocotyls of other species (33), extrapolation to the present experiments is difficult because our seedlings received omnidirectional WL simultaneously with the unilateral FR treatment.

The important point is that in our experiments, curvature was induced over a range of FR fluence rates (Fig. 4), where a 2-fold change of fluence rate (i.e. equivalent to the fluence rate differential that could be expected between opposite flanks of a 2 mm diameter, green hypocotyl [33]) should produce a sizable (about 0.1 mm h^{-1}) difference in elongation rate (Fig. 5). Simple geometrical relations indicate that such a difference in elongation between the "illuminated" and "shaded" flanks would yield a bending rate of about $2.9 \text{ degrees h}^{-1}$, which is roughly similar to the bending rates measured during the initial 2 h in our experiments (Fig. 3).

The question at this point is whether a phytochrome-mediated phototropic mechanism plays a role in the curvature responses of young seedlings to the proximity of green neighbors (Fig. 2). The observation that hypocotyl bending responses were larger in WT than in *lh* seedlings (Fig. 8, C and D, controls) is consistent with such a possibility, but certainly cannot be taken as definite evidence. In fact, it is well known from a number of other studies that an important action of phytochrome in phototropism is to alter the pattern of response to unilateral B light mediated by a specific photoreceptor (e.g. ref. 34). Therefore, the observed differences between WT and *lh* seedlings might simply reflect an effect of phytochrome-B on the curvature response to the steep south-to-north B light gradient (Table I; Fig. 7C) created by the presence of a green canopy. However, when that B light gradient was experimentally eliminated by placing a B-absorbing filter on the southern side of the plants (Fig. 7D), a significant southward curvature was still observed in the

hypocotyls of WT plants (Fig. 8D). Moreover, when the B-absorbing barrier was placed on the southern side of *isolated* plants, the northward curvature responses of WT and *lh* seedlings were similar (Fig. 8, A and B). These and previous data (6) suggest that the lack of phytochrome-B does not affect the (steady-state) curvature induced by lateral B light in de-etiolated cucumbers under natural light fluences. If we therefore assume that the actions of phytochrome and the B-absorbing photoreceptor are roughly additive in this system, we can calculate that about 46% of the total bending induced by the proximity of a green canopy is due to radial R:FR gradients perceived by phytochrome.

The observation that the hypocotyl is the main site of perception of lateral FR (Fig. 6) is consistent with results obtained in other dicotyledonous seedlings irradiated with B light or WL (16, 17, 28, 31) and with the hypothesis that it is the R:FR gradient established across the hypocotyl that elicits the bending response. This observation is very important with respect to the ecological significance of stem phototropism. In open plant stands, the presence of neighboring individuals can alter the light environment of vertically oriented stems well before there is any mutual shading at leaf level (refs. 7–9; Fig. 7 of this article). These alterations influence the rate of internode elongation and may convey critical information to plants that are competing with neighbors for colonizing the aerial environment (8). According to our data (Fig. 7), the radial light gradients perceived by the stems are related to the spatial distribution of neighbors around the plant. Tropic responses to these gradients would improve the efficiency with which a seedling collects light in a patchy light environment, as the probability of new leaves being actively projected into light gaps would increase. It has been reported recently that seedlings of *Portulaca oleracea*, a plant with a plagiotropic shoot system, tend to avoid growing toward plant neighbors or plastic objects that back-scatter radiation with a low R:FR ratio. Part of the response in this case appeared to be because main stems were unlikely to become recumbent toward natural or simulated neighbors (25). Our results indicate that in light-grown cucumbers, phototropic mechanisms controlled by the B-absorbing photoreceptor(s) and by phytochrome are responsible for the negative bending responses elicited by the proximity of neighboring plants.

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