

Rapid Suppression of Growth by Blue Light

OCCURRENCE, TIME COURSE, AND GENERAL CHARACTERISTICS¹

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ABSTRACT

The inhibition of stem elongation in dark-grown seedlings by blue light was studied with marking techniques and with a high-resolution, growth-measuring apparatus. Blue light rapidly suppresses growth in a variety of cultivated species. In some species, the inhibition persists only during the period of irradiation, after which time growth quickly returns to the high dark rate, whereas, in other species, the light response has an additional long-term component which lasts for at least several hours in the dark. The long-term inhibition may be mediated by phytochrome, whereas the rapid, short-term component is specific to a blue-light receptor.

The rapid inhibition of growth in cucumber (*Cucumis sativus* L.) requires high-energy blue irradiation, which is perceived directly by the growing region of the hypocotyl and inhibits all regions below the hook to the same extent. Detailed investigation of the kinetics of the inhibition in cucumber and in sunflower (*Helianthus annuus* L.) shows that, after a short lag period (20 to 30 seconds in cucumber, 60 to 70 seconds in sunflower), the growth rate declines in an exponential fashion to a lower rate, with a half-time of 15 to 25 seconds in cucumber and 90 to 150 seconds in sunflower. Excision of the hypocotyl greatly reduces the sensitivity of the growth rate to blue-light inhibition. Because of the rapid kinetics, the blue-light photoreceptor cannot affect cell enlargement by altering the supply of growth hormone or the sensitivity to hormones but probably operates more directly either on the biochemical process which loosens cell walls or on cell turgor.

Light strongly inhibits stem elongation in higher plants. Although many studies have shown that phytochrome mediates a significant part of this response to light (17, 20, 21, 28, 29), there are several lines of evidence indicating the involvement of a blue-light receptor, distinct from phytochrome, in the control of stem growth (10, 14, 26, 27). Meijer (19) has shown that blue irradiation rapidly inhibits the growth of etiolated cucumber seedlings, whereas, red and far-red irradiations only slowly affect growth after a lag of 60 min. Similarly, Gaba and Black (10) found a difference in the timing of blue and red inhibition in light-grown cucumber. Such findings are compelling evidence for the action of a distinct blue-light photoreceptor in the light-growth responses of cucumber. In contrast, with continuous and end-of-day irradiation experiments, Wildermann *et al.* (29) found no indication of the involvement of a blue-light photoreceptor in the control of *Sinapis* hypocotyl growth. Although coarse-resolution measurements suggest that a rapid response to blue light may also occur in other species (14, 27), high-resolution measurements have been

published only for cucumber (1, 19).

Besides the question of what photoreceptor mediates light-growth responses, the suppression of growth by blue light is of particular interest (because of its short lag and rapid kinetics) for an understanding of the mechanism and control of plant growth. Chemical agents such as auxins, gibberellins, and metabolic inhibitors have been used extensively for studies on the process of cell enlargement (6, 12, 18, 23). Precise control of the duration and concentration of the application of such agents for high-resolution kinetic studies of growth is technically limited by problems of uncertain uptake and slow diffusion of the chemical into and out of the tissue. Light, which does not have these disadvantages, might be a very useful probe for investigation of plant growth.

The experiments reported herein were conducted with three goals in mind: (a) to determine if the rapid growth inhibition by blue light is unique to cucumber or common to other species; (b) to investigate in detail the timing, location, and other characteristics of the rapid inhibition; and (c) to determine if excised sections would show the same light response as do intact plants.

MATERIALS AND METHODS

Plant Material. Seeds were soaked overnight in running tap water, sown in wet vermiculite, and grown in complete darkness at 30 C to a height of 3 to 5 cm. Those plants to be measured in the continuous growth-measuring apparatus were sown in 7-dram plastic vials with drainage holes. The seeds used and their sources were as follows: cucumber (*Cucumis sativus* L. cv. Burpee's Pickler and cv. Lemon), pea (*Pisum sativum* L. cv. Hiderma and cv. Mammoth Melting), and zucchini (*Cucurbita pepo* L. cv. Fordhook), all from W. Atlee Burpee Co., Riverside, CA; sunflower (*Helianthus annuus* L. cv. Black Russian) from JL Hudson Co., Redwood City, CA; cucumber (*C. sativus* L. cv. Levo) from Nunhems Zaden BV, Haalen, Holland; sunflower (*H. annuus* L. cv. Peredovik and cv. Sputnik) from Northrup King & Co., Woodland, CA; pea (*P. sativum* L. cv. Progress No. 9) from Ferry Morse Seed Co., Mountain View, CA; and mung bean (*Phaseolus aureus* L.) and adzuki bean (*Phaseolus angularis* L.) from a local supermarket.

Light Sources. Except as noted, blue light was obtained from two 150-w Dicro Blue flood lamps (General Electric) filtered through 6 cm saturated copper sulfate solution and through one or more blue Plexiglas plates (Rohm and Haas no. 2424, 3.18 mm thickness). The spectral characteristics of the blue light is shown in Figure 1. Light fluence rates were changed by adding blue or grey (Rohm and Haas no. 2064, 3.18 mm thickness) Plexiglas plates. Red, far-red, and green light was obtained from two 150-w flood lamps filtered through 6 cm water and the appropriate plastic filter (CBS Red 650, CBS Far-red 750, and CBS Green 545, from Carolina Biological Supply Co., Burlington, NC). [See Poff and Norris (22) for a description of these filters.] Light fluence rates were measured with an Eppley eight-junction bismuth-silver thermopile (previously calibrated against a standard lamp from

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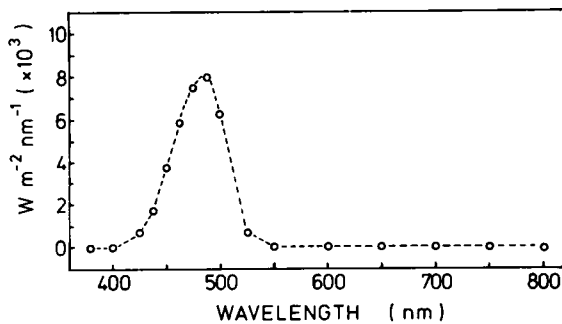


FIG. 1. Spectral distribution of light from the blue-light source, as measured with model SR spectroradiometer (Instrumentation Specialty Co.).

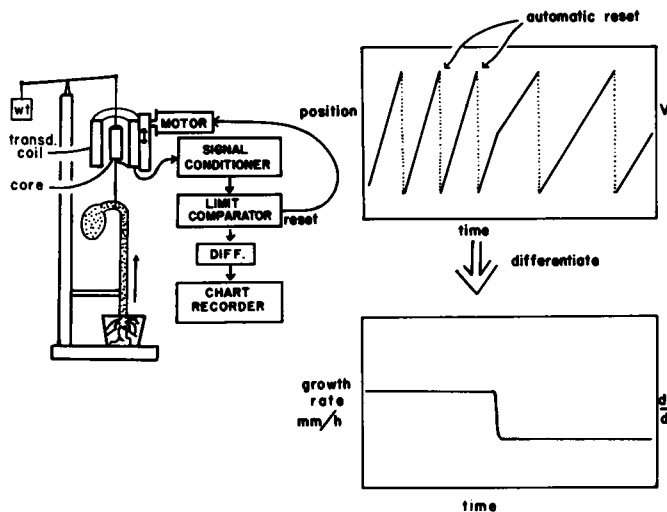


FIG. 2. Diagram of the continuous growth-measuring apparatus. Elongation of the seedling in a vermiculite-filled vial raises the attached transducer core, generating a voltage proportional to position. This voltage is electronically differentiated to give a direct record of the growth rate. A reset circuit maintains the transducer core within its linear range by activating a DC motor. [See Green and Cummins (12) for more details.]

the National Bureau of Standards) in conjunction with a Keithley 150B microvoltmeter. Measurements were made with and without a Corning 7-56 IR transmitting filter in order to subtract out the IR portion of the radiation present in the green, red, and far red sources. The copper sulfate solution in the blue light source did not transmit any detectable IR energy.

A special green safelight was built from a small panel-meter light bulb (no. CM47) and a 6-v battery. The bulb was enclosed in a small light-proof case having a 2.5-cm round window at one end, filtered by two layers of amber Roscolene acetate and one layer of green Roscolene acetate. The lamp was connected to the battery by a long, flexible cord and could be directed at the growth-measuring apparatus while the seedlings were being attached, with minimal irradiation of the plants. In most cases, the seedlings were directly illuminated with the dim green light for 10 to 15 s. Extensive experiments with cucumber have indicated that the rapid blue-light response is not affected by short periods of red, far-red, or green light.

Growth Measurements. The elongation rate of plants was continuously measured with an apparatus modified after Green and Cummins (12) (Fig. 2). It consisted of a position transducer (Linearsyn differential transformer, Hewlett-Packard model 595DT-100, used with a Hewlett-Packard model 311A transducer amplifier-indicator), a custom-made electronic differentiator

module, and an automatic reset circuit to keep the transducer within its linear range. Plants were attached to the transducer with the aid of the green safelight and allowed to stabilize their growth rate for 1 to 2 h before a light treatment was given. In general, seedlings were connected to the transducer core-assembly by looping a hook on the bottom of the assembly around the hook of the stem. This method is quick and minimizes the handling and mechanical disturbance of the plant but has the potential disadvantage that hook opening could contribute to the apparent growth rate. Such an artifact was not found to be a problem as long as the upward tension on the plant was not large (less than 1 to 2 g). The usual upward tension for the experiments reported here was approximately 0.1 g. Other attachment methods were tried, for instance, clamping or tying the core assembly just below the hook, but the characteristics of the light-growth response remained the same.

The dark growth rate of intact seedlings of most species tested was found to be quite variable. Slow oscillations with a period of about 1 h were common. Seedlings often showed quite erratic growth during the first h of being placed in the growth apparatus, and any mechanical disturbance of the plant would transiently alter the growth rate. In general, it seemed that those plants with the highest growth rates showed the greatest tendency to oscillate.

For experiments in which parts of the seedling were shielded from light, the core assembly was carefully tied to the hypocotyl about 1 to 3 mm below the hook and either the region below the attachment point (that is, the growing region) or the hook and cotyledons above the attachment point were covered with an opaque covering. To shade the growing region, two layers of black plastic tubing, somewhat larger in diameter than the stem diameter, were slit lengthwise and carefully placed around the hypocotyl. To shade the hook and cotyledons, the upper portion of the seedling was completely enclosed with an aluminum foil covering. Although the growth of the plant was temporarily disturbed by the procedure of applying the shading material, a normal growth rate usually resumed after about 1 h. Light treatments were given only to those plants which showed a full and stable recovery to the normal dark growth rate.

The light source in experiments with the growth transducer apparatus was located on one side of the seedling, with a mirror on the opposite side to minimize the light gradient across the stem. Phototropic bending of the etiolated stem did not occur under these conditions. However, cucumber and sunflower seedlings were found to be very geotropically sensitive and care was needed not to tilt the plant while attaching it to the position transducer.

For those experiments using excised portions of seedlings, 10 to 20 seedlings/group were cut under dim green safelight and floated in open Petri plates (9 cm diameter) on 15 ml distilled H₂O or of a freshly prepared solution of IAA, with or without 1% sucrose. Excised portions consisted of either 18-mm hypocotyl segments cut directly below the hook or the whole upper 18-mm portion of the seedling, including hypocotyl, hook, and cotyledons, where the 18 mm were measured from the top of the hook to the excision point on the hypocotyl. After 4 h incubation in the dark or in blue light, the lengths of the portions were measured under a dissecting microscope to the nearest 0.2 mm.

To measure the distribution of growth along the hypocotyl axis, seedlings were marked under dim green safelight with a rubber stamp having 1.4-mm gradations. After growth in the dark or in the blue light for 6 h at 30°C, the distances between the marks were measured under a dissecting microscope. Relative growth rates were calculated by the formula:

$$\text{relative growth rate} = \frac{\ln(D2) - \ln(D1)}{6 \text{ h}}$$

where D1 and D2 are the distances between the marks at the beginning and at the end of the experiment, respectively.

RESULTS

Occurrence and Pattern in Blue-light Responses. The possible existence of a rapid growth response to blue irradiation was tested in a variety of species by continuous, high-resolution measurements of the rate of elongation of the stem. Table I summarizes the results of the survey, showing that the rapid inhibition by blue light occurs in a variety of plants and that two patterns of response could be discerned. The simplest response pattern (Fig. 3A) consists of a rapid decrease of the growth rate (after a lag of 20 to 240 s, depending on species), with a full recovery of the previous rate upon return to the dark. No subsequent decrease in the growth rate is seen, even when growth is monitored for several hours after the light treatment. However, because of the variability of the dark growth rate of seedlings, this technique would not detect a small (10 to 15%) reduction in the growth rate. The second response pattern (Fig. 3B) consists of both a rapid decrease in the growth rate and a long-term inhibition of growth in the dark, lasting for at least several hours after the light treatment. Alaska pea consistently showed a transient recovery of the growth rate, often exceeding the previous dark rate by 50 to 60%, before subsequently decreasing to a lower rate (Fig. 3B). In contrast, Hiderma pea showed no transient recovery whatsoever following return to the dark. Thus, although the rapid growth inhibition by blue light was found in a variety of plants, only some of these species showed a prolonged inhibition in the dark (Table I).

Only blue light was effective in inducing the rapid growth inhibition in both cucumber (Burpee's Pickler) and in pea (Alaska); green, red, and far-red irradiations were ineffective. In cucumber, short periods (5 to 30 min) of irradiation at very high fluence rates (green, 73 w m^{-2} ; red, 35 w m^{-2} ; and far-red 34 w m^{-2}) caused no significant growth effect. Continuous illumination with red light, on the other hand, inhibited growth beginning about 90 min after the onset of irradiation. Similarly in Alaska pea, 5 to 20 min red light did not induce the rapid-growth suppression caused by blue light but did produce a response which mimicked the long-term component of blue-light inhibition. About 30 to 40 min after the start of red irradiation, the growth rate began a decline which continued in the dark for several hours (Fig. 4). A curious feature of the light-growth response in pea is brought out (Fig. 4): when the light is turned off, there is a very rapid, temporary drop in the rate, followed by an overshoot in the

Table I. Growth Responses of Intact Seedlings to Blue Irradiation

The growth rate of individual dark-grown seedlings was measured continuously during and after a 15-min irradiation with 5.0 w m^{-2} blue light. Plants responding by a decrease in growth rate within 5 min of the start of irradiation were scored positive for rapid inhibition. Plants whose growth rate returned to a high level within 0.5 h and remained high for at least 3 h were scored positive for dark recovery.

Plant	Rapid Inhibition	Dark Recovery
Cucumber		
Burpee's Pickler	+	+
Levo	+	-
Lemon	+	-
Sunflower		
Black Russian	+	+
Peredovic	+	+
Sputnik	+	+
Azuki bean	+	+
Zucchini	+	+
Pea		
Alaska	+	-
Hiderma	+	-
Progress No 9	+	-
Mung bean	+	-

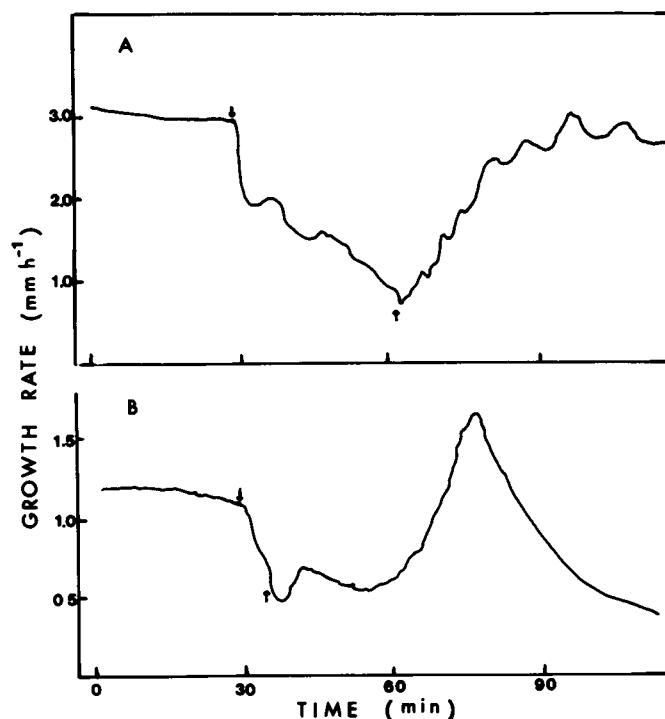


FIG. 3. Growth responses to blue irradiation. Seedlings which are irradiated for a short time with 5.0 w m^{-2} blue light exhibit two patterns of response, as typified in A and B. A, cucumber (cv. Burpee's Pickler) shows only a rapid, short-term inhibition of growth; B, Alaska pea responds with both the rapid, short-term response and a more long-term inhibition which continues for at least 6 h in the dark. The arrows indicate the time for the start and the end of the irradiation.

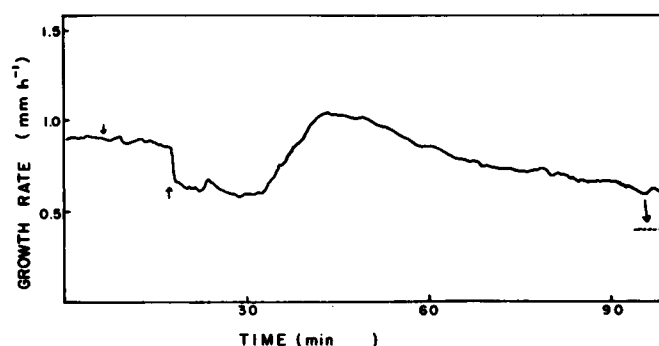


FIG. 4. Effect of red light on the growth of Alaska pea. Red light (fluence rate, 35 w m^{-2}) was turned on and off at the time indicated by the arrows. (---) (far right), stable growth rate eventually attained.

recovery, *i.e.* the growth rate transiently rises to a higher value than the preirradiation value. This "light-off" response was also often seen with blue irradiations and in species other than Alaska pea (Fig. 3). It seemed to appear only after periods of irradiation greater than 5 min and seemed more pronounced at higher fluence rates. Aside from this peculiarity, red light did not cause an immediate suppression of growth, as did blue light. The kinetics of the growth response to red and to blue irradiations suggests that the blue-light response in Alaska pea may be a composite of two different light-response systems: a very rapid inhibition, mediated by a pigment which absorbs only in the blue end of the visible spectrum, and a more slowly acting long-term inhibition, mediated by a pigment absorbing both in the red and in the blue regions.

Further studies focused on the blue-light inhibition in cucumber (cv. Burpee's Pickler) because its large and rapid response has only a short-term component and, thus, could be repeatedly evoked in a single seedling. A dose-response curve (Fig. 5) was obtained by irradiating plants for 5 min at various fluence rates and then taking the ratio of the growth rate at the end of the light treatment over the growth rate just preceding the light treatment. Despite considerable variability in the response, the graph shows that (a) the rapid inhibition is a high-energy response, and (b) there is an approximately linear relationship between the logarithm of the light dose and the amount of inhibition. Other measures of growth inhibition were tried, e.g. calculating the amount of growth lost due to the light, but variable recovery made such a measure too noisy and uncertain. However, there is a conceptual difficulty in interpreting these data in the classical dose-response sense, in that the response (decline in growth rate) is occurring at the same time that the light dose is given. Better characterization of the growth response was needed to resolve this difficulty.

Response Kinetics. The typical response of cucumber to 15 to 30 min blue irradiation consists of a very fast drop in the growth rate when the light is first turned on, followed by a much slower decline (Fig. 3A). Consistently, there is a transient plateau or even short recovery before the growth rate begins the second, more gradual decline. Upon return to the dark, there is a recovery to the dark rate, often with oscillations. A closer examination of the initial decrease in the growth rate shows it to consist of a short lag period followed by a smooth decline to the transient plateau level (Fig. 6A). The dose-response data thus represent a measure of this plateau as a function of fluence rate.

The decline of the growth rate to the lower value has the appearance of an exponential approach to an asymptote. This exponential character is verified in Figure 6B where the logarithmically transformed data fall along a straight line. If just a short light pulse (10 to 20 s) is given, the rate goes through the complete exponential decay and then recovers over a 20- to 30-min period. In such cases, the light response (exclusive of recovery) can be neatly and fully characterized by three parameters: the lag time before onset of inhibition, the half-time (or time constant) of the exponential decline in rate, and the lower rate (asymptote) eventually attained. In cucumber, the lag lasts 20 to 30 s and the half-time is about 15 to 25 s.

A similar analysis of the blue-light response in sunflower (cv. Black Russian) (data not shown) also shows it to consist of a short lag followed by an exponential decay of the rate. Sunflower has a slower response than cucumber, with a lag of 60 to 70 s and a half-time of about 90 to 150 s.

Sites of Light Perception and Response. In the experiments above, there was no way to determine where along the length of the hypocotyl the growth that had been measured with the dis-

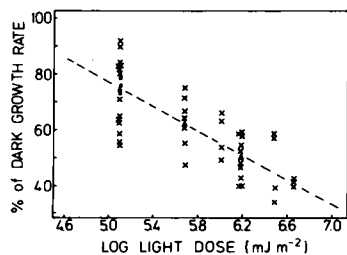


FIG. 5. Growth response of cucumber as a function of light dose. Blue light at fluence rates of 0.4 to 10 W m^{-2} was given for 5 min and the inhibition of the growth rate (as a percentage of the dark value) at the end of the irradiation is plotted as a function of light dose. (x), individual values; (▲), means; (○) (at the lowest dose), responses for a 30-s (instead of a 5-min) light treatment.

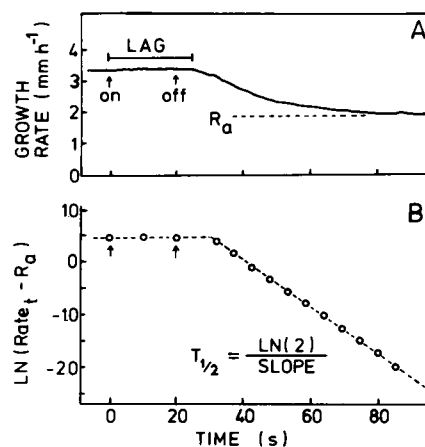


FIG. 6. High-resolution time course of the suppression of growth by blue light. A, a 20-s pulse of blue light (fluence rate, 4.0 W m^{-2}) was given to a cucumber seedling (cv. Burpee's Pickler) at the time indicated by the arrows. The resulting decrease in growth rate may be characterized by the lag time, the half-time, and the asymptote (lower rate). B, logarithmic plot of growth rate versus time. The data of A were transformed by taking the $\ln(\text{rate at time}_t - \text{asymptotic rate})$ ($\text{Rate}_t - R_a$) and then plotted against time. The straight line indicates a single component exponential decay to the lower rate.

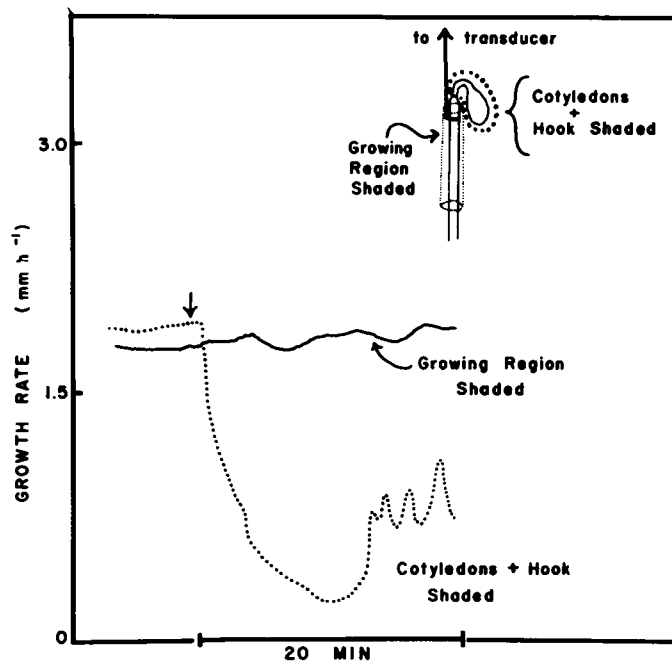


FIG. 7. Location of the blue-light photoreceptor for hypocotyl growth inhibition. Portions of cucumber seedlings (cv. Burpee's Pickler) were shaded as described. Irradiation for 20 s at 4.0 W m^{-2} resulted in growth inhibition only if the growing region was illuminated.

placement transducer had occurred. The whole plant was irradiated and only the total growth of the hypocotyl was measured. Two questions of interest were: In what part of the plant was the photoreceptor located and which region of the hypocotyl was inhibited by light?

The first question was answered by covering either the growing region of the hypocotyl or the upper portion of the plant, consisting of the hook and cotyledons, with an opaque covering, and then irradiating with blue light. It is clear from the results (Fig. 7) that, in cucumber, the growing region itself perceives the blue light,

rather than the hook or cotyledons perceiving the light and transmitting a stimulus to the hypocotyl.

The second question was answered by marking the hypocotyl at 1.4-mm intervals, letting the plants grow in the dark or in light, and measuring the displacement of the marks from each other at the end of 6 h. From these data the distribution of growth along the hypocotyl axis was calculated. The results (Fig. 8) show that blue light evenly inhibits all parts of the growing region below the hook.

Response in Excised Sections. Several attempts were made to evoke the blue-light response in excised cucumber hypocotyls, since such a system would be particularly advantageous for physiological studies on growth. However, despite the fact that blue light is perceived by the hypocotyl and so quickly suppresses hypocotyl growth in the intact plant, excised hypocotyls are much less responsive to light. Table II shows the growth of cucumber hypocotyls under various experimental conditions. Clearly, excised portions of the plant grow at a much slower rate than similar portions on an intact plant. Hypocotyl segments barely extend at all, whereas segments which are still attached to the cotyledons elongate at less than one-half of the rate of similar intact pieces.

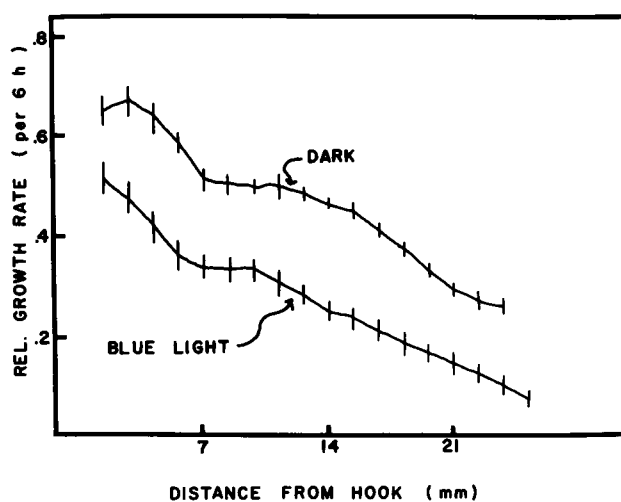


FIG. 8. Growth distribution along the cucumber hypocotyl in the dark and in the light. The relative growth rate of different parts of the hypocotyl for plants kept in the dark or in blue light (fluence rate, 1.5 W m^{-2}) for 6 h was measured with marking techniques. There were 10 seedlings/treatment. Vertical bars indicate \pm SE of the means. This experiment was performed three times with similar results.

Table II. *Suppression of Cucumber Hypocotyl Growth by Blue Light*

The elongation of cucumber (cv. Burpee's Pickler) hypocotyls under different experimental conditions was measured after 4 h in the dark or in 7.0 W m^{-2} blue light. Hypocotyls either were left intact on the plant, were completely excised, or were excised leaving the cotyledons still attached. Initial length was 18 mm. IAA concentration was 6 mg/liter in a 1% sucrose solution. Value are means \pm SE, with 10 hypocotyls/treatment. Each treatment was repeated at least twice with similar results.

Hypocotyl Condition	Increase in Length in		Inhibition
	Dark	Light	
	mm		%
Intact	8.50 ± 0.20	1.67 ± 0.07	+80
Excised segments on water	1.18 ± 0.04	0.77 ± 0.09	+35
Excised segments on IAA, sucrose	3.87 ± 0.11	4.80 ± 0.82	-24
Segments with cotyledons on water	4.13 ± 0.20	3.30 ± 0.12	+20
Segments with cotyledons on IAA, sucrose	4.75 ± 0.19	5.69 ± 0.26	-20

The light responsiveness of such segments is also greatly diminished in both absolute and relative magnitude: the growth of excised segments on water is so slow that any growth response is difficult to measure, whereas those with cotyledons grow at a rate of about 1 mm h^{-1} in the dark, of which only 20% is inhibited by blue light, compared to 80% in whole plants.

Hypocotyl segments can be stimulated to grow by addition of IAA and sucrose, but this stimulated growth is not inhibited by blue light. In fact, contrary to the condition in whole plants, such segments with or without cotyledons grow faster in the light than in the dark (Table II). This contrary effect of light on the growth of excised segments appears only at the higher concentrations of IAA (Fig. 9). The threshold concentration for growth stimulation by IAA is the same in both dark and irradiated sections, indicating that the affinity of the IAA-receptor is unchanged. Note that, even at the highest concentration tested, the growth rate of the excised segments is still only one-half of the rate in the intact plant and that the light-growth response is of the same (small) magnitude throughout most of the concentration range.

DISCUSSION

The results of these experiments show that the rapid growth inhibition by blue light, first reported by Meijer (19), is not unique to cucumber but also occurs in a variety of other species. They also show that, in some plants, a short pulse (10 s to 5 min) of blue light evokes only a rapid inhibition of growth which is fully reversible, whereas in other plants it evokes both the rapid growth inhibition and a more prolonged inhibitory response. Although phytochrome absorbs light in the blue region, the rapid growth inhibition is clearly mediated by a photoreceptor other than phytochrome, since red and far-red irradiations are ineffective in inducing the rapid response. This evidence, however, does not exclude a possible concomitant role for phytochrome in the growth response; it only argues that phytochrome alone cannot mediate the rapid response and that a specific blue-light photoreceptor must be involved. Experiments with simultaneous irradiations of blue and far-red light would be necessary to resolve this question.

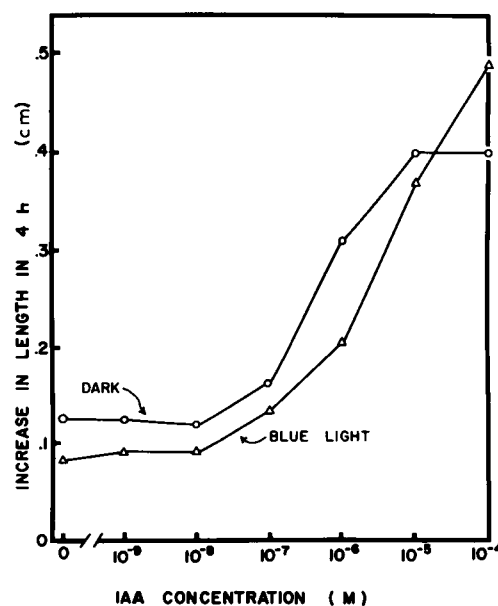


FIG. 9. Growth of cucumber segments in different IAA concentrations. Eighteen-mm hypocotyl segments of Burpee's Pickler cucumber were incubated at 30°C in the dark or in blue light (7.0 W m^{-2}) and lengths were measured after 4 h. Plotted values are the mean increases in length of 15 segments for each treatment. Standard errors of the means were all less than 0.015 cm.

of the possible extent of phytochrome involvement in the rapid response. The prolonged inhibition observed in some species, on the other hand, may well be mediated via a blue-light effect on the photostationary state of phytochrome because red light gives a similar time course of inhibition. More work is needed to confirm this aspect of the blue-light response. It is notable that some varieties of cucumber totally lack the long-term inhibition, whereas others have a pronounced secondary inhibition. Meijer (19) studied a cucumber variety with a pronounced long-term inhibition, whereas Gaba and Black (10) apparently used a variety without a long-term inhibition. Such differences in the degree of the prolonged inhibition must be an important aspect of the differential sensitivity among species for blue- and red-light inhibition noted by Thomas and Dickinson (29). It is likely that a rapid (nonphytochrome) response of the type characterized here could easily be masked by a superimposed phytochrome effect, particularly when only long-term measurements of growth are made, as in the experiments of Wildermann *et al.* (29).

Whether the blue-light photoreceptor which mediates this rapid growth response is the same as that which mediates phototropism is still unresolved. Comparisons between the two blue-light responses are hampered by the lack of information on the characteristics of phototropism in dicots. However, the rapid growth inhibition by blue light studied here differs in several respects from the phototropic response extensively studied in oat and corn coleoptiles. First, the timing of the two responses is very different. Phototropic bending in coleoptiles begins only about 25 min after the start of irradiation (7), whereas the growth inhibition in cucumber and sunflower seedlings is nearly fully reversed by this time. Second, the minimum light dose for any significant growth inhibition in cucumber falls well into the second positive region for phototropism (8, 25) and smaller doses are ineffective. Third, one can demonstrate a spatial separation between the light-sensitive and the response zones for coleoptile phototropism, but no such separation exists for the rapid growth response to blue light in cucumber hypocotyls.

In these last two characteristics, the rapid blue-light growth response is similar to the so-called base response observed in oat-coleoptile phototropism (7, 11). According to the view of Curry (7), the base response is induced only when the whole coleoptile (not just the tip) is asymmetrically irradiated with a high dose of blue light (in the second positive region), and the resulting curvature does not propagate but develops at the same time along the length of the organ. This view of the base response is similar to the old idea of Blaauw (2) that phototropic bending is due to a stronger light-growth reaction on the illuminated side of the organ than on the dark side and, at first glance, the rapid blue-light response seems to be a good candidate for such a mechanism of phototropism. More recently, however, Blaauw and Blaauw-Jansen (3) have maintained that the distinction between the tip and the base responses is an artifact of uncontrolled red-light effects. Furthermore, the rapid growth inhibition by blue-light in cucumber did not cause curvature of the hypocotyl. Even in cases where the seedling was irradiated from one side only (that is, when the mirror opposite the light source was removed) and the plant's growth rate dropped to half of the dark rate, no bending of the hypocotyl occurred. Thus, the rapid growth response to blue light seems to be distinct from the phototropic system.

The results of the shading experiments show that the photoreceptor for the rapid inhibition in etiolated cucumber is located in the growing region of the hypocotyl. With more long-term measurements of growth in radish and in light-grown cucumber, Jose (14) and Black and Shuttlesworth (4) have concluded that blue light acts directly on the growing hypocotyl, although their measuring technique could not adequately resolve whether this conclusion applied only to the long-term light response or to the very rapid response as well. In contrast, the site of red-light perception

is often different from the growing region. For example, red light is perceived by the hook in radish (14), by the cotyledons in light-grown cucumber (4), and by the coleoptile tip in rice (9), but the response in each of these cases occurs in the more basal growing regions. This difference in the site of perception and the site of response in red-light inhibition implicates the transmission of a stimulus or hormone of some kind. Indeed, red-light inhibition of growth is often associated with, and perhaps mediated by, changes in the auxin and gibberellin systems (5, 9, 16, 24).

In contrast, the rapidity of the blue-light response precludes its possible mediation by a hormone such as auxin or gibberellin. For example, stimulation of elongation by auxin typically has a latent period of 10 to 15 min (23), but the lag for the growth response to blue light in cucumber is only 20 s. Even if light instantly reduced either the concentration of auxin or the sensitivity of the tissue to auxin, one would reasonably expect a lag of 10 min before growth was inhibited. Lack of auxin involvement is also supported by the results of the experiments with excised hypocotyls floating on solutions of different IAA concentrations, where blue light inhibits growth to the same extent throughout the physiological range of IAA concentrations. Kinetic arguments similarly exclude gibberellin involvement.

The rapid blue-light growth response characterized here offers a potentially useful probe for studying the mechanism of cell enlargement and its control. It is easier to control the duration and intensity of light than it is to control the application of chemical substances, such as hormones, fusaric acid, and metabolic inhibitors, which take time to diffuse into and out of the tissue. Furthermore, the response of cucumber and sunflower to light has both simpler kinetics and a shorter lag than for the responses to other agents. Unfortunately for such studies, excised hypocotyls lose much of their sensitivity to light, so that whole plants must be used in the experiments. Although a similar loss of light sensitivity and even reversal of the sign of the response upon excision have been observed in other plant systems (13, 15, 21, 30), the reason for this major difference in the growth of intact and excised tissues is still unknown.

The short lag and the rapid kinetics of the blue-light growth response in cucumber and in other plants suggest that the blue-light photoreceptor acts directly on one or more steps in the process leading to cell enlargement. Such action must involve either the alteration of the (biochemical) process which loosens the cell wall or a reduction in the turgor pressure of the cell (or both). In another paper (manuscript in preparation), I will present evidence that blue light inhibits growth by modifying the yielding properties of the cell walls.

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LITERATURE CITED

1. ADDINK C, G MEIJER 1972 Kinetic studies on the auxin effect and the influence of cycloheximide and blue light. In DJ Carr, ed, *Plant Growth Substances* 1970. Springer-Verlag, New York, pp 68-75
2. BLAAUW AA 1919 Licht und Wachstum. III. Meded Landbou Wagen 15: 89-204
3. BLAAUW OH, G BLAAUW-JANSEN 1970 Third positive (c-type) phototropism in the *Avena* coleoptile. *Acta Bot Néerl* 19: 764-776
4. BLACK M, J SHUTTLEWORTH 1974 The role of the cotyledons in the photocontrol of hypocotyl extension in *Cucumis sativus* L. *Planta* 117: 57-66
5. BOWN AW, DR REEVE, A CROZIER 1975 The effect of light on the gibberellin metabolism and growth of *Phaseolus coccineus* seedlings. *Planta* 126: 83-91
6. CLELAND RE 1977 The control of cell enlargement. In DH Jennings, ed, *Integration of Activity in Higher Plants*, Symp Soc Exp Biol 31: pp 101, 115
7. CURRY GM 1969 Phototropism. In MB Wilkins, ed, *Physiology of Plant Growth Development*. McGraw-Hill, London, pp 245-276
8. DENNISON DS 1979 Phototropism. In W Haupt, ME Feinleib, eds, *Encyclopedia of Plant Physiology*, New Series, Vol 7. Springer-Verlag, New York
9. FURUYA M, DJ PION, T FUJII, M ITO 1969 Phytochrome action in *Oryza sativa* L. III. The separation of photoreceptor site and growing zone in coleoptiles and auxin transport as effector system. *Dev Growth Differ* 11: 62-76
10. GABA V, M BLACK 1979 Two separate photoreceptors control hypocotyl growth

- in green seedlings. *Nature* 278: 51-54
11. GALSTON AW 1959 Phototropism of stems, roots and coleoptiles. In W Ruhland, ed, *Encyclopedia of Plant Physiology*, Vol 17/1, Springer, Heidelberg, pp 492-617
 12. GREEN PB, WR CUMMINS 1974 Growth rate and turgor pressure. Auxin effect studied with an automated apparatus for single coleoptiles. *Plant Physiol* 54: 863-869
 13. IDLE DB 1957 Studies in extension growth. II. The light-growth responses of *Vicia faba* L. *J Exp Bot* 8: 127-138
 14. JOSE A 1977 Photoreception and photoresponses in the radish hypocotyl. *Planta* 136: 125-129
 15. KAZAMA H, M KATSUMI 1978 Effects of light on auxin-induced elongation of light-grown cucumber hypocotyl sections. *Plant Cell Physiol* 19: 1137-1144
 16. KENDE H, A LANG 1964 Gibberellins and light inhibition of stem growth in peas. *Plant Physiol* 39: 434-440
 17. LOCKHART, JA 1959 Studies on the mechanism of stem growth inhibition by visible radiation. *Plant Physiol* 34: 457-460
 18. MARSHALL DC, D PENNY 1976 High-resolution measurement of transient changes in the growth rate of intact lupin seedlings. *Austr J Plant Physiol* 3: 237-246
 19. MEIJER G 1968 Rapid growth inhibition of gherkin hypocotyls in blue light. *Acta Bot Néerl* 17: 149-
 20. MUIR RM, KC CHANG 1974 Effect of red light on coleoptile growth. *Plant Physiol* 54: 286-288
 21. PJON C, M FURUYA 1967 Phytochrome action in *Oryza sativa* L. I. Growth responses of etiolated coleoptiles to red, far-red and blue light. *Plant Cell Physiol* 8: 709-718
 22. POFF KL, KH NORRIS 1967 Four low-cost monochromatic sources of known equal intensities. *Plant Physiol* 42: 1155-1157
 23. RAY PM 1974 The biochemistry of the action of indoleacetic acid on plant growth. *Rec Adv Phytochem* 7: 93-122
 24. RUSSEL D, AW GALSTON 1969 Blockage by gibberellic acid of phytochrome effects on growth, auxin responses, and flavonoid synthesis in etiolated pea internodes. *Plant Physiol* 44: 1211-1216
 25. STEYER B 1967 Die Dosis-Wirkungsrelationen bei geotroper und phototroper Reizung: Vergleich von Mono- mit Dicotyledonen. *Planta* 77: 277-286
 26. THOMAS B, HG DICKINSON 1979 Evidence for two photoreceptors controlling growth in de-etiolated seedlings. *Planta* 146: 545-550
 27. TURNER MR, D VINCE 1969 Photosensory mechanisms in the lettuce seedling hypocotyl. *Planta* 84: 368-382
 28. VANDERHOEF L, WR BRIGGS 1978 Red light-inhibited mesocotyl elongation in maize seedlings. I. The auxin hypothesis. *Plant Physiol* 61: 534-537
 29. WILDERMANN A, H DRUMM, E SCHAFER, H MOHR 1978 Control by light of hypocotyl growth in de-etiolated mustard seedlings. I. Phytochrome as the only photoreceptor pigment. *Planta* 141: 211-216
 30. WOLF F 1979 Effects of light quality upon the growth of *Avena* coleoptiles. *Z Pflanzenphysiol* 91: 1-6