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Light-Stimulated Apical Hook Opening in Wild-Type *Arabidopsis thaliana* Seedlings[1]

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Apical hook opening and cotyledon unfolding are characteristic responses that occur during deetiolation of dicotyledonous seedlings. Light-stimulated apical hook opening and cotyledon unfolding in etiolated *Arabidopsis thaliana* seedlings appears to involve the activities of multiple photosensory systems. Red, far-red, and blue light are all effective in stimulating these responses in *Arabidopsis*. Stimulation of hook opening by red light and low fluence blue light is inductive, far-red reversible, and exhibits reciprocity, as is characteristic of many low fluence-dependent phytochrome-mediated responses. Far-red and high-fluence blue light appear to stimulate hook opening and cotyledon unfolding through high-irradiance-response systems during long-term light treatments. Although a phytochrome high-irradiance-response system presumably mediates the responses in far-red light, the responses to high-fluence blue light may be mediated by a blue light-specific photosensory system.

One of the most important developmental programs initiated in a plant is the switch from etiolated to deetiolated growth. Growth responses affected by this developmental switch include stem-growth inhibition, apical hook opening, cotyledon unfolding and expansion, leaf and root growth, and the acquisition of photosynthetic competence. One of the most morphologically striking of these is the apical hook opening response (Withrow et al., 1953). In dark-grown epigeal plants, the cotyledons and the most apical portion of the hypocotyl fold back toward the long axis of the hypocotyl to form a "U"-shaped structure: the apical hook. Upon exposure to light, the hook opens, cotyledons enlarge and unfold, and Chl is synthesized. Light-stimulated hook opening has generally been considered a phytochrome-mediated response because exposure to red light causes hook opening (Withrow et al., 1957; Lane and Kasperbauer, 1965; Caubergs and De Greef, 1975; Powell and Morgan, 1980). However, in at least two species, blue light-stimulated hook opening has been observed that does not appear to be mediated by phytochrome (Mohr and Noble, 1960; Kujawski and Truscott, 1974; Silk, 1980).

Arabidopsis has proven to be a valuable model system for studying light-dependent processes in higher plants (Koornneef et al., 1980; Khurana and Poff, 1989; Chory et al., 1989; Boylan and Quail, 1991; Deng et al., 1991; Liscum and Hangarter, 1991; Nagatani et al., 1991; Whitelam and Smith, 1991; Liscum et al., 1992; Young et al., 1992). In this paper, the effects of light on apical hook responses in wild-type seedlings of *Arabidopsis* have been examined. These studies provide the first detailed analysis of light-stimulated hook opening in *Arabidopsis* and indicate that multiple photosensory systems are involved in red, blue, and far-red light-stimulated apical hook opening and cotyledon unfolding in etiolated *Arabidopsis* seedlings.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Wild-type *Arabidopsis thaliana* (L.) Heynh. ecotypes Columbia, homozygous for the recessive *gl1* mutation (Koornneef et al., 1982), and Landsberg *erecta* (Redei, 1962) were used. Seeds were surface sterilized for 20 min in 1.5% (w/v) sodium hypochlorite, rinsed several times with sterile H_2O, and planted in polystyrene Petri dishes containing growth medium consisting of 0.5× Murashige and Skoog salts (Murashige and Skoog, 1962) and 0.8% (w/v) agar. Seeds were incubated for 2 to 3 d at 4 ± 1°C, then exposed to red light for 30 min to induce uniform germination (Liscum et al., 1992). The red light-treated seeds were incubated in darkness at 23 ± 2°C for an additional 71.5 h and then moved to the various light treatments for the indicated times.

Light Sources

White light was provided by a 1:1 mixture of cool white fluorescent lamps (F40CW; Philips Lighting Co., Salina, KS) and warm white fluorescent lamps (F40CW; General Electric Co., Cleveland, OH). The red light source for induction of germination was as described by Liscum et al. (1992).

Blue light for fluence rate-response and reciprocity experiments was obtained by filtering light from four halogen flood lamps (150 W Quartzline; General Electric Co.) through 7 cm of 1.5% (w/v) $CuSO_4 \cdot 7H_2O$ and Rohm and Haas blue plexiglass No. 2045 (3.18 mm thick; Dayton Plastics, Columbus, OH). For pulse experiments, one halogen lamp was used with 3 cm of 1.5% $CuSO_4 \cdot 7H_2O$, 3 cm of H_2O, and blue plexiglass. The resulting spectral output had peak intensity at 480 nm and a 100-nm half-bandwidth.

Red light for fluence rate-response and reciprocity experiments was obtained by filtering light from four halogen flood lamps through 3.5 cm of 1.5% $CuSO_4 \cdot 7H_2O$ and one layer of Rohm and Haas red plexiglass No. 2444 (3.18 mm thick; Dayton Plastics). This filter combination cut off wavelengths

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below 580 nm and had peak intensity at 630 nm. For pulse experiments, light from one halogen lamp was filtered through 3 cm of 1.5% $CuSO \cdot 7H_2O$, 3 cm of H_2O, and Rohm and Haas red plexiglass No. 2423 (3.18 mm thick; Dayton Plastics). This filter combination cut off wavelengths below 580 nm and had peak intensity at 644 nm. Less than 15% of the total irradiance from these sources was from wavelengths greater than 700 nm.

Far-red light for fluence rate-response experiments was obtained by filtering light from one halogen flood lamp through 5 cm of H_2O and one layer of far-red plexiglass No. FRF 700 (3.18 mm thick, Westlake Plastics Co., Lenni, PA). The fluence rate for this light source was measured for wavelengths between 710 and 750 nm because Pfr absorbs maximally at 730 nm. Wavelengths above 750 nm were assumed to be inactive in the responses tested here. For pulse experiments, light from one halogen lamp was filtered through 3 cm of H_2O and a 734-nm interference filter with a half-bandwidth of 10 nm.

Fluence rates were adjusted by changing voltage, distance between the seedlings and the light source, and/or using neutral density filters such that the spectral quality remained constant. Fluence rates at the level of the seedlings were measured with an LI-189 quantum photometer or an LI-1800 portable spectroradiometer (LiCor, Inc., Lincoln, NE). In all experiments that involved long light exposures, the H_2O and $CuSO_4$ solutions that were used as light filters were cooled by running cold tap water through copper tubing submerged in the solutions.

Measurement of Hook Opening and Cotyledon Unfolding

At the end of the treatments, the seedlings were carefully pulled from the agar and placed onto transparent tape. Images of the seedlings were projected from a photographic enlarger (3.5× magnification), and the angle of the apical hook was measured to the nearest degree (see inset in Fig. 1). Light-stimulated hook opening was calculated by subtracting the angle of the apical hook of seedlings that were kept in darkness from the angle observed after light treatment. Although the apical hook was treated as a simple angle in this work, it should be noted that the morphological changes that occur during hook opening are more complex.

Cotyledon unfolding is expressed as the percentage of seedlings with cotyledons that were at least visibly curved outward away from the axis of the seedling as a result of differential cell enlargement and division on the adaxial and abaxial sides of the cotyledon. For example, the seedling shown for the 3.5-h treatment in Figure 2 would be scored as having cotyledons unfolding because the outward curvature is apparent. In contrast, the seedling shown for the 2-h treatment would be scored as closed because, although the cotyledon tips are not tightly appressed, they do not show outward curvature. Using this procedure, cotyledons that are just beginning to unfold are lumped together with those that have fully opened. Unless otherwise indicated, each data point represents the mean response from a minimum pooled sample size of 75 seedlings from at least three replicate experiments.

RESULTS

Apical Hook Opening and Cotyledon Unfolding in Darkness

Etiolated, wild-type seedlings of *Arabidopsis* exhibited appreciable apical hook opening in darkness as shown in Figure 1, but cotyledon unfolding did not occur within the 5-d growth period examined here. The kinetics for apical hook opening in darkness were similar for the two ecotypes used here, except that Landsberg *erecta* exhibited a slightly slower initial rate of opening. The majority of seedlings had opened hooks and the cotyledons were unfolded after 2 weeks of growth in darkness (data not shown).

Light-Stimulated Apical Hook Opening and Cotyledon Unfolding

Apical hook opening and cotyledon unfolding occurred sequentially when 3-d-old, etiolated, wild-type *Arabidopsis* seedlings were transferred to fluorescent white light (Fig. 2). Hook opening was noticeable after about 2 h in white light. By 3.5 h, the hooks were nearly completely opened and the cotyledons were beginning to unfold. After 6 h of continuous white light, the hooks were opened completely and the cotyledons had unfolded in most of the seedlings. Deetiolation of the apical hook was completed after about 12 h of continuous irradiation. Similar kinetics for hook opening have been reported for etiolated *Cuscuta* seedlings after transfer to fluorescent (Lane and Kasperbauer, 1965) and incandescent white light (Kujawski and Truscott, 1974).

Figure 3 shows the fluence rate-responses for apical hook opening in wild-type *Arabidopsis* seedlings exposed to 14 h of blue, red, and far-red light. In blue light, hook opening exhibited a log-linear response with a threshold of about 0.01 μmol m^{-2} s^{-1} and saturation at about 10 μmol m^{-2} s^{-1}. The threshold for far-red light was also around 0.01 μmol m^{-2} s^{-1}

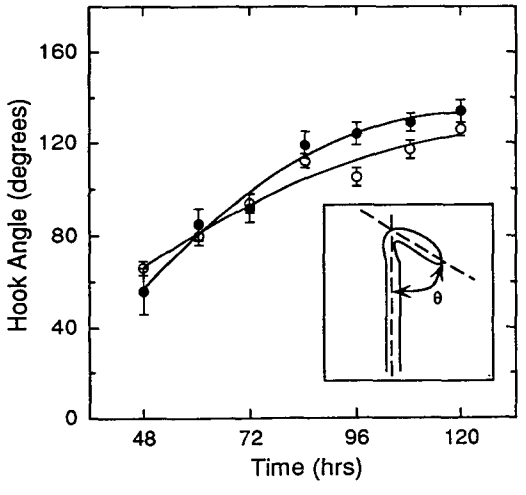

Figure 1. Time course of apical hook opening in dark-grown *Arabidopsis* seedlings. The vertical error bars represent the SE values. Curves were fit by regression analysis. The inset demonstrates how hook angles were determined from projected images. O, Columbia; ●, Landsberg *erecta*.

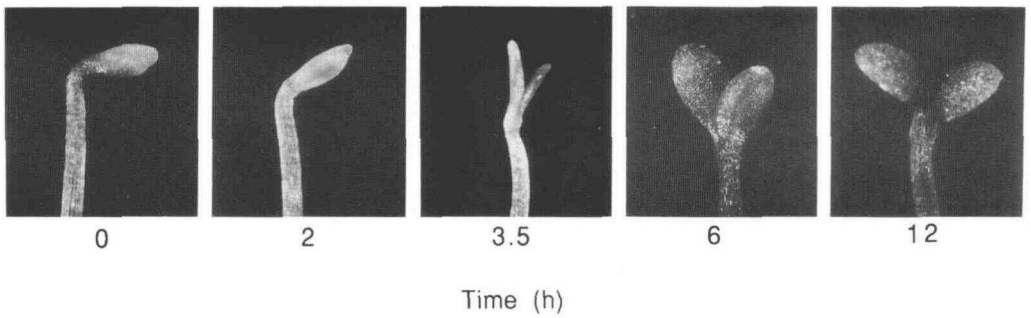

Figure 2. Representative photographs of apical hook opening and cotyledon unfolding in *Arabidopsis* in white light. Three-day-old, dark-grown seedlings were transferred to white fluorescent light (50 ± 5 μmol m^{-2} s^{-1}). Representative seedlings were then photographed after the indicated times.

but saturation occurred at about 3 μmol m^{-2} s^{-1}. The hooks were completely open at saturation in blue and far-red light. Red light-stimulated hook opening exhibited a log-linear response with a threshold below 0.01 μmol m^{-2} s^{-1} and saturation at about 1 μmol m^{-2} s^{-1}. The fluence-rate dependence for red light-stimulated hook opening in *Arabidopsis* is in the range of those observed for other species (Withrow et al., 1957; Lane and Kasperbauer, 1965; Caubergs and De Greef, 1975; Powell and Morgan, 1980).

In blue and far-red light, the threshold for cotyledon unfolding is at a fluence rate just below saturation for hook opening (Figs. 3 and 4). In addition, although the hooks didn't open completely in red light at any fluence rate tested (Fig. 3), cotyledon unfolding occurred on more than 50% of the seedlings at fluence rates greater than 1 μmol m^{-2} s^{-1} (Fig. 4). This indicates that, although hook opening may be related to cotyledon unfolding, it is not a prerequisite for cotyledon unfolding and the two processes may therefore have divergent signal transduction pathways.

Although Columbia and Landsberg *erecta* represent polymorphic genetic backgrounds (Chang et al., 1988; Nam et al., 1989), the dark-grown pattern and deetiolation responses of the apical hook appear to be conserved (Figs. 1, 3, and 4). Thus, only Columbia was used in the remaining experiments.

Reciprocity and Photoreversibility of the Light-Stimulated Hook Opening Response

To further characterize the photobiology of hook opening, reciprocity relationships were examined in red and blue light (Fig. 5). Red light-stimulated hook opening was essentially reciprocal over at least 4 orders of magnitude of exposure time. Thus, short pulses of red light were nearly as effective for activating the hook-opening response as continuous irradiation. These results are consistent with the red light-stimulated hook-opening response being an inductive phytochrome response as observed in other species (Withrow et al., 1957; Lane and Kasperbauer, 1965; Caubergs and De Greef, 1975; Powell and Morgan, 1980).

Because blue light stimulated hook opening over a wider range of fluence rates than did red light (Fig. 3), reciprocity relationships were examined with low- and high-fluence blue light. Apical hook opening in low-fluence blue light showed reciprocity over at least 3 orders of magnitude of exposure time (Fig. 5). However, reciprocity failed in high-fluence blue light. These data suggest that two different signal transduction systems operate in blue light-stimulated hook opening: a "low-fluence-requiring system" that is dependent only on the number of incident photons, and a "high-fluence-requiring system" that is dependent upon exposure time and fluence rate. The former is typical of an inductive response, whereas the latter is typical of a high-irradiance response (Kronenberg and Kendrick, 1986).

If the red light-stimulated hook-opening response is an inductive phytochrome response, it should be far-red reversible, as is red light-stimulated hook opening in other species (Withrow et al., 1957; Lane and Kasperbauer, 1965; Caubergs and De Greef, 1975; Powell and Morgan, 1980). Similarly, the low-fluence, blue light-stimulated hook-opening response may also operate via a photoreversible phytochrome system (Bertsch, 1963; Downs and Siegelman, 1963; Wellmann, 1971, 1974).

Table I demonstrates that when a red pulse sufficient to cause 30° of opening or blue light pulse sufficient to cause 18° of opening was followed by a far-red light pulse of an equivalent fluence to the red or blue pulse, the effect of the inductive pulse was negated. These results suggest that hook opening in red light and low-fluence blue light is induced via a photoreversible phytochrome signal transduction system. In addition, the results in Table I suggest that hook opening in continuous far-red light (Fig. 3) may be dependent upon a phytochrome high-irradiance-response system because pulses of far-red light did not induce hook opening.

The kinetics for the loss of photoreversibility are shown in Figure 6. The effectiveness of far-red light for reversing red light-stimulated hook opening in wild-type seedlings of *Arabidopsis* decreased as the dark time between red and far-red light exposure increased up to 20 min. It took 12 to 13 min for 50% of the red light-induced signal to escape from far-red photoreversibility, and at intervening dark periods longer than 20 min photoreversibility reached its minimum.

DISCUSSION

The effects of light quality and quantity on light-stimulated apical hook opening and cotyledon unfolding were investigated in etiolated *Arabidopsis* seedlings. Fluence rate dependencies showed that red light was less effective than far-red

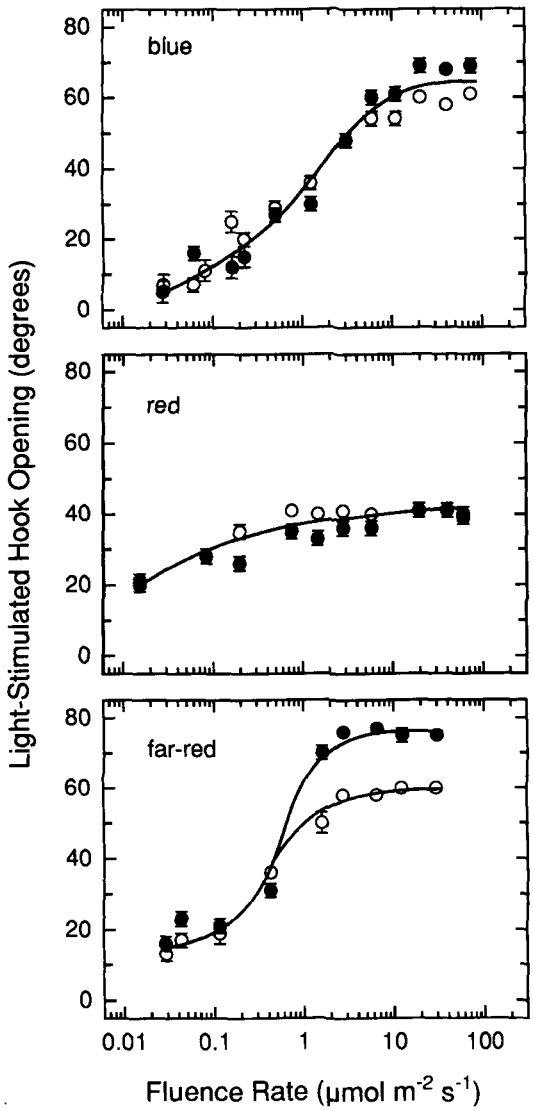

Figure 3. Fluence rate-response curves for blue, red, and far-red light-stimulated hook opening in *Arabidopsis* seedlings. Three-day-old, dark-grown seedlings were transferred to continuous blue, red, or far-red light provided from above. After 14 h, the angle of the apical hook was measured. In this experiment, the apical hooks of dark controls were opened to 114 ± 2° for Columbia (○) and 100 ± 3° for Landsberg *erecta* (●). Error bars represent the SE for the light-treated seedlings. For some data points, the SE was less than the size of the symbol. Curves were drawn by inspection. Note that the magnitude of the response to red light is less than that for the other colors.

or blue light for stimulating hook opening. In addition, red-light stimulation of hook opening showed reciprocity and was far-red reversible. It took about 15 min of dark time after red-light treatment to lose 50% of the far-red reversibility. Other species show similar effects of red and far-red light (Klein et al., 1957; Withrow et al., 1957; Lane and Kasperbauer, 1965; Caubergs and De Greef, 1975; Porath and Atsman, 1977; Powell and Morgan, 1980). Stimulation of hook opening in *Arabidopsis* by low-fluence blue light also showed reciprocity and exhibited far-red photoreversibility. The far-red reversibility of the inductive effects of red light and low-fluence blue light indicate that phytochrome is involved in light-stimulated hook opening in *Arabidopsis*.

In addition to the inductive effects of red light and low-fluence blue light, hook opening in *Arabidopsis* also appears to be mediated by high-irradiance-response systems, as indicated by the responses to far-red and high-fluence blue light. For example, in contrast with the effects of low-fluence blue light on hook opening, the response to high-fluence blue light does not exhibit reciprocity (Fig. 5). To our knowledge, blue-light light stimulation of hook opening has not been observed in most species. Notable exceptions are *Cus-*

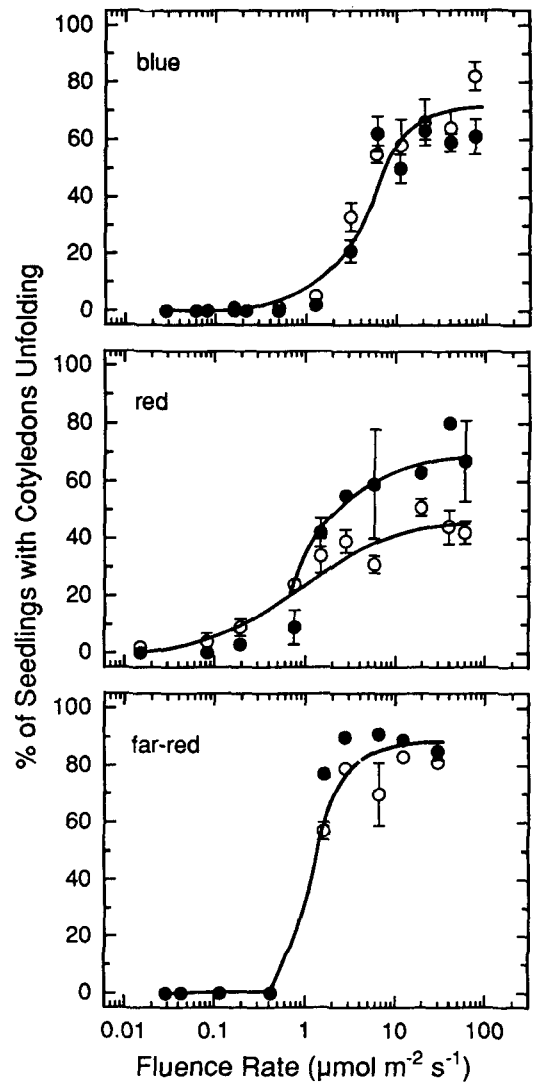

Figure 4. Fluence rate-response curves for blue, red, and far-red light-stimulated cotyledon unfolding in *Arabidopsis* seedlings. Seedlings were handled as described in Figure 3, and cotyledon unfolding was visually scored as described in "Materials and Methods." Error bars represent the percent SE. For some data points the SE was less than the size of the symbol. Curves were drawn by inspection. ○, Columbia; ●, Landsberg *erecta*.

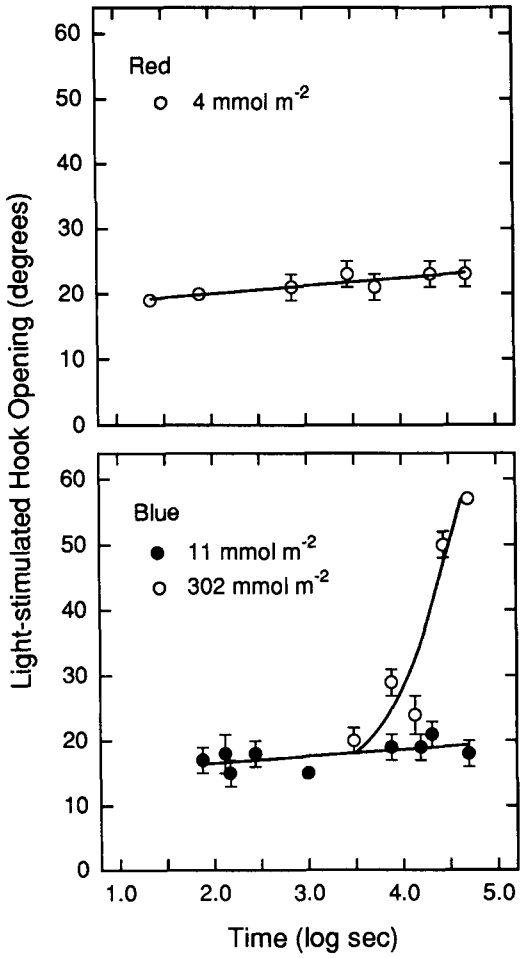

Figure 5. Reciprocity relationships of the hook-opening response. Three-day-old, dark-grown Columbia seedlings were exposed to red or blue light given from directly above at various combinations of fluence rates and exposure times to achieve the indicated fluence. The fluence of red light used in these experiments was equal to a 14-h exposure at a fluence rate that stimulated the hooks to open by about 20°. For blue light, the low- and high-fluence treatments used were photon equivalents of 14-h exposures to low- and high-fluence rates, respectively, that stimulated the hooks to open by about 18° and 60°, respectively. The longest light exposure was 14 h and the shortest was 24 s. When required, seedlings were transferred to the dark so that all seedlings were allowed to grow for 14 h after the beginning of light exposure. The apical hooks for dark controls were opened to 114 ± 2°. Error bars represent the SE for the light-treated seedlings. Curves were drawn by inspection.

cuta (Kujawski and Truscott, 1974) and lettuce (Mohr and Noble, 1960; Silk, 1980). However, because cotyledons do not develop in *Cuscuta*, the hook and hook-opening response are not necessarily analogous to hypocotyl and epicotyl hooks and hook responses of dicotyledonous plants. In addition, whereas blue light stimulates hook opening in etiolated *Arabidopsis* seedlings, apical hooks in lettuce must be induced to close by a red-light treatment before blue light will stimulate opening. The effects of far-red light in *Arabidopsis* also appear to be atypical because far-red light-stimulated hook opening

Table I. *Far-red photoreversibility of light-stimulated hook opening*

Hook opening was stimulated in 3-d-old, dark-grown Columbia seedlings by 5 min of red light (116 μmol m^{-2} s^{-1}) or 10 min of blue light (78 μmol m^{-2} s^{-1}). Far-red light, of a fluence equal to the inductive treatments, was given 30 s after the inductive treatments. Control seedlings were exposed to far-red light alone at the same fluence given for the red or blue pulses. Hook opening was allowed to develop in the dark for a total of 14 h after the start of light exposure. Data represent the mean ± SE for light-stimulated samples minus the value for dark controls (114 ± 2°). The numbers in parentheses equal the pooled sample size from a minimum of three independent experiments. R, Red; FR, far-red; B, blue.

Light Treatment	Light-Stimulated Hook Opening
R	31 ± 1° (150)
FR	0 ± 2° (206)
R-FR	1 ± 2° (147)
B	18 ± 2° (230)
FR	2 ± 2° (144)
B-FR	1 ± 2° (178)

has only been reported for *Cuscuta* (Lane and Kasperbauer, 1965; Kujawski and Truscott, 1974), *Cucumis* (Porath and Atsman, 1977; Porath et al., 1980), and after red light-induced hook closure in lettuce (Mohr and Noble, 1960).

The fluence rate-response curves for red, blue, and far-red light-stimulated hook opening (Fig. 3) are very similar to those generated for the inhibition of hypocotyl elongation in wild-type *Arabidopsis* (Young et al., 1992). These results suggest that light-stimulated hook opening and inhibition of

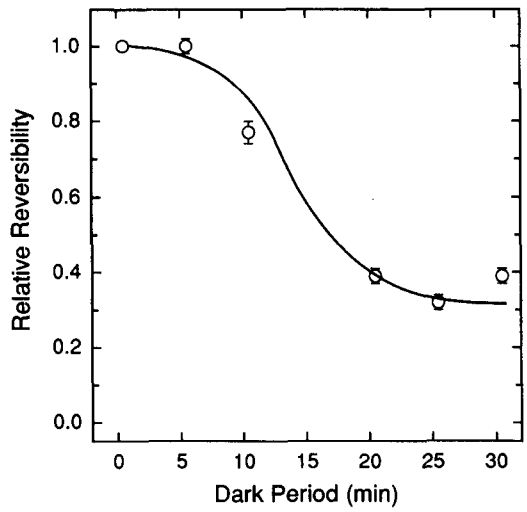

Figure 6. Kinetics for the escape from far-red photoreversibility of red light-stimulated hook opening. Three-day-old, dark-grown Columbia seedlings were given 5 min of red light (116 μmol m^{-2} s^{-1}) followed, after various times in the dark, by 15 min of far-red light (39 μmol m^{-2} s^{-1}). Hook opening was allowed to develop in the dark for a total of 14 h after the start of light exposure. The shortest delay time between red and far-red treatments was 30 s, and it resulted in complete reversibility of the red-light induction. Data are expressed relative to this treatment. Error bars represent the SE. Curves were drawn by inspection.

hypocotyl elongation may have common signal transduction systems. This is to be expected because the apical hook is a region of the hypocotyl that has undergone differential cell elongation during the development of the seed to give rise to the "U"-shaped hook structure; however, in other studies apical hook opening and inhibition of hypocotyl elongation did not appear to be closely related photobiological processes (Mohr and Noble, 1960; Janes et al., 1976; Porath et al., 1980).

Although the threshold for light-stimulated unfolding of the cotyledons was slightly lower for red light than for blue or far-red light, unfolding occurred at fluence rates that were at least 100-fold greater than those required for the stimulation of hook opening in all light conditions tested. The requirement for relatively high fluence rates (>1 μmol m^{-2} s^{-1}) suggests that cotyledon unfolding is a high-irradiance response. This possibility is currently being investigated in several photomorphogenic mutants.

The results presented here indicate that the apical hook-opening response in wild-type *Arabidopsis* is controlled by multiple signal transduction pathways, including low-fluence and high-irradiance phytochrome systems and a blue light-sensitive high-irradiance photosensory system. Phytochrome probably acts as the photoreceptor for red light and low-fluence blue light stimulation of hook opening because a terminal far-red light pulse can negate the effects of red and low-fluence blue light pulses. Presumably, the far-red high-irradiance response acts via a phytochrome photoreceptor, but the nature of the high-irradiance blue-light photoreceptor is unknown.

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