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Photobiology of Phytochrome-Mediated Growth Responses in Sections of Stem Tissue from Etiolated Oats and Corn[1]

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ABSTRACT

The far-red reversibility of the phytochrome-controlled stimulation of elongation of coleoptile sections by low fluence red light has been characterized in subapical coleoptile sections from dark-grown *Avena sativa* L., cv Lodi seedlings. The fluence dependence of the far-red reversal was the same whether or not the very low fluence response is also expressed. The capacity of far-red light to reverse the red light-induced response began to decline if the far-red light was given more than 90 minutes after the red irradiation. Escape was complete if the far red irradiation was given more than 240 minutes after the red irradiation. Sections consisting of both mesocotyl and coleoptile tissue from dark-grown *Avena* seedlings were found to have physiological regulation of the very low fluence response by indole 3-acetic acid and low external pH similar to that seen for sections consisting entirely of coleoptile tissue. The fluence-dependence of the red light-induced inhibition of mesocotyl elongation was studied in mesocotyl sections from dark grown *Zea mays* L. hybrid T-929 seedlings. Ten micromolar indole 3-acetic acid stimulates the control elongation of the sections, while at the same time increasing the sensitivity of the tissue for the light-induced inhibition of growth by a factor of 100.

In previous papers, the physiology of phytochrome-mediated stimulation of coleoptile elongation induced by red light, both in terms of the nature of the change in elongation rate (15), and the nature of the coupling of the phytochrome signal to the response (13, 14) were described. A major finding was that alterations in the physiological state of the coleoptile cells can alter phytochrome signal transduction processes considerably. Decreasing the extracellular pH in section tissue caused the sensitivity of the sections to R[3] to increase by as much as a factor of 10,000 (13, 14). Certain assumptions about the responses seen have been made in interpreting the results, and assessing their significance. In the main, these assumptions have been: (a) that the performance of isolated coleoptile sections is relevant to the behavior of intact seedlings, (b) that the physiological altrations brought about by the changes in the extracellular milieu affect all of the cells of the section relatively equally, and (c) that the alterations in apparent light sensitivity of the sections is in fact an alteration in the properties of phytochrome signal transduction.

It is implicit in the last assumption that the high sensitivity (or VLF) response is a phytochrome-mediated response. Action spectroscopy studies of two such responses (1, 16, 17) suggest that the VLF responses may be phytochrome-mediated. The previous finding that the VLF and LF responses share control of the light-induced growth in a reciprocal manner (13) also suggests that the VLF may be phytochrome-mediated, and a similar relationship between VLF and LF responses has been found for phytochrome regulation of photodormancy in seeds (20).

Some experimental approaches can be used to test the validity of other aspects of these assumptions. The photobiology of the effects of FR on phytochrome responses has been used to examine similar assumptions to those mentioned above (1–3, 5, 6). The initial study of the FR reversibility of R-induced elongation (13) merely confirmed that the LF response was FR reversible in this system, and that growth in response to R in the VLF range was not reversible by FR. The sensitivity of the LF response to FR under different conditions was not examined, and the kinetics of the escape of the LF R-induced growth from FR reversibility were not obtained. Results of these studies address assumptions (a) and (c).

Experiments studying the regulation of the VLF in different tissues can test all three assumptions. A study of longr sections, which are a combination of mesocotyl and coleoptile tissue, will permit detection of any tissue/tissue interaction in the response (8, 9), and will change both the number of cut ends that each tissue has exposed to the medium and the relative percentage of tissue in proximity to those cut surfaces. By studying isolated mesocotyl sections, the modulations of the VLF by the extracellular milieu can be tested for a phytochrome-mediated inhibition of growth, instead of a stimulation (7, 18, 19), separating the direct action of the physiological alteration which induces the VLF (always a stimulator of elongation), from the action of phytochrome.

Results from the experiments described should further define the nature of the physiological regulation of phytochrome signal transduction. Taken together, these findings support the assumptions listed above. Further, the findings draw attention to a difficulty in establishing where, in the shoots of intact seedlings, the events of phytochrome photoreception occur (11).

MATERIALS AND METHODS

Light Sources. The fluorescent light source previously referred to as 'B' (14) was used for the R irradiations in the FR reversal experiments, and was also used for the VLF and LF R irradiations, using the protocols described. For irradiations with FR, a custom-built 1000 W light source was used. The FR source consisted of an Olesen 17288 15.2 × 22.9 cm elipsoidal spot lamp and a light-tight housing with a platform which held a 20 × 20 × 7.6 cm plastic box. The bottom of the box was a Rohm and Haas FRF 700 plastic color filter with one sheet of orange cinemoid (No. 5A) attached. During irradiations the box was

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[3] Abbreviations: R, red light; FR, far-red light; LF, low fluence; VLF, very low fluence.

filled with 1 L of deionized H_2O (depth 2–3 cm). The fluence rate of the FR source was measured with a Skye 660/730 quantum meter (Skye Instruments, Isle of Skye, Scotland) which measured the FR fluence only between 725 and 735 nm. For the FR fluence-response experiments, the fluence rate was varied using Whatman filter paper filters, and for the R fluence-response experiments performed on mesocotyl sections, the light source previously referred to as 'A' was used as described (14).

Plant Material. Seedlings of *Avena sativa* L. cv Lodi were grown in complete darkness, as described (15). Seedlings of *Zea mays* L. Trojan Hybrid T 929 were grown for 72 to 76 h in complete darkness as described (13). Subapical *Avena* coleoptile sections, 5.7 mm in length, were cut from 72 h old seedlings as described previously (15). Sections of *Avena* seedlings which were a composite of coleoptile and mesocotyl tissue were obtained from 72 h old dark grown seedlings using the same cutter used for *Zea* coleoptile sections (13). Seedling shoots were loaded tip down into the cutter, and this time the subapical sections produced were 10.9 mm in length, cut beginning from 3 mm below the coleoptile tip. Mesocotyl sections were cut from *Zea* seedlings by locating the node between the coleoptile and mesocotyl by touch, and removing the coleoptile and enclosed leaves with a razor blade. The mesocotyl tissue was then placed, node down, into the cutter used for the composite *Avena* sections. Mesocotyl sections, 10.7 mm in length, beginning from 3 mm below the node, were obtained. *Zea* mesocotyl segments were used because of difficulty obtaining such tissue from *Avena*, and *Zea* coleoptile sections have been shown to exhibit similar induction of a VLF response to that seen in *Avena* coleoptile sections (13).

Buffers, Incubation Conditions, and Growth Measurements. All sections were placed on buffered aqueous medium in mini-Petri dishes (20 × 60 mm) immediately after cutting. The standard medium consisted of: 2.5 mM Mes, 2.5 mM fumaric acid, 5% (w/v) sucrose, and 80 μM chloramphenicol. The pH was adjusted with NaOH and HCl to either pH 5.9 or 4.5. IAA was added, as noted, from a 0.1 M stock in ethanol, which was stored at −20°C. Potassium was added as K_2SO_4, as noted. For the experiments using *Zea* mesocotyl sections, the buffer was 5 mM K-phosphate, pH 5.9, plus 5% sucrose. After all sections for a given treatment were harvested, irradiations were performed. The beginning of irradiation (the first irradiation when two were used) was used as the start time for a 12 h incubation. The incubation was in complete darkness, on a rotary shaker operating at 100 rpm. At the end of the 12 h incubation, growth was measured as described previously (15).

RESULTS

Figure 1 shows the fluence-response data for the reversal of the R-induced increase in coleoptile section length by FR. The incubation conditions (pH 5.9, no IAA) were such that R-induced growth is potentiated almost exclusively by the LF response (14). The R fluence used was a fluence which saturates the LF response. The FR irradiation was given immediately following the R irradiation. Several irradiations with FR alone are also shown. At 3000 μmol m^{-2} FR, the FR alone treatment yields almost identical section length to that obtained after R followed by FR, indicating maximum FR reversal.

Figure 2 shows similar fluence-response data for FR reversal of the R-induced growth when the sections are incubated at pH 4.5. For both panels, the R fluence used was sufficient to saturate the LF response. In Figure 2A, the treatment with pH 4.5 evokes a VLF response (14), causing FR to induce 50% of the maximum capacity for light-induced elongation. The reversal of the R-induced growth by FR is to the level of elongation induced by FR alone. The FR reversal is saturated at about 1000 μmol m^{-2}.

As seen in Figure 2B, the capacity to express a VLF response, evoked by the pH 4.5 treatment, was inhibited by the inclusion

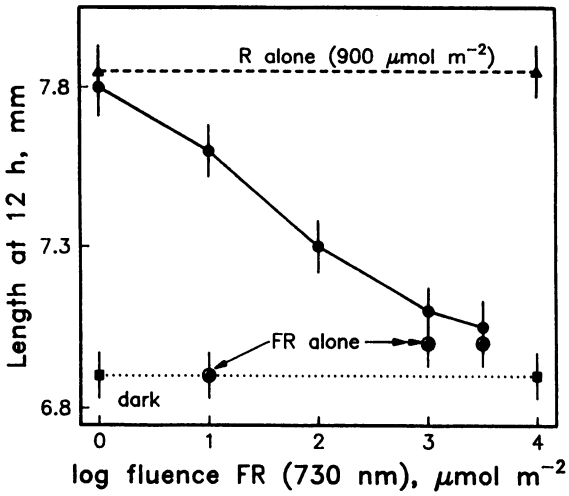

FIG. 1. Fluence dependence for the FR reversal of the LF R induced growth response. *Avena* coleoptile sections were incubated in pH 5.9 buffer with no IAA for 12 h in 2.5 mM Mes/2.5 mM fumaric acid. R and FR irradiations were given as in "Materials and Methods". The solid line is the fluence-response curve for FR following R (at 900 μmol m^{-2}). The dashed line indicates the final length for sections given only the R irradiation, and the dotted line indicates the final length of the dark control sections. The three circumscribed diamonds indicate the lengths of sections given only FR at the fluences indicated. Results shown are the average of three replicate experiments. Error bars indicate the average SE for the three replicates.

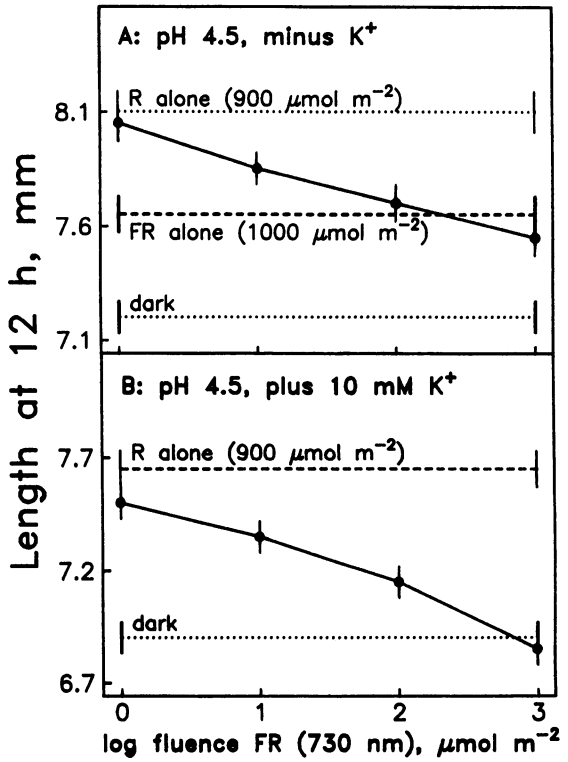

FIG. 2. Fluence dependence of FR reversal of LF R-induced growth of sections incubated at pH 4.5. *Avena* coleoptile sections were incubated as in Figure 1, but in pH 4.5 buffer, either without (Fig. 2A) or with (Fig. 2B) 5 mM K_2SO_4. The solid lines are the FR fluence-response curves, and the broken lines indicate the final lengths for the R only, FR only, and dark control treatments. Error bars indicate SE for each experiment.

of 10 mM K^+ in the incubation medium. The R-induced growth was less in this experiment than in either Figures 1 or 2A, but this slight inhibition of growth by K^+ was not always observed (see Table I). FR evokes no detectable elongation, even at 1000 μmol m^{-2} (data not shown). The fluence-response curve for FR-reversal of R-induced elongation is not changed relative to that seen in Figure 2A, and the saturation of the FR-reversal is again near 1000 μmol m^{-2} FR.

The time course for the escape of the R-induced growth from reversal by FR is shown in Figure 3. The incubation conditions were the same as in Figure 1, as was the R fluence which the FR was to counteract. The FR fluence (3000 μmol m^{-2}) was the saturating fluence for FR reversal when the FR was given immediately after the R irradiation. The duration of the R irradiation was 2 to 3 min, and the FR irradiation required 50 to 80 s. The kinetic determinations of the FR escape were made under conditions where only the LF response is expressed (Fig. 1). Escape does not begin until at least 90 min after the irradiation, and is not complete until 240 min after R irradiation. The onset of escape is the same for sections incubated in pH 4.5 buffer plus 10 mM K^+ (Table I).

The growth responses to light, IAA, and low pH buffer were studied in coleoptile portions of *Avena* sections consisting of both coleoptile and mesocotyl tissue. Figure 4 summarizes the growth responses to VLF and LF R, with IAA and pH treatments as shown. The variability of the growth responses shown is in large part a function of the range of the initial proportions of the composite sections. The initial length of the coleoptile portions of the sections are shown as the baseline value in Figure 4. The mean value exhibited a SE of 0.2 mm. The SE is much higher than those seen for the initial length of isolated coleoptile sections (15). The small size and low elongation rate of the mesocotyl portions of the composite sections did not allow for detection of changes in the growth responses to light in this tissue (data not shown).

Table I. *Escape from Far-Red Reversibility of Red Light-Induced Elongation in Avena Coleoptile Sections*

Coleoptile sections from dark grown *Avena* seedlings were incubated in pH 4.5 Mes/fumarate buffer (2.5 mM/2.5 mM) with 10 mM K^+ as in Figure 2B, and irradiated as in Figure 3.

Elongation of Coleoptile Sections						
D	R	FR	Dark period between R and FR (min)			
			1	60	90	120
			mm ± *SE*			
7.00 ±0.06	7.95 ±0.07	7.00 ±0.06	7.00 ±0.08	6.90 ±0.07	7.10 ±0.09	7.25 ±0.08

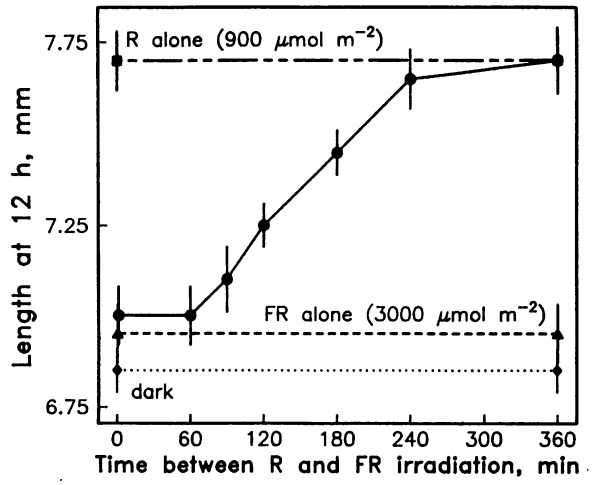

FIG. 3. Time course for the escape of the R-induced growth from FR reversibility. *Avena* coleoptile sections were incubated as in Figure 1. The solid line is the curve for the effect of increasing the time between R and FR irradiations. The broken lines are the final lengths for R only, FR only, and dark treated sections. Irradiations were with the R and FR fluences shown. Results are the average of three replicate experiments. Error bars represent the average SE for the three replicates.

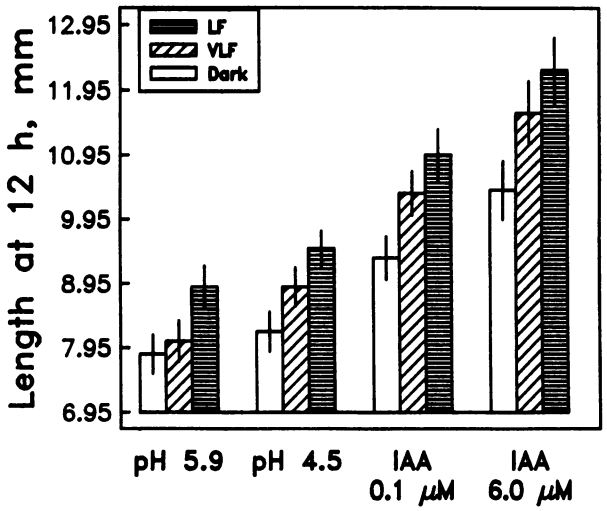

FIG. 4. Responses of coleoptile portions of composite *Avena* sections to light, IAA, and pH 4.5 and pH 5.9 buffer. Sections were obtained, incubated and irradiated as described in "Materials and Methods". Lengths of coleoptile portions of tissue are shown. Baseline value shown is the average initial length. Results shown are the average of three replicate experiments. Error bars represent average SE for the three replicates.

Treatment of sections with both 0.1 and 6 μM IAA, induced greater elongation in the dark controls, relative to the pH 5.9, minus IAA, treated sections. Treatment of sections with pH 4.5 buffer, as well as the IAA treatments, also induced the capacity of the sections to respond to VLF R. The pattern of the responses to buffer pH, IAA, and VLF and LF R was constant over three replicate experiments for each type of treatment. The LF irradiated sections were always longer than the VLF treated sections, for the three treatments evoking a VLF, over all three replicates. The VLF response in sections incubated in pH 5.9 minus IAA medium was never larger than the dark control by an amount more than the combined standard error for the two responses.

The low pH and IAA treatments also caused an increase in the magnitude of the total capacity of the sections to elongate in response to R, although the VLF component of the growth response increases partially at the expense of the LF component. When the responses to pH 5.9 minus IAA and pH 5.9 plus 6 μM IAA are compared, IAA treatment yields less than a 2-fold increase in R-induced elongation, while causing a 4-fold increase in dark elongation. The relative contribution of the VLF and LF components to the total growth response may not be exactly parallel between the coleoptile sections and the coleoptile tissue in the composite sections.

The capacity of IAA to induce a VLF response was tested in *Zea* mesocotyl sections. The effect of IAA was tested rather than the effect of low external pH because the cuticle resistance to buffer penetration was not known for this tissue, and the larger sections used would require good penetration of the tissue by buffer, whereas IAA is transported polarly through mesocotyl tissue (8), and may also pass freely through the cuticle (4, 12).

In Figure 5, the effect of IAA on the fluence-dependence of

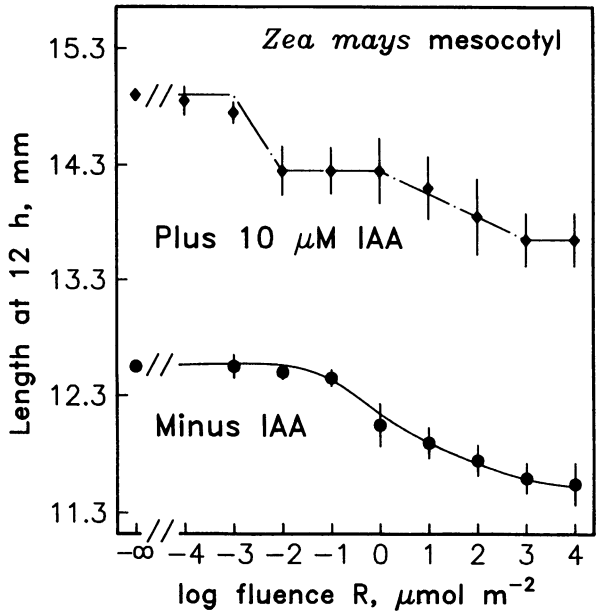

FIG. 5. Effect of 10 μM IAA on the fluence dependence of the R-induced inhibition of mesocotyl elongation of *Zea mays*. Mesocotyl sections were harvested into 5 mM K-phosphate, pH 5.9, and irradiated with R as described in "Materials and Methods". Results shown are the average of four replicate experiments. To compensate for variability between experiments, lengths were normalized to the dark control response for each replicate. Error bars indicate SD for the normalized replicates.

the R-induced inhibition of *Zea* mesocotyl elongation is shown. It is clear that 10 μM IAA stimulates elongation, but also increases the sensitivity to light for the R-induced inhibition of elongation by approximately 100-fold. Although the variability of the growth responses in the presence of IAA was somewhat high, the pattern shown was seen in all four replicates. The induction of a VLF response by IAA is very similar to the effect of IAA in increasing the light sensitivity of *Zea* coleoptile sections (13).

DISCUSSION

The FR-reversal studies in Figures 1 and 2 indicate that the LF response has the same FR fluence requirement for reversal whether or not the VLF response is expressed at the same time. For two external conditions which cause sections to show only an LF response to R, the fluence-dependence of the FR reversibility is the same, independent of the means by which the VLF response is suppressed (no IAA, nonpermissive pH; or permissive pH but high K^+). In sum, the responses to FR are similar to those seen in intact tissue (10).

The kinetic determinations of the escape from FR reversibility shown in Figure 3 are quite similar to those obtained by Hopkins and Hillman (6). Although apical coleoptile sections (the tips of which are an internal source of IAA) (21) were used, and tissue was handled under dim green bench lights, the onset of escape was found to occur at approximately 2 h after irradiation as seen here. In the earlier study, complete escape did not occur until 6 to 8 h after R irradiation, unlike the findings presented here, where escape was complete after 4 h. Escape from FR reversibility indicates the time at which the Pfr is no longer required for the signal transduction process to be completed. Since there is little or no escape from FR reversibility during the first 90 min after irradiation, the signal transduction process cannot have progressed beyond the requirement for Pfr. The complete escape of the response from FR reversibility at 240 min indicates that the response is decoupled from any requirement for Pfr long before the response is complete (15).

The time during which the IAA, or low external pH must be present in order to induce the VLF response is a window from 1 h before to 2 h after irradiation (14). A small component of the LF R-induced growth escapes from FR reversibility during the first 2 h after irradiation, but this component appears only after 90 min after irradiation. Overall, the kinetics of the escape from FR reversibility and the kinetics of the IAA-induction of the VLF are similar, and this similarity is consistent with the assumption that the induction of the VLF by IAA is an effect of IAA on the process of phytochrome signal transduction.

The FR escape kinetic determinations are, of necessity, a direct measure of the signal transduction of the LF phytochrome response only. The signal transduction for the VLF response may be different. However, there is indirect evidence that the kinetics of the VLF signal transduction are likely to be similar to those seen for the LF response. The lag time for the beginning of the actual increase in elongation rate caused by red light for both the VLF and LF responses is at least 2 h from the time of irradiation (15). The shared kinetics of the VLF and LF responses in this case suggests a shared signal transduction process. The combination of the kinetics of the growth responses to VLF and LF R, and the kinetics of the escape from FR reversibility, give some confidence to the assumption that phytochrome signal transduction is being altered by the changes in physiological conditions (14).

In the experiments with composite *Avena* sections, it appears that the reduction of cut surfaces of coleoptile tissue from two to one does not appear to alter the capacity of either low external pH or 0.1 μM IAA to induce the response to VLF R. The ratio of VLF- to LF-induced growth in the composite coleoptile tissue may be reduced relative to the isolated coleoptile sections, when both are treated with 6 μM IAA. But in general it appears that the majority of cells in the tissue are responding to the external conditions, not just those in proximity to a cut surface.

The experiments with *Zea* mesocotyl sections test an alternative to the assumption that phytochrome signal transduction is being directly affected by the incubation conditions. The alternative hypothesis is that the VLF signal is always transduced, but only expressed when external conditions permit the elongation process itself to be changed. The results of the mesocotyl section experiments would require this hypothesis to postulate a single factor which releases the capacity of VLF R both to stimulate elongation, and inhibit elongation in two different tissues. In addition to lending support to the hypothesis that phytochrome signal transduction is directly affected by physiological conditions, the demonstration of the phemonenon in a second tissue and species adds generality to the findings.

In a similar study (18), it was reported that the addition of IAA to the incubation medium eliminates the R-induced inhibition of elongation in *Zea* mesocotyl sections. Here, it was found that there is a considerable inhibition of elongation by R, whether or not the sections are incubated with IAA. This discrepancy can be resolved by noting that the previous study was performed under dim green bench lights. Since IAA induces a VLF response in this tissue, a large fraction of the light-induced inhibition of growth would be induced by the green light when sections were incubated with IAA (*cf.* 10). Therefore the 'dark controls' for the plus IAA experiments would also show a reduced elongation, to the point where the effect of additional R might be negligible.

The results of both the experiments with *Zea* mesocotyl sections, and with the composite sections are relevant to the specific zones of photoreception for both the VLF and LF phytochrome responses postulated by Mandoli and Briggs (11). The coleoptile sections used here and in the previous papers (13–15) do not contain the tissue region to which these zones of photoreception

have been localized, while the composite sections both of the zones identified, and the mesocotyl sections come from a different species. No differences between the physiological regulation of the photobiology of the three types of sections have been observed. So if the process by which phytochrome acts in excised tissue is different from that which occurs in the intact seedling, the excised tissue can mimic the intact system by a process which is indifferent to the zones of photoreception identified for the intact seedling responses.

The results presented by Mandoli and Briggs (11) do not require an explanation which invokes discrete zones of photoreception to account for the growth responses to irradiation of narrow regions of intact seedling shoots. The original analysis only considered the effects of unidirectional light guiding along the axis of the shoot to explain the response of shoot regions to light given at a considerable distance from the responding region. The possibility remains that the light is distributed roughly in parallel with the regions showing a growth response to the local irradiation. Under this interpretation, phytochrome would control growth on a cell by cell basis, with each cell responding to its own cellular pool of phytochrome. It is also possible that, in the intact plant, the phytochrome-mediated response to light is effected by both a signal propagated from the zones of photoreception and by a cell by cell response.

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