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Phytochrome Control of Two Low-Irradiance Responses in Etiolated Oat Seedlings[1]

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ABSTRACT

Light-induced coleoptile stimulation and mesocotyl suppression in etiolated *Avena sativa* (cv. Lodi) has been quantitated. Etiolated seedlings showed the greatest response to light when they were illuminated 48 to 56 hours after imbibition. Two low-irradiance photoresponses for each tissue have been described. Red light was 10 times more effective than green and 1,000 times more effective than far red light in evoking these responses. The first response, which resulted in a 45% mesocotyl suppression and 30% coleoptile stimulation, had a threshold at 10^{-14} einsteins per square centimeter and was saturated at 3.0×10^{-12} einsteins per square centimeter of red light. This very low-irradiance response could be induced by red, green, or far red light and was not photoreversible. Reciprocity failed if the duration of the red illumination exceeded 10 minutes. The low-irradiance response which resulted in 80% mesocotyl suppression and 60% coleoptile stimulation, had a threshold at 10^{-10} einsteins per square centimeter and was saturated at 3.0×10^{-8} einsteins per square centimeter of red light. A complete low-irradiance response could be induced by either red or green light but not by far red light. This response could be reversed by a far red dose 30 times greater than that of the initial red dose for both coleoptiles and mesocotyls. Reciprocity failed if the duration of the red illumination exceeded 170 minutes. Both of these responses can be explained by the action of phytochrome.

Blaauw *et al.* (1) and Vanderhoef *et al.* (29) have shown that dose-response curves for the effect of red light on elongation growth of etiolated oat and corn tissues are composed of two or more steps. Oat mesocotyl suppression showed three steps with the first detectable response, called here very low irradiance response (VLIR[2]), at 10^{-5} and final saturation near 4.0×10^{-4} nE cm^{-2} (1). Blaauw *et al.* (1, 2) characterized the VLIR in oat mesocotyl suppression, which reduced mesocotyl length by 15% compared to the dark control, as irreversible by FR and inducible by wavelengths of light through the green and FR spectral regions (wavelengths tested were 519, 600, 735, 770, 790 nm). The second response of oat mesocotyls (LIR), suppression of elongation by 50%, was characterized by FR reversibility, and the third (95% inhibition) by its time dependence. Stimulation of oat coleoptile growth by light showed a parallel "mirror image" pattern although the magnitude of the response was not as dramatic (1). In corn, Vanderhoef *et al.* (29) found that mesocotyl suppression by R occurred in two steps similar in magnitude to the second and third steps found in oats (1). They did not find in corn the very sensitive response detected in oats. Generally, the characteristics of the two responses of the corn mesocotyl were similar in magnitude, relative sensitivity, R/FR reversibility, and time dependence to those described for oats (29, *cf.* 1). Corn coleoptiles, however, under the conditions used to study mesocotyl suppression, showed no response at all to R for doses from 10^0 to 10^5 nE cm^{-2} for any wavelengths from 600 to 700 nm (Vanderhoef, unpublished). Other workers have also failed to obtain reproducible red light responses with coleoptiles (*e.g.* 17).

The vast literature on photomorphogenesis in *Avena* was confusing for two major reasons: first, growth of the etiolated seedlings was highly variable, and second, the responses to light were often not reproducible. This report described the elongation growth of etiolated oat coleoptiles and mesocotyls in a growth system in which these problems have been solved and which has facilitated analysis of large groups of seedlings.

METHODS

Growth of Uniform Etiolated Seedlings. A 9 × 6 cm piece of absorbent paper (Kimpak, K-41 Perf'd, Kimberly-Clarke) was placed in the middle of a 17 × 3.5 cm glass plate so that one long side of the paper and glass were even. Groups of 25 dry oat seeds (*Avena sativa* L. cf. Lodi, Lot No. 0170-B, Dakota Seed and Grain Co., Inc., Watertown, SD) with husks present were placed side by side onto strips of masking tape 12.7 mm in width (Scotch Brand, Part No. 6201, 3M Co.) with the embryos against the tape. About 5 cm of bare tape extended on either side of each group of seeds. A group of seeds was then laid against absorbent paper with the bare ends of the tape affixed to the glass plate beyond the paper. The ends of the seeds farthest away from the embryo and the padding were even with the aligned edges of the glass plate and paper, and any projecting glumes, etc., were excised. These dry-mounted seeds could be stored for several weeks at 4 C without loss of viability. They were imbibed by inserting this asembly with the seeds up into distilled H_2O just to the level of the middle of the seeds for 0.5 h in absolute darkness. Uniformity of germination and growth was improved if the seeds themselves were not entirely submerged during imbibition. The plates were then transferred to racks which held them at an angle 45° from the vertical with the seeds up and the other edge of the absorbent paper immersed about 5 mm deep in distilled H_2O in plastic boxes. These boxes were then tightly closed and kept in darkness until seedling treatment. The absorbent paper under the seeds acted as a wick to provide water to the seedlings for the duration of the experiments. This method yielded from 20 to 24 seedlings of uniform length per plate. Seedlings which had been planted and grown in this manner were indistinguishable from those planted and grown without masking tape (data not shown).

Illumination and Analysis. Plates of 25 seedlings were illuminated from above and then returned to the dark for 24 h before harvest. No safe lights were used at any time prior to harvest

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[2] Abbreviations: VLIR, very low-irradiance response; FR, far-red light; R, red light; G, green light; LIR, low-irradiance response; HIR, high-irradiance response.

except when indicated (Fig. 2). Illuminations were automated with a custom-built sequential gate timing system equipped with a Uniblitz microsecond "programmable" shutter (model no. 225L0A0T5; 25 mm aperture). Seedlings were harvested, secured to plastic sheets with clear tape, and photocopied. Length measurements were taken directly from these images with an Alvin planimeter or a computerized digitizer. Each treatment is usually the average of 50 to 100 seedlings (2–4 plates): standard errors of coleoptile or mesocotyl mean length were between 1.0 and 3.5%. Growth increments

$$\frac{\text{(Illuminated Final Length} - \text{Dark Initial Length)}}{\text{(Dark Final Length} - \text{Dark Initial Length)}},$$

(cm/24 h), had combined standard errors from 5 to 7% (*e.g.* Fig. 4).

Light Sources. Incandescent light (General Electric, CWD 300W, 3,200 K) passing through a 6 mm IR-absorbing filter (Leitz, Germany), 3 cm of water, and finally through a Rohm and Haas red or far red plastic filter (2444 or RFR, respectively: Corth Plastics, Inc., Redwood City, CA) provided broad band light (Fig. 1). Per cent transmittance with a Corning 7-56 filter (visible absorbing, IR transmitting) was zero. A custom-built 650 w light source (22) provided high intensity FR for doses exceeding 300 nE cm^{-2}. Overhead gold fluorescent tubes (Sylvania, F40G0) filtered through one layer each of Rohm and Haas blue (2424) and green (2092) plastic provided 0.0002 nE cm^{-2} s^{-1} green safe light at bench level (about 142 cm from front surface of fluorescent tubes) with a major peak at 525 nm and a shoulder at 534 nm (Fig. 1, *cf.* 24). Light intensities were measured with a Licor radiometer (model no. L10185A) or with an Eppley eight junction bismuth-silver thermopile in conjunction with a Keithley 150B microvoltmeter that had been previously calibrated against a standard lamp (National Bureau of Standards). Light intensity was varied with distance, neutral density filters (Bausch and Lomb), and/or a variety of light scattering agents such as opal glass and Kimwipes. All lamp voltages were kept constant.

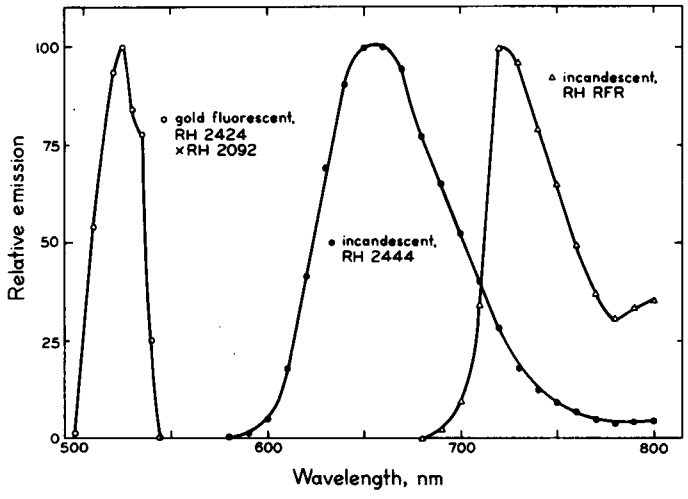

FIG. 1. Spectral energy distributions for green, red, and far red actinic light sources were calculated by multiplying the manufacturers' emission curves by the transmission of each of the filters used (not shown). Transmission of each filter was measured on a Cary 17 spectrophotometer. Data were normalized so that peak emission corresponds to 100% relative energy for each curve shown. G: gold fluorescent tubes (Sylvania F40G0) filtered through one layer each Rohm and Haas blue (2424) and green (2092) plastic. R and FR: warm white incandescent light (General Electric: CWD, 300 w, 3,200 K) passed through both a 3-cm water and a heat filter (Leitz, Germany) and then through either Rohm and Haas red (2444) or far red (RFR) plastic.

RESULTS

Response Optimization. Growth in total length of etiolated Lodi oat remained linear ($y = 7.53x + 0.16$, $r^2 = 0.98$) from about 56 to 122 h after the start of imbibition. Mesocotyls and coleoptiles, however, showed maximal growth at different times (Fig. 2). The increment in mesocotyl length (cm/24 h) was highest for dark-grown seedlings during the growth interval starting at 64 h. Growth rates declined thereafter until by 122 h, mesocotyl growth had ceased (not shown). The coleoptile growth rate continued increasing slowly from 64 until 96 to 98 h when it reached a maximum. Subsequently (from 98 to 122 h), the growth rate of the coleoptile declined. From 15 to 30% mesocotyl suppression and 10 to 20% coleoptile stimulation were commonly seen as a result of handling the plants for 10 min under a green safe light (total dose 0.12 nE cm^{-2}; Fig. 2). Since the mechanical effects of handling the seedlings proved statistically insignificant in several

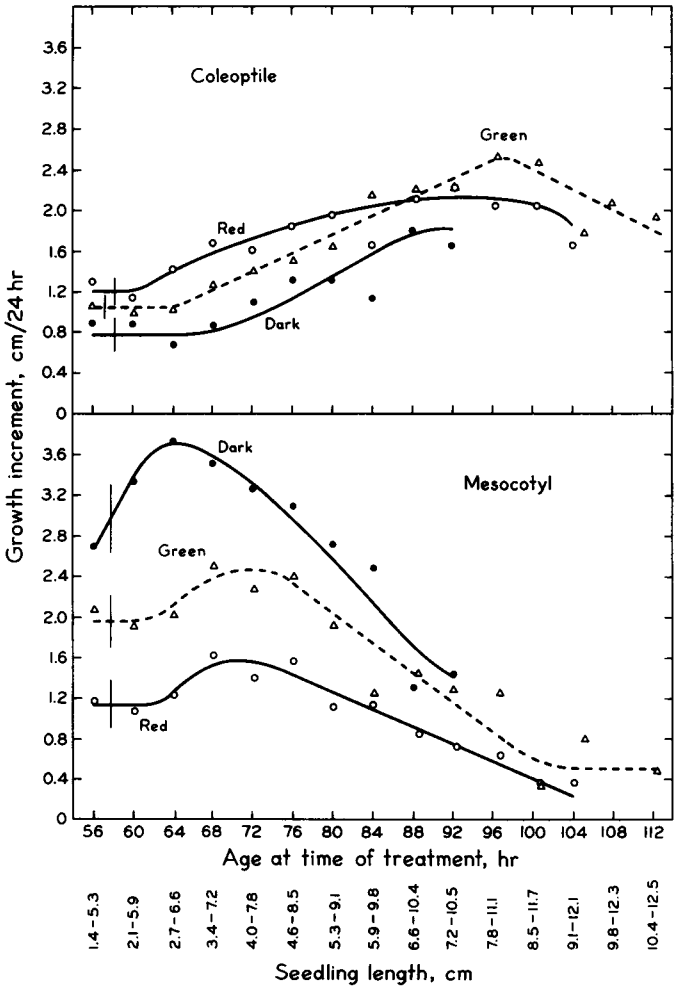

FIG. 2. Growth increments of mesocotyls and coleoptiles were measured 24 h after treatment and plotted as a function of age at the time of treatment. Age was measured from the start of imbibition. Approximate total seedling lengths are also indicated along the abscissa as an index of physiological age. Dark-grown plants (dark controls) were undisturbed until harvest. R dose was 20 s duration for a total dose of 4.0 nE cm^{-2} and was delivered in the presence of green safe lights (0.0002 nE cm^{-2} for 10 min). "Green" seedlings are those that were removed from light-tight growth cabinets to a bench under overhead green safe light (24) for 10 min. Humidity remained at or above 85%. During these 10 min, groups of seedlings were moved into position for R illumination but were not illuminated. Vertical bars represent the range of values obtained in replicate experiments.

experiments in which oat seedlings were mechanically disturbed in absolute darkness or under green safe lights (results not shown), this effect is attributed solely to the green safe light. A dose of 4.0 nE cm^{-2} of R further suppressed mesocotyl elongation and slightly affected coleoptile elongation as compared with the G-treated controls but did not change the pattern of elongation during the 24 h immediately after treatment (Fig. 2).

A dose-response curve for R conducted under green safe lights when seedlings were 72-h-old showed a threshold for mesocotyl suppression at 0.04 nE cm^{-2} and saturation at 25 nE cm^{-2} (not shown). Although the mesocotyl showed a sizeable response over this range (70%), the coleoptile was only slightly stimulated (12%) and the response became saturated over a surprisingly small dose range (from 0.06–1.7 nE cm^{-2}). Since green safe light seemed to induce both oat mesocotyl suppression and coleoptile stimulation (Fig. 2) (16), we reasoned that the small stimulation of the coleoptile might be amplified and some experimental variability eliminated by repeating the R dose-response curves without the G. All subsequent experiments were conducted without any safe lights. The response of the coleoptile or mesocotyl to a given dose of R (oat: 6, 8, Mandoli, unpublished; corn: 4) or white light (oat: 27, 28) varied as a function of seedling age at the time of illumination: both corn and oat tissues were quite sensitive to light when they were from 48- to 60-h-old. All subsequent experiments were initiated with seedlings from 54- to 56-h-old. The growth technique used permitted handling groups of seedlings in complete darkness.

The length of time between illumination and harvest was also critical to the magnitude of the responses obtained, since at these low doses, the changes in growth rate were not permanent (cf. 25). If R-irradiated seedlings are grown for 48 rather than 24 h after the irradiation, the magnitude of the coleoptile and mesocotyl responses to R decreases by 25% (data not shown).

Dose Response Curves. Oat coleoptile stimulation and mesocotyl suppression each showed two levels of response to R, G, or FR over a range of doses which spanned seven orders of magnitude (Fig. 3). The coleoptile and mesocotyl showed approximately equal and opposite responses to light as shown when the growth increment (cm/24 h) was normalized to the dark control (Fig. 3). This relationship was not obvious if the absolute increments in length (mm) were plotted (*cf.* Fig. 2). Some of the variability at very low doses was the result of technical difficulties in preventing light leaks through the leaves of the shutter; at higher doses, the light leak was comparatively insignificant.

The threshold for the VLIR to R in Lodi oat occurred at 10^{-5} nE cm^{-2}, became saturated at 5×10^{-3} nE cm^{-2}, and resulted in 35% mesocotyl suppression and 30% coleoptile stimulation (Fig. 3, top). The LIR to R in Lodi oats had a threshold at 0.1 nE cm^{-2}, became saturated at 30 nE cm^{-2} (Fig. 3, top), and resulted in 80% mesocotyl suppression and roughly 65% coleoptile stimulation.

The dose-response curve for G had the same general shape as that for R and showed that G was one-tenth as effective as R in eliciting these photoresponses in oats (Fig. 3, center). FR could induce the VLIR and probably some LIR but was 1,000-fold less effective than R (Fig. 3, bottom). The small amount of mesocotyl LIR which was induced by FR (30–1,000 nE cm^{-2}; Fig. 3) is reproducible (Fig. 7). The variability of the coleoptile response precludes resolution of an effect of these doses on the coleoptile at this time (Figs. 3, 7).

Reciprocity Tests. Reciprocity for the VLIR at a total dose of 0.03 nE cm^{-2} R was valid from 1 to 600 s (Fig. 4). The same total dose delivered over a period of time longer than 600 s resulted in a greater response from both mesocotyls and coleoptiles (Fig. 4). Reciprocity for the LIR (total dose 1.0 nE cm^{-2} R) was essentially valid over four orders of magnitude (Fig. 5). The small slope of the regression line from 1 to 10^4 s was significantly different from a slope of zero ($P >> 0.05$) for the mesocotyl but was insignificant ($P < 0.01$) for the coleoptile.

FR Reversibility. FR reversibility of the VLIR and the LIR that had been induced with R were tested to determine the involvement of the photomorphogenic pigment, phytochrome. Since FR alone would induce these responses in oats (Fig. 3), the photoreversal obtained with FR could at best be expected to return seedlings to the response level for FR, not to the level of the dark controls. To test the VLIR, a 10% response was produced with a dose of 10^{-4} nE cm^{-2} R and followed 5 min later with an equivalent or greater dose of FR (Fig. 6). The resulting data did not show FR reversal of the VLIR but rather described a curve identical to the one predicted from summation of the individual responses of R and FR (Fig. 6; *cf.* Fig. 3). To test the LIR, 70% mesocotyl suppression was produced with a dose of 1.0 nE cm^{-2} R and, again, followed 5 min later with an equivalent or greater dose of FR (Fig. 7). Significant FR reversal was obtained with a FR dose roughly 30 times greater than that of the initial R dose (Fig. 7). The FR reversal of the coleoptile LIR stimulation paralleled that obtained for mesocotyl suppression.

DISCUSSION

The R photoresponses of etiolated seedlings of *Avena sativa* are 10 to 100 times more sensitive than the blue light-induced phototropic responses of *Avena* (3, 5). The most sensitive R photoresponse characterized here (VLIR) and by Blaauw *et al.* (1) rivals the sensitivity of phytochrome-mediated root geotropism (23, 26). These photoresponses have thresholds between 10^{-14} and 10^{-15} E cm^{-2}.

Oat mesocotyls showed the greatest response to light when irradiated between 48 and 60 h after imbibition, and coleoptile responses were greatest when seedlings were irradiated 64 to 80 h after imbibition (Fig. 2; Mandoli, unpublished). Although similar data have been obtained by Thomson (28) for Victory oat, direct comparisons were impossible since an incandescent source of unspecified intensity was used. Goodwin (6) and Hamada (8) both obtained the largest mesocotyl response to light when seedlings were irradiated between 24 and 48 h after imbibition. Examination of these various reports revealed that the greatest mesocotyl response to light was always obtained when the seedlings were irradiated just before the exponential increase in growth occurred. The threshold and saturation values for the VLIR in Lodi oats were in good agreement with those determined by Blaauw *et al.* (1) for Victory oats. Data of Huisinga (11) on coleoptile and mesocotyl sections showed a similar threshold value. Vanderhoef *et al.* (29) did not see this very low-energy response in corn. Oats (both Lodi and Victory) and corn mesocotyls had similar threshold and saturation values for the LIR (1, 29). No third (HIR) response (*cf.* 1, 29) was detected in this study.

The relative magnitudes of the VLIR and LIR presented here are generally triple those reported for oat mesocotyl and coleoptile by Blaauw *et al.* (1, 2) and roughly double those reported for the LIR in corn mesocotyl (29). There are four differences in procedure which might account for these discrepancies in the response of intact oat seedlings: (*a*) age at time of illumination; (*b*) length of growing time between illumination and harvest; (*c*) the presence or absence of hulls during growth and irradiation; and (*d*) the unspecified or uncontrolled use of safelights. The magnitude of the photoresponses of the corn (4) and the oat coleoptile (Fig. 2; 6, 8, 27, 28) is strongly dependent on seedling age at the time of illumination. Although Blaauw *et al.* (1) irradiated their seedlings at 48 rather than 56 h after imbibition, the response of their seedlings should be comparable to the response of the seedlings used in this study (see also 8).

Vanderhoef (unpublished) did not detect any coleoptile response in corn from 10^0 to 10^5 nE cm^{-2} for wavelengths between 600 and 700 nm. Also, the variability seen by many previous

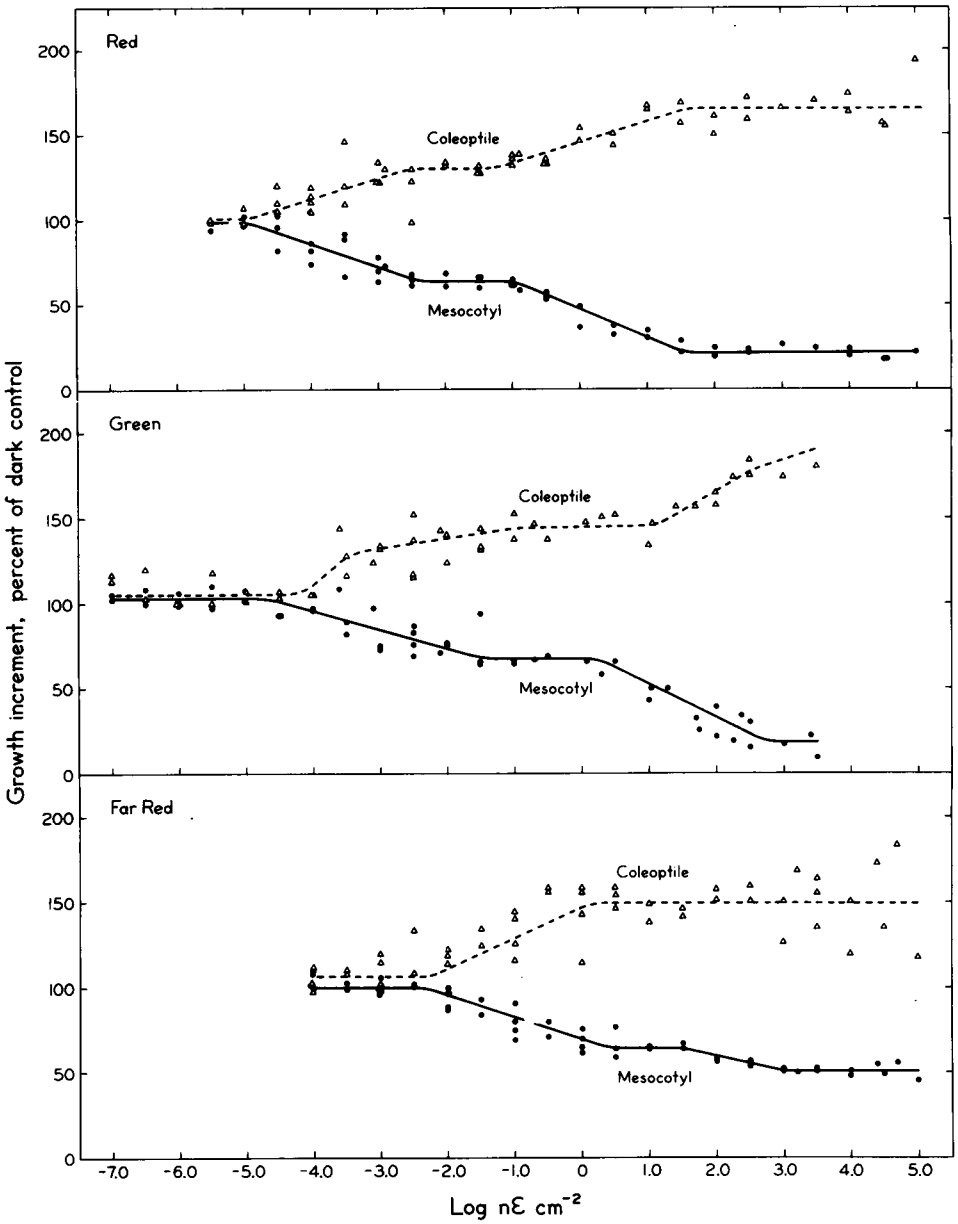

FIG. 3. Dose-response curves for R, G, and FR. Growth increments (cm/24 h) of mesocotyls and coleoptiles expressed as a function of the dark controls (100% response for mesocotyl = 2.50 cm; for coleoptile = 0.75 cm). No safe lights of any kind were used. Reciprocity fails only for the last two or three doses of R and G shown. Seedlings were 56-h-old at the time of illumination.

investigators in the "dark" controls (*e.g.* Fig. 1 in 1, and 12, 19), in the response of the mesocotyl (*e.g.* 25, 30, 31), and the coleoptile (*e.g.* 9, 10, 17, Vanderhoef, unpublished) might largely be attributed to the uncontrolled use of green safelights. Unfortunately, investigators often do not make clear whether or not safelights were used (*e.g.* 1). In a few cases, although the authors were aware of these effects, experimentation proved impossible without them (14, 25).

The photoresponses of etiolated *Avena* seedlings can be accounted for on the basis of a single pigment. The difference in the threshold values of the dose-response curves for R, G, and FR, both for the VLIR and LIR, correspond well to the relative photoefficiency of phytochrome phototransformation *in vivo* at these wavelengths (20). These data do not suggest involvement of a separate green-absorbing photoreceptor as suggested elsewhere for other systems (13).

Published action spectra for the inhibition of the oat mesocotyl are numerous but none were found for the coleoptile. The value of these spectra for the mesocotyl response is questionable as a result of reciprocity failure for the doses given (12, 30, 31, 32) or of the use of a single dose for all wavelengths examined without regard for quantum efficiency (6, 18, 32). Goodwin and Owens (7) reported some data for brief irradiations at doses sufficient to induce 10% mesocotyl suppression (compared with a green-irradiated control, so this response was probably a LIR). Although these data indicated peaks at 623 and 577 nm, the data were too scanty to draw any conclusions as to the nature of the photoreceptor. In addition, since none of the authors cited above avoided safelights in their experiments, the actual dose of photomorphogenically active light given is unknown. Blaauw *et al.* (1) have completed a reliable though scanty action spectrum for the VLIR. This spectrum has a peak at 673 and a slight rise at 400 nm (their Fig. 11). Hence, the VLIR had an action spectrum compatible with the known absorption maxima of phytochrome while a

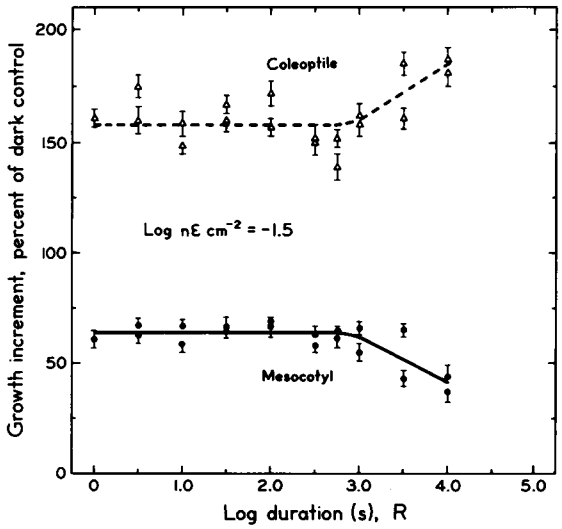

FIG. 4. Reciprocity of oat R-induced VLIR graphed as a function of the log duration of illumination. Total dose was held constant at 0.03 nE cm^{-2}. Combined standard error bars for the growth increment ratios are given.

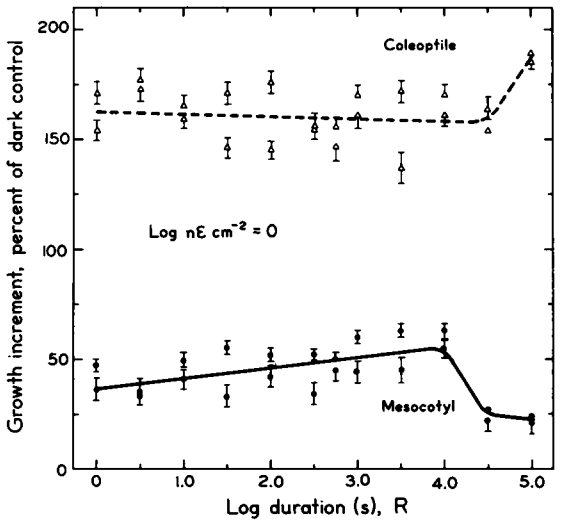

FIG. 5. Reciprocity of oat R-induced LIR graphed as a function of the log duration of illumination. Total dose was held constant at 1.0 nE cm^{-2}. Per cent response and combined standard error bars for the growth increment ratios are given as in Figure 4.

reliable spectrum for the oat LIR was unavailable (*cf.* LIR action spectrum for corn mesocotyl: 29). In summary, available action spectrum data, though not ideal, also implicate phytochrome as the photoreceptor for both VLIR and LIR.

FR can only convert from 1 to 3% Pr to Pfr *in vivo* (20) but could saturate the VLIR and induce part of the LIR (Fig. 3). We conclude that less than 4% Pfr was sufficient to saturate the VLIR (*cf.* 14) and could induce but not saturate the LIR (Fig. 3). Hopkins and Hillman (10) and Hillman (9) correlated the photostationary states of phytochrome *in vivo* with elongation of *Avena* coleoptile segments. Their data (Fig. 1 in 10) suggest that less than 5% Pfr saturated the VLIR and was above the threshold for LIR. Their data show saturation of a R/FR reversible response, the LIR, with more than 48% of the maximum obtainable Pfr [*i.e.* 75% of the total phytochrome present (21)] (their Fig. 1). Loercher (14) correlated the photostationary state of phytochrome in excised mesocotyls with mesocotyl inhibition in intact oat seedlings. He

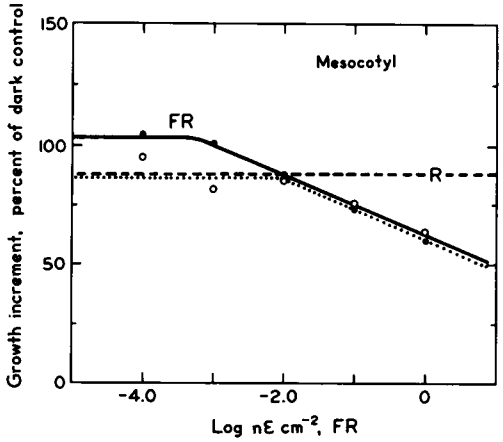

FIG. 6. Attempt at R/FR reversibility of mesocotyl VLIR. Coleoptile response (not presented) was similar. A 1-s pulse of R sufficient to induce the VLIR (10^{-4} nE cm^{-2}) was followed 5 min later with a FR pulse equal to or greater than the dose of R (○). The effect of FR pulse alone is also shown (●). In all cases, the complete irradiation series was completed in less than 10 min, before VLIR reciprocity failure (Fig. 4).

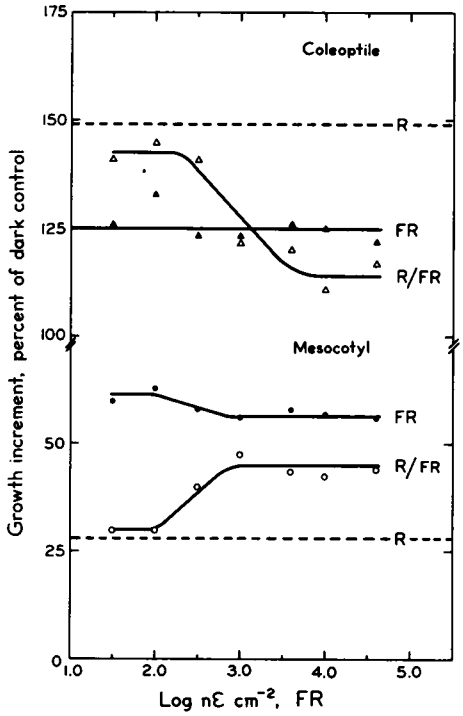

FIG. 7. R/FR reversibility of mesocotyl and coleoptile LIR. Half saturation LIR induced by R (1.0 nE cm^{-2}) was followed by the indicated doses of FR. Detailed irradiation protocol and symbols as in Figure 6.

apparently did his experiments on whole seedlings in darkness. He showed that LIR mesocotyl inhibition increased with the logarithm of Pfr concentration in the tissue (14). His data also indicate that 3% Pfr saturated the VLIR (assessed here by the per cent response he obtained in the presence of 3% Pfr) and was slightly above the LIR threshold (Fig. 2 in ref. 14). Interpretation of these data for comparison with data presented in this report was complicated by the fact that Hopkins and Hillman (10) used excised coleoptiles to monitor physiological response and because both groups prepared tissue segments for measurements of photostationary states under G's. Both groups expressed photostationary states as a per cent of the maximum obtainable Pfr, and normalized physiological response to either the dark control (14)

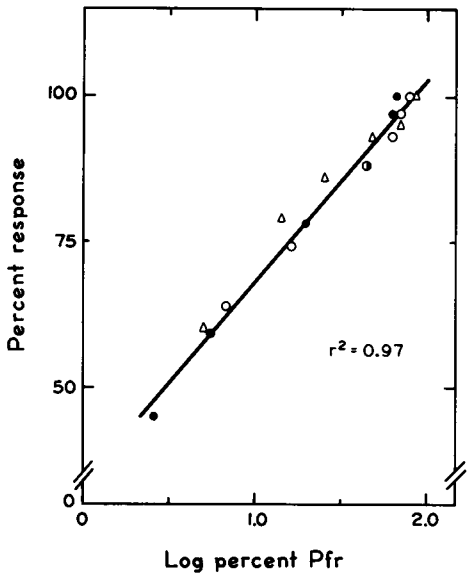

FIG. 8. Photostationary state of phytochrome measured *in vivo* correlated with per cent response of excised oat coleoptiles (Δ; data from 10) and intact oat mesocotyls (● and ○; data from 14). Filled symbols represent seedlings in which photostationary state was established with R only, open symbols those in which the photostationary state was achieved using both R and FR. Note that here, 100% Pfr is equivalent to only 75% of the total pool (21).

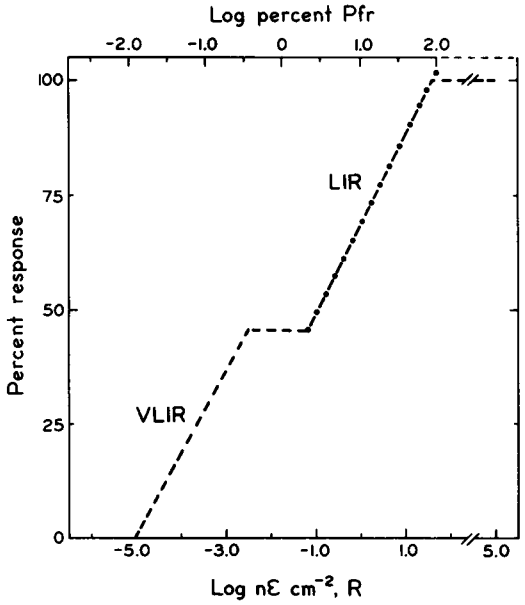

FIG. 9. Regression lines for mesocotyl and coleoptile responses, VLIR and LIR, to R [-----] normalized to the per cent of the total response obtained (from Fig. 3, top). The linear regression for mesocotyl data from Loercher (14) and coleoptile data from Hopkins and Hillman (10) (Fig. 8) which compare per cent response with the per cent photoconvertible Pfr have also been reproduced here [· · · · ·]. We have assumed that threshold and saturation for LIR (expressed as per cent response) in their experiments and ours are the same.

or the maximum response obtained (10). Despite differences in procedure and the tissue used, the data of both groups describe the same relationship between physiological response (LIR) and per cent Pfr ($r^2 = 0.97$; Fig. 8).

If we now normalized our data for the coleoptile and mesocotyl with the maximum response obtained in our dose-response curves (Fig. 3) and superimposed the regression line calculated from Figure 8, we could estimate the per cent maximum Pfr required for threshold and saturation of both the VLIR and LIR (Fig. 9) on the assumption that we are dealing with a single molecular species of phytochrome. The VLIR had a threshold at 0.01% Pfr and became saturated when only 0.4% Pfr was present. The LIR threshold occurred with 2% Pfr and finally became saturated with 87% Pfr present.

The third response (HIR) found in oats (1) and in corn (29) occurred from about 10^3 to 10^5 nE cm^{-2} R and was not found in this study (Fig. 3). The evidence to date indicates that this response is a HIR and is therefore induced by low intensities given over a long period of time (15). The irradiations used to generate the dose-response curves presented here were probably either too short in duration (R, FR) or of insufficient dose (G) to evoke this response.

LITERATURE CITED

1. BLAAUW OH, G BLAAUW-JANSEN, WJ VAN LEEUWEN 1968 An irreversible red-light-induced growth response in *Avena*. Planta 82: 87–104
2. BLAAUW OH, G BLAAUW-JANSEN 1975 On the relationship between red light dose and the sensitivity to the reversing effect of far-red light. Z Pflanzenphysiol 76: 333–338
3. BRIGGS WR 1963 The phototropic responses of higher plants. Annu Rev Plant Physiol 14: 311–352
4. DUKE SO, AW NAYLOR, JL WICKLIFF 1977 Phytochrome control of longitudinal growth and phytochrome synthesis in maize seedlings. Physiol Plant 40: 59–68
5. ELLIOT WM, J SHEN-MILLER 1976 Similarity in dose responses, action spectra and red light responses between phototropism and photoinhibition of growth. Photochem Photobiol 23: 195–199
6. GOODWIN RH 1941 On the inhibition of the first internode of *Avena* by light. Am J Bot 28: 325–332
7. GOODWIN RH, OH OWENS 1948 An action spectrum for inhibition of the first internode of *Avena* by light. Bull Torrey Bot Club 75: 18–21
8. HAMADA H 1929 Über die Beeinflussung des Wachstums des Mesokotyls und der Koleoptile von *Avena*—Keimlingen durch das Licht. Mem Coll Sci Kyoto Imp Univ Ser B 6: 121–238
9. HILLMAN WS 1966 Responses of *Avena* and *Pisum* tissues to phytochrome conversion by red light. Plant Physiol 41: 907–908
10. HOPKINS GW, WS HILLMAN 1966 Relationships between phytochrome state and photosensitive growth of *Avena* coleoptile segments. Plant Physiol 41: 593–598
11. HUISINGA B 1964 Influence of light on growth, geotropism and guttation of *Avena* seedlings grown in total darkness. Acta Bot Néerl 13: 445–487
12. JOHNSTON ES 1937 Growth of *Avena* coleoptile and first internode in different wavelength bands of the visible spectrum. Smithson Misc Collect 96: 1–19
13. KLEIN RM 1979 Reversible effects of green and orange-red radiation on plant cell elongation. Plant Physiol 63: 114–116
14. LOERCHER L 1966 Phytochrome changes correlated to mesocotyl inhibition in etiolated *Avena* seedlings. Plant Physiol 41: 932–936
15. Mancinelli AL, I Rabino 1978 The "high irradiance responses" of plant photomorphogenesis. Bot Rev 44: 129–180
16. MANDOLI DF, WR BRIGGS 1979 Growth characteristics of etiolated *Avena sativa* L. (cv Lodi) in response to red and green light. Carnegie Inst Wash Year Book 78: 140–144
17. MER CL 1953 An examination of the factors affecting variability in the growth of the mesocotyl and of the coleoptile of etiolated *Avena* seedlings. Ann Bot 17: 569–578
18. MER CL 1966 The inhibition of cell division in the mesocotyl of etiolated oat plants by light of different frequencies. Ann Bot 30: 17–23
19. MER CL, DR CAUSTON 1967 Analytic studies of the growth of the etiolated seedling of *Avena sativa* II. The effects of growth-modifying factors on cell division and extension. New Phytol 66: 665–681
20. PRATT L, WR BRIGGS 1966 Photochemical and nonphotochemical reactions of phytochrome *in vivo*. Plant Physiol 41: 467–474
21. PRATT LH 1978 Molecular properties of phytochrome. Photochem Photobiol 27: 81–105
22. QUAIL PH, WR BRIGGS 1978 Irradiation-enhanced pelletability: requirement for phosphorylative energy *in vivo*. Plant Physiol 62: 773–778
23. QUAIL PH, WR BRIGGS 1978 Light-enhanced geotropic sensitivity in maize roots: possible involvement of phytochrome. Carnegie Inst Wash Year Book 77: 336–339
24. SCHIFF JA 1972 A green safelight for the study of chloroplast development and other photomorphogenetic phenomena. Methods Enzymol 24: 321–322
25. SCHNEIDER CL 1941 The effect of red light on growth of the *Avena* seedling with special reference to the first internode. Am J Bot 28: 878–886

26. TEPFER DA, HT BONNETT 1972 The role of phytochrome in the geotropic behavior of roots of *Convolvulus arvensis*. Planta 106: 311–324
27. THOMSON BF 1950 The effect of light on the rate of development of *Avena* seedlings. Am J Bot 37: 284–291
28. THOMSON BF 1951 The relation between ages at time of exposure and response of parts of the *Avena* seedling to light. Am J Bot 38: 635–638
29. VANDERHOEF LN, PH QUAIL, WR BRIGGS 1979 Red light-induced mesocotyl elongation in maize seedlings. Plant Physiol 63: 1062–1067
30. WEINTRAUB RL, ED MCALISTER 1942 Developmental physiology of the grass seedling. I. Inhibition of the mesocotyl of *Avena sativa* by continuous exposure to light of low intensities. Smithson Misc Collect 101: 1–11
31. WEINTRAUB RL, L PRICE 1947 Developmental physiology of the grass seedling. II. Inhibition of mesocotyl elongation in various grasses by red and violet light. Smithson Misc Collect 106: 1–15
32. WOLF FT 1979 Effects of light quality upon the growth of *Avena* coleoptiles. Z Pflanzenphysiol 91: 1–6