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Phytochrome-Mediated Cellular Photomorphogenesis[1]

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ABSTRACT

Red light-induced cell elongation and division in intact, etiolated oat (*Avena sativa* cv Lodi) seedlings have been assessed. The middle of coleoptile was especially responsive in the very low fluence range whereas the region immediately below the coleoptile tip and the two regions just above the coleoptilar node were more responsive than the entire organ in the low fluence range. These responses in the coleoptile are both the result of an increase in cell elongation. Coleoptile cell division is slightly inhibited in the very low and slightly stimulated by red light in the low fluence range.

The one-sixth of the mesocotyl closest to the node is more suppressed in its growth than is any other region in the very low fluence range. However, the low fluence response involved the entire mesocotyl equally. In the apical one-sixth of the mesocotyl, a strong suppression of cell division and a weak suppression of cell elongation occurs. In the lower five regions of the mesocotyl, red light in both fluence ranges suppresses only cell elongation. Apparently, the difference between red light-induced oat growth stimulation and suppression primarily involves differences in the response of the cell elongation process.

Mandoli and Briggs (17) characterized two phytochrome-mediated photoresponses in etiolated oat tissues. The VLF[2] response resulted in 45% mesocotyl growth suppresstion and 30% coleoptile growth stimulation over the 24 h subsequent to a brief pulse of R. The VLF was detected at 10^{-4} μmol m^{-2} and became saturated at 3×10^{-2} μmol m^{-2}. The LF response resulted in 80% mesocotyl suppression and 60% coleoptile stimulation. The LF response was detected at 10^{0} μmol m^{-2} and became saturated at 3×10^{2} μmol m^{-2} of R.

Phytochrome controls organ morphogenesis, but reliable data on cellular morphogenesis are scarce. The use of unsafe working lights (R or green light) for seedling manipulations (7, 8, 11, 23), fluences far above saturation (white light, Ref. 2; R, Refs. 1, 7, 8, 20, and 22), and the analysis of cellular morphogenesis only through experiments that average cellular responses over the entire organ (20) are limitations of the studies available concerning the effect of phytochrome photoconversion on cellular morphogenesis in seedlings. None of the studies available reports reciprocity data even for extremely long exposures.

Several studies have analyzed and compared large regions (thirds) of organs (oat, Ref. 8, *cf.* Ref. 7; wheat, Refs. 20 and 22; corn, Refs. 13 and 14) and/or assessed cell morphogenesis at a given position relative to an anatomical structure (*e.g.* coleoptile tip or node) (20, 23). The former studies do not provide very high resolution and the latter assumed that cells in an organ were stationary (10). Although Huisinga (12) performed experiments in total darkness and analyzed very small regions of both the oat coleoptile and mesocotyl, his study was confined to excised seedlings and presents data only for individual seedlings given fluences in the LF range. The data collectively indicate that changes both in cell division and elongation affect organ morphogenesis. Unfortunately, the evidence often cited as the strongest (for intact R-irradiated seedlings; Refs. 2 and 9), employed unquantitated 'safe' R and only calculated changes in cell number from data on mean cell length from whole organs (8) on the assumption that cellular packing and cell position in an organ were constant.

An additional problem is that, although phytochrome has been found throughout the etiolated oat seedling (4, 6), the sites of photoperception in oat seedlings (1.5–2.5 mm above the node and 4.5–6.5 mm below the node; Ref. 17), do not match the areas where phytochrome is most heavily concentrated: the coleoptilar node and tip (4). Thus, the phytochrome absolute concentration in a given cell may be less important than that cell's ability to respond to R and to affect the particular response being assayed, in this case, stimulation of coleoptile and suppression of mesocotyl growth.

A technique has been developed which allows 54-h-old, intact etiolated seedlings to be marked at 1-mm intervals in total darkness (12). These marks can be used to monitor growth responses of specific regions of the coleoptile and the mesocotyl to R. The response of these regions in each organ can then be compared to the sites of photoperception and the sites at which the highest concentrations of phytochrome have been found. The relative contributions of cell elongation and cell division to these responses in each region have been assessed for R in the VLF and LF response ranges.

MATERIALS AND METHODS

Growth of Seedlings. Seedlings of oats (*Avena sativa* cv Lodi) were grown according to Mandoli and Briggs (17) with the following two modifications. Seeds were dehusked and imbibed for 0.5 h by laying the glass, paper, and tape assembly in a pan of water 0.5 cm deep, such that none of the seeds were covered, but the paper was allowed to soak completely. Seeds were then transferred to racks and grown as by Mandoli and Briggs (17). The entire imbibition process and all manipulations were done in total darkness. Seedlings were used at 54 h postimbibition since organ growth, cell elongation, and cell division are maximal at this time (26). Analysis of growth of whole organs was completed five times (1 plate/fluence in each experiment, each plate with about 20 usable seedlings).

Illumination and Marking. Seeds were grown in darkness for 54 h, and then illuminated with R according to Mandoli and Briggs (17). Fluence rates were varied with Balzer's neutral density filters, and measured with a Licor Quantum Radiometer (model LI0185A). A device for marking seedlings in the dark was utilized (Fig. 1). Seedlings, still adhering to the masking tape on which they were grown, were laid on a flat Plexiglas plate. A Plexiglas bridge with thin fishing lines (0.25 mm in diameter) stretched

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

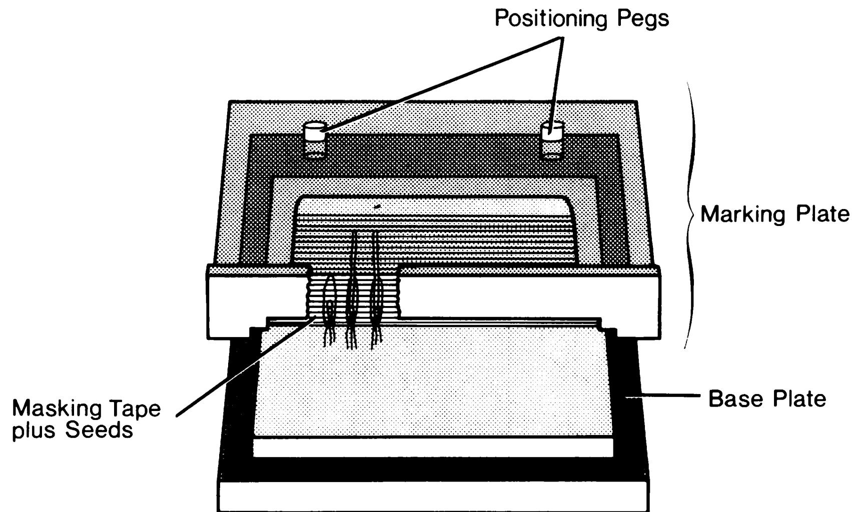

FIG. 1. Device used for marking seedlings in complete darkness. Horizontal lines represent fishing lines (0.25 mm in diameter) spaced at 1-mm intervals.

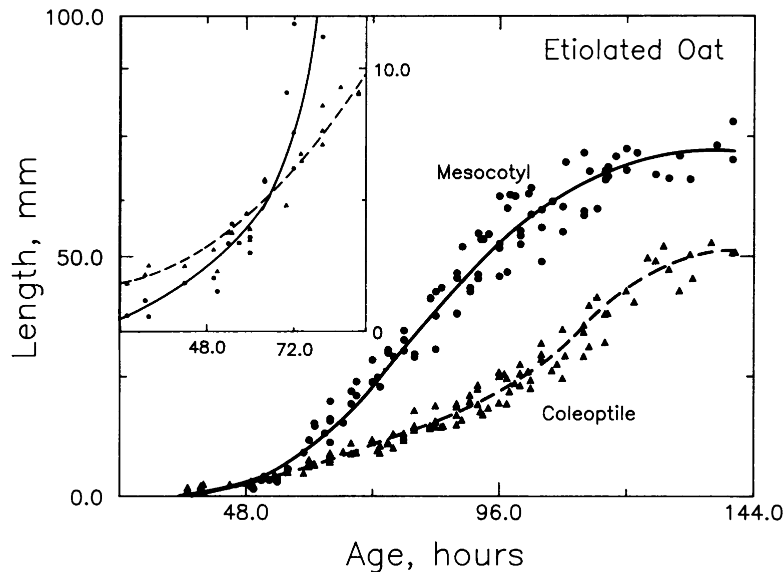

FIG. 2. Growth of coleoptile (▲) and mesocotyls (●) of *Avena sativa* cv Lodi (lot 170-B) in complete darkness at 22°C and 95% humidity is given in mm from imbibition to 144 h. Each point represents the mean length of a population of 25 to 100 seedlings measured from photocopied plants with a computerized digitizer (17). SE range from 1 to 3% for a given population (*i.e.* per point).

across it was then used to mark the seedlings. The bridge was positioned by fitting two drill holes in the bridge structure onto two positioning pegs which protruded from the flat Plexiglas plate. The fishing lines, which had been painted with a nontoxic, water-insoluble lamp black/oil emulsion, were pressed onto the seedlings. These fishing lines left an average of five marks separated by approximately 1-mm intervals on each seedling. Marking was done in total darkness either immediately after illumination or after a mock irradiation in the case of the dark controls.

Harvest and Analysis. Plants were grown in total darkness for 24 h after illumination and marking, and then harvested in white light. The plants were photocopied and length measurements were made directly from these images with a computerized digitizer. Mean coleoptile and mesocotyl lengths were determined for each fluence given and for the dark initial and dark final controls.

The distance from either the coleoptilar node or tip to each lamp black mark was also measured for individual seedlings. These data from all seedlings given a single fluence (20 seedlings/experiment; three coleoptile and five mesocotyl experiments) were combined to yield the average position of each mark. Inasmuch as an average of five marks was left on each organ of the seedlings used, growth of 16.6% regions between each mark on both organs could be compared among seedlings given different fluences. These 16.6% regions were chosen because they best represented the actual number of marks per seedling, and maximized the number of measurements for the average position of the marks.

At the time of harvest, cellular dimensions were measured by a technique adapted from Van Volkenburgh and Cleland (28). Seedlings were painted with clear nail polish, and the polish was allowed to dry for 10 min. The nail polish formed imprints of the seedling epidermis, showing both cell outlines and the lamp black marks left by the marking technique. Imprints were then mounted on plain microscope slides and viewed at 50× with a dissecting microscope. A camera lucida attached to the dissecting scope allowed cell outlines to be traced. In each experiment, 10 cells were traced for each region at fluences below threshold, at half-saturation and just above saturation of both the VLF and LF responses (Fig. 4). Tracings for all regions of the dark initial and

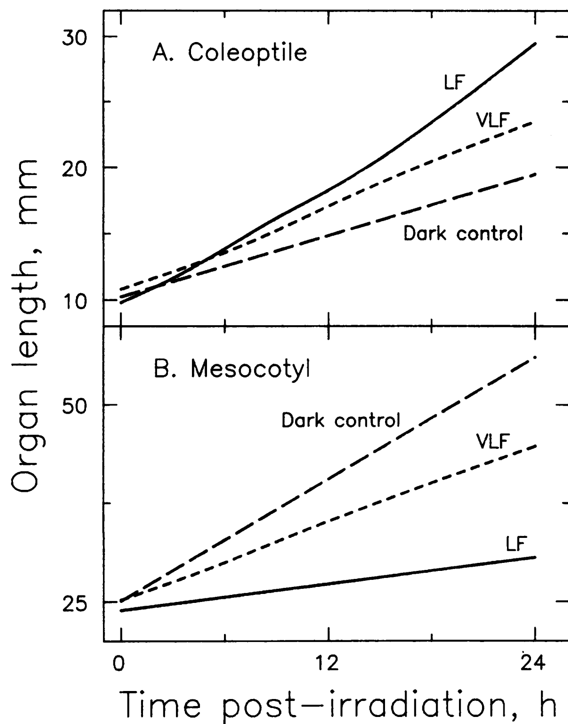

FIG. 3. Growth kinetics of oat organs grown in darkness from 54 to 78 h postimbibition or given a fluence of R sufficient to saturate the VLF or LF response of the coleoptile (A) and mesocotyl (B). Regression lines represent data hourly for the first 6 h and at 9, 12, and 24 h postirradiation. Experiments were performed three times and all $r^2 > 0.97$.

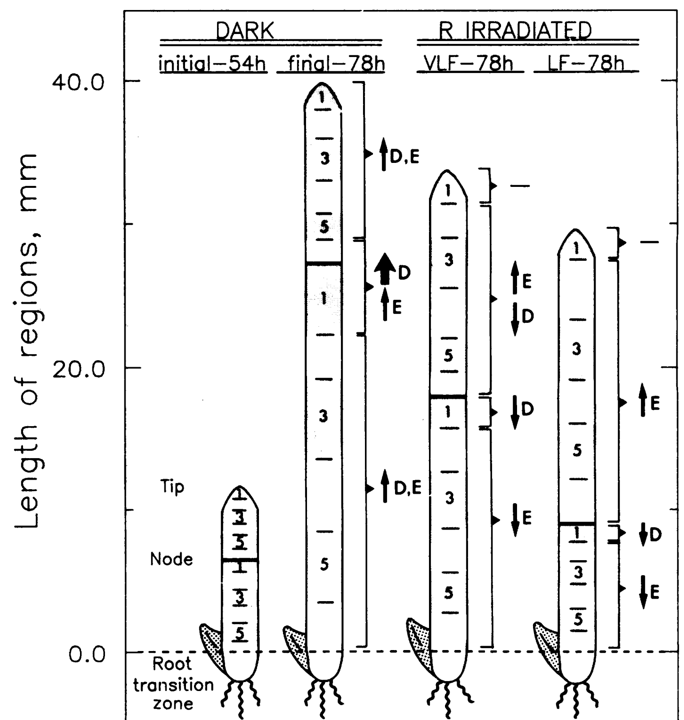

FIG. 4. Summary of the regional growth analysis. Diagrams represent the dark initial control, dark final control, and seedlings which have received irradiations just above saturation of either the VLF or the LF photoresponses. D refers to cell division, and E to cell elongation. The thickness of the arrow denotes the strength of the average regional response to R in relation to the average response of all other regions within an organ (thin arrow <5-fold; thick arrow >5-fold effect). The orientation of the arrow signifies either stimulation or suppression of the process.

Table I. *Regional Growth Responses to R in the Coleoptile and Mesocotyl of Avena sativa (cv Lodi)*

	Dark Final Control				
Regions	Coleoptile		Regions	Mesocotyl	
	VLF	LF		VLF	LF
mm	%		*mm*	%	
0.0–0.9	127 ± 7	122 ± 5	0.0–1.0	43 ± 3	25 ± 3
0.9–1.6	126 ± 11	221 ± 9	1.0–2.0	96 ± 9	45 ± 5
1.6–2.6	117 ± 12	141 ± 7	2.0–3.2	68 ± 5	29 ± 6
2.6–3.7	152 ± 12	128 ± 6	3.2–4.4	62 ± 5	32 ± 7
3.7–4.7	95 ± 12	190 ± 8	4.4–5.5	63 ± 4	35 ± 6
4.7–5.3	133 ± 8	207 ± 5	5.5–6.4	76 ± 3	38 ± 4

dark final controls were also taken. All tracings were then measured with a computerized digitizer. For this analysis, a total of three experiments was performed (all of the previously mentioned mesocotyl experiments and three of the five coleoptile experiments), and the results were pooled by averaging together all cell length measurements made for each region at a particular fluence. Discussion of these data will always refer to a region as it was measured in the dark initial control. For example, the coleoptile region adjacent to the node will always be at mm 4.7 to 5.3 even though it actually measured as the region from mm 9.2 to 10.7 or 11.7 to 14.8, depending on the fluence of R perceived. The response of a given irradiated region will be expressed as a percentage of the response of that region of similar plants which had been manipulated for R exposure but not irradiated.

Cell numbers per region were measured by a technique adapted from Brown and Rickless (5). Seedlings were cut with a razor blade at the position of the lamp black marks, and the primary leaf tissue was removed from each coleoptile with tweezers. In

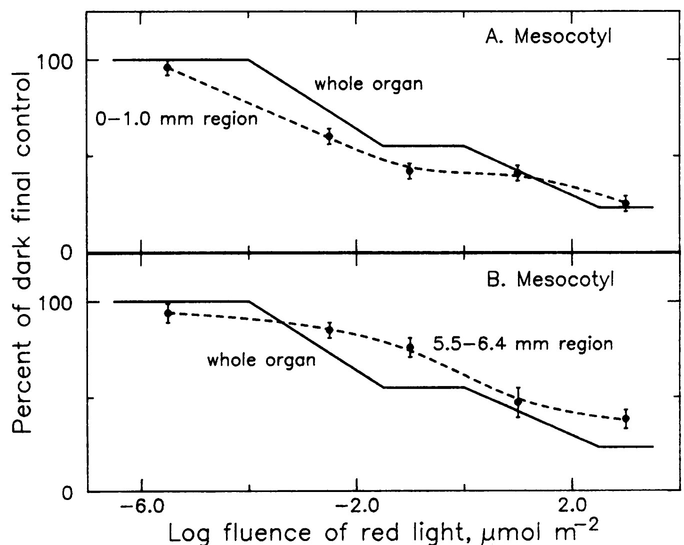

FIG. 5. Fluence response curves for two mesocotyl regions. Solid lines are fluence response curves for the whole mesocotyl growth reproduced from Mandoli and Briggs (17). Dotted lines represent R growth responses of regions consisting of one-sixth of the whole organ (the 0.0–1.0-mm region which is closest to the node, and the 5.5–6.4-mm region which is closest to the base). SE are indicated for each symbol. Five experiments with a total of 700 seedlings were analyzed. For the coleoptile, 100% = 12.7 ± 0.5 mm; for the mesocotyl, 100% = 27.3 ± 0.5 mm.

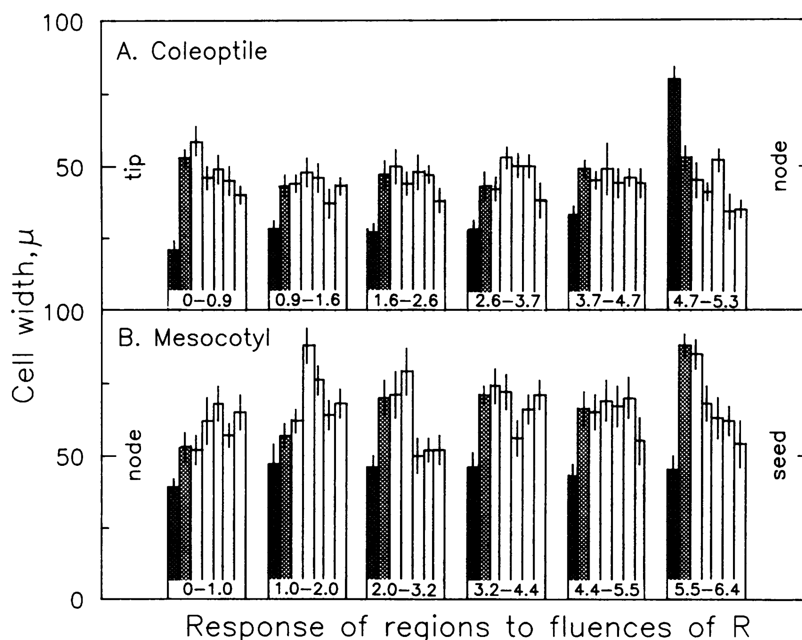

FIG. 6. The effect of R on cell width in distinct regions of the coleoptile and mesocotyl. The seedlings analyzed are the same seedlings used in all other analyses (whole organ analysis [not shown] and Figs. 4, 7, and 8). The bars representing each of six regions, moving left to right from tip to node in the coleoptile (A) and node toward the seed in the mesocotyl (B) each consist of the dark initial control, the dark final control, and five groups of seedlings given fluences (from left to right) (a) below threshold, (b) at half-saturation, (c) just above saturation for the VLF, (d) at half-saturation, and (e) at just above saturation for the LF response. Numbers at the base of bars are the regions of each organ with reference to the dark initial control (Fig. 4).

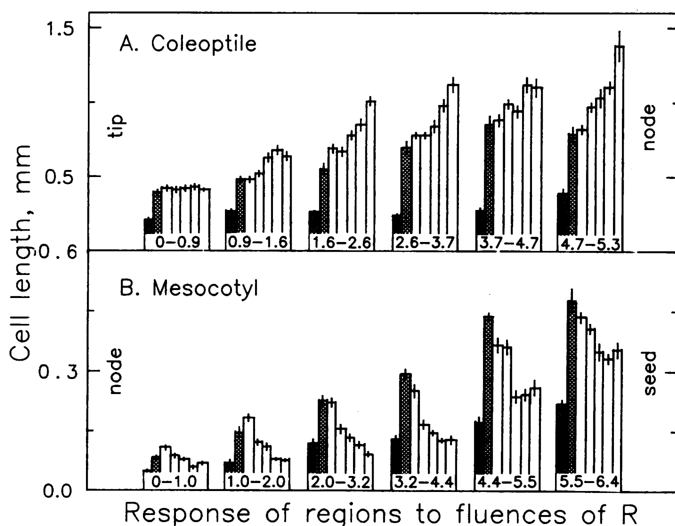

FIG. 7. The effect of R on average cell length within distinct regions of the coleoptile and the mesocotyl. Organization as in Figure 6.

each experiment, 10 of the same regions for a particular fluence were dissolved in a 1 ml solution of 5% chromic acid. After 3 d at 25°C, seedling sections were disrupted by several passages through a syringe (Stylex 21 × 1.5). Ten counts were then made of a known volume of the 1-ml cell suspension. It was possible, given the volume of suspension counted, the average number of cells counted, the volume of the cell suspension, and the number of regions per suspension, to calculate the average number of cells per region. Seedlings from two experiments (10 counts/cell suspension for each experiment) were analyzed for coleoptile, and three for mesocotyl cell numbers. The same plants were used in analyzing the whole organ response, the regional responses, and the cellular responses to R.

RESULTS

Etiolated Organ Growth Rates in Dark and R-Irradiated Seedlings. Growth of coleoptiles (▲) and mesocotyls (●) of *Avena sativa* (cv Lodi) in complete darkness is shown in mm from imbibition to 144 h (Fig. 2).

Growth kinetics of oat organs grown in darkness or given a fluence of R sufficient to saturate the VLF or LF responses (Fig. 3) show that changes in growth rate induced by R are effected within the first hour postirradiation and persist for at least 24 h. Similar data have been obtained for longer R pulses (min) (Victory oats, Ref. 24; corn, Ref. 27). These data validate the use of a simple 'end point' determination of cell numbers and cell lengths in the following analyses.

Growth Response of Etiolated Oat Seedlings to R. The consequences of irradiating intact etiolated oat seedlings with R were analyzed at three levels: whole organ, regions of the organ, or the cells themselves. The R fluence-response curves for oat coleoptile and mesocotyl matched those obtained previously (2, 17) for intact, whole organs (not shown).

A R pulse which saturates the VLF induced the greatest response in the 2.6 to 3.7 mm region below the tip of the coleoptile (Table I). The variability in these data on the coleoptile response (7–12% SE) precludes further resolution of the VLF effect on this organ (Table I).

The coleoptile regions immediately below the tip and adjacent to the node showed the greatest responses to a R fluence which saturated the LF response (Table I, Fig. 4). These regions were each about twice the length of the dark final control: extending to 221 and 190 to 207% of the dark final controls. The least responsive regions in the LF range were the tip and central region of the coleoptile.

In the mesocotyl, the region nearest the node was most suppressed by R, particularly in the VLF response range (Figs. 4 and 5, Table I). In response to a fluence saturating the VLF, this region was suppressed to 43% of the dark final control (Table I). The lower five regions were less affected. The mesocotyl base was least

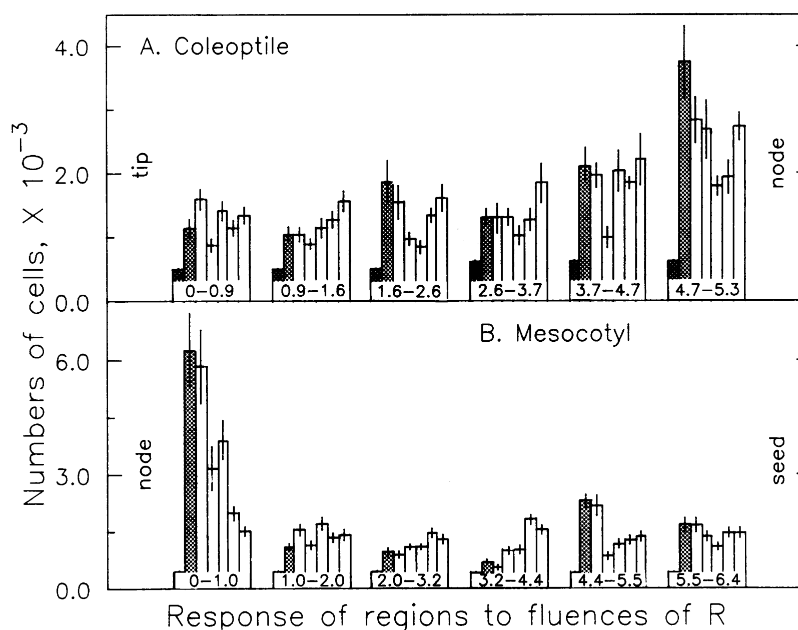

FIG. 8. The effect of R on cell number per region within distinct regions of the coleoptile and the mesocotyl. Organization as in Figure 6.

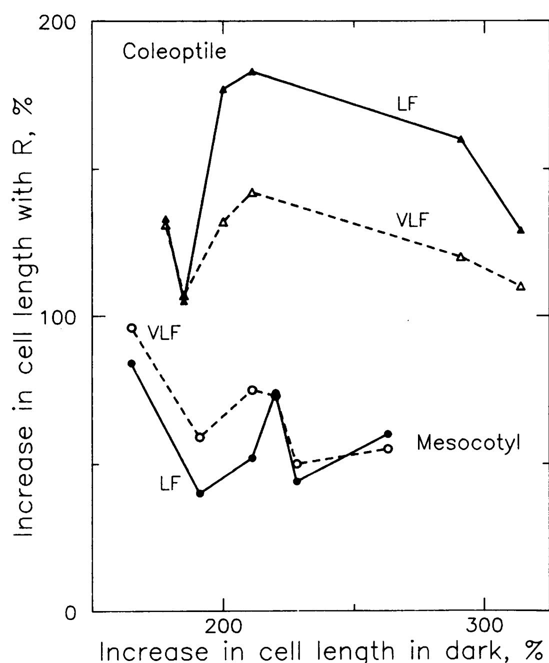

FIG. 9. The effect on cell length of R fluences (vertical axis: light final/dark final) which saturate either the VLF or LF is graphed in relation to the increase in cell length over this dark, 24-h growth period (horizontal axis: dark final/dark initial). On the vertical axis, 100% equals cell length in the dark final control for the comparable coleoptile region. On the horizontal axis, 200% means cell length has doubled over this dark, 24-h growth period.

affected by a VLF-saturating fluence (Table I, Fig. 5, panel B).

In response to a fluence of R which saturates the LF response, again the region nearest the node showed the greatest suppression (Table I). However, the disparity between suppression in this region and suppression of growth in the other regions was smaller in the LF range than in the VLF range. Again, least affected was the base of the mesocotyl, but the standard errors make this difference marginally significant. What shows in striking fashion (Fig. 5) is that the VLF predominates in the apical region of the mesocotyl while the LF predominates in the basal region.

Cell Width. In the top five regions of the coleoptile, cell width increases an average of 177% (from about 27 to 47 μm) between the dark initial and dark final controls (Fig. 6). In the region adjacent to the node, average cell width declines 66% in the same dark growth period (from 80 to 53 μm). In the mesocotyl, average cell width increases in all regions to at least 153% in the 24-h dark period (from about 44 to 68 μm). The oldest cells near the seed almost double in width (45 to 88 μm).

Coleoptile cell width showed no large changes with increasing fluences of R in any of the regions except possibly that adjacent to the node (Fig. 6A). Mesocotyl cell width increases in response to fluences at or below half-saturation for the organ VLF but the increase is less with higher fluences of R (Fig. 6B). This response pattern however, appears to be highly dependent on the age of the cells; more differentiated cells near the seed either do not respond or show only inhibition of increase in cell width to R.

Cell Length and Division in the Coleoptile. In completely etiolated seedlings, coleoptile epidermal cells in the three uppermost regions approximately double in length (Fig. 7A). Cell length triples in the center of the coleoptile (2.6–4.7 mm) and doubles in the region nearest the node. In the coleoptilar tip, no changes in cell length induced by R were detected. In the regions of the coleoptile from 0.9 mm below the tip to the node, cell length increases with increasing fluences of R. Stimulation of cell elongation ranges from 11 to 44% of the dark final control in response to a fluence of light which saturates the VLF response, and from 33 to 84% of the dark final control for a R irradiation which saturates the LF response (Fig. 7A).

Coleoptile cell number per region increases from 2- to 6-fold in the dark controls with the greatest increase (*i.e.* the meristem) occurring near the node (Fig. 8A). Red irradiation in the VLF range slightly suppresses this normal cell proliferation whereas R fluences in the LF range do not (Fig. 8A).

Cell Length and Division in the Mesocotyl. Mesocotyl cell length increases from 49 to 218 μm in the 54-h etiolated seedling as one progresses from the meristematic region near the node to the seed. All mesocotyl cells approximately double in length in the ensuing 24 h if the plants remain in the dark (Fig. 7B). In general, mesocotyl cells are less than one-half as long as coleoptile cells (Fig. 7, A and B). In all regions of the mesocotyl, cell

elongation is suppressed by increasing fluences of R. In the uppermost region of the mesocotyl, cell length was slightly suppressed (8% over the dark final control) by R which saturates the VLF response. In the rest of the mesocotyl, suppression of cell elongation by an irradiation which saturates the VLF response ranged from 30 to 50% of the dark final control. Red irradiation which saturates the LF organ response suppresses cell length to 79% of the dark final control in the region from just below the node and from 30 to 60% of the dark final control for the rest of the mesocotyl.

Cell number per region in the mesocotyl increases in the dark, for seedlings 54 to 78 h old (Fig. 8B). In the region closest to the node, cell number increases 10-fold whereas in the lower five regions cell numbers only double or triple. No consistent changes in mesocotyl cell numbers were seen in response to R in the regions from 1.0 mm below the node down to the base (Fig. 8B). However, in the meristem (0.0–1.0 mm), R induces either a 50 or a 76% decrease in cell number at fluences sufficient to saturate the VLF or the LF response, respectively.

DISCUSSION

In summary (Fig. 5), the data presented here are consistent with previous studies which show either (a) the relative distribution of organ growth (7, 12–14), (b) that meristematic activity in the mesocotyl is limited to the upper portion closest to the coleoptilar node (*e.g.* 8), or (c) calculations that indicate R generally reduces the increase in cell number in the mesocotyl (8). R has very little effect on cellular morphogenesis in the tip region of the coleoptile. R stimulates coleoptile cell elongation, suppresses mesocotyl cell elongation and inhibits cell division in both.

Cellular morphogenesis induced by R is affected differently in distinct regions of both the coleoptile and the mesocotyl (Fig. 4). Hence, fluence response curves for whole organs should be viewed as an average of those regions and the heterogeneous population of cells which comprise them. This study does not present complete fluence response curves for cellular morphogenesis and so does not indicate whether a given cell has distinct VLF and LF responses.

Note that the cell lengths and widths were measured for epidermal cells, while cell numbers were measured for all nonvascular cells. Preliminary studies of tissue sections (not shown) suggest that cortical cells do not differ in any dramatic way from epidermal cells in their growth responses. The measurements and calculations of Iino (14) on corn mesocotyl support this suggestion.

Mandoli and Briggs (18) found the sites of photoperception for phytochrome-mediated responses in oat seedlings 1.5 to 2.5 mm above the node and 4.5 to 6.5 mm below the node. The site of photoperception above the node is inside the boundaries of the two growth regions near the node where the greatest percentage of the coleoptile LF growth response was found. However, the region just below the coleoptile tip was also strongly stimulated by an LF-saturating fluence, but this was not a site of photoperception (18). In comparing the sites of photoperception with the regional growth analysis done in this study, we see there is a rough correlation between the regions of greatest growth response and the photoperceptive sites. However, it is apparent that the VLF and LF growth responses occur to some degree throughout the seedling, especially in the mesocotyl LF range, and are not restricted to the sites of photoperception.

Phytochrome has been detected throughout oat seedlings and is known to be most concentrated in the coleoptilar tip and node (4, 6), but an absolute correlation between the amount of phytochrome present and the photomorphogenic growth response is not indicated in these data. The seedlings used here were not the same age as those used in studies of phytochrome localization in oat cited above but phytochrome distribution in another grass species does not change with age (rice, Ref. 21). Growth stimulation in the coleoptile tip (0.0–1.0 mm in this study) was 43% less than that found in the whole organ LF response while growth in the region adjacent to the tip where the phytochrome absolute concentration is lower was 221% of the dark final control in response to an LF-saturating fluence. Similarly, growth responses in the regions adjacent to the coleoptilar node were greater than the overall organ response; the mesocotyl region closest to the node accounted for by far the greatest percentage of the VLF response, and the two coleoptile regions closest to the node show the greatest LF response (Table I). Phytochrome concentrated in the tip and node may be fortuitous or may be important for responses other than those measured here.

Does light simply accelerate the maturation sequence in *Avena* cells as has been proposed (9, 25, 26)? Figure 9 shows the degree to which R effects epidermal cell elongation in particular cells (vertical axis) as a function of the elongation potential of the comparable dark controls (horizontal axis). The amount of elongation occurring in a dark, 24-h growth period is taken here as a measure of the cellular stage of development. Coleoptile cells which are rapidly elongating (300% or tripling in length during this 24 h of darkness) are less stimulated to elongate by R than are cells which are not yet in such a rapid elongation phase (200% elongation during this 24-h growth period). However, the mesocotyl cell response is the inverse: R inhibits cells to a progressively greater degree at more rapid stages of elongation (Fig. 9). These data corroborate calculations of cell length by Iino (14) which were based on cell numbers present in the fifth row of the mesocotyl cortex in corn.

A similar analysis of the effect of R on cell division (not shown) was done for all the available data (from Fig. 8). When the increase in cell numbers with R was plotted as a function of the increase in cell numbers in the dark (*cf.* Fig. 9 for cell elongation) it was clear (a) that R affected cell division in those regions where cells were most rapidly dividing (*i.e.* meristematic regions) but (b) that the effect of R on cell division was the same in both coleoptile and mesocotyl cells. That morphogenesis can proceed in the absence of cell division in *Avena* has been shown with γ-irradiated plants (Ref. 16; see Ref. 10 for general treatment of growth problems). In sum, the hypothesis that light accelerates cell maturation seems too simplistic to explain the diametrically opposed responses to R found in etiolated oat organs. From these data (Fig. 9) and those experiments which indicate that phytochrome influences cell wall properties (3, 19, 29), it appears that future experiments on this question should focus on the process(es) of cell elongation rather than cell division in these tissues.

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