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Effect of Red Light on the Phototropic Sensitivity of Corn Coleoptiles[1]

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Summary. The effect of red light in alteration of the phototropic sensitivity of corn coleoptiles (*Zea mays* L., cultivar Burpee Barbecue Hybrid) is investigated. Phototropic dosage-response curves for etiolated coleoptiles are compared with those for coleoptiles receiving 1 hour of continuous red light immediately prior to phototropic induction. In the former case, only curvature comparable to the first positive curvature of oat coleoptiles is obtained. There is no evidence for first negative curvature and only minimal second positive curvature. The reciprocity law proved valid for all curvatures obtained. With red light, the sensitivity of the first positive curvature was decreased over ten-fold and there was clear appearance of second positive curvature for which the reciprocity law was not valid. Once again there was no evidence for negative curvature. Time course studies indicated that within 1 hour of the beginning of red light treatment at 25°, reactions leading to the decrease in phototropic sensitivity of the first positive component had gone to completion whether the red light was continuous or consisted of a single 1 second exposure followed by a 1 hour dark period. An action spectrum for the red-induced change in phototropic sensitivity showed a marked peak near 660 mμ with a small broad shoulder between 610 and 630 mμ, characteristic of phytochrome-mediated responses. The effect of red light could be fully reversed by low dosages of far-red light, but longer doses of far red were less effective. Large dosages of far-red light alone induced the same alteration in phototropic sensitivity as did red light.

In recent years, there have been numerous studies of the influence of red light on the subsequent phototropic sensitivity of coleoptiles of various grasses (1, 3, 4, 9, 15, *27*, *28*). The consequences of red light treatment for phototropic sensitivity are extremely complex, depending upon the plant chosen and the conditions under which the red light treatment is administered (10). To date, there has been no report of attempts to determine the threshold energy required for this red light response, although it is clearly very low (3, 9). Furthermore, there has been only one demonstration of partial reversibility of the response by far-red light, under rather special conditions of multiple light treatments (9). Indeed Blaauw-Jansen (4) clearly showed that relatively long exposures of far-red light had precisely the same effect as red light in altering the phototropic sensitivity of *Avena* coleoptiles.

The complexity of the effect of red light on phototropic sensitivity has been explored in detail by Zimmerman and Briggs (*27*, *28*) for *Avena* coleoptiles. Red light reduces the sensitivity of first positive curvature in *Avena* (system I: positive curvatures, reciprocity law valid) by a factor of 10. First negative curvature (system II: negative curvatures, reciprocity law valid) is affected in the same manner, i.e. with a 10-fold decrease in sensitivity. A recent study by Blaauw and Blaauw-Jansen (3) confirmed the above results for system I curvature but did not explore system II curvature. Red light, by contrast, dramatically increased the sensitivity of second positive curvature in *Avena* (system III: positive curvature, reciprocity law not valid, response time-dependent and intensity-independent over at least a 100-fold intensity range). Asomaning and Galston (1) have reported a system III-type response to red light for barley coleoptiles, system III being the only type of curvature that they were able to obtain.

The purpose of the present paper is 3-fold: first, to investigate the time course for the phototropic sensitivity change under a variety of conditions; second, to obtain an action spectrum for the red light effect on system I curvature; and, third, to investigate the influence of far-red light and attempt to resolve the apparent controversy mentioned above.

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Corn was selected as experimental material since there was already a large amount of information available concerning its phototropic behavior (7, 8, 9).

Materials and Methods

Corn (*Zea mays* L.), Burpee cultivar Barbecue Hybrid, Lot 29234, was used throughout these experiments. The growth procedure adopted here is essentially the same as one described by Briggs (9). Modifications, where made, will be noted in each case.

All the manipulations prior to the day of an experiment were carried out in a dark room kept at 25° (± 2°) with relative humidity of greater than 92 %. However, all light exposures except one for mesocotyl suppression (see below) were given in another dark room with constant temperature (24° ± 2°) but without controlled humidity. In both rooms the working lights were 15 watt fluorescent bulbs wrapped in 2 layers of amber and 1 layer of green cellulose acetate. This combination of celluloid filters showed greater than 0.1 % transmission only in the narrow region of 522 to 563 mμ (26). With cultivar Barbecue Hybrid, no phototropic effects or red light-induced changes in phototropic sensitivity were found to be caused by these green working lights.

In some cases the seedlings were exposed to 3 hours of intense red light when they were 46 to 49 hours old. This treatment was found to suppress mesocotyl growth markedly. Seedlings so treated yielded the greatest number of plants with desired straightness and uniform height at the time of phototropic induction. The possible effect of this mesocotyl suppression on the subsequent phototropic sensitivity of the coleoptile is discussed elsewhere (11).

Light sources used for these experiments are described elsewhere (11) as well as techniques used for measuring light energy (27). For the far-red light source, a 150-watt incandescent light bulb, two 5 cm water filters, and a narrow band interference filter (Baird Atomic) with its transmission maximum around 730 mμ were used. The area that could be illuminated with sufficient but uniform intensity through these filters was approximately 10 × 10 cm^2. The intensity measured directly with the thermopile was ca. 9.6×10^2 ergs cm^{-2} sec^{-1} at the level of the plants.

When the plants were about 80 hours old, the coleoptile was between 1.3 to 1.8 cm long and the mesocotyl 0.5 to 0.8 cm in the mesocotyl-suppressed plants (in non-suppressed plants, 1.5 to 2.0 cm and 1.0 to 2.0 cm, respectively). Plants were selected for experiments if the coleoptiles were straight. Efforts were made to select 8 or 9 plants of uniform height in a given row. The selected plants were placed in a wooden rack in such a way that the long transverse axes of the coleoptiles were perpendicular to the length of the rack. The racks were then transferred to a light-tight box for transport to the second dark room mentioned above.

The sets of plants were removed from the box and vials were marked to indicate their positions relative to the rack. When the ruby red light source was used in preliminary experiments, plants were illuminated from above for varying lengths of time up to 2 hours. In case a period of dark incubation was called for, prior to phototropic induction, the plants were placed in a light-tight cabinet in the second dark room. When the monochromator was used, the plants were placed in a prearranged position for the individual exposures to the monochromator output. The distance between the exit slit of the monochromator and the plants was kept greater than 40 cm. The illumination in the latter case was unilateral. No detectible difference in terms of subsequent red light-induced phototropic sensitivity change was noted between plants illuminated from above and ones that were unilaterally irradiated. Blue light used for phototropic induction was obtained from a high pressure mercury lamp, described by Zimmerman and Briggs (27), and a Baird-Atomic 436 mμ interference filter. Phototropic curvatures were allowed to develop for 100 minutes following the start of phototropic induction, and were then shadowgraphed.

Far-red reversal of the red light-induced phototropic sensitivity change was tested by immediately exposing the red-treated plants to far-red light for varying lengths of time. For reasons to be discussed in detail in the following section, the time from the onset of red light exposure to subsequent phototropic induction was normally 60 minutes. Thus, there were cases in which the plants given a short red light exposure followed by far-red exposure were stored in the dark until phototropic induction. As noted previously, the far-red source used in these experiments permitted illumination of only a limited area. Therefore, rows of only 5 plants could be irradiated simultaneously instead of the usual 8 or 9.

The curvatures recorded on shadowgraphs were measured with a goniometer and then averaged. In a given experiment, usually 2 or more rows were treated in an identical manner, and the average of each row was represented as a point on a graph. In order to minimize daily fluctuation in phototropic sensitivity (e.g. 7, 15) the experimental conditions as well as growing schedules of the plants were rigidly standardized. In addition, a large number of rows of plants, to serve as a control group, were tested in a series of preliminary experiments. They were given a dosage (1.5×10^{-9} Einsteins cm^{-2}) of 436 mμ blue light without the red light pretreatment (see below for further discussion). Under these conditions, very little curvature (3.5° ± 1.2°) was obtained. All subsequent phototropic experiments included 1 or more rows of this control. If the control row(s) of a given experiment indicated that it came from the same hypothetical population as the initial group of controls mentioned above, the entire experiment was accepted and the average values of individual rows were considered to be comparable with similar values in other experiments in a given series. The final control value was computed from the control values thus obtained as well as from the initial group of controls. Thus the sample size for the controls increased to approximately 200 such average values by the end of this investigation. On the basis of this final control value, the earlier experiments were re-examined. Such re-examination showed no fundamental change in the evaluation of individual experiments. The percentage of rejection of experiments on this basis remained rather small. Further statistical treatment of data will be discussed below where appropriate.

Results

Phototropic Dosage-Response Curves. In order to have a system defined in terms of phototropic behavior of the coleoptiles, phototropic dosage-response curves covering approximately 5 log units of dosages of 436 mμ blue light were obtained with and without red light pretreatment.

In figures 1 and 2, phototropic response is plotted against log of blue light dosage. Exposure times ranged from 30 seconds to 1800 seconds. Figure 1 represents the combined results of 4 experiments in which plants received no red light other than that used for mesocotyl suppression. Mesocotyl suppression itself was shown to have little effect on the phototropic sensitivity of the coleoptile at the time of the experiments (9). In figure 2 are presented similar results of 7 experiments in which plants were given 1 hour (see below) of continuous red light (intensity: 4.4 × 10^{-3} ergs cm^{-2} sec^{-1}) from the ruby red bulb source immediately preceding phototropic induction with blue light. Each point represents an average of 8 to 9 individual curvatures.

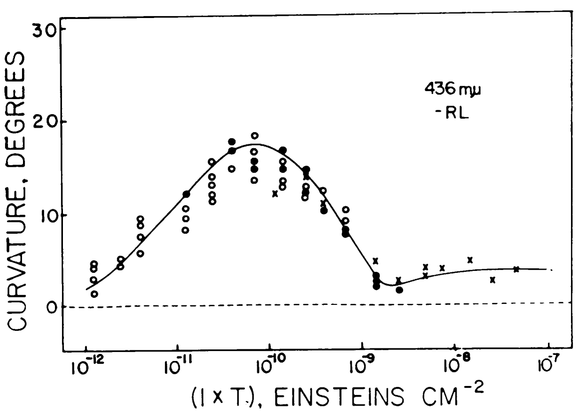

Fig. 1. Phototropic dosage-response curves for completely etiolated corn coleoptiles at 3 intensities of blue light. Blue light intensities: 4.0 × 10^{-13} (○), 4.0 × 10^{-12} (●), and 4.0 × 10^{-11} (×) Einsteins cm^{-2} sec^{-1} at 436 mμ.

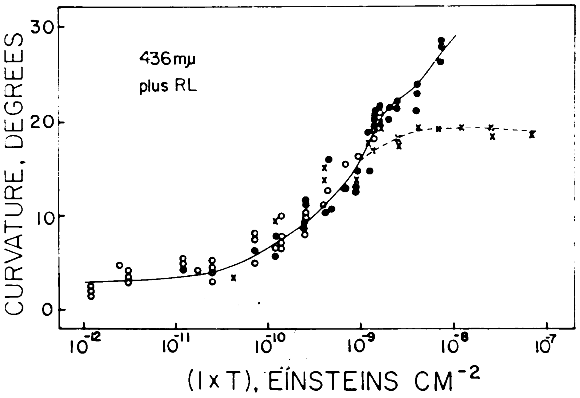

Fig. 2. Phototropic dosage-response curves for red light pretreated (2 hr) corn coleoptiles at 3 intensities of blue light. Blue light intensities: 4.0 × 10^{-13} ○, 4.0 × 10^{-12} (●), and 4.0 × 10^{-11} (×) Einsteins cm^{-2} sec^{-1} at 436 mμ.

Within the dosage range covered in this study, the response curve for the etiolated coleoptiles (fig 1) includes a well defined system I curvature range (ca. 1.0 × 10^{-12} – 1.5 × 10^{-9} Einsteins cm^{-2}). Although the curvature response declined almost to 0 at about 1.5 × 10^{-9} Einsteins cm^{-2} there is no indication of system II (negative) curvature. Furthermore, virtually no system III curvature was observed within the dosage range tested. The reciprocity law was apparently valid [a criterion used to define system I curvature (27, 28)] as the points for a given dosage obtained with more than 1 intensity are statistically not different from each other.

With the red-light pretreated plants, a response curve (fig 2) of rather different shape was obtained. It appears that system I curvature shifted more than a full log unit to the right, reflecting a decrease in sensitivity to blue light. That the major part of the ascending portion of this curve represents system I curvature is supported by the apparent validity of the reciprocity law in the dosage range of approximately 2.0 × 10^{-11} to 2.0 × 10^{-9} Einsteins cm^{-2}. In addition, when the plants were tested with still lower blue light dosages than shown in figure 2 no curvature resulted. Thus, the possibility that the system I curvature may have shifted to the left may be eliminated. In the system I curvature range, the magnitude of maximum curvature in the red-treated plants is slightly greater than that of the non-treated (cf. 3, 4). However, the difference between the 2 is not statistically significant. For blue light dosages greater than 2.0×10^{-9} Einsteins cm^{-2} the failure of the reciprocity law supports the suggestion that this portion of the curve represents, in part, system III curvature, with increased sensitivity to blue light as a result of red light pretreatment (cf. 27, 28).

A comparison of the 2 curves shown in figures 1 and 2 indicates that, at a specific dosage of 436 $m\mu$ blue light (1.5×10^{-9} Einsteins cm^{-2}; intensity 4.0×10^{-12} Einsteins cm^{-2} sec^{-1}; exposure time: 360 sec), the red light-pretreated plants yielded a near maximum curvature (fig 2) while the etiolated plants gave almost negligible (ca 3°) curvature (fig 1). Thus this particular dosage was chosen to assay the red light effect in an operational sense. The red light effect so measured reflects almost entirely the decrease in system I phototropic sensitivity mentioned above. This choice could be justified for the following 3 reasons: (1) the large difference in the curvature (ca 20°) obtained between red-treated and untreated plants, (2) a minimum amount of system III curvature from the non-treated plants, and (3) the amount of information already available concerning auxin relationships under comparable situations (8, 9). The controls used throughout this study were etiolated seedlings phototropically induced with the same dosage of blue light. Thus, the red light effect investigated in this study involved primarily the system I curvature response of corn coleoptiles.

Time Course Studies of the Red Light Effect. The red light effect was studied first by determining its time course using the ruby red bulb source described earlier. Rows of 9 to 10 plants were exposed to red light from above for varying lengths of time prior to phototropic induction. Figure 3 shows results of 4 experiments (open circles) in which the red light intensity was 4.4×10^{3} ergs cm^{-2} sec^{-1}, and those from an additional 4 experiments (closed circles) with red light intensity of 1.4×10^{3} ergs cm^{-2} sec^{-1}. Each point on the graph represents an average of 9 to 10 individual curvatures.

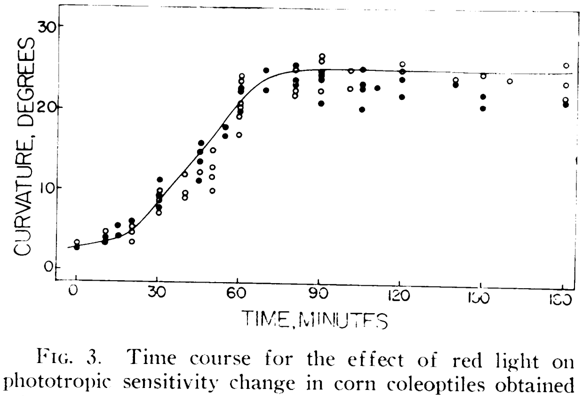

FIG. 3. Time course for the effect of red light on phototropic sensitivity change in corn coleoptiles obtained with continuous red light exposure. Red light intensities: 4.4×10^{3} (○), and 1.4×10^{3} (●) ergs cm^{-2} sec^{-1}; phototropic induction with 436 $m\mu$ (dosage: 1.5×10^{-9} Einsteins cm^{-2}).

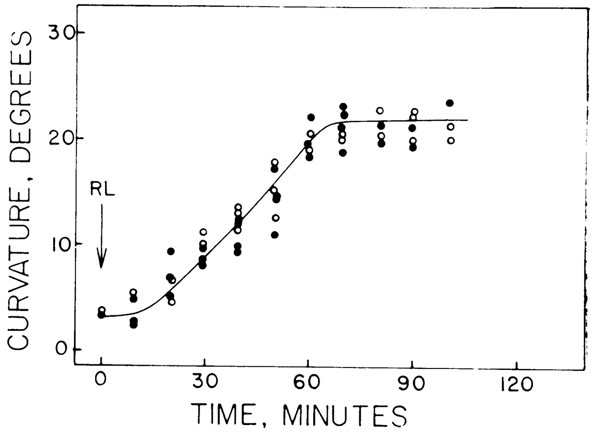

FIG. 4. Time course for the effect of red light induced by 5 seconds (○) and 1 second (●) exposures to red light (intensity: 1.4×10^{3} ergs cm^{-2} sec^{-1}) and followed by dark incubation at 24° prior to phototropic induction with 436 $m\mu$ (dosage: 1.5×10^{-9} Einsteins cm^{-2}) in corn coleoptiles.

As can be seen from the graph, the curvature obtained increases, after a slight lag, to a maximum with about 1 hour of exposure to red light, and stays there for another 2 hours, the longest exposure time tested in this series of experiments. No significant differences in the shapes of the curves obtained with 2 different intensities are noted. The curves are in close agreement with one obtained by Briggs (9), who used white light for phototropic induction. His dosages, however, also induced a maximum system I curvature in the red light-treated plants. The results shown in figure 3 indicate that the red light-sensitive physiological system might, in fact, be very quickly saturated by the continuous red light exposure to the various light intensities employed, and that the attainment of the maximum phototropic sensitivity change might depend, to some extent, on the time elapsed after the onset of the red light exposure. In figure 4 are presented results from 2 experiments (open circles) with a total red light dosage of 7.0×10^{3} ergs cm^{-1} (5 sec exposure) and those from 5 experiments (closed circles) in which a single 1 second exposure (dosage: 1.4×10^{3} ergs cm^{-2}) was given. Phototropic sensitivity during the subsequent dark period was followed as before. Clearly, the lowest dosage tested (1.4×10^{3} ergs cm^{-2}) was still sufficient to evoke the full expression of the red light-induced phototropic sensitivity change, if 60 minutes were allowed following the inception of red light treatment prior to phototropic induction.

The crude light source was inadequate for exposures of less than 1 second in this series of

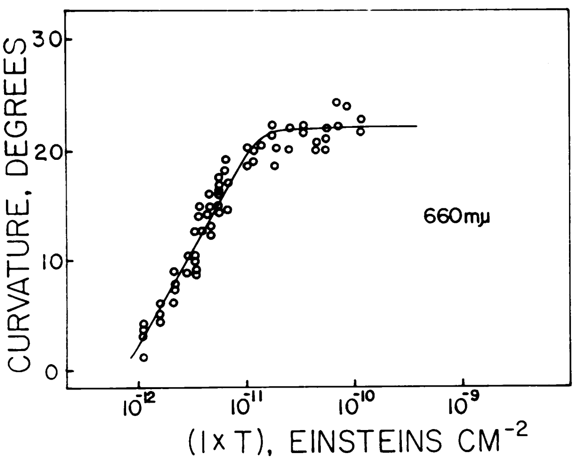

FIG. 5. Dosage-response curve for the effect of red light (660 mμ) in corn coleoptiles. Phototropic induction with 436 mμ (dosage 1.5 × 10^{-9} Einsteins cm^{-2}) exactly 60 minutes after beginning of the red light treatment.

experiments. Therefore a grating monochromator was used to determine red light dosage-response relationships at a variety of wavelengths at far lower energy ranges than had been possible thus far. In all subsequent experiments, plants were stimulated phototropically exactly 60 minutes after the beginning of red light treatment.

Action Spectrum. The method of action spectrum determination adopted involved a comparison of the number of Einsteins required to produce a given change in phototropic sensitivity at 10 mμ intervals in the region 600 to 700 mμ. An alternative method of determining threshold energies was avoided because of the difficulties involved in establishing minimal responses.

Determination of response curves at several wavelengths showed that the shapes of such curves were essentially similar: they showed initial log-linear portions and subsequent levelling off as the dosages were greatly increased, as shown in figure 5. At a given wavelength, intensities were kept as low as possible. The exposure times varied from 2 to 60 seconds. In a few cases, however, exposures as long as 240 seconds were administered. Efforts were made, however, to limit exposure times within 3 to 10 seconds whenever possible. Thus, often more than 1 intensity had to be used at each wavelength. Within the intensity-time combinations tested the reciprocity law was found to be valid.

Figure 5 shows the combined data from 8 experiments performed with 660 mμ red light. These experiments were carried out in the course of several months. However, the spread of such data is no greater than that in a single experiment. Similar response curves, although with fewer points, were obtained in much the same manner as described above at 10 mμ intervals from 600 mμ to 700 mμ. In all cases, the dosage ranges tested for each wavelength involved those inducing a phototropic sensitivity shift of from 0 to 10° which cover a major portion of the log-linear response range. Figures 6 to 9 show the initial log-linear portions of such response curves for a number of wavelengths. For convenience, 3 such response curves were placed in each graph and the abscissa shifted 1 log unit to the right for each wavelength. The ordinate shows increase in phototropic curvature in degrees, where this increase represents difference between individual mean curvature and the mean of non-irradiated controls.

Regression lines were calculated by the method of least squares for each response curve to give the best straight line fit in the log-linear portion

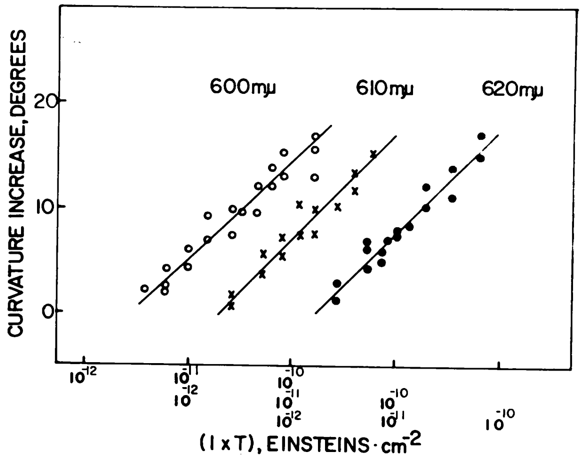

FIG. 6. Log-linear portions of dosage-response curves for the effect of red light in corn coleoptiles obtained for various wavelengths (600 mμ, 610 mμ and 620 mμ). Phototropic induction as in figure 5.

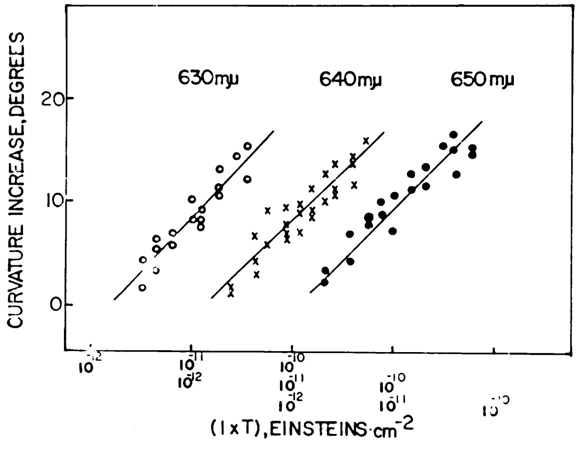

FIG. 7. Log-linear portions of dosage-response curves for the effect of red light in corn coleoptiles obtained for various wavelengths (630 mμ, 640 mμ, and 650 mμ). Phototropic inductions as in figure 5.

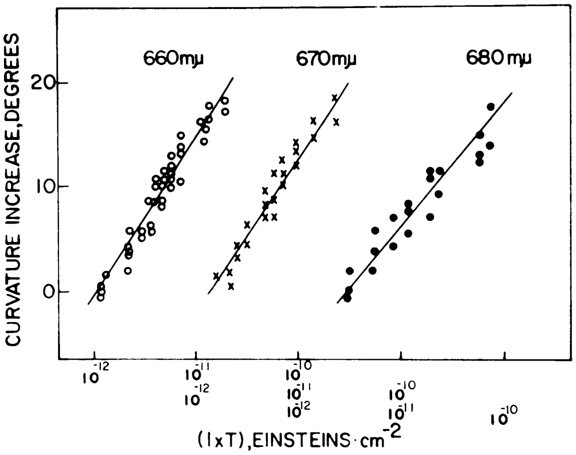

FIG. 8. Log-linear portions of dosage-response curves for the effect of red light in corn coleoptiles obtained for various wavelengths (660 mμ, 670 mμ, and 680 mμ). Phototropic induction as in figure 5.

Table I. *Regression Analysis of Phototropic Curvature and Incident Energy*

Regression equation	Coeff. of determination, R^2
$C_{600\,m\mu} = 0.915 + 7.762 \log E$ (0.887)*	0.855
$C_{610\,m\mu} = 0.276 + 10.014 \log E$ (1.003)	0.926
$C_{620\,m\mu} = 2.579 + 7.873 \log E$ (0.794)	0.883
$C_{630\,m\mu} = 0.388 + 11.846 \log E$ (1.303)	0.883
$C_{640\,m\mu} = 3.978 + 7.147 \log E$ (1.000)	0.773
$C_{650\,m\mu} = 3.143 + 9.382 \log E$ (0.995)	0.881
$C_{660\,m\mu} = 6.054 + 10.443 \log E$ (0.672)	0.831
$C_{670\,m\mu} = 5.966 + 10.163 \log E$ (2.030)	0.676
$C_{680\,m\mu} = -0.507 + 11.054 \log E$ (0.902)	0.920
$C_{690\,m\mu} = -2.566 + 8.171 \log E$ (0.641)	0.931
$C_{700\,m\mu} = -0.879 + 7.075 \log E$ (0.639)	0.885

* Figures in parentheses indicate standard errors of regression coefficients.

of the curve. The least-square values of a and b were estimated from the regression equation $C = a + b \log E$, where C = degrees curvature, a = intercept, b = regression coefficient, and E = incident energy in Einsteins cm^{-2}. High values of coefficients of determination (R^2) indicate that the proportion of variation in curvatures attributable to the log of E (our explanatory variable) is high. Furthermore, the estimates of the slopes (b) are highly significant as seen by the estimates of standard errors of regression coefficients. The values of estimated slopes are all significant at more than the 95 % confidence level. The statistical results are summarized in table I.

From these estimated regression equations the incident moles of quanta of red light required to produce a 5, 8, or 10° increase in curvature were reciprocal of the moles of incident quanta required to produce fixed responses is plotted against the wavelengths in figure 10. A major peak is present

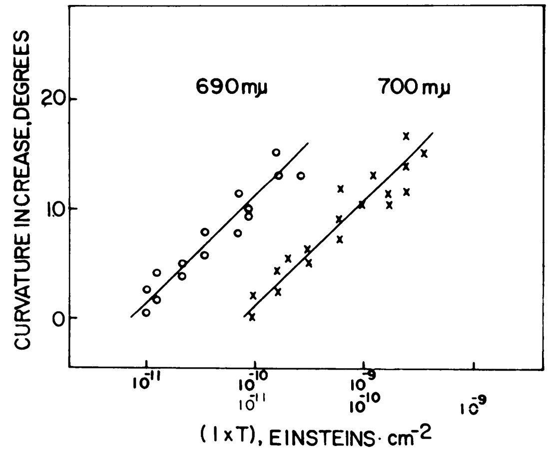

FIG. 9. Log-linear portions of dosage-response curves for the effect of red light in corn coleoptiles obtained for various wavelengths (690 mμ and 700 mμ). Phototropic induction as in figure 5.

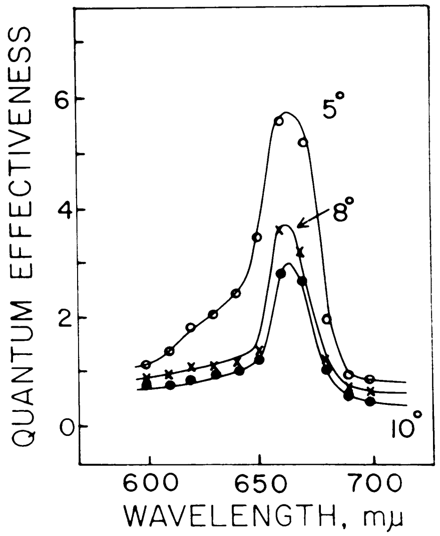

FIG. 10. Action spectra for the red light-induced phototropic sensitivity change in corn coleoptiles. Quantum effectiveness is expressed as the reciprocal of the mole of incident quanta required to produce fixed responses: 5° (○), 8° (×), and 10° (●) curvature increases. Phototropic induction with 436 mμ (dosage: 1.5 × 10^{-9} Einsteins cm^{-2}) was started exactly 60 minutes after beginning of red light treatment.

at the 660 mμ region at all response levels. A small broad shoulder is also seen in the 610 to 630 mμ region at the lowest response level (5°).

Far-Red Effects. The following series of experiments were carried out to determine whether the red light-induced phototropic sensitivity shift could be reversed by subsequent far-red irradiation. A series of 6 experiments was performed in which plants were first exposed to red light (660 mμ) at a dosage (1.8×10^{-11} Einsteins cm^{-2}) more than sufficient to induce a maximum red light response. Within 1 minute after the end of the red light exposure the plants were irradiated with far-red light (intensity: 9.6×10^2 ergs cm^{-2} sec^{-1}) for varying lengths of time up to 60 minutes. As mentioned earlier, when shorter far-red light exposures were given, the plants were kept in the dark until exactly 60 minutes after the onset of the initial red light exposure, at which time they were subjected to the usual phototropic induction with blue light.

In table II the results from these 6 experiments are summarized. The mean curvatures of 4 or more rows of 5 plants treated in an identical manner are shown in column 3. Far-red light clearly reverses the red light-induced effect. Indeed, the *t* tests performed on the non-aggregated data show that the differences between the non-red-treated controls and the groups irradiated with red and followed by far-red dosages of less than 4.6×10^5 ergs cm^{-2} are not significant.

However, it is equally clear that increasingly greater dosages of far-red light are progressively less effective in reversing the red light effect. The combined effect of the red and the far-red light becomes almost indistinguishable from the effect of red light alone as the far-red dosage is increased to 3.5×10^6 ergs cm^{-2}, the highest dosage tested in this series.

Table II. *The Effects of Various Far-red Light Treatments Immediately Following Red Light Exposure on Phototropic Sensitivity of Corn Coleoptiles*

Far-red light intensity: 9.6×10^2 ergs cm^{-2} sec^{-1}; red light dosage: 1.8×10^{-11} Einsteins cm^{-2} at 660 mμ; phototropic induction with 436 mμ.

Far-red dosage ergs cm^{-2}	Exposure time min	Mean curvature degrees
1.7×10^5	3	3.6
2.3×10^5	4	3.9
2.9×10^5	5	3.9
4.6×10^5	8	4.6
5.8×10^5	10	6.1
8.6×10^5	15	7.2
1.2×10^6	20	9.3
1.7×10^6	30	9.7
2.3×10^6	40	13.2
3.5×10^6	60	17.2
Controls:		
No red or far-red light:		3.4
Red light only:		21.6

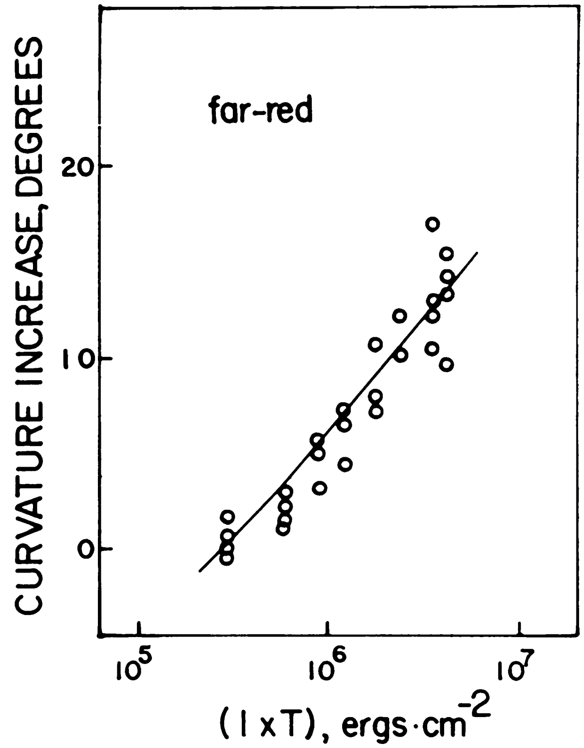

FIG. 11. Dosage-response curve for the effect of far-red light (intensity: 9.6×10^2 ergs cm^{-2} sec^{-1}) in corn coleoptiles. Phototropic induction with 436 mμ (dosage: 1.5×10^{-9} Einsteins cm^{-2}).

The next logical step was an examination of the influence of far-red light alone on this phototropic system. In a series of 3 experiments, far-red dosage-response relationships were examined by exposing plants to far-red light of the same intensity as in preceding experiments for varying lengths of time up to 70 minutes. As in the case of the experiments involving red light, phototropic induction by blue light was started exactly 60 minutes after the beginning of the far-red exposure, except in the cases where exposures to far-red light exceeded 60 minutes. In the latter cases, phototropic induction was started immediately after the end of the exposure to far-red light.

The results of these experiments reveal that, with increase in far-red dosage, phototropic sensitivity changed in an almost identical manner as in the preceding experiments (table II). The differences between the non-irradiated (but phototropically induced) controls and the plants given less than 5.8×10^5 ergs cm^{-2} of far-red light are not significant as revealed by the *t* tests performed on the non-aggregated data. In order to facilitate comparison with the red light dosage-response curves, the data obtained were plotted in figure 11 as increase in phototropic curvature in degrees against log ($I \times t$). Although the units of dosage are not given in Einsteins cm^{-2}

as in figures 6 to 9, the familiar log-linear nature of the initial portion of the curve is seen as in figures 6 to 9 (the regression equation was not used). Thus, when a far-red dosage greater than 8.6×10^5 ergs cm^{-2} is applied to this phototropic system, the effect appears almost indistinguishable from that of red light.

Discussion

The phototropic dosage-response curves of corn (cultivar Barbecue Hybrid) coleoptiles for system I curvature show a general similarity to those obtained with *Avena* (3, 23, 27) although the phototropic sensitivity of the latter is greater than that of corn. However, in the case of completely etiolated corn coleoptiles (fig 1) there is no indication of the presence of system II curvature as is the case in *Avena*. Marked reduction in curvature, however, leading almost to 0°, occurred in the light dosage range greater than that causing system I curvature. Similar observations were made by Briggs (7) in another cultivar of corn. In addition, within the dosage range tested in the present study, there is only a slight indication of system III curvature in corn, as contrasted with the *Avena* coleoptile.

With plants that had been pretreated with red light (fig 2) a major difference from the case of *Avena* is found in the failure of corn to show any reduction in curvature in the range of blue light dosages between systems I and III. Zimmerman and Briggs (27) were able to demonstrate such a reduction in *Avena* with high intensities of blue light, while comparable reduction could not be detected in the present study despite the employment of 3 different intensities. As pointed out earlier, however, the apparent failure of the reciprocity law in the high dosage range indicates that this portion of the curve represents system III curvature, at least in part.

The blue light dosage selected for the purpose of assaying the red light effect clearly falls within the range that induces, in corn coleoptiles, system I curvature responses as defined by Zimmerman and Briggs (27, 28). Thus the red light effect studied here is comparable with that first observed by Curry (15) in the *Avena* coleoptile.

As observed by Blaauw and Blaauw-Jansen (3), the red light effect on phototropic sensitivity change is time-dependent. In the present study with corn coleoptiles, 60 minutes were found to be necessary after the beginning of the red light exposure to evoke a full expression of the red light effect. Compared with other known phytochrome-mediated responses, the present case represents one of the shortest time courses found along with that of geotropic sensitivity change (25), since most other responses are morphogenic in nature and take long hours before changes are detectable at the morphological level. The data on the red light effect on the coleoptile growth obtained by earlier workers (2, 19, 24) dealt mostly with long-term observations.

Somewhat more pertinent data on growth rate changes following red light exposure (1 hr) are found in the work of Curry et al. (16). A graph showing distribution of growth rate by zones along the *Avena* seedling shows an almost 10 % increase in the tip 5 mm zone and a near 20 % increase in the 6 to 8 mm subapical zone of the coleoptile compared with the etiolated seedling. An increase in the magnitude of system I curvature which Blaauw-Jansen (4) observed in *Avena* coleoptiles treated with continuous red light prior to phototropic induction, and which was observed in the present study (with plants treated with continuous red light) to a certain extent may, in part, be explained by such acceleration of growth rate following red light treatment. However, the majority of the experiments presented in this study was performed with very short exposures involving small amounts of red light energy and with the plants phototropically induced exactly 60 minutes after the red treatment. The results of a few exploratory experiments to measure, by means of a travelling microscope (under green light), any change in the growth rate of corn coleoptiles under the above mentioned experimental conditions failed to reveal any significant differences between the red-treated and non-treated coleoptiles in the 3 hour period following a red light irradiation. These experiments were carried out both with completely etiolated and mesocotyl-suppressed groups of seedlings.

A comparison of the present action spectrum with the action spectra for a number of phytochrome-mediated processes (e.g. 18) with figure 10 shows a general similarity in the wavelength region 600 to 700 mμ. Thus, the action spectrum and the far-red reversibility found in the present study clearly indicate that this process is phytochrome-mediated. As pointed out earlier, the failure to observe far-red reversibility of the red light effect by Blaauw-Jansen (4) may be due to the long far-red exposure (40 min) used.

An examination of the data indicates, however, that the amount of incident energy necessary to induce a given degree of change in phototropic sensitivity is considerably smaller than the comparable red light energy required for other known phytochrome-mediated systems. With lettuce seed, for example, the red light energy necessary to induce 50 % response (promotion of germination) was shown to be 2.5×10^4 ergs cm^{-2} (6). It is likely that the red light effect investigated in the present study on the phototropic sensitivity shift in corn coleoptiles may involve a more sensitive physiological system than the other responses mentioned above (11). In the etiolated corn coleoptiles, lack of other pigments absorbing in the red region of the spectrum, as well as their favorable anatomical arrangements (e.g., thin layers of exposed cells) may partly account for the high sensitivity observed.

The action spectrum presented in figure 10 agrees fairly closely with that obtained for in vivo transformation of phytochrome in etiolated corn Barbecue Hybrid coleoptiles (21), as well as with one for the photoconversion of the isolated pigment from etiolated *Avena* seedlings (12). Although the absorption spectra of partially purified phytochrome from etiolated corn coleoptiles are not available, such spectra have been presented recently for phytochrome from *Avena* coleoptiles (22). A comparison of figure 10 with the absorption spectrum for the red-absorbing form of the pigment from *Avena* shows a close similarity in the wavelength region 600 to 700 mμ.

The results from the study of far-red reversibility of the red light effect are of some interest. As is well known most of the physiological responses mediated by phytochrome have been shown to be reversible by far-red irradiation. However, there have been occasional reports in which prolonged far-red exposures produced results similar to those from red exposures. For instance, prolonged treatments with far red (rather than red) in the middle of the dark periods have been shown to be inhibitory to flowering in such short-day plants as *Xanthium,* soybean (17), *Chenopodium* (20), and *Chrysanthemum* (14). In the latter case, 9 minutes of far-red light given after an inhibitory treatment with red light repromoted flowering, but a prolonged far-red irradiation (81 min) following the red treatment failed to reverse the red light effect. Flowering was also inhibited by 81 minutes exposure to far red without prior red light treatment. Borthwick (5) argued that the red light-like action of prolonged far-red light might be caused by a small amount of P_{FR} maintained during the far-red irradiation, acting over a prolonged period of time. Similar reasoning may be applied in the present case. Blaauw-Jansen's (4) failure to obtain far-red reversibility of the red light effect on *Avena* phototropism may have been due to the long far-red exposure used (40 min).

A similar instance of far-red light producing the same action as red light has also been reported in a study involving in vivo dark transformations of phytochrome in etiolated corn seedlings (13). The destruction of photoreversible phytochrome, which occurs only when P_{FR} is present, was studied by using various light sources which maintained different ratios of $P_{FR}:P_R$ at the photostationary state. Butler and co-workers found that the rate of destruction was saturated when 10 % of the phytochrome was maintained as P_{FR}. Destruction was still measurable when less than 1 % of the pigment was maintained as P_{FR}. By prolonged irradiation with far-red light a low level of P_{FR} can be maintained by virtue of the long wavelength-absorption tail of P_R. The relationships between the spectrophotometric status of phytochrome and the phytochrome-mediated phototropic sensitivity change in corn studied here are discussed in detail in another paper (11).

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