

Second Positive Phototropism in the *Avena* Coleoptile

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Abstract. A method has been developed whereby the second positive phototropism can be observed separately from the first positive and negative phototropic responses which also occur in oat coleoptiles. Although the second positive phototropic response has often been referred to as the base response, photoreception for it is shown to occur mainly in the apical 3 mm of the coleoptile. The Bunsen-Roscoe reciprocity law, so typical of first positive phototropism, does not apply to the second positive responses, and the amount of curvature increases linearly with the duration of the stimulus. However, although this linear proportionality between stimulus duration and response is the major factor determining response at all intensities tested, the intensity of the stimulus does influence the response somewhat. The action spectrum for the response shows no activity above 510 nm and has peaks at 375 and 450 nm. In all but one particular it closely resembles the action spectrum for the first positive phototropism, and it is concluded that the same, or similar, pigments may well be the photoreceptors for both types of response. The identity of this blue light absorbing pigment is not known.

Despite the availability of action spectra for the first positive phototropism in oats (15, 17), the photoreceptor for this response has not been definitely characterized (9, 17). Furthermore, the early experiments on phototropism demonstrated that in addition to first positive phototropic curvatures, oat coleoptiles also exhibit negative and second positive types of response (1, 4). From a study of the dose-response curves for phototropism in *Avena* and of theoretical models for these data, Zimmerman and Briggs (19, 20) suggested that *Avena* coleoptiles possess 3 different photoreceptor systems for the 3 types of phototropic response—first positive, negative, and second positive. If this be the case, then the photoreceptive pigment for the second positive type of curvature would be different from that for the first positive phototropism and might be identified from an action spectrum for the second positive response. For this reason, and in order to characterize the little-known second positive response more clearly, the present experiments on second positive phototropism in coleoptiles of *Avena* were undertaken.

Although the second positive phototropic response, which occurs with large stimulus energies or long stimulus durations, has not been extensively studied, there are strong indications that the Bunsen-Roscoe reciprocity law, which holds for first positive phototropism, is not applicable to it (2, 5, 17). This law states that the response depends only on the total

energy of the light dose and is not influenced by the intensity or duration of the stimulus. Thimann and Curry (17) suggested that curvatures of the second positive phototropic type are determined mainly by the duration of the stimulus, and Briggs (2) provided strong evidence for this hypothesis by showing that second positive responses of oat coleoptiles to stimuli of equal energy, delivered with various intensities of light, increased with increasing stimulus duration. Furthermore, when Zimmerman and Briggs (20) subtracted the responses predicted by their theoretical models for first positive and negative phototropism from their phototropic dose-response curves, the remaining responses, assumed to be of the second positive type, increased linearly with stimulus duration and were not affected by a 10-fold variation in intensity. Unfortunately the overlap of first positive responses by second positive ones when low intensity light is used (1, 17, 19) has prevented a direct study of the characteristics of the second positive phototropic response. For this reason it seemed essential to develop a method of isolating second positive curvatures, and thus to study them alone. In this paper such a method is described and used to elucidate both some general properties of the system and its action spectrum.

Materials and Methods

Seeds of *Avena sativa* var. Victory, obtained from the U.S.D.A. Branch Experiment Station at Aberdeen, Idaho, were husked and soaked for 2 hr in distilled water. The soaked seeds were planted individually on 1.5% agar slanted in 1.5 ml vials, which were placed in deep petri dishes, covered to maintain a high humidity. The dishes were placed

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in a growth room maintained at $25^{\circ} \pm 1^{\circ}$ and exposed to 22 to 24 hr of red light at a distance of about 50 cm from a 25 watt ruby red bulb, where the intensity was about 1.5×10^4 ergs $\text{cm}^{-2} \text{sec}^{-1}$. This treatment completely inhibited the growth of the mesocotyl. The plants were then placed in a light-tight cabinet in the growth room. At 70 to 72 hr from the time of soaking, when the coleoptiles were 2.5 to 3.0 cm tall, they were exposed to 1 to 2 hr of the same red light to bring the sensitivity changes caused by red light to a maximum (5, 19). Exposure to the stimulus followed this treatment.

The seedlings were selected for straightness and positioned (in their vials) in racks so that the narrow side of the coleoptile would be exposed to the stimulus beam. Ten plants at a time were exposed to each stimulus, the entire coleoptile being illuminated unless otherwise stated. Monochromatic light, of band width 5 nm, was obtained from a 150 watt xenon lamp and a Bausch and Lomb high-intensity grating monochromator. The monochromator, located in a part of the growth room partitioned from the rest by a black curtain, was encased in a light-tight box provided with a shutter. Intensity was usually varied by changing the distance of the plants from the exit slit of the monochromator, but in a few cases neutral density filters were employed. For stimulus times of less than 1 sec the shutter mechanism was used, while for longer stimuli the shutter was operated by hand and timed with a stop watch. If only the bases of the plants were to be exposed, aluminum foil caps of the appropriate size were placed on the coleoptiles during stimulation.

Immediately after exposure to the stimulus, the vials containing the plants were rotated 90° around a vertical axis and placed in position before a film holder containing Kodabromide paper. A shadowgraph was taken with phototropically inactive green light; the plants were left in position, and a second shadowgraph was taken 100 min after the time of the start of the stimulus. The double shadowgraphs were measured twice with a goniometer; the 2 sets of values for each plant were compared and averaged, and if a discrepancy of more than 3° occurred in the 2 measurements of each plant, it was corrected by a third measurement. Standard errors for the means of these measurements were no more than 2° , and rarely more than 1.5° . Each value in the plotted data rests on measurements of not less than 50 plants.

A Reeder vacuum thermocouple connected to a Keithley microvoltammeter was used to measure light intensities. Absolute values of intensity were determined with an 8-junction bismuth-silver Eppley thermopile which had been calibrated against a standard lamp by the manufacturer. Variation of intensity with distance from the monochromator was determined with an Evans electro selenium microphotometer used with a neutral density filter. Since the readings on the photometer indicated that the

intensity of the light decreased as the square of the distance from the monochromator (except much closer to the monochromator than any plants were placed), intensities in the range where this relation was valid were calculated using this assumption.

Results

Isolation of the Response. In preliminary experiments the dose-response curves for 5 intensities of 475 nm light were determined. The results are plotted in figure 1 and are in agreement with the data of Zimmerman and Briggs (19) on the shape of the dose-response curves at a series of intensities of stimulus light. Negative responses were not observed because the stimulus intensities reached with the narrow slit width were not sufficiently high. Since the first positive responses depend only on the total stimulus energy, the 5 curves coincide in the region of the lower energy doses. In the higher energy region where the second positive responses occur, the curves do not overlap, and the second positive curvature is initiated at increasingly lower energies as the stimulus intensity decreases. The explanation of the onset of second positive curvature at progressively decreasing energy levels is given by the theory that the second positive responses depend primarily on the stimulus *duration*, irrespective of the total energy contained in the stimulus. For instance, the time required to deliver the dose of 1000 ergs/ cm^2 decreases from over 1600 sec at the lowest intensity to 21 sec at the highest intensity. With long stimulus durations the second positive responses overlap those of the first positive, and the difficulty of studying responses observed in this way is clearly illustrated in figure 1.

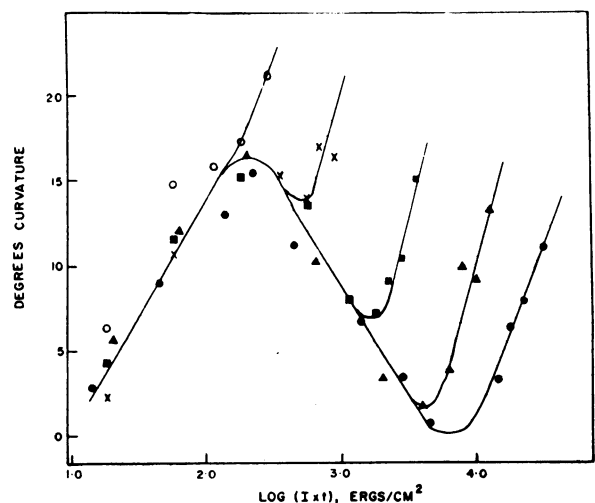


FIG. 1. Dose-response curves for phototropism in oat coleoptiles at 5 different intensities of 475 nm light. ●) 48 ergs $\text{cm}^{-2} \text{sec}^{-1}$ (80 I in fig 3), ▲) 24 ergs $\text{cm}^{-2} \text{sec}^{-1}$ (40 I in fig 3), ■) 6 ergs $\text{cm}^{-2} \text{sec}^{-1}$ (10 I in fig 3), ×) 1.5 ergs $\text{cm}^{-2} \text{sec}^{-1}$ (2.5 I in fig 3), ○) 0.6 ergs $\text{cm}^{-2} \text{sec}^{-1}$ (I in fig 3).

There is 1 situation in which the second positive responses can be isolated, namely when high intensity light is used for the stimulus. Such a situation is illustrated by the responses of the coleoptiles to the highest intensity of light used in figure 1. Here there is an "indifferent" responsive region between first and second positive curvatures, the plants showing no response to a stimulus of this energy. First positive responses occur only with stimulus energies lower than those in this indifferent zone; and because the intensity being used is high, the stimulus durations are not long enough to cause significant second positive curvatures. It is possible, however, to use this system to obtain isolated second positive responses by following a high intensity dose with one of a lower intensity. Thus, if a high intensity light dose, causing an indifferent response, is given unilaterally to the experimental plants and is immediately followed by a second unilateral stimulus of any intensity, lasting several hundred sec, the plants now respond with a positive curvature. Such curvatures take place when the sum of the energies of the 2 stimuli is greater than the energies that cause first positive or negative curvatures. Evidence will be presented below that these curvatures have the characteristics of second positive responses as described above. The initial stimulus used in most of the experiments was a dose of 4800 ergs/cm² of 475 nm light, delivered in 100 sec. The second stimulus was usually given for 200 sec or more. In the action spectrum experiments, the initial dose was changed to 5700 ergs/cm², delivered in 100 sec, at 470 nm.

Characteristics of the Response. Authors have occasionally used the terminology "tip response" and "base response" in referring to first and second positive curvatures, respectively, to suggest that photoreception and response for the 2 types of phototropism occur in different regions of the coleoptile (18). However, in the experiments of Arisz (1) and of Zimmerman and Briggs (19) only the apical 3 mm tips of the coleoptiles were stimulated, but nevertheless second positive responses were observed. Thus, as pointed out previously (17), the term "base response" is inappropriate for second positive phototropism. In addition, the "base responses" observed with 260 to 330 nm light (7) differ in dose-response characteristics from second positive phototropism so that these responses may well represent a type of phototropic curvature distinct from those occurring with wavelengths of light above 350 nm.

With the experimental method used here, a comparison of the responses of plants bearing 3 mm apical caps with those of plants stimulated along their entire length showed that light-reception in the tip of the coleoptile accounts for 75 to 80% of the responses observed in these experiments. For instance, in 1 experiment capped plants responded to a stimulus consisting of the initial 100 sec high intensity dose followed by 400 sec of 6 ergs cm⁻²

sec⁻¹ at 475 nm with a curvature of $3.7^\circ \pm 0.9^\circ$ while plants without caps curved $14.5^\circ \pm 1.5^\circ$ to the same stimulus combination. Only with illumination lasting 1000 sec or more did capped plants give curvatures of over 10° . Thus, the responses described in these experiments are primarily tip responses, and the photoreception and resulting response that undoubtedly can occur in the base of the coleoptile during some second positive curvatures (1, 17) play a minor role here.

The characteristics of the response in plants stimulated with the 2-dose method described above were examined at 1 wavelength, 475 nm. Figure 2

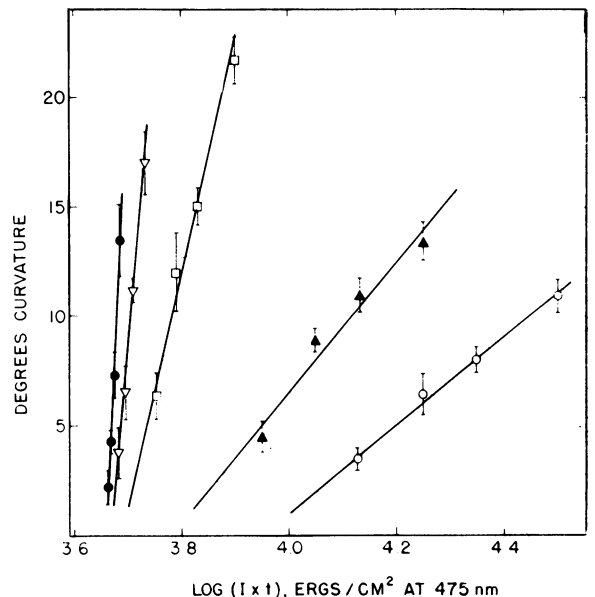


FIG. 2. Phototropic responses of oat coleoptiles stimulated with an initial dose of 4800 ergs/cm² at 475 nm [$\log AI \times t = 3.68$], and a second dose delivered in 5 intensities of 475 nm light: (○) 48 ergs cm⁻² sec⁻¹, (▲) 24 ergs cm⁻² sec⁻¹, (□) 6 ergs cm⁻² sec⁻¹, (△) 1.5 ergs cm⁻² sec⁻¹, (●) 0.6 ergs cm⁻² sec⁻¹. Stimuli of 4 durations were given at each intensity. The responses are plotted against the logarithm of the total energy of the stimulus. Standard errors are indicated.

shows the responses to the second doses at 5 intensities, as a function of the logarithm of the total stimulus energy. All the plants received the initial dose of 4800 ergs/cm² [$\log (I \times t) = 3.68$], and were then exposed to a second stimulus, lasting 200 to 600 sec, with 475 nm light. When the curvature is thus plotted against dose, it is evident that the reciprocity law does not apply to these responses; equal stimulus energies do not produce equal curvatures. At any 1 intensity the response increases with increasing dose and therefore with increasing stimulus duration.

The indication that second positive responses depend on the stimulus duration is directly tested in figure 3, where the data shown in figure 2 are

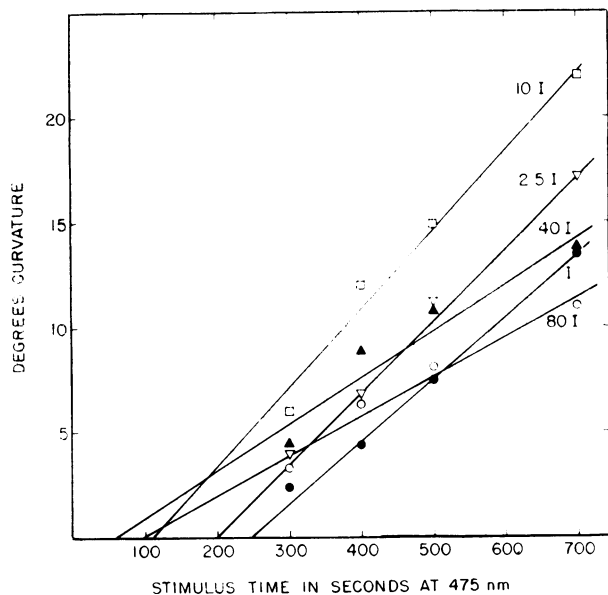


FIG. 3. Responses of oat coleoptiles plotted against the stimulus duration. The initial 100 sec of all the stimuli gave the same dose of 4800 ergs/cm² at 475 nm. The second parts of the stimuli were delivered with 5 intensities of 475 nm light: (○) 48 ergs cm⁻² sec⁻¹, (▲) 24 ergs cm⁻² sec⁻¹, (□) 6 ergs cm⁻² sec⁻¹, (△) 1.5 ergs cm⁻² sec⁻¹, (●) 0.6 ergs cm⁻² sec⁻¹. Lines drawn through the data for each intensity were calculated by the least squares method. Standard errors for these data are indicated in figure 2.

re-plotted against the duration of the stimulus. The first 100 sec represent the duration of the initial stimulus received by all the plants, bringing them to the zone of indifference. For any 1 intensity of the second dose the response is seen to increase linearly with stimulus duration. However, the intensity does modify the slope or X-intercept of the line relating response to stimulus duration, so that all the data points do not fall on 1 line. To illustrate the influence of stimulus intensity on second positive phototropism, the responses of plants to stimuli of constant duration have been plotted against the logarithm of the intensity of the second stimulus. The result is shown in figure 4. Response is maximal at an intensity of 6 ergs cm⁻² sec⁻¹, higher and lower intensities causing decreased responses. The decrease in response at high intensities is not caused by heat radiating from the monochromator, since water filters placed in front of the monochromator made no difference in the response. It must be emphasized that at any 1 intensity of the second dose, stimulus duration is the factor determining the amount of curvature, and response increases linearly with duration. The modifying effect (on this linear relationship) of the intensity of the stimulus has not been observed previously, although it is possible that the decreased phototropic responsiveness reported with very large light doses (1) is a manifestation of this phenomenon. On the other hand the

existence of a second indifferent and a third positive region of the phototropic dose-response curve (4) has not been substantiated in these experiments.

The Action Spectrum. In the highest intensity region, where curvature decreases with increasing intensity, the spectral sensitivity of the response could not be investigated thoroughly since sufficiently high intensity light was not available throughout the spectrum. However, measurements of the responses of coleoptiles to a quantum flux for the second stimulus of 3.5×10^{12} quanta/cm² sec⁻¹, lasting 400 sec, indicated that light of wavelength between 440 and 480 nm was most effective in bringing about the decrease in response, and that at this intensity 495 nm and 355 nm light did not appear to cause any depression in response.

The action spectrum for second positive phototropism was determined in the low intensity stimulus region, where response increases with increasing intensity. Since the duration of the stimulus is the major factor determining the response, the durations of the stimuli in all these experiments were held constant by using an initial high intensity stimulus of 100 sec, followed by a second stimulus of 400 sec. To determine the effect of the intensity of the second stimulus on the second positive phototropic response at all the wavelengths investigated, 2 quantum fluxes, 0.53×10^{12} and 1.2×10^{12} quanta cm⁻² sec⁻¹, were employed at each wavelength. The wavelengths were spaced every 20 nm from 355 to 435 nm and every 10 nm from 445 to 495 nm. The experiments at each wavelength and quantum flux were repeated 4 or 5 times, and the data are presented in table 1. As shown, the change in response for a change in quantum flux of 1 log unit is found to be reasonably constant with wavelength in this intensity region. The values for the slope calculated at 455 and 475 nm are much smaller than the others,

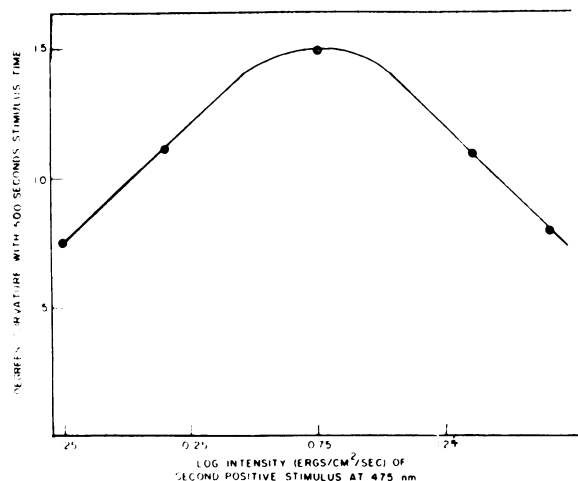


FIG. 4. Variation of responses to stimuli of fixed (500 sec) duration at 5 intensities of 475 nm light. Initial 100 sec stimulus of 48 ergs cm⁻² sec⁻¹ received by all the plants. The response is plotted against the logarithm of the intensity of the second stimulus (400 sec duration). Standard errors are indicated in figure 2.

Table I. *Variation of Response With Intensity and Wavelength of the Second Stimulus*

Response is measured in degrees curvature \pm standard error. The slopes are determined in the intensity region where response is increasing with intensity. An initial 100 second stimulus of $57 \text{ ergs cm}^{-2} \text{ sec}^{-1}$ at 470 nm was given to all the plants.

| Wavelength | Response to 400 sec of $0.53 \times 10^{12} \text{ quanta/}$ $\text{cm}^2 \text{ sec}^{-1}$ | Response to 400 sec of $1.2 \times 10^{12} \text{ quanta}$ $\text{cm}^{-2} \text{ sec}^{-1}$ | Slope: Response/log (Intensity) |
|------------|--|---|---------------------------------------|
| <i>nm</i> | <i>deg of curvature</i> | | |
| 355 | 7.9 ± 0.8 | ... | ... |
| 375 | 12.6 ± 0.9 | 19.3 ± 1.5 | 19.1 |
| 395 | 11.5 ± 1.3 | 17.3 ± 1.4 | 16.6 |
| 415 | 12.9 ± 0.6 | 18.2 ± 1.7 | 15.1 |
| 435 | 14.9 ± 1.2 | 20.2 ± 0.9 | 15.1 |
| 445 | 17.7 ± 1.0 | 22.0 ± 0.9 | 12.3 |
| 455 | 17.8 ± 1.1 | 20.7 ± 1.7 | 8.3 ¹ |
| 465 | 17.4 ± 0.6 | 22.4 ± 0.6 | 14.3 |
| 475 | 16.0 ± 0.8 | 17.4 ± 2.1 | 4.0 ¹ |
| 485 | 14.1 ± 0.9 | ... | ... |
| 495 | 6.8 ± 0.8 | ... | ... |
| Avg slope | | | 15.4 |

¹ Values not included in calculation of average slope (see text).

and in these cases it seems reasonable to assume that the higher quantum flux initiated the processes causing the decreased curvatures observed at high intensities.

For the action spectrum, the data on the responses of the coleoptiles to the 2 quantum fluxes were used to extrapolate or interpolate to the quantum flux required for a standard response. The standard response chosen was 15° , and the quanta contained in a second stimulus, lasting 400 sec, required to produce this standard response were determined graphically from the data on the responses to the 2 quantum fluxes investigated. The reciprocal of this value is plotted against wavelength in the action spectrum, figure 5. At the 2 wavelengths, 455 and 475 nm, where the slopes of the lines relating response to logarithm of stimulus intensity deviated

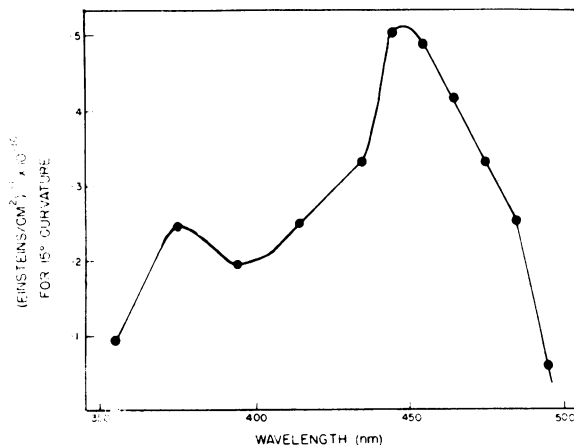


FIG. 5. Action spectrum for the second positive phototropic response in *Avena* coleoptiles. The reciprocal of the energy, in Einsteins/cm², of the second stimulus, when delivered in 400 sec, for a 15° curvature is plotted against the wavelength of the second stimulus.

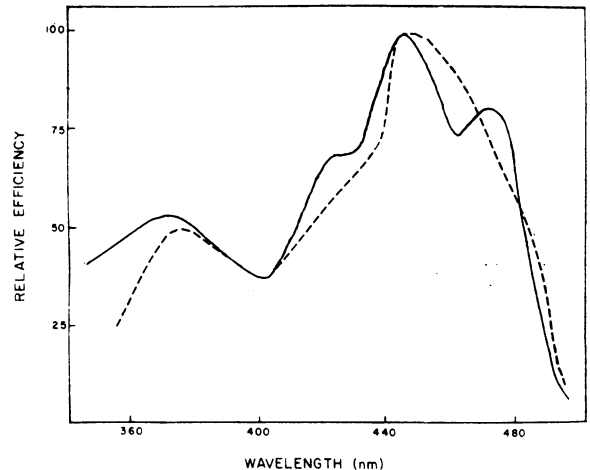


FIG. 6. A comparison of the action spectrum for first positive phototropism in oat coleoptiles, solid line from (16), with the action spectrum for second positive phototropism (dashed line).

greatly from the other values, the quantum flux required for the standard response was determined by assuming that the slope of the line relating response to quantum flux through the point at $0.53 \times 10^{12} \text{ quanta cm}^{-2} \text{ sec}^{-1}$ was the average slope of $15.4^\circ/\log$ unit.

In the action spectrum shown, the peaks fall at about 375 and 450 nm, and no activity is observed above 510 nm. The resemblance of this action spectrum to the 1 for first positive phototropism in *Avena* (17) is striking, and the 2 are graphed together in figure 6. In both action spectra the peaks in the near ultraviolet are based on observations at only a few wavelengths, so the details of the shape in this spectral region are not well defined. Both action spectra have a valley at 400 nm, but above this point certain differences are discernible.

Because of the lengthy experiments involved, the points for the second positive action spectrum are further apart than those for the first positive response. For this reason a shoulder at 425 nm in the second positive action spectrum may well have been missed. The major peak in the action spectrum for first positive phototropism is at 445 nm and for the second positive phototropism it is at 445 to 455 nm. The ratio of the height of the near ultraviolet peak to this one is in both cases very close to 1:2. The absence of a second peak around 475 nm in the second positive action spectrum is the major discrepancy between the 2 action spectra. Unfortunately there is a large change in the lamp output at about this wavelength. Additional experiments on the second positive response in this spectral region were carried out using a second stimulus of 0.53×10^{12} quanta $\text{cm}^{-2} \text{sec}^{-1}$ lasting 400 sec at the wavelengths 465, 470, and 475 nm. The experiment was repeated 6 times, and the results are shown in table II. These experiments indicate that the second positive phototropic action spectrum may well have a second peak around 475 nm. Since the presence of such a peak has not yet been satisfactorily demonstrated in detailed experiments with varying stimulus intensities, however, it has not been included in the action spectrum for the response. Nevertheless, the similarities between the 2 action spectra are strong, and we conclude that the same, or very similar, pigments appear to be involved in photoreception for these 2 phototropic responses.

Table II. *Additional Action Spectrum Data*

Responses to an initial sec stimulus of 57 ergs $\text{cm}^{-2} \text{sec}^{-1}$ at 470 nm plus 400 sec of 0.53×10^{12} quanta $\text{cm}^{-2} \text{sec}^{-1}$ at the test wavelength.

| Wavelength | Curvature \pm standard error |
|------------|-------------------------------------|
| nm | deg |
| 465 | $16.8^\circ \pm 1.3$ a ¹ |
| 470 | $13.6^\circ \pm 0.4$ b ¹ |
| 475 | $17.8^\circ \pm 1.4$ a ¹ |

¹ a, b Values with different letters are significantly different at the 95 % confidence level.

Discussion

The method of isolating second positive phototropism used in these experiments has permitted a characterization of the effects of stimulus duration, intensity, and wavelength on the response. Haupt (10) and Meyer zu Bentrup (12), working on the photo-induction of polarity of germination in *Fucus* zygotes and *Equisetum* spores, used a method similar to the one developed in these experiments. The dose-response characteristics of the low and the high energy types of polarity induction are similar to those for first and second positive phototropism in coleoptiles, and the wavelengths of light effective for the responses are also in the blue and near ultraviolet. However, studies on the spectral sensi-

tivity of the polarity induction processes indicated that the low and high energy responses might have different action spectra (12), while it appears that the 2 kinds of positive phototropism have similar action spectra.

The experiments reported here agree with earlier evidence (2, 5, 20) that second positive phototropic responses are determined by the duration of the stimulus rather than by the total energy of the stimulus. Zimmerman and Briggs (20) reported that a 10-fold change in intensity had no influence, detectable with their method, on the linear relationship between response and stimulus duration. However, the present experiments cover a larger intensity range with a more direct method and bring out the fact that the stimulus intensity does indeed have some modifying effect on the second positive response. The means whereby stimulus intensity and duration affect the response are not known. Perhaps the decreased responsiveness at high intensity is caused by bleaching or photo-oxidation of the photoreceptor. Zimmerman and Briggs (20) suggested that the second positive response is determined by the length of time during which a photoequilibrium is maintained between an inactive and an active form of the photoreceptor. A modification of this scheme in which the equilibrium concentration of the active form of the photoreceptor is intensity-dependent would provide 1 possible mechanism to explain the secondary effect of intensity.

In these experiments the minimum stimulus duration required for initiation of second positive phototropic bending is 100 sec. Curry (5) estimated that a duration of about 240 sec was required, while Zimmerman and Briggs' (20) data indicated that the second positive type of response was initiated with the start of the stimulus. These differences are probably related to the different methods used to observe the response. With the 2 dose method used in these experiments the intensity and duration of the initial dose might influence the point of onset of the second positive responses, but it was not found possible to test this factor thoroughly.

The similarity between the action spectra for first and second positive phototropism accords strikingly with the demonstration of Pickard and Thimann (13) that lateral transport of auxin occurs during both types of response in coleoptiles. There are 2 possible interpretations of these facts. One is that the 2 photoreceptors are indeed the same, the apparent discrepancy at 475 nm being due to experimental imperfections. The oat coleoptile would then present the remarkable phenomenon of having 2 different types of response (each with its characteristic kinetics) both mediated by the same photoreceptor and brought about by the same effector, namely auxin asymmetry. However, the great differences in dose-response characteristics between the 2 types of positive phototropism, as well as the opposite effects of red light pretreatment (in decreasing the sensitivity of the first positive and

increasing that of the second positive) (19, 20) have not yet permitted the formulation of a model in which first and second positive phototropism are related to the same photoreceptive mechanism. The alternative interpretation of the data is that the photoreceptors in fact differ slightly; perhaps the same pigment is conjugated with 2 different proteins. Zimmerman and Briggs (20) indeed suggested separate photoreceptor systems for first and second positive responses. Each system would have its own dose-response characteristics, but the end result, lateral transport of auxin, would be the same. One would be tempted to draw an analogy with mammalian vision where 2 different types of photoreceptors, the rods and the cones, operate in low or high light intensities respectively, but both bring about the sensation of light, and both contain very closely related pigments.

The phototropic photoreceptor has not been identified from the action spectrum for first positive phototropism. The same must at present be the situation for the second positive photoreceptor. The problem has been discussed in detail in references (3), (9), and (17). Suffice it to say here that neither type of pigment, flavin, or carotenoid, suggested as the photoreceptor, has an absorption spectrum precisely matching the action spectra. The idea, discussed by Briggs (3) and Thimann (16), that flavins and carotenoids participate together in light absorption for the phototropic response is, indeed, reasonable, but proof for this or any other theory is lacking.

The identity of the photoreceptor for blue-light-reactions such as phototropism is an important unsolved question in plant physiology. Reactions with action spectra similar to those for phototropism in oats are found throughout the plant kingdom: a few examples of such responses are phototropism in *Phycomyces* (6, 8) whose action spectrum is virtually identical with that for first positive phototropism in *Avena*, photo-stimulation of respiration in *Chlorella* (11) with peaks at about 375 and 460 nm, light-stimulated carotenoid synthesis in *Fusarium* (14) and chloroplast phototaxis in *Lemna* (21) with peaks at 382, 452, and 485 nm. In none of these has the photoreceptor been unequivocally identified. The experiments reported here add yet another response to the list of these blue-light-reactions and provide an additional reason for continued efforts to identify this photoreceptor.

Acknowledgments

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