Phototropism and Local Adaptation in *Phycomyces* Sporangiophores

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ABSTRACT Phototropic responses to unilateral ultraviolet stimuli were studied
to determine whether the response of one side of the cell is affected by the pre-
vious exposure of the opposite side to ultraviolet. It has been found that the direc-
tion of bending is not parallel to the stimulus direction, but is along a straight
line rotated 17° clockwise from the stimulus direction. This deviation indicates
that the photoreceptors may be in a state of continual clockwise rotation. If before
the stimulus the cell is exposed briefly to ultraviolet and rotated through 90°,
the response is not along the 17° line, but is deviated a greater or lesser amount,
depending on whether the 90° rotation is clockwise or counterclockwise. This
difference is evidence that the first ultraviolet exposure leaves a persistent
patch of light-adapted receptors and the shaded part of the cell remains dark
adapted. The phototropic stimulus straddles the edge between light- and dark-
adapted regions, and the differing responses of the two regions affects the direc-
tion of phototropic bending. A phototropic mechanism is proposed which
combines the features of local adaptation and photoreceptor rotation.

INTRODUCTION

The phototropic response of *Phycomyces* to blue light depends on the intra-
cellular intensity distribution (Dennison, 1965), but steady-state phototropic
bending is difficult to explain, since the growth-response mechanism is acti-
vated only by changes in light intensity. Delbrück and Reichardt (1956)
proposed a model in which the growth response is a result of a mismatch be-
tween the light intensity and the light level to which the sporangiophore is
adapted. After exposure to a constant intensity for several minutes, the
sporangiophore becomes adapted to that intensity, and the growth rate
approaches a constant value, regardless of the intensity. When the intensity
is abruptly changed, however, the level of adaptation does not immediately
adjust to the new intensity level, and consequently the growth rate deviates
for a time from its previous value. When the cell is illuminated unilaterally,
each cellular photoreceptor element should become adapted to its local light
intensity and thus lead to the same growth on all sides of the cell. One would

therefore predict that the tropic response to unilateral illumination would die out after 5 or 10 min, in direct contradiction with the fact of steady-state phototropism (Dennison, 1965).

An alternative has been suggested by Jaffe (Cohen and Delbrück, 1959) and by Bergman et al. (1969), who propose that while the intracellular intensity distribution is highly nonuniform, the corresponding level of adaptation might be smoothed out to some degree. Thus, particularly in regions of strong inhomogeneity of illumination, there would be a mismatch between the light intensity and the level of adaptation, even in the steady state. The experiments reported here were undertaken to discover whether the level of adaptation spreads uniformly around the cell's circumference, or remains relatively localized.

The experimental design was suggested by the work of Delbrück and Varjú (1961) who studied the phototropic response to narrowband ultraviolet stimuli. Ultraviolet was chosen because, although a very effective growth stimulus, it is very strongly absorbed by the cell contents. As a result it is effective only on the illuminated side, and the optical properties of the cell can be safely ignored. Delbrück and Varjú showed that adapted regions do in fact remain localized in the longitudinal direction; the "edge" does not smooth out appreciably with time. Our purpose is to show that a similar adapted region on one side of the cell also maintains its edge and does not blur over into the nonadapted side.

Our experimental approach is to expose one side of the cell to a short ultraviolet stimulus, and then rotate the cell 90° and illuminate again. The second stimulus thus strikes the edge between light- and dark-adapted regions. We would expect that if this edge remains sharp with time, there should be a greater response from the dark-adapted region than from the light-adapted region. This differential response should then be detectable as a lateral skewing of the phototropic response away from the dark-adapted region. On the other hand, if adaptation spreads uniformly around the cell, no such differential response and no such skewing should occur.

MATERIALS AND METHODS

Cultures are prepared by inoculating vials containing 4 % potato dextrose agar with vegetative spores of a sexually minus strain of *Phycomyces blakesleeanus* derived from type 1555 of Northern Regional Research Laboratories. The spores are diluted from a stock suspension, heat shocked at 45°C for 10 min, and added to each vial at a surface density of about 5 spores/cm². Culture vials are kept in a box humidified to 80 % and illuminated continuously by white light (two 7 W incandescent lamps at 10 cm) until ready for use. Sporangiophores between 28 mm and 36 mm, from cultures 5 days old or more, are selected for experimental use. During experiments the room humidity is maintained near 80 %, and the temperature during culture and experimentation is kept in the range from 20°C to 22°C by an air conditioner.

The apparatus is built around a motor-driven turntable with a vertical axis of rotation and fitted with an angular scale. The turntable is mounted on a threeway movable stage. A culture vial containing a single sporangiophore is centered on the turntable, where it can be subjected to three types of illumination. A blue light source consisting of an incandescent lamp plus Corning 5-61 filter (Optical Sales Department, Corning Glass Works, Corning, N.Y.) at an intensity of 0.35 μW/cm^2 and impinging on the sporangiophore at an angle of 55° from vertical is used to straighten and equilibrate the sporangiophore during a 30 min period of 2 rpm rotation. This blue light intensity was selected so that the sporangiophore is adapted to a standard level in the normal range (Bergman et al, 1969) and, after a 30 min dark period (see protocol below), will be adapted to a low enough intensity to give a strong but not saturating response to the ultraviolet stimuli. A red light source (phototropically inert) is used for making photographic exposures. A timer turns the red light on for a period of 3 s once every minute. The ultraviolet source is a deuterium lamp whose output passes through a visible-blocking filter and a Bausch & Lomb 500 mm grating monochromator (Bausch & Lomb Inc., Rochester, N.Y.) set at a wavelength of 285 nm. To vary the ultraviolet intensity, the entrance slit is varied while the exit slit is kept at 3.00 mm. The ultraviolet intensity at the sporangiophore position is measured with a Photovolt photometer (Photovolt Corporation, New York) with an ultraviolet-sensitive photomultiplier tube. Ultraviolet intensities of 175, 1,200, 4,800, and 9,400 arbitrary units (U) are used. The ultraviolet beam passes from the exit slit through a quartz lens and iris diaphragm. The diaphragm is imaged as a 2 mm diameter spot on the sporangiophore by a concave mirror of 18 inch focal length. The sporangiophore is adjusted so that the center of the 2 mm spot is located 1 mm below the sporangium at about the midpoint of the 17 min experimental run (see protocol below).

The direction and speed of the phototropic response are recorded photographically from above. A 35 mm macro-objective lens (Ernst Leitz, Wetzlar, Germany) is focused at ×4 on the sporangium. The intensity of the red light is adjusted so that only its tiny reflection spot in the spherical sporangium produces a dense image point on Kodak High Contrast Copy film (Eastman Kodak Co., Rochester, N.Y.). To reduce the size and increase the sharpness of this reflection, the top of the sporangium is coated with a light oil by carefully dipping the inverted sporangiophore in an oil film on a glass slide. A millimeter scale is photographed on each length of film as a size and direction reference. For analysis the film is placed in a Vanguard Motion Analyzer (Vanguard Instrument Corp., Melville, N.Y.), which projects the images at ×8 onto a ground-glass screen. The instrument is equipped with measuring cross-hairs for the X- and Y-coordinates of the projection screen, and these are used to read off the coordinates of desired points along the photographic record. Distances and angles between pairs of points are then calculated by computer.

Since the results depend quite critically on the procedure, it seems useful to present here a typical experimental protocol. First, the experimental room is humidified to approximately 80 %, by adjusting the rate of flow of low pressure steam into the room. After 5 min, a culture vial with a suitable sporangiophore is placed at the center of the turntable and rotation at 2 rpm in blue light is begun. After 30 min the

blue light is turned off and rotation is continued in darkness (except for red light) for an additional 28 min. The air conditioning is turned off to reduce room air currents 4 min before the rotation is stopped. Also, during the last 10 min of rotation, the sporangiophore is centered precisely on the axis of rotation by gently sliding the glass turntable top in its grease-covered base until no lateral movement is observed in the horizontal microscope. This alignment is necessary since the ultraviolet spot is centered on the rotational axis. Just before the rotation is stopped, the turntable is adjusted vertically so that the stimulus spot will be centered 1 mm below the sporangium at about the midpoint of the experiment (assuming a typical growth rate of 2–3 mm/h). Also, the camera must be positioned so that the critical images, covering minutes 10 through 16, are in sharpest focus. To a certain extent the tendency of vertical growth to move the sporangium up and out of focus is compensated by bending. At 30 min after turning off the blue light, the first ultraviolet exposure (1 min) is begun by opening the monochromator shutter. The entrance slit is set to 1.5 or 3.0 mm for this exposure (4,800 or 9,400 U, respectively), which marks "time zero"— the start of the experimental run. At time 1 min the exposure is terminated by closing the shutter. After the shutter is closed, the turntable is rotated through the desired angle (for example 90° counterclockwise), and the camera shutter is opened and locked. At time 2 min the red photo light is turned on for a 3 s exposure and the timer activated to continue the red exposures at 1 min intervals. Before time 3 min, the monochromator slit is narrowed to 0.15 or 0.50 mm (175 or 1,200 U, respectively). At time 3 min, the monochromator shutter is opened to begin the second ultraviolet exposure, which continues for the rest of the experiment. The experiment is terminated at minute 17, after a total of 16 exposures have been recorded on the film.

RESULTS

Fig. 1. shows photo records of two representative experiments in which the first ultraviolet exposure was at an intensity of 4,800 U, the second at 175 U, and the sporangiophore was rotated 90° (clockwise or counterclockwise) between ultraviolet exposures. To visualize these records one should imagine looking down on the trail traced out by the sporangium as the sporangiophore bends in response to the stimuli. The stimulus directions are shown as if the ultraviolet stimulus directions instead of the sporangiophore were rotated between ultraviolet exposures.

From image no. 3 to no. 8, the sporangiophore bends away from the direction of the first ultraviolet exposure. This is to be expected, since the 1 min ultraviolet stimulus impinges on a relatively dark-adapted cell and should cause a positive light growth response on the proximal side of the cell. More remarkable is the fact that the response is a relatively straight line oriented some 30°–40° clockwise from the stimulus direction. This indicates that some cellular mechanism may cause the response region to be rotated clockwise (see Discussion).

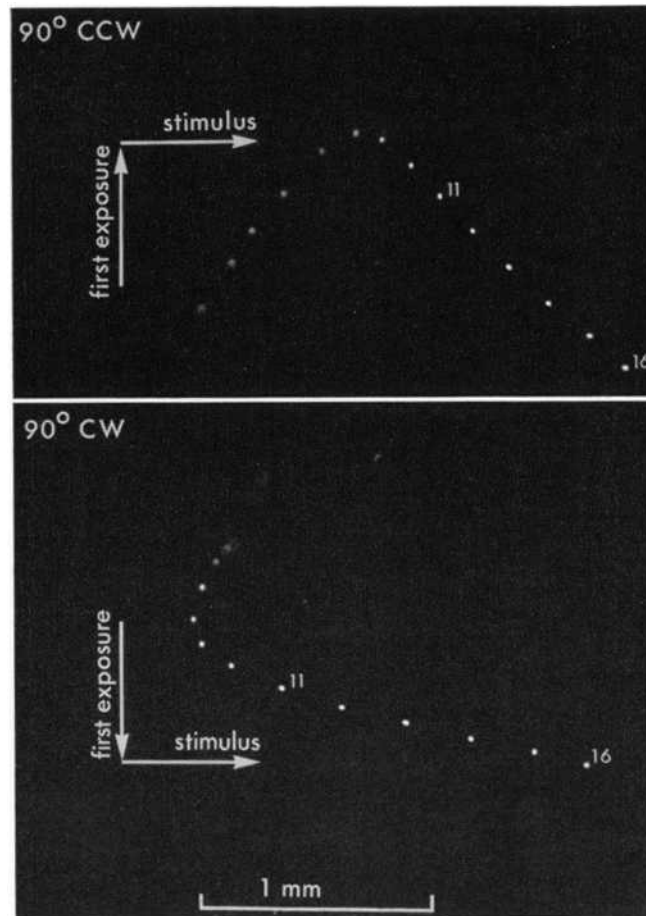From image no. 7 to no. 9 (8.5–10.5 min after the first ultraviolet exposure

FIGURE 1. Photographic records of phototropic responses to ultraviolet stimuli after a 1 minute preexposure to ultraviolet. The direction of bending, α, is measured between the stimulus direction and the line connecting the 11th and 16th images, as described in the text. Above: sporangiophore rotated 90° counterclockwise (*ccw*) after the first ultraviolet exposure, $\alpha = 42.7°$. Below: sporangiophore rotated 90° clockwise (*cw*) after the first ultraviolet exposure, $\alpha = 15.5°$. In the early part of each record the images become sharper as the sporangiophore grows upwards into the plane of best focus.

and 5.5–7.5 min after the beginning of the second ultraviolet exposure[1]) the bending direction changes quite abruptly. After turning this corner the bending is now in a nearly straight line oriented away from the direction of the second ultraviolet stimulus, but rotated clockwise from that direction. It is remarkable and highly significant that this clockwise deviation is much

[1] The first photographic exposure is made precisely at minute 2, but owing to an erratic feature of the timer, the second exposure occurs at times up to 50 s after minute 3. The mean time shift is 30 s. All later exposures are at precisely 1 min intervals after the second exposure.

greater if the sporangiophore rotation was counterclockwise than if it was clockwise. For purposes of measurement, the bending direction is taken as that of a straight line connecting the position of images 11 and 16, thus corresponding to the average bending direction during the interval 9.5–14.5 min after the beginning of the second ultraviolet stimulus. The angle of bending, α, is defined as the acute angle between the second ultraviolet stimulus direction and the direction of bending. In the experiment shown in Fig. 1, α, = 15.5° for a clockwise rotation of 90° and α = 42.7° for a counterclockwise rotation of 90°. In repeated experiments, mean values of α = 14° for 90°

TABLE I

THE EFFECT OF ROTATION ANGLE AND ULTRAVIOLET INTENSITY ON THE
SPEED AND DIRECTION OF THE PHOTOTROPIC RESPONSE

Angle of rotation	Ultraviolet intensity*		$\alpha\ddagger$	$s\S$
	I	II		
110° CCW	4,800	175	35 ± 2	0.22 ± 0.02
" "	4,800	1,200	43 ± 7	0.25 ± 0.02
" "	9,400	175	31 ± 2	0.17 ± 0.01
70° CW	4,800	175	10 ± 4	0.29 ± 0.003
" "	4,800	1,200	3 ± 5	0.27 ± 0.02
" "	9,400	175	11 ± 2	0.22 ± 0.02
90° CCW	4,800	175	42 ± 2	0.19 ± 0.02
70° CCW	"	"	27 ± 3	0.18 ± 0.01
90° CW	"	"	14 ± 4	0.32 ± 0.02
110° CW	"	"	21 ± 4	0.28 ± 0.01
Rotated 360°	"	"	17 ± 2	0.23 ± 0.01

* Intensity is in arbitrary units. I and II refer to first and second ultraviolet exposures, respectively.
‡ α is the bending direction in degrees measured from the second ultraviolet stimulus direction.
§ s is the bending speed in millimeters per minute.
Both s and α are calculated from the sporangium positions at the 11th and 16th photographic images, except for the series at an intensity of 1,200 U for the second ultraviolet stimulus, in which the 9th and 14th images are used.
Values are means of five replicate experiments (exception: seven for 90° clockwise) and are given ± the standard error of the mean.

clockwise rotation (seven experiments) and α = 42° for 90° counterclockwise rotation (five experiments) were obtained (see Table I). This large difference in bending angle reflects the different aftereffects persisting in the cell after the two different conditions of initial ultraviolet exposure.

These results are presented in polar form in Fig. 2, which clearly shows the much greater value of α for counterclockwise 90° rotation. Significantly, the difference is in the direction one would expect. Assuming that the preexposed region would remain at a higher level of adaptation than the other cell half, one would expect the part not preexposed to give the greater growth response and thus shift the response direction as shown.

The conditions of clockwise and counterclockwise 90° rotation represent oppositely asymmetrical preexposure conditions, and it is of some interest to know if the values of α resulting from uniform preexposure fall midway between 14° and 42°. Uniform exposures are made by substituting a 1 min period of ultraviolet rotation (2 rpm) for the usual 1 min static preexposure. The cell is thus irradiated uniformly around its circumference during the first ultraviolet exposure. As in the 90° rotation experiment, the response is a relatively straight line, but instead of two distinct response segments there is only one, beginning at the 8th or 9th exposure, or 6.5–7.5 min after the beginning of the second ultraviolet exposure. Thus the uniform ultraviolet pre-
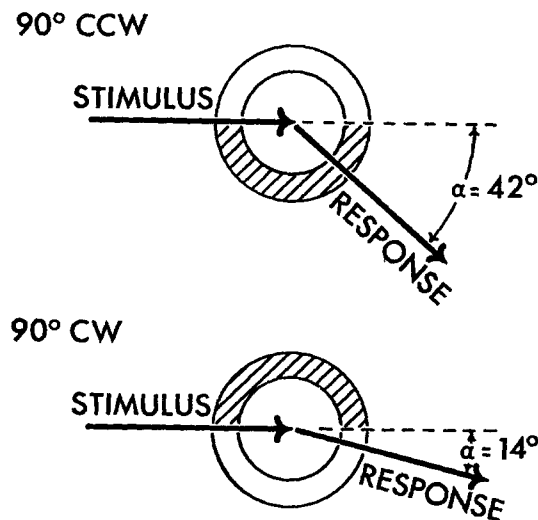

FIGURE 2. The relation between the preexposed area (cross-hatched), the stimulus direction, and the phototropic response direction. Above: sporangiophore rotated 90° counterclockwise (*ccw*) after the first ultraviolet exposure. Below: sporangiophore rotated 90° clockwise (*cw*) after the first ultraviolet exposure. Values of α are means from Table I.

exposure elicits only a single linear response beginning at about the same time the second segment begins for a 90° rotated sporangiophore, replacing the initial linear response segment by an extra latency period of 5–6 min. The bending direction is measured from image no. 11 to no. 16 as before, and the results of five experiments give an average value of α = 17°. Very clearly, therefore, the rotations of 90° clockwise and counterclockwise do not give deviations symmetric about the value of α = 17° for uniform preexposure. This suggests that due to some intracellular mechanism the preexposed, adapted region has undergone some amount of clockwise rotation before the response direction (second segment) becomes established. This suggests a series of experiments in which the clockwise and counterclockwise rotations differ from 90°.

The results of such a series are given in Table I and Fig. 3. In all cases intensities are 4,800 and 175 U for the first and second ultraviolet exposures, respectively. Besides the pair at 90° clockwise and counterclockwise, experiments were done at 110° counterclockwise −70° clockwise and 70° counterclockwise −110° clockwise. These values of α are plotted in Fig. 3 together with the value of α from the experiments in which the sporangiophore is rotated at 2 rpm during the first ultraviolet exposure (here the rotation angle is considered 0°). Although the data are somewhat fragmentary, they support the generalization that the values of α observed for clockwise rotation are clearly smaller than those observed for counterclockwise rotation. Also, there
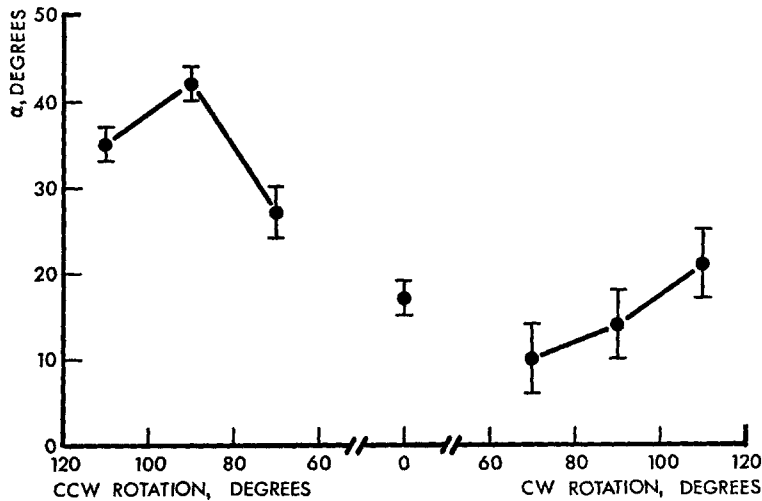

FIGURE 3. Effect of rotation angle upon the direction of the phototropic response. Ultraviolet intensities are 4,800 U for the first exposure and 175 U for the second exposure. The value of α for 2 rpm rotation during the first ultraviolet exposure is plotted at a rotation angle of 0°. The length of each vertical bar is twice the standard error of the mean. *ccw*, counterclockwise rotation; *cw*, clockwise.

appears to be a trend towards smaller values of α as the clockwise rotation decreases from 110° to 70°. The values of α for rotations of 110° counterclockwise and 70° clockwise (α = 35° and 10°, respectively) come the closest to bracketing the value of α = 17° for uniform preexposure. This again indicates that some rotation is built into the response mechanism and this inherent rotational tendency is partially offset by shifting the center of symmetry of the counterclockwise-clockwise rotation pairs.

The effects of increasing the intensity of either the first or the second ultraviolet exposure are shown in Table I. It is clear that increasing the intensity from 4,800 to 9,400 U for the first exposure has almost no effect on α, and increasing the intensity from 175 to 1,200 U for the second exposure increases

α for counterclockwise rotation and decreases it for clockwise rotation. In the latter case, the intensity increase causes the response (second straight segment) to begin about 2 min earlier; therefore for this series the response is measured from image no. 9 to no. 14 (instead of no. 11 to no. 16). The center of symmetry is not significantly affected by these variations.

Variation in rotation angle and stimulus intensity affect the rate of phototropic bending as well as its direction. Bending speed is calculated as the linear horizontal distance in millimeters between the sporangium position at image no. 11 and that at no. 16 (or nos. 9 and 14, respectively), divided by 5 min. Values of these bending speeds at various rotation angles are given in Table I. The bending speed for uniform first ultraviolet exposure is 0.23 mm/min, with higher speeds for clockwise rotation angles and lower speeds for counterclockwise angles. Conversion of these distances into the more usual units of degrees per minute can be done approximately by assuming a 2 mm lever arm (radius) between the sporangium top and the bending pivot point.[2] Such a bending speed is typical of that normally encountered in the phototropic response to blue light (Bergman et al, 1969), but is considerably less than that found at 280 nm (typically 20°/min). This is due to the high level of adaptation resulting from the 30 min exposure to blue light before the start of the experiment. Such relatively low bending speeds are necessary to avoid the large angles that would complicate the photographic recording system and to ensure that the experiment lasts long enough to approximate a phototropic steady state. The difference in bending speed between clockwise and counterclockwise rotation angles is significant and may be related to some kind of intracellular rotational asymmetry (see Discussion).

The effect of variation in ultraviolet intensity on bending speed is also presented in Table I. For rotation angles of 110° counterclockwise −70° clockwise, the bending speed is significantly decreased by the increase in intensity of the first ultraviolet exposure from 4,800 to 9,400 U, showing the importance of the persistent aftereffects of the first ultraviolet exposure. In contrast, the effect of a relatively larger increase in the second ultraviolet exposure intensity is very slight.

DISCUSSION

The results clearly show that the first ultraviolet exposure sets up some kind of laterally asymmetric state within the cell, which persists for a relatively long time. This asymmetry is detected by the large difference in the direction of phototropic bending, depending on which side of the cell was previously exposed to ultraviolet. These differences are in the direction predicted by the

[2] If s is the horizontal sporangium velocity in millimeters per minute and θ is the bending speed in degrees per minute, then $\theta = \sin^{-1} (s/2)$.
For example, if s is 0.23 mm/min, θ is about 6.5°/min.

hypothesis that the side not previously exposed gives the greater growth response, and are thus consistent with the hypothesis that the first ultraviolet exposure produces a persistent patch of light-adapted photoreceptors in the cell at or near the cell wall. When the second ultraviolet exposure begins, this light-adapted patch would then give a smaller growth response than the photoreceptor patch on the opposite side.

It should be remembered that the level of adaptation is not itself a directly observable entity, but can only be inferred on the basis of the size of response resulting from a particular stimulus. Thus in the uniform adaptation theory of phototropism, the unequal growth rate is supposed to arise from the continued local disparity between the intensity at the bright focal line and the adaptation level there. To the extent that it is assumed that the local growth rate is determined only by the local intensity and the local level of adaptation, then our experimental results clearly contradict the hypothesis that the level of adaptation is uniform across the cell. We have shown that the local growth responses to a symmetric stimulus are not the same on the two sides of the cell; hence the above assumption leads directly to the conclusion that differences persist in the level of adaptation on the two sides.

These results not only appear to rule out a uniform lateral spreading of the level of adaptation, but in addition they indicate the existence of intracellular asymmetry. The most clearcut evidence of asymmetry is the 17° clockwise deviation in response direction for a cell uniformly adapted on all sides. It is tempting to ascribe this deviation to the spiral growth pattern of the cell, which causes the top of the growing zone (and sporangium) to rotate clockwise at about 10°/min. From the top to the bottom of the growing zone, the cell wall rotation rate drops from 10°/min to zero (see also Cohen and Delbrück 1958), and one might therefore think that the clockwise deviation is due to the occurrence of twist below the region of bending. But this explanation is untenable since it predicts that the clockwise deviation would steadily increase with time, leading to a curved bending trajectory with its concave portion to the right as seen from above. In fact the trajectories are either very nearly straight or slightly curved and concave to the left. Alternatively, the 17° clockwise deviation in response direction might be explained by assuming that the light receptors are in clockwise rotation and that a time delay intervenes between receptor stimulation and the establishment of the bending response. Thus the 17° shift would be equal to the product of the rotation rate and the duration of the time delay. However, we still have no adequate understanding of the remarkable fact that the bending trajectory is relatively straight in spite of the rotation of the cell wall and the light receptors.

Asymmetry is also suggested by the speed and direction of the response to the second ultraviolet stimulus. Clockwise and counterclockwise 90° rota-

tions result in response directions unequally displaced from the 17° line. A reasonable explanation of this is that the adapted area has rotated by the time the second response direction is established. This is supported by the closer approach to symmetric response directions when the rotations are 110° counterclockwise and 70° clockwise. From the available data it is not possible to infer just how far the adapted region must have rotated, but it is probably greater than 20°.

It is puzzling to note the consistently greater bending speed for clockwise rotation than for counterclockwise. In both cases, the second stimulus falls on the edge between preexposed and non preexposed areas, but in the clockwise case it is the leading edge of the non-preexposed area, and in the other case it is the trailing edge. Could there be a difference between leading and trailing edges? This is possible, but a more appealing explanation assumes the dark-adapted photoreceptors are rotating clockwise and therefore undergo different stimuli in the two cases. For 90° clockwise rotation, the dark-adapted area is moving from a position of relative shade towards a position of higher intensity and hence would experience an increasing stimulus level. In contrast, for 90° counterclockwise rotation the dark-adapted area is moving from a brighter position towards a more shaded position and would therefore experience a decreasing stimulus level. Therefore we might expect a weaker response in the latter case, as found experimentally.

In summary, we have presented evidence that adaptation may be a relatively localized phenomenon and that some structures relating to photosensitivity may be in constant clockwise rotation. This not only makes the uniform adaptation theory of phototropism less attractive, but it also suggests a new possibility, namely a rotational theory of phototropism. Such a theory would postulate that the receptors adapt locally and that they rotate in a regular clockwise manner. Then the cause of steady-state phototropism is simply that these receptors are alternately dark adapted and then stimulated as they pass through the dark and light regions of the intracellular illumination pattern. Preliminary experiments, in which sporangiophores are mechanically rotated during an ultraviolet phototropic stimulus, were carried out in collaboration with K. Foster (Foster, 1972) and although inconclusive, seem to lend support to the rotation theory. Further experiments are currently in progress.

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