

Tropic Responses of *Phycomyces* Sporangiophores to Gravitational and Centrifugal Stimuli

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ABSTRACT A low-speed centrifuge was used to study the tropic responses of *Phycomyces* sporangiophores in darkness to the stimulus of combined gravitational and centrifugal forces. If this stimulus is constant the response is a relatively slow tropic reaction, which persists for up to 12 hours. The response is accelerated by increasing the magnitude of the gravitational-centrifugal force. A wholly different tropic response, the transient response, is elicited by an abrupt change in the gravitational-centrifugal stimulus. The transient response has a duration of only about 6 min. but is characterized by a high bending speed (about 5°/min.). An analysis of the distribution of the transient response along the growing zone shows that the active phase of the response has a distribution similar to that of the light sensitivity for the light-growth and phototropic responses. Experiments in which sporangiophores are centrifuged in an inert dense fluid indicate that the sensory mechanism of the transient response is closely related to the physical deformation of the growing zone caused by the action of the gravitational-centrifugal force on the sporangiophore as a whole. However, the response to a steady gravitational-centrifugal force is most likely not connected with this deformation, but is probably triggered by the shifting of regions or particles of differing density relative to one another inside the cell.

INTRODUCTION

Sporangiophores of *Phycomyces* have long been the object of research concerned with the phenomenon of irritability. Most of the work has been concerned with the sensitivity of the sporangiophores to light, as manifested by the phototropic response and by the light-growth response. These responses may also be elicited by other environmental stimuli, such as humidity changes and gradients (Walter, 1921), ionizing radiation (Forssberg, 1943), infrared radiation (Wortmann, 1883), ultraviolet radiation (Curry and Gruen, 1957), and gravity. It seems reasonable that all these responses involve changes in the rate of elongation of the cell wall. This suggests that the terminal portions of the pathway from stimulus to response might be shared by these different reactions,

although the initial part of each pathway, concerned with stimulus reception, must obviously be different.

The interaction of the light and gravity responses may reveal the extent of a common stimulus-response pathway. Several observations of such interactions have been made. Elfving (1883) found that the geotropic response was inhibited if the sporangiophore was illuminated uniformly on all sides, and Pilet (1956) found that a light pretreatment reduced the geotropic bending rate subsequently observed in darkness. A different mode of interaction was noted by Oehlkers (1926) and by Dennison (1958). Illumination of a sporangiophore by a horizontal beam leads to a stable tropic equilibrium in which the mean direction of growth is about 20° above horizontal. This equilibrium is evidently the result of an interaction between prototropism and geotropism.

It is first necessary to establish in some detail the nature of the geotropic response in the absence of light. The experiments of Sachs (1879) showed that geotropism is a rather weak orienting factor in the growth of sporangiophores. However, Schwarz (1881) found that the application of a centrifugal force of 17 g 's caused a much stronger geotropic response. A consistently strong geotropic response would be preferable to a weak and variable one for purposes of studying the effect of light on gravitational sensitivity. Thus the present series of experiments, using a centrifuge, was begun in the hope of finding suitably vigorous responses to gravitational stimuli stronger than natural gravity.

MATERIALS AND METHODS

The experimental material is a "minus" strain of *Phycomyces blakesleeana*, originally derived from strain 1555 of the National Regional Research Laboratory. After heat-shocking for 10 minutes at 45°C, vegetative spores are inoculated in aqueous suspension into 3 ml glass vials, each containing about 2.8 ml of sterile 5 per cent potato dextrose agar (Difco). The cultures are kept at 21.0°C ± 0.5°C, in a ventilated, moist chamber (relative humidity about 90 per cent) and are illuminated from above by a white 15 watt incandescent lamp at a distance of 60 cm. Sporangiophores begin to appear by the 3rd day after inoculation, but those used in experiments are from cultures that are 4 to 7 days old. The sporangiophores used in experiments are always in stage IV (sporangium darkening, growth rapid) and have a total length of 20 to 30 mm.

The centrifuge used in these experiments (Fig. 1) consists of a disk, 2 feet in diameter, mounted on a vertical axle driven by an electric motor through a flexible rubber belt and a pair of "step" pulleys. By shifting the drive belt to various steps of the pulleys, and by varying the voltage supplied to the motor, constant speeds of 10 to 250 RPM can be maintained by the disk. The speed of the axle is monitored by an electrical tachometer connected to its lower end. Up to ten cultures may be mounted

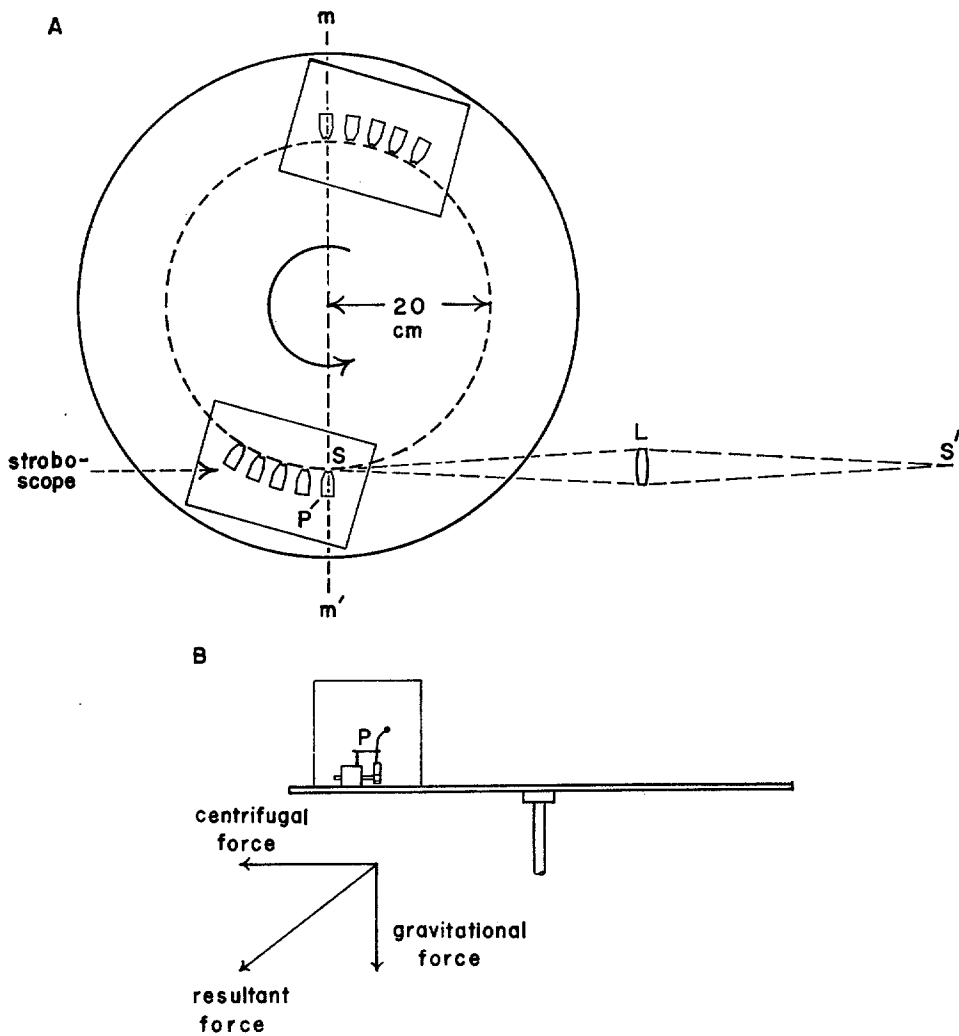


FIGURE 1. Top and side views (schematic) of the centrifuge disk. In A, the top view, the stroboscope lamp is in the midst of a flash, illuminating the sporangiophore at *S*. The lens, *L*, focuses the image of *S* at the point *S'*. This image may be recorded on photographic film or examined directly with a microscope. The sliding contact switch under the disk enables the stroboscope to flash when any one of the ten sporangiophores is at the position *S*. In B, the disk is shown in side view, as cut by the diameter *mm'*. The notched platform, *P*, is shown supporting a sporangiophore. Only one mounting and one lucite box are shown. The vectorial addition of the gravitational and centrifugal forces acting on the sporangiophore is also indicated.

in adjustable holders on the centrifuge disk (see Fig. 1). Each culture vial is cleared of all but one sporangiophore, which is steadied in a V-shaped notch cut in a small lucite platform mounted over the vial holder. Each of the ten notches is fixed at 20.0 cm radius and thus fixes the position of each sporangiophore. The cultures are covered

by two lucite boxes to protect them from air currents, and the atmosphere is kept moist by a wet sponge inside each box. An air conditioner maintains the temperature of the room air at $20.5 \pm 0.5^\circ\text{C}$.

A Cenco-Edgerton stroboscope lamp, fitted with a dark red gelatin filter, is used to observe the sporangiophores while the centrifuge is in motion. The radiation from this combination was found to be phototropically inert. During all experiments the sporangiophores were in darkness, except for this and other similarly filtered illumination. The stroboscope is triggered by a sliding contact mounted on the centrifuge disk. The sliding contact passes over ten fixed pins spaced in such a way that, depending on which pin is energized, any of the ten cultures may be illuminated when it passes through the same fixed point. The stroboscope illumination is directed along a line tangent to a circle 20 cm in radius on the disk (see Fig. 1). Also along this line is placed a lens which forms an unmagnified image of the flash-illuminated sporangiophore at a point several feet from the disk. This primary image can be observed by a Gaertner low-power microscope fitted with a protractor eyepiece, or it can be recorded on photographic film. For the latter, the camera body of a 35 mm-single-lens reflex camera is used to hold the film. To make exposures, the shutter is opened just long enough to permit one stroboscopic flash to occur.

RESULTS

I. Responses to a Steady Gravitational Stimulus

If the centrifuge is held at a constant speed, a sporangiophore riding on the turntable will experience a steady force that is both centrifugal and gravitational in origin. This force results from the vectorial addition of two components, one resulting from the centripetal acceleration and one resulting from the gravitational acceleration. The magnitude of the resultant vector varies from a minimum, equal to that of the gravitational acceleration, to a maximum limited by the maximum speed of the centrifuge. The direction of this resultant varies between vertical and horizontal. We will denote the centripetal vector RCF (Relative Centrifugal Force) and the resultant vector RGF (Resultant Gravitational Force). The magnitudes of these vectors will be given as multiples of the acceleration due to gravity, 980 cm/sec^2 .

In the first series of experiments a sporangiophore is placed on the centrifuge disk, oriented so that the growing zone is approximately perpendicular to the direction of the resultant at a particular centrifuge speed. The centrifuge is maintained at this speed while the resultant position angle (Fig. 2) of the upper portion (usually the upper 1.0 mm) of the growing zone is measured at regular time intervals. Experiments were performed at RGF values of 4.35, 2.26, 1.47, 1.10, 1.01, and 1.00.

We may characterize the results as follows:—

1. Generally, the resultant position angle tends to drop from initial values of near 90° towards a final value of 0° . This is the classic manifestation of

negative geotropism, although many geotropic organs do not exhibit such simple behavior (Bennet-Clark, Younis, and Esnault, 1959).

2. There is a 30 minute delay between the time of starting the centrifuge and the time of onset of the main tropic response. During this lag period there may be a small reverse reaction, or the position angle may remain more or less constant.

3. The rate of bending is greatest when the position angle is large and drops as the position angle approaches zero. The experimental curves do not

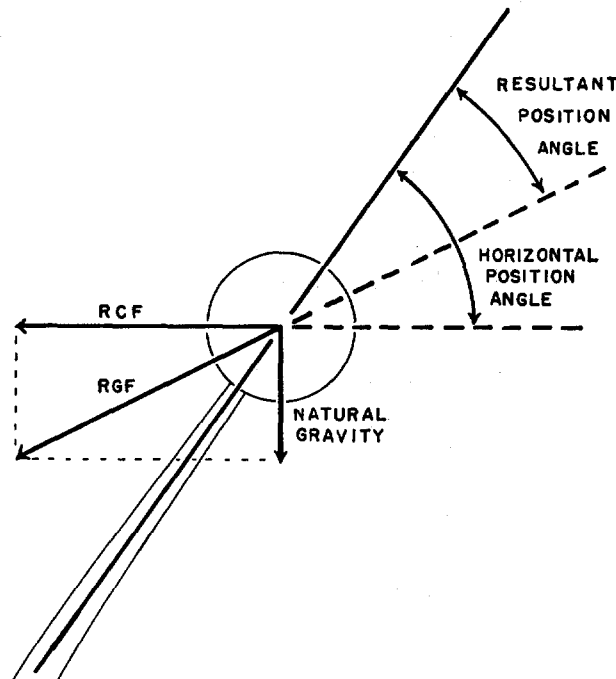


FIGURE 2. The resultant position angle and the horizontal position angle of a sporangio-phore.

seem to follow the well known sine law of geotropism, which in its simplest form predicts that the bending rate should be proportional to the sine of the resultant position angle.

4. The curves show various short period perturbations. Some of these appear to be regular oscillations of periods from 10 min. to nearly 1 hour, while most appear to be irregular.

5. The bending rate for any given position angle increases with RGF.

For each of the six RGF values the data were combined in the following way. For one RGF value, the data for each sporangio-phore were plotted on a separate sheet of cross-section tracing paper. The sheets for all the sporangio-phores were moved with respect to one another in a direction parallel to the

time axis until all the data seemed to fall into a single group, as judged by eye. The justification for this shifting of the time axis lies in the fact that it was not practical to begin experiments with all sporangiophores at the same position angle. Sporangiophores under the same conditions but starting at different position angles gave results that were similar, but shifted with respect to each other along the time axis.

When the combined data for the six RGF values were compared, it was found that the observations fell into three distinct groups. The data for RGF of 4.35 and 2.26 were distinct from each other and distinct from the remaining data. However, the observations for RGF values of 1.47, 1.10, 1.01, and 1.00 did not differ significantly. Thus the RGF must exceed 1.47 to produce a geotropic response greater than the response to natural gravity.

In Fig. 3, the three groups of results are given, with a smooth curve drawn by eye for each group. The curves have been adjusted along the time axis so that they pass through a common point at a position angle of 90°. Increasing the RGF increases the speed of the response; for example, at 45°, the bending speeds of the three groups are 0.17, 0.32, and 0.63 degrees per minute, respectively.

Pilet (1956) studied geotropism in *Phycomyces* sporangiophores under natural gravitation and found that preillumination greatly reduced the geotropic bending rate. The initial geotropic bending rates observed by Pilet were of the order of 0.05 degree per minute for preilluminated sporangiophores. This is about one-fifth of the bending rate observed under similar conditions in the present experiments (for RGF of 1.00). This disparity may be connected with the abnormally low growth rates (0.30 mm per hour) observed by Pilet.

In Fig. 3, the scatter in the observations increases markedly on going to lower values of the RGF. This is a confirmation of Sachs' observation that the geotropic response (to natural gravity) is essentially weak and hence easily affected by chance variation as well as specific factors such as humidity gradients. But this variability is greatly reduced at high RGF values, where the response is more rapid. This more rapid and uniform response at high RGF will be more useful for future study of the effect of light on the geotropism of *Phycomyces* sporangiophores than the relatively weak and variable response to natural gravity.

II. Responses to Changes in the Gravitational Stimulus

In the course of the experiments just presented, a new geotropic response was discovered, which was quite distinct from the response to a steady gravitational acceleration. This new response is a *transient* one, occurring only after a change in the gravitational stimulus.

The transient response has two phases (Fig. 4). The first phase occurs in-

stantaneously upon changing the RCF, is in the direction of increased force, and is simply the result of the flexure of the sporangiophore. The sporangiophore sags passively outward, and hence the "horizontal position angle"

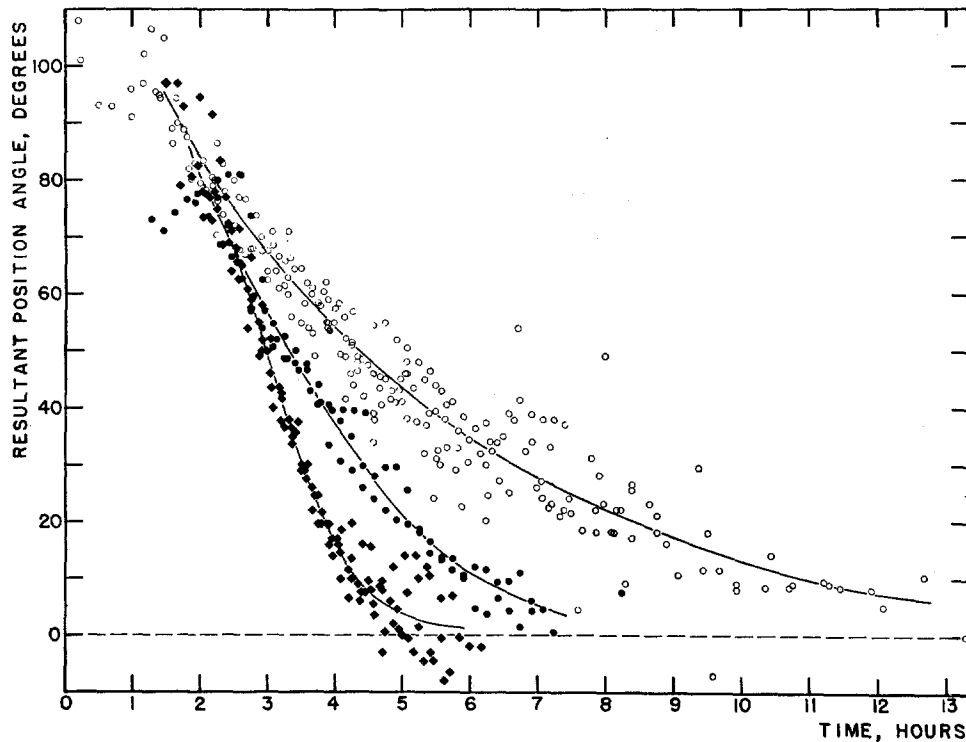


FIGURE 3. Summary of observations of the long term geotropic response of sporangiophores subjected to steady centrifugal and gravitational forces. The upper curve (open circles) summarizes the results of experiments at RGF values of 1.47, 1.10, 1.01, and 1.00. A total of twenty-eight sporangiophores is represented in the upper curve. The middle curve (solid circles) summarizes the results of experiments at an RGF of 2.26; three sporangiophores are represented. The lower curve (diamonds) summarizes the results of experiments at an RGF of 4.35; five sporangiophores are represented. The three summary curves have been shifted along the time axis so as to intersect at a position angle of approximately 90° . Within each summary curve, data for individual sporangiophores were shifted along the time axis to produce the least scatter in the combined data (see text).

(Fig. 2) increases abruptly. Similarly, a decrease in the RCF causes an abrupt and immediate decrease in the horizontal position angle.

The second phase of the transient response is termed the active phase and has the following characteristics:

1. The active phase commences within 2 min. after the beginning of the change in the RCF.

2. During the active phase, the tropic bending speed is of the order of 5 degrees per min.

3. The active phase lasts until about 7 min. after the beginning of the stimulus.

4. At the end of the active phase, the sporangiophore may exhibit a small reverse response. The reverse response is usually only about 4 min. in duration, and its magnitude usually does not exceed 10 per cent of the main response. It is often undetected.

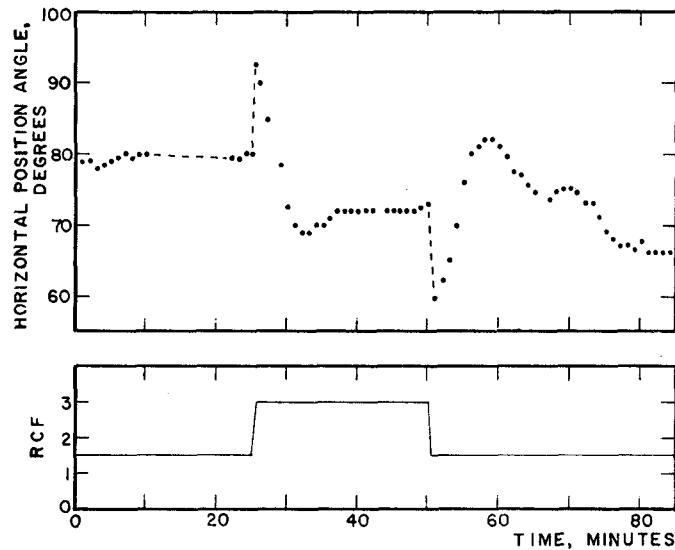


FIGURE 4. The transient geotropic responses of a sporangiophore to a step-up and a step-down in centrifugal force (RCF). The passive phase of each response is indicated by a vertical dashed line.

5. The direction of the active phase of the response is related not to the direction of the RCF, but to the direction of the *change* of the RCF. Thus, when the RCF is lowered from 3.0 to 1.5, the direction of *change* in the RCF is inward, although the RCF itself is always in the outward direction. The main active phase is always in a direction *opposite* to that of the change in RCF; hence an increase in RCF leads to an inward active response, and a decrease in RCF leads to an outward active response. The small reverse responses are always in a direction opposite to that of the main response.

6. The transient responses are superimposed on the relatively slow (0.5 degree per min.) geotropic response characteristic of a steady gravitational stimulus. Because of characteristic variations in the response to a steady gravitational stimulus the latter cannot always be detected in a short period of time.

7. The magnitude of the active phase, defined as the net change in the

position angle during the main response, was found to increase as the change in the RCF is increased. This proportionality between stimulus and response was not examined in detail.

To examine the possible role of the passive phase in triggering the active phase of the response, a detailed analysis was made of the extent to which each portion of the growing zone participates in the passive and active phases of the transient response. For this purpose, stroboscopic photographs were taken at frequent intervals during the transient response. These photographs were analyzed by projecting them at high magnification onto white paper. A pencil mark is then made at 0.5 mm intervals (about 2 inch intervals on the projected image) along the midline of the sporangiophore, starting at the lower edge of the sporangium. In this way, the upper part of the sporangiophore is subdivided into nine 0.5 mm straight sections, each mark joining two adjacent sections. By means of straight-edge and protractor, the difference in angle between adjacent segments is measured with an over-all precision of $\pm 1^\circ$. The sporangiophore is thus treated as a chain of rigid 0.5 mm sections which can flex only at the joints between them. By examining the *changes* in the angles at these joints throughout the series of photographs, the responses of various parts of the growing zone can be measured.

Taking the passive phase of the response at each joint as the change in the angle during the change in the RCF, we can plot this quantity as a function of position along the growing zone. Similarly we take as the active phase of the response at each joint the change in the angle (excluding the passive phase) up to the beginning of the reverse response. These values are given in Fig. 5, along with the passive and active curves from another experiment.

The most obvious feature of these results is the *dissimilarity* between the passive and active curves. Thus the active phase is not a simple mechanical restoration of the passive phase, since this would give a proportional relation between passive and active phase for all sections, and hence similar curves.

The shape of the active response curves is quite similar to that of the light sensitivity curves of Cohen and Delbrück (1959). They also resemble the curves of elemental growth rate of Castle (1959), and the "twist" (but not "stretch") curves of Cohen and Delbrück (1958). The active response curve is similar to the distribution of protoplasmic thickness (Dennison, unpublished data), which has a broad maximum around 1.0 mm. In these comparisons, the peak of the active phase response curve, at 1.0 to 1.5 mm, seems to be a little farther down the growing zone than the peak on the other curves. However, the nature of the curvature measurements does not permit fine position discrimination.

The passive response tends to be rather constant along the length of the growing zone although the bending moment is *not* constant, since the sporangium exerts a greater torque about the lower portion of the growing zone

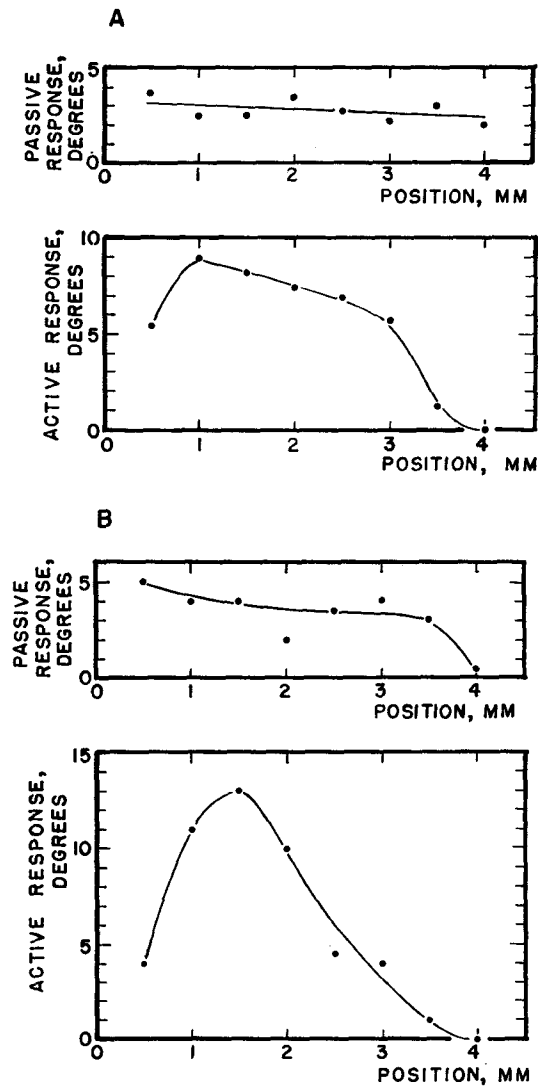


FIGURE 5. Active and passive phases of the transient response as functions of position along the sporangiophore. The position is measured from the base of the sporangium downward. The experimental points represent the total amount of bending response that occurred between the 0.5 mm straight line segments above and below each position along the sporangiophore. A and B are two separate experiments.

than about the upper portion. The moment of force (in dyne-centimeters) exerted at each joint by the sporangium was calculated, assuming a lateral acceleration of 5.4 (RGF) and a sporangium mass of 2×10^{-4} gm. Dividing the amount of passive bending at each joint by this torque gives the flexibility of each segment of the sporangiophore in units of degrees of bending per dyne-

centimeter of torque. The resulting curve is quite similar to the curve of cell wall extensibility found by Roelofsen (1950) when he studied the stretching of the growing zone under internally applied hydrostatic pressure. This similarity is quite reasonable since the passive bending is the result of extension and compression of the cell wall under externally applied force.

We have concluded that the active phase is a true tropic response and not merely a "mechanical rebound," but it seems possible that the passive phase, involving the mechanical distortion of the cell wall, may itself serve as the

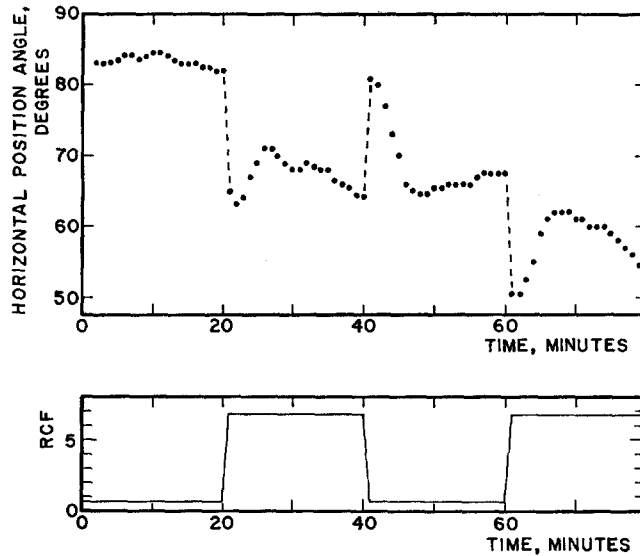


FIGURE 6. The transient responses of a sporangiophore immersed in FC-43. The fluid has a density of 1.87. As in Fig. 4, the passive phase of the response is indicated by a vertical dashed line.

primary stimulus for the active phase. To test this idea, an experiment was performed in which the air surrounding the sporangiophore was replaced by a fluid whose density (1.87) is considerably greater than that of the cell. The fluid, perfluorotributylamine, (fluorochemical FC-43 of the Minnesota Mining and Manufacturing Co.) has no apparent effect on the growth of the sporangiophore except for the suppression of phototropism (Delbrück and Shropshire, 1960). When a sporangiophore is centrifuged in this fluid (a sturdy cell of lucite was constructed to hold the fluid and specimen), the external stresses are reversed since the dense fluid buoys up the sporangiophore. Internally, however, the situation is unchanged, and any purely internal gravitational sensory apparatus should function the same as before.

The results of a representative experiment in FC-43 are given in Fig. 6. It is evident that the active phase of the transient response is reversed, as

well as the passive phase. The increase in RCF produces a passive reaction *inwards* and an active reaction *outwards*. Similarly, a decrease in RCF produces an outward passive phase and an inward active phase. In comparing Fig. 6 with Fig. 4 it will be noted that in FC-43 the magnitude of the active phase seems to be smaller in relation to the passive phase than it is in air. This difference was not observed consistently and is probably due to different specimen responsiveness.

Since the transient response is reversed by FC-43, it is evidently a direct result of forces applied externally to the sporangiophore. We may further postulate that the primary stimulus for this response is the *alteration* of the forces acting on the sporangiophore and the resulting physical distortion of the cell.

To confirm this hypothesis it must be shown that the transient response results from mechanical deformation of the growing zone under constant gravity. Several preliminary experiments were performed as follows. A sporangiophore is positioned vertically and a glass filament, 0.1 mm in diameter and 20 cm long, is lowered from above so that its tip lies on one side of the sporangium. To allow for the growth and rotation of the sporangium, the filament tip is coated with light oil, which forms a flexible bond between the filament and the sporangium. Thus when the filament is moved laterally the sporangium is pulled to one side by the oil surface-tension. It was found by calibrating the filament that a lateral force of about 0.5 mg could be applied to the sporangium by moving the upper end of the filament through a horizontal distance of 4 mm.

Representative results are shown in Fig. 7. The sporangiophore responds to a purely mechanical deformation in the same manner as it does to a change in gravitational force in air and in FC-43. One slight difference is apparent in the reverse portion of the active phase, which is of greater magnitude and duration than in the gravitational experiments. The reason for this is not clear.

Thus far we have shown that the transient response is due to the change in external forces acting on the sporangiophore and the resulting deformation. We may now ask whether the steady geotropic response is likewise due to externally acting forces, or whether it is due to some internal mechanism that is sensitive to acceleration. To settle this point, several long term centrifugation experiments were performed with FC-43.

A sporangiophore undergoing centrifugation at constant speed in FC-43 is subject to exactly the same resultant acceleration as in air. In air this acceleration causes an external force to act on the sporangiophore in a direction parallel to the resultant and also causes localized forces to act on internal regions of the cell which differ from one another in density. In FC-43, the internal action is unchanged, but the external force is reversed in direction and reduced somewhat in magnitude.

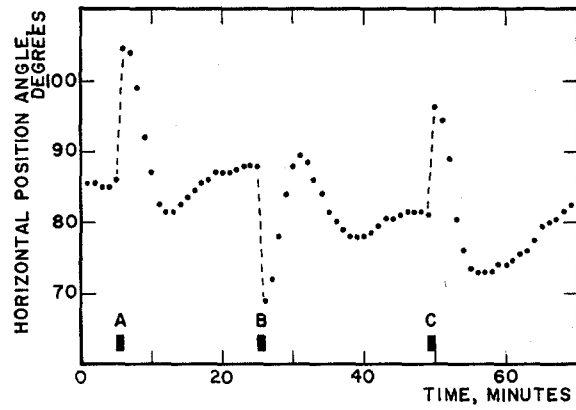


FIGURE 7. Transient responses of a sporangiophore to a laterally applied force. At *A*, a force of approximately 0.5 mg was applied laterally to the sporangium, using a glass fiber. At *B*, the force was released, and at *C* it was reapplied. The passive phase of each response is indicated by a vertical dashed line.

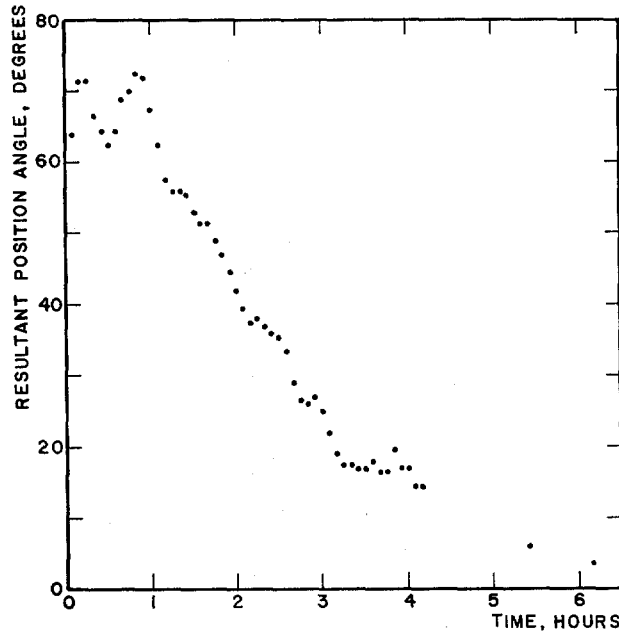


FIGURE 8. The long term response of a sporangiophore in FC-43. The RGF in this experiment was 4.35.

The results of a long term experiment in FC-43 at an RGF of 4.35 are given in Fig. 8. The main features of the response are similar to those of responses in air, although the time delay seems to be longer and the bending speed less. It is not clear whether these differences are significant or merely due to

variations between sporangiophores. These results indicate that the long term response is *not* due to the deformation of the growing zone under external forces. If this were so, the *direction* of the long term response would be reversed in FC-43. On the contrary, the long term response to a steady gravitational stimulus must be due to its action on a strictly internal sensory apparatus.

DISCUSSION

The experimental evidence that has been presented suggests the following hypothesis: gravity and centrifugal force produce bending responses in sporangiophores by means of at least two separate sensory systems. The evidence further suggests that the sensory elements for the transient response respond to the mechanical deformation of the cell wall under externally acting forces, whereas the sensory elements for the long term response do not respond to such mechanical deformation.

The principal evidence for the dual nature of the gravity-sensing system comes from a comparison of the results of experiments in FC-43 with the results obtained in air. In the denser medium the transient response is reversed in direction, but the long term response is substantially unchanged. The fact that the two responses may be "uncoupled" from one another in this way is strong evidence for supposing the two responses to have separate sensory mechanisms. This hypothesis is further supported by the observation that the transient response may be elicited by applying a transverse force to the sporangium. Thus it appears that the transient response itself has no direct connection with gravity at all, but results as a by-product of the mechanical forces arising from the action of gravity and centrifugal force on the relatively massive sporangium.

What are the likely mechanisms of these two sensory systems? Since the transient response is so closely related to the deformation of the growing zone under external force, it is reasonable to suppose that these receptors are themselves closely associated with the cell wall. Thus the stretching or compression of the wall would stimulate or retard the rate of cell wall elongation.

Since the long term response is not triggered by deformation of the cell wall we may suppose that its sensory mechanism involves particles or inclusions inside the cell which differ in density from the medium surrounding them. The application of gravity or centrifugal force would then cause a force, proportional to the density difference, to act between these objects. The resulting displacements of the objects would then trigger the release of substances affecting the rate of growth. The principal problem is, of course, to identify the structures whose displacement triggers the geotropic bending.

The protoplasm and vacuole constitute two liquid phases of differing density

within the growing zone. The densities of the vacuole and protoplasm of the alga *Nitella flexilis* have been found (Kamiya and Kuroda, 1957) to differ by 0.3 to 0.5 per cent, the protoplasm being denser. In sporangiophores the protoplasm forms a layer inside the cell wall, the vacuole occupying the core of the cell. A transverse gravitational force should cause the denser protoplasm to move to the "lower" side of the cell, forming a thicker layer there than on the upper side. If such a movement occurs within the cell, it should be microscopically observable during centrifugation. To explain the long term geotropic response we must postulate further that this thickening of the protoplasmic layer causes a more rapid elongation of the adjacent cell wall.

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