

Avoidance and Rheotropic Responses in *Phycomyces*

Evidence for an "Avoidance Gas" Mechanism

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ABSTRACT If a mature sporangiophore is placed next to a barrier that is moving in a clockwise direction, it grows both away from the barrier and into the wind; the wind is generated by the moving barrier itself. When the barrier is moving in a counterclockwise direction, the sporangiophore grows towards both the barrier and the wind. The net direction of growth appears to be the vector sum of the rheotropic response and the avoidance aiming error and does not involve the classic stationary-barrier avoidance response. Our experiments all support the suggestion that the avoidance response, the rheotropic response, and the variety of reported wind responses can be explained by the presence of a self-emitted, growth-stimulating avoidance gas. We present data that suggest that it is the direction of the net flux (mass transfer) of this gas that determines both the direction and the magnitude of the sporangiophore growth. We further suggest that the region of the cell wall showing maximum mass transfer will show a minimum growth rate, i.e., the direction of growth will always be in the direction of maximum mass transfer. If water is the avoidance gas, then it would follow that the total hydration of the cell wall in an aqueous salt solution should result in cell wall softening; cell wall softening has been correlated directly to cell wall growth. Using the Instron technique, we now show that submerging the entire sporangiophore in an aqueous salt solution for 4 min causes an increase in cell wall extensibility.

INTRODUCTION

The avoidance response of the sporangiophore of *Phycomyces* was first reported more than a hundred years ago by Elfving (1881). Although extensive studies were done by him and his colleagues on the avoidance response, their work was forgotten until the response was independently rediscovered by Shropshire (1962). Numerous suggestions have been offered to explain the avoidance response mechanism, the organism's uncanny ability to sense and then grow away from close barriers (Johnson and Gamow, 1971; Cohen et al., 1975; Bergman et al., 1969; Lafay et al., 1975). The most frequently given hypothesis

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is that the *Phycomyces* is positively responding to some self-emitted, growth-stimulating "avoidance gas" released from the sporangiophore's growing zone (GZ), whose concentration around the GZ is somehow modified by the presence of a barrier. If the presence of a barrier causes an asymmetry in the "avoidance gas" concentration around the GZ, then the "avoidance gas" flux from the GZ must also be asymmetric. We are suggesting that when the avoidance gas is symmetrically distributed about the GZ and is thus symmetrically released from the GZ, the growth is symmetric; asymmetric growth occurs when the gas is asymmetrically released. This hypothesis can be experimentally tested by measuring the direction and the magnitude of the avoidance response when a sporangiophore is subjected to a barrier that is either stationary or moving. From our present studies using both moving and stationary barriers, we have concluded that the direction of asymmetry of the postulated "avoidance gas" accurately predicts the direction of growth of a *Phycomyces*. These studies and the conclusions from these studies do not depend on the nature of the "avoidance gas" or identify the "avoidance gas;" cell wall extensibility experiments of hydrated, living cell walls suggest that the "avoidance gas" is water.

MATERIALS AND METHODS: EXPERIMENTAL PROCEDURES

Wild-type *Phycomyces blakesleeanus* sporangiophores, NRRL1555(-), originally obtained from M. Delbrück, California Institute of Technology, were grown in shell vials containing 5.0% potato dextrose agar (PDA) with 1.0% yeast extract. The shell vials were incubated under diffuse incandescent light in a high-humidity room with a temperature range between 22 and 27°C.

Stationary and Moving-Barrier Experiments

The stationary and the moving barriers consisted of an aluminum wheel 30.4 cm in diameter and 1.9 cm thick. With a wheel this size, the avoiding area of the rotating barrier closely approximates a flat plate. The wheel, hence termed the barrier, was designed to be rotated in either a clockwise or counterclockwise direction by means of a reversible AC-DC motor. For the experiments described in this report, the motor was set for a wheel velocity of ~12 rpm, i.e., 17 cm/s. Each experiment is initiated when the barrier, either spinning or stationary, is brought within 1 mm of the sporangiophore. Before each experiment, a sporangiophore is light-adapted to a GE cool, white circular fluorescent bulb (8-in Diam, 22 W). The same light program is continued throughout an entire experiment. The relative humidity in the laboratory is maintained at 50% at all times. Two 35-mm cameras were positioned, one directly above the avoiding sporangiophore and one normal to it. The circular fluorescent light was positioned just below the upper camera. To record the exact trajectory of the avoiding sporangiophore, the film in the upper camera was not advanced during exposures; exposures were made every 10 min.

The initial trajectory of the sporangium, as seen from above, clearly defines the aiming error. We have defined the aiming error (Fig. 4) to be the angle of the initial trajectory away from the barrier that occurs as a result of an avoidance stimulus (Gamow and Böttger, 1982). In practice, this is the trajectory that occurs for ~20 min after the initiation of the avoidance stimulus. The camera, positioned normal to the sporangiophore, was used for the most part to ensure that the sporangiophore was correctly aligned with respect to the barrier. Since the sporangiophore does not avoid

in a plane normal to the lower camera, the data from the film can only approximate bending angles and growing speeds. Fig. 1 shows the rotating barrier, the circular light source, the two cameras, and the vial containing the test sporangiophore.

Cell Wall Extensibility Measurements

Changes in the extensibility of the cell wall as a function of hydration were measured using our standard technique (Ortega et al., 1975). Briefly, the test sporangiophore was adapted to red light for 20 min. Tensile loads were applied to the stage IVb sporangiophore using an Instron model T.M. tension-compression machine (Instron Corp., Canton, MA) equipped with a model A load cell set at high sensitivity (2 g full scale). Tensile loads are transmitted to the sporangiophore using a 0.2-mm Nichrome wire hook (McMaster Carr Supply Co., Chicago, IL) placed directly beneath the head. The sporangiophore is loaded and unloaded to a load of 240 mg. This procedure is termed strain hardening (SH) (Ortega et al., 1975) and was developed to ensure that the sporangiophore extensibility is invariant when repeatedly loaded to this value. The sporangiophore is then unloaded for 4 min and loaded once again to 240 mg, which allows us to determine the amount of relaxation that has occurred during the first 4-min relaxation period. This extensibility value is called control No. 1 (C-1). The sporangiophore is again strain hardened, unloaded, placed in a dilute salt solution (Sutter, 1975) for 4 min, and the extensibility at 240 mg load is once again measured. This extensibility we have called the hydration response (HR). The effect of the Sutter solution treatment is determined by subtracting the C-1 control, measured cell wall extensibility, from the HR cell wall extensibility; this value has been called the magnitude of the increase in extension (Ortega et al., 1975), and is represented by E_H when the extensibility is the result of a hydration response.

RESULTS

Barrier Effects

STATIONARY BARRIER A single mature stage IVb sporangiophore, in its growth pot, was placed 1 mm away from our aluminum wheel barrier, previously described and shown in Fig. 1. The growth trajectory of these sporangiophores was away from the barrier but displaced in a clockwise direction (as seen from above) in respect to a line drawn normal to the barrier and tangent to the sporangium. This initial clockwise displacement from the barrier, known as the avoidance aiming error, occurs as a direct result of the sporangiophore's innate rotation rate of $\sim 15^\circ/\text{min}$ and the latency of the sporangiophore's response to an avoidance stimulus (Gamow and Böttger, 1982). One such experiment is shown in Fig. 2A, in which the aiming error is +42.5 degrees. The average clockwise displacement, the aiming error, for 14 different sporangiophores was 38.8 ± 23 degrees. As can be seen in Table I, the scatter of the data is much larger for the stationary barrier than for the moving barrier, presumably because in the absence of a large induced wind current, the small random air currents in the laboratory exert relatively large effects.

CLOCKWISE-MOVING BARRIER The procedure is identical to the one described above except the barrier is rotating in a clockwise direction at ~ 12 rpm, resulting in a barrier speed of 17 cm/s. At the beginning of each

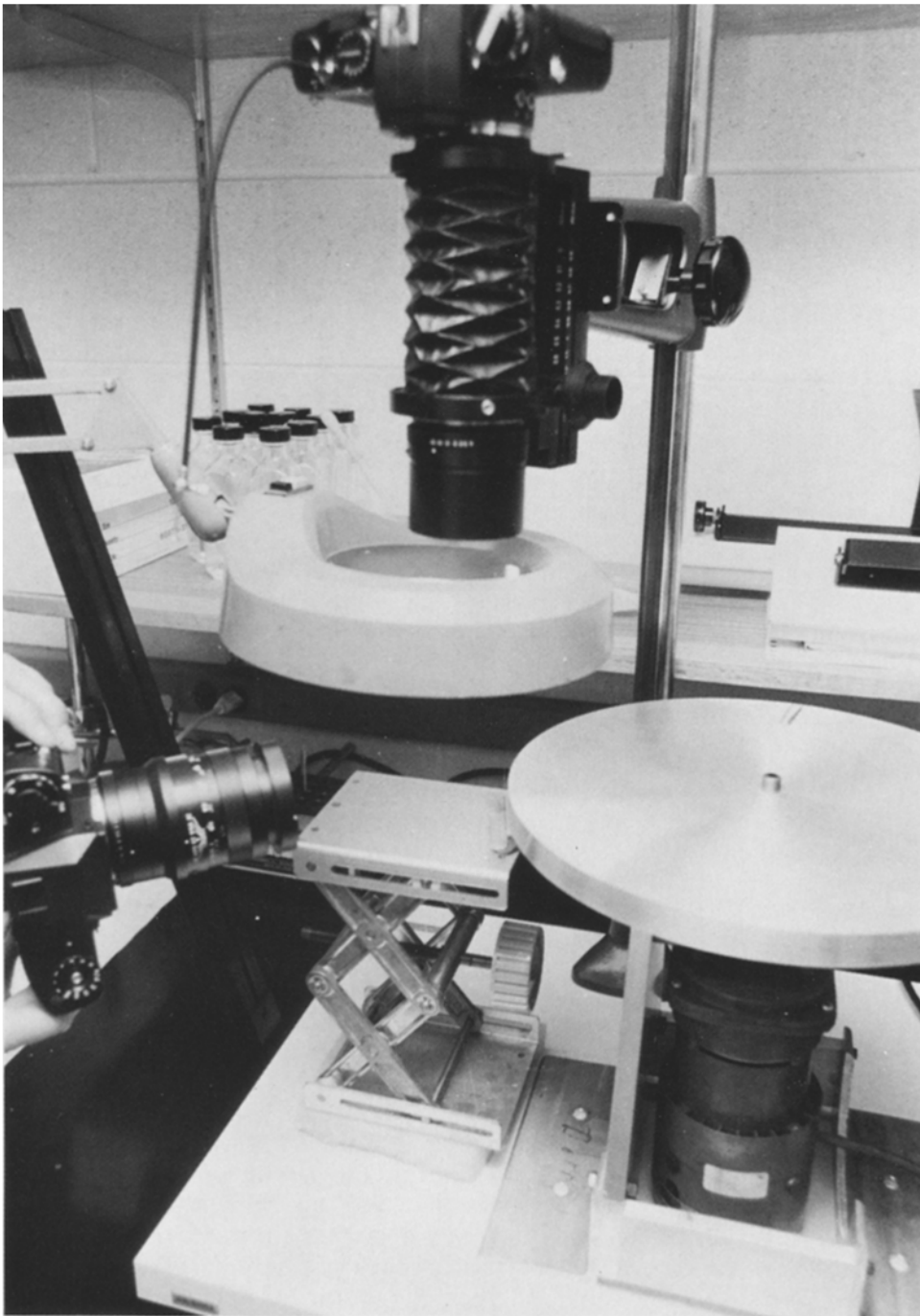


FIGURE 1. A photograph of the moving barrier apparatus. The barrier can be rotated in either a clockwise or counterclockwise direction. A mature stage IVb sporangiophore in a glass shell vial can be seen on a stand next to the barrier. A vertical 35-mm camera and a circular light source are placed directly above the sporangiophore. A second camera is shown in a horizontal position.

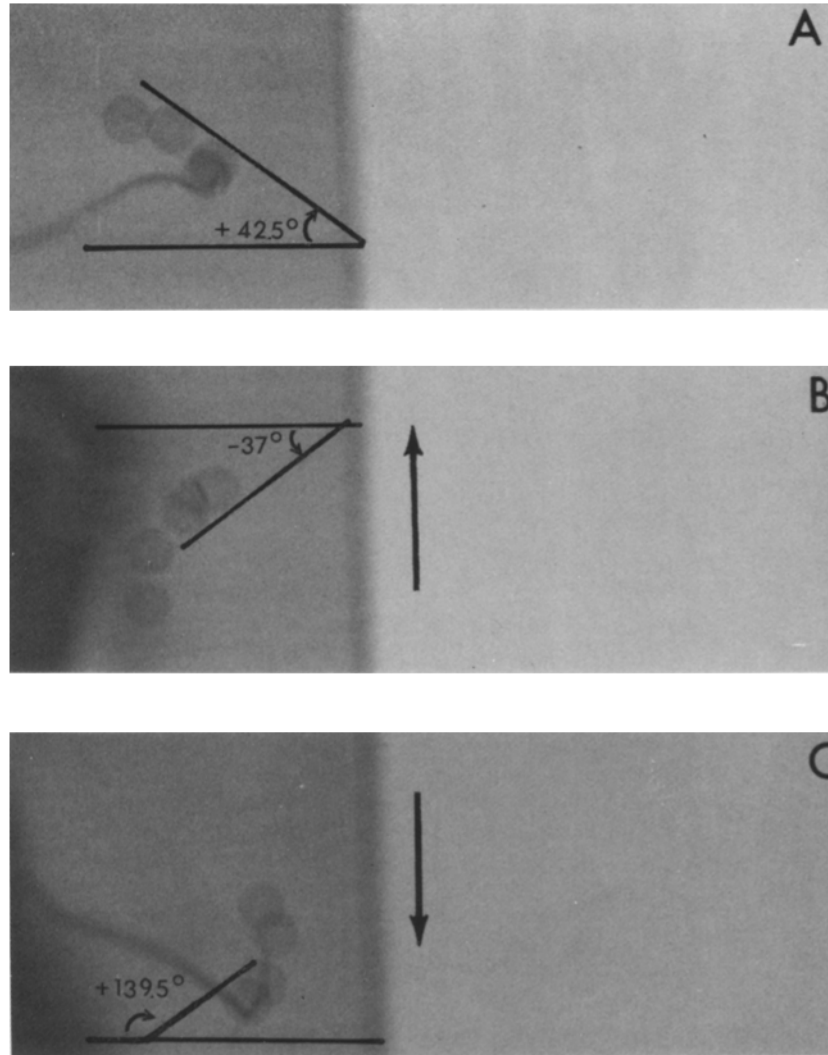


FIGURE 2. A. At the beginning of the experiment, a mature stage IVb sporangiophore is placed ~ 1 mm from a stationary aluminum barrier. The film in the vertical camera is not advanced but an exposure is made once every 10 min. In this particular experiment, the sporangiophore does not bend directly away from the barrier but shows an aiming error of $+45.5^\circ$. B. Identical to A except the barrier was moving in a clockwise direction, indicated by the arrow, at a barrier velocity of 17 cm/s. In all experiments, the rotating barrier was moved to within 1 mm of a stationary sporangiophore. In this particular experiment, the deviation of bend from the normal, in respect to the barrier, was -37° . C. Identical to B except the barrier was not rotating in a counterclockwise direction. The bending angle in this particular experiment was $+139.5^\circ$. In all the experiments, the trajectory represents the initial pathway taken by the sporangiophore.

experiment, the already spinning barrier is brought within 1 mm of the sporangiophore. The gradient of the induced wind was calculated theoretically using a boundary layer theory (Schlichting, 1979) but was also experimentally determined by J. F. Lafay and J. Matricon (personal communication), who initially pioneered the moving-barrier experiments. Fig. 2B shows one such experiment; as can be clearly seen in this figure, the sporangiophore grows both into the wind and away from the barrier. In contrast with a stationary barrier, the aiming error angle is now negative, i.e., -37° . As shown in Table I, the average counterclockwise displacement for five different experimental sporangiophores was $-66.8 \pm 20^\circ$. Fig. 3 shows the theoretically calculated induced flow gradient that is generated when the surface of the barrier has a velocity of 17 cm/s in a clockwise direction. Also schematically shown in Fig. 3 is a sporangiophore whose trajectory is both into the wind and away from the barrier. It is important to note that the induced flow velocity is greater on the barrier side than on the opposite side.

TABLE I
ANGULAR DISPLACEMENT MEASUREMENTS AS DEFINED IN
FIG. 4

Stationary barrier	Clockwise-moving barrier	Counterclockwise-moving barrier
+5°	-90°	+121°
+42°	-72°	+90°
+60°	-76°	+139°
0°	-37°	+106°
0°	-58°	
+44°		
+11°		
+68°		
+63°		
+26°		
+37°		
+37°		
+8°		
+30°		
<u>+30.8° ± 23°*</u>	<u>-66.8° ± 20°</u>	<u>+113.8° ± 20°</u>

* SEM.

COUNTERCLOCKWISE-MOVING BARRIER Again, the procedure is identical to the one described above except the barrier is now moving in a counterclockwise direction at a velocity of 17 cm/s. In this case, the trajectory of the sporangiophore is both into the wind and into the barrier; one example of this is shown in Fig. 2C with a shown aiming error of $+139.5^\circ$. Table I shows the data from four different experimental sporangiophores with an average value of 113.8 ± 20 degrees.

Fig. 4 is a schematic representing the average aiming error of all our experimental data.

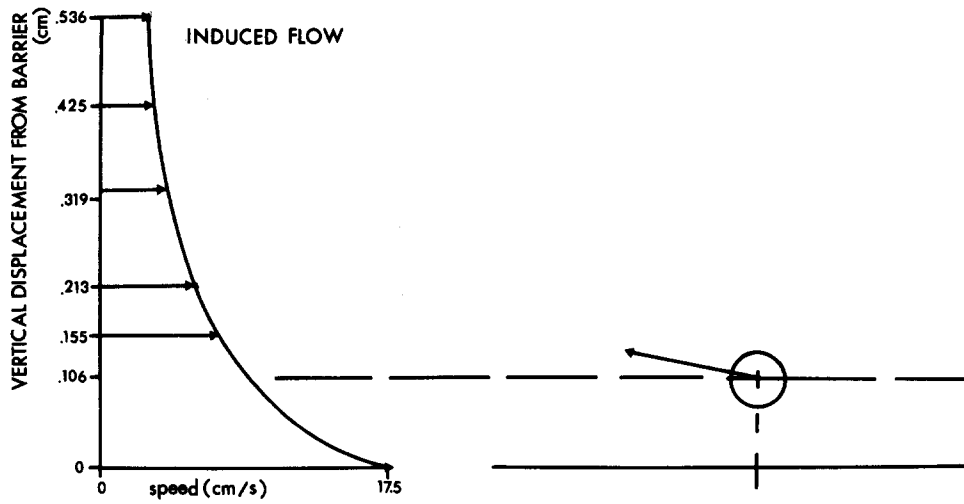


FIGURE 3. The calculated wind gradient as induced by a clockwise-moving barrier having a velocity of 17 cm/s. The shape of this gradient was also experimentally determined by Lafay and Matricon (personal communication). Also shown schematically is the sporangiophore's head, the sporangium, that is placed ~ 1 mm from the barrier. The arrow depicts the direction of the trajectory, i.e., away from the barrier and into the wind.

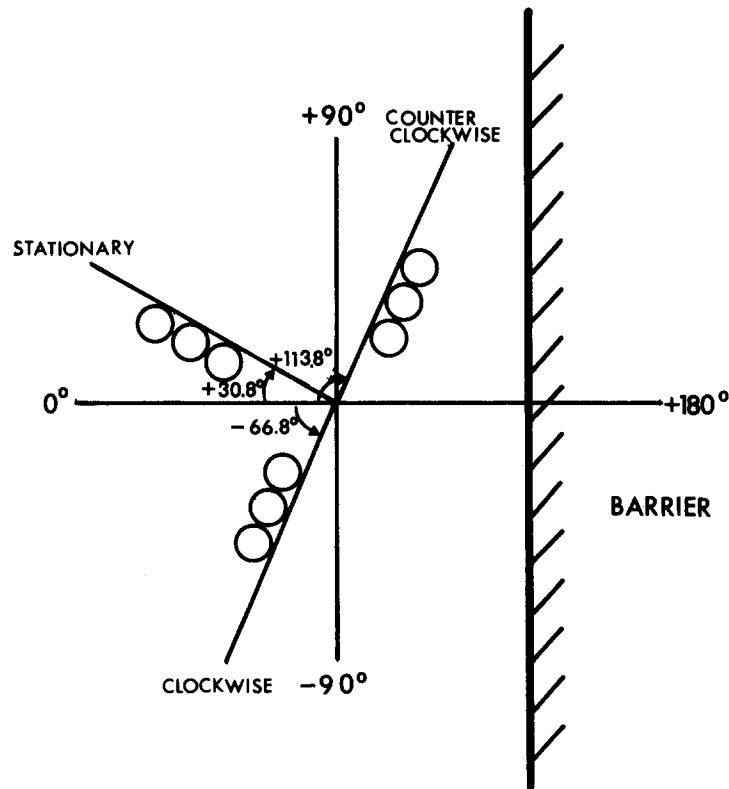


FIGURE 4. A schematic representation of all of our data averaged and shown in Table I.

Effect of Hydration on Cell Wall Extensibility

Using a procedure identical to the one we developed (Ortega et al., 1975) to measure the effect of light on cell wall extensibility, we have measured the effect of cell wall hydration on cell wall extensibility. As described in Materials and Methods, the experimental value we obtain is called the magnitude of extensibility (E_H). The E_H is obtained by subtracting the extensibility (in micrometers) that occurs after 4 min of relaxation in air from the amount of extensibility that occurs after the sporangiophore is submerged for 4 min in Sutter solution. Fig. 5 shows one such experiment. We have repeated this experiment 12 separate times and have obtained an average value for E_H of $28.6 \pm 14 \mu\text{m}$. It is interesting to note that this value is significantly higher than the magnitude of the increase in extension that occurs after a saturating light stimulus (E_L), which has been found to be $16.8 \pm 14 \mu\text{m}$ (Ortega et al., 1975).

DISCUSSION

From a wide variety of published and unpublished experiments, it is clear that the growth behavior of the *Phycomyces* cell wall is strongly influenced by the flow of air currents adjacent to the growing surface of the cell wall. It is well documented that if a sporangiophore is placed between a double barrier (Ortega and Gamow, 1970) or within a small glass house (Cohen et al., 1975), it will show a transient increase in growth rate. Removal of the double barrier (Ortega and Gamow, 1970) or the glass house (Cohen et al., 1975) results in a decrease in the growth rate. It is also known that the changes in cell wall growth are accompanied by changes in cell wall mechanical extensibility; increased growth rates are accompanied by the softening of the cell wall (Ortega and Gamow, 1976). Consistent with these results is the fact that the cell wall becomes softer when the sporangiophore is enclosed in a double barrier (Ortega and Gamow, 1977) and becomes stiffer when placed in a miniature wind tunnel and subjected to a laminar wind flow of 5 cm/s (Blum, 1981). This last result is of significance because it is known that the sporangiophore responds to a laminar wind by growing into it; this is known as the rheotropic response (Cohen et al., 1975). Finally, and perhaps most importantly, it has been reported that substances as different as distilled water (Thimann and Gruen, 1960), vacuum grease, or protein solution (Cohen et al., 1975), when placed on one side of the GZ, cause an increase in growth rate in just that region of the GZ, i.e., the sporangiophore grows actively in a direction away from the side where the substance was placed. As noted by Cohen et al. (1975), "these effects represent extreme cases of avoiding a barrier." These experiments suggest that if the rate of flux of some yet unknown substance from the cell wall is either decreased or eliminated, the cell wall in that region will become more extensible and thus will grow faster.

The response to a double barrier, the house response, and the rheotropic response all suggest that any change in the concentration and/or distribution of the avoidance gas that occurs in the immediate vicinity of the GZ will change the sporangiophore's growth properties. The fact that vacuum grease,

protein solution, or water, when placed on the GZ, also directly change the growth properties suggests to us that the important parameter is the rate that avoidance gas is emitted from the cell wall, i.e., the rate of mass transfer. We have reached this conclusion because it is inconceivable that substances as

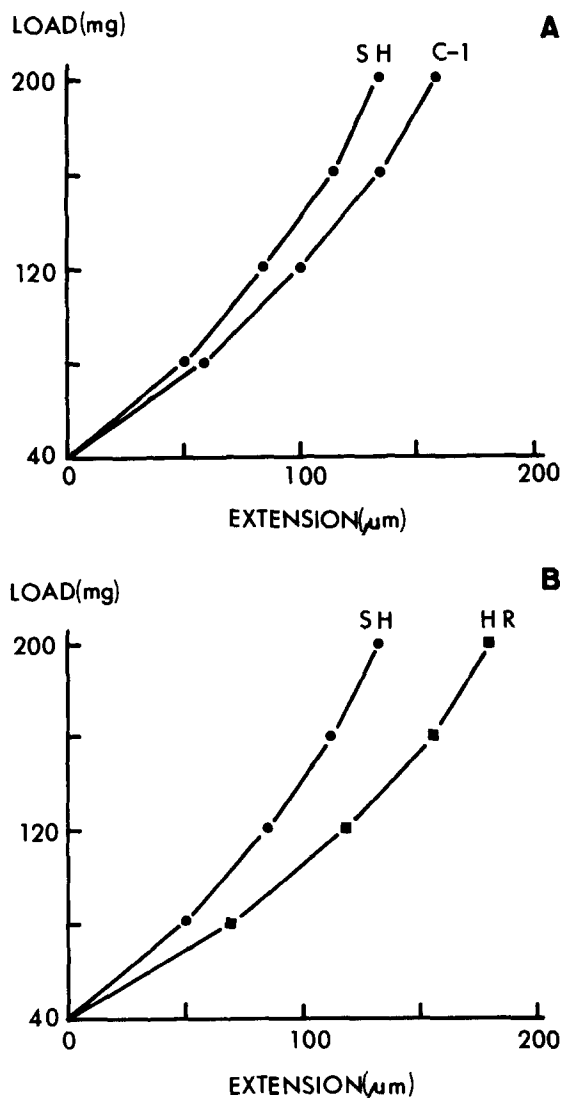


FIGURE 5. A. As described in the text, a sporangiophore is strain hardened, SH, and then allowed to relax for 4 min. As a result of this relaxation, the sporangiophore is now more extensible. The difference between SH and the 4-min control (C-1) is the amount of extension that occurs as a result of only relaxation. B. Identical to A except after SH, the sporangiophore was unloaded and submerged 4 min in Sutter solution and then the extensibility was measured again; this increase in extensibility is the hydration response, HR, extensibility minus the SH extensibility.

different as vacuum grease, protein solution, and water all possess the specific growth-stimulating properties of the emitted avoidance gas.

As a result of these experiments, we have developed the following general working hypothesis:

The rate of growth of the sporangiophore is a result of the internal turgor pressure, which provides the driving force of cell wall extension. The rate of cell wall extension is a function of the extensibility of the cell wall. The extensibility of the cell wall decreases when some critical substance(s), a volatile gas, is removed from the cell surface (or from within the cell wall), and the extensibility increases when the substance(s) is not actively removed but allowed to leave the cell only by diffusion. This critical substance has been termed the avoidance gas.

We believe that our present moving-barrier experiments support our working hypothesis. The initial moving-barrier experiments were conceived and executed by Jean-Francois Lafay and Jean Matricon while they were visiting Max Delbrück at the Cold Spring Harbor Laboratories. They were surprised that the sporangiophore appeared to grow both away from the barrier and into the wind when the barrier was rotating in a clockwise direction. They were puzzled because it would seem that any "avoidance gas" released from the sporangiophore would be carried away faster on the barrier side, thus resulting in a response direction opposite to the one found in the case of a stationary barrier; they expected the sporangiophore to grow into the barrier (J.-F. Lafay and J. Matricon, personal communication). Although the detailed geometry of the fluid flow of a volatile gas emitted from a cylinder next to a moving barrier is far from simple or obvious, we now know that the fact that the sporangiophore grew away from the clockwise-moving barrier is, for the most part, an avoidance aiming error effect (Gamow and Böttger, 1982) and not an avoidance effect. The net direction of growth appears to be the vector sum of the rheotropic response and the avoidance aiming error and does not involve the classic stationary-barrier avoidance response. The fact that the sporangiophore does grow into the barrier when the barrier is rotating in a counterclockwise direction and away from the barrier in the clockwise case beautifully illustrates this. We must thus conclude, both for the clockwise- and the counterclockwise-moving barriers, that the major response is the rheotropic response (Cohen et al., 1975), i.e., the sporangiophore grows into the wind. The fact that it does not grow directly into the wind generated by the moving barrier is explained by the presence of the avoidance aiming error. The existence of an aiming error in *Phycomyces* was first reported by Dennison and Bozof in 1973, and these studies were further extended in 1977 by Dennison and Foster, in their in-depth study of the phototropic response. Mature stage IVb sporangiophores all show spiral growth in that they rotate at an angular velocity of $\sim 15^\circ/\text{min}$ as they elongate. If the photoreceptors are rotating in a sporangiophore that is being stimulated by a unilateral light source, the photoreceptors are constantly receiving different stimuli intensities in respect to a stationary light source. Because of both its clockwise rotation and its latency of response, the time interval between the initiation of the

stimulation and the response, one would expect first, that the sporangiophore would not grow directly towards the unilateral light source, and second, that the sporangiophore would also not adapt to the unilateral light source. Dennison and Foster (1977) have presented evidence that both phenomena, the lack of adaptation and the aiming error, are a direct result of the cell's rotation. To quote from their paper: "Conversion to a continuous temporal stimulus ensures that phototropism never adapts as long as the spatial asymmetry is maintained." This quote appears to be as true for the avoidance response as it is for the phototropic response. The avoidance response shows adaptation to a symmetrical avoidance stimulus, a double barrier (Ortega and Gamow, 1970), whereas in a tropostat, in which the barrier is constantly repositioned in respect to the growing zone (Bergman et al., 1969), the response can be indefinite. A similar aiming error occurring as a result of an asymmetric avoidance stimulus, i.e., a single barrier, has been reported (Gamow and Böttger, 1982).

If one considers only the direction of maximum mass transfer of an avoidance gas leaving the cell wall as a result of a moving barrier, and assumes that this direction will be further adjusted by the aiming error, one finds that the direction of maximum transfer would be into the wind and away from the barrier in the clockwise-moving barrier case; into the wind and into the barrier in the case of the counterclockwise-moving barrier. The windward side of the GZ will be the region of *maximum* mass transfer, and the region of the cell wall directly opposite this region, the leeward side, would show the minimum flux of the avoidance gas and thus the maximum gas concentration. Our present data are in full agreement with the prediction that the direction of bending, taking into account the aiming error, is the same as the direction of maximum mass transfer. For the stationary-barrier case, the net direction of mass transfer of the avoidance gas must occur in the region of the GZ opposite the barrier. This follows from the fact that a buildup of an avoidance gas on the barrier side will decrease the net flux of this gas on this side. Because of the avoidance aiming error, the sporangiophore does not bend directly away from the barrier but at some positive angle to the barrier. For the stationary-barrier case, the avoidance gas can only be transported by diffusion. In the rheotropic response using a wind tunnel, the avoidance gas can only be transported by advection. In the moving-barrier case, the avoidance gas must be transported by *both* advection and diffusion; therefore, advection and diffusion must both play a role in the final response. Which component dominates depends on the barrier distance and the barrier velocity. If the barrier were very close, say 100 μm to the GZ, and the barrier were moving at a reasonably slow speed, the asymmetry of the net flux at equilibrium would be largely dominated by diffusion. For larger barrier distances and larger barrier velocities, the net flux would be dominated by advection. Diffusion-dominated flows result in the avoidance response; advection-dominated flows result in the rheotropic response. The relative weights of these two components simply depend on the two critical parameters: barrier distance and barrier velocity. The fact that the sporangiophore grows into the counterclockwise-moving barrier suggests

to us that at a barrier speed of 17 cm/s and a barrier distance of 1 mm that we have used, the advection component dominates. It also follows that since the advection flow resulting from the moving barrier is asymmetric, so must be the diffusion component; in other words, the avoidance response, pure gaseous diffusion, must always play some role in all the moving-barrier experiments. The importance of the moving-barrier experiments is that the experimental results are entirely consistent with our working hypothesis, i.e., the GZ emits a stimulatory "avoidance gas" whose direction of net flux determines the direction of sporangiophore growth, and furthermore, both the avoidance response and the rheotropic response are explained by the same mechanism. Our experiments do not distinguish between our proposed model in which the critical parameter is the rate of mass transfer and the classical receptor model in which avoidance gas receptors are distributed along the GZ surface. Conceptually, we favor the former because it has always been difficult to conceive how the same structure could contain both the receptors and the emitters.

Our analysis using stationary and moving barriers sheds no light on the nature of the "avoidance gas" itself. R. J. Cohen has determined that at least 22 different gases are released from the growing sporangiophore (personal communication). Of the gases he identified, none of them appears to be a viable candidate because all caused a decrease in growth rate when added in vapor form to a container containing a mature stage IVb sporangiophore (Cohen et al., 1979). Russo et al. (1977) have reported that ethylene could be a possible candidate. We believe that water may still be a possible candidate. On the positive side, it is released from the GZ at a rate of ~ 1 nl/min (Bergman et al., 1969), but on the negative side, the avoidance response does not appear to change in magnitude when avoidance experiments are performed at different relative humidities (Bergman et al., 1969). To our knowledge, this experiment has never been quantitatively done. In 1975 Cohen et al. reported no change in growth rate when the humidity in the growth chamber was stepped up from 68 to 96%. Because the differential change in growth that occurs as a result of an avoidance stimulus is small compared with the change in growth needed to measure a growth response, this result sheds little light on the nature of the avoidance gas. The critical experiment whether the avoidance response would indeed occur in a true 100%-humidity, isothermal chamber in which all convective currents have been eliminated has also not been reported. The fact that the cell wall mechanical extensibility increases after an avoidance stimulus (Ortega and Gamow, 1977), coupled with our present finding that the cell wall extensibility increases after being placed in aqueous salt solution, Sutter solution, suggests to us that water may indeed be the "avoidance gas." This follows simply from our proposed model that a decrease in mass transfer of water through the cell wall and cuticle complex results in an increase in cell wall growth. Based on this model, we can further speculate that the primary molecular event is cell wall hydration. The fact that when the entire sporangiophore is submerged in an aqueous salt solution we obtain cell wall softening lends support to this speculation.

Another valid interpretation of this experiment is that the water is inhibiting the escape, the mass transfer, of the avoidance gas, creating a situation similar to either the double barrier effect in which we know that the extensibility of the cell wall also increases or when a water droplet or some vacuum grease is placed on the sporangiophore which also stimulates cell wall growth. The fact that the avoidance response fails to occur under water (Johnson and Gamow, 1971) also suggests that the "avoidance gas" may be water. Recently, we have repeated these experiments using the Sutter salt solution as a growth medium, and although we have obtained good growth rates and good light growth responses, we have never observed an avoidance response.

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