

Phycomyces: Detailed Analysis of the Anemogeotropic Response

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ABSTRACT Stage IVb sporangiophores of *Phycomyces* grow into the wind—the anemotropic response—and away from gravity—the geotropic response. A procedure has been designed to measure the equilibrium bend angle that results when the two stimuli are given simultaneously over a long period of time. This angle will be referred to as the anemogeotropic equilibrium angle. This measurement of a sensory response is analogous to the photogeotropic equilibrium angle in which the variable stimulus is light instead of wind. We have found that the anemogeotropic angle, measured relative to the vertical, increases with both increasing wind speed and increasing relative humidity of the wind stimulus. This finding is new and argues against a major prediction of the mass transfer model that anemogeotropism and relative humidity are inversely related. Data from these anemogeotropic experiments further suggest that the self-emitted gas responsible for both the anemotropic response and the avoidance response is water.

INTRODUCTION

In 1961, Varjú et al. studied the interplay between the phototropic response and the geotropic response in *Phycomyces* sporangiophores. These early studies led to a modern technique known as photogeotropic analysis (Bergman et al., 1973), which is now used to quantitatively assay phototropic sensitivity in photosensory-defective mutant strains of *Phycomyces*. The experimental procedure consists of measuring the equilibrium angle that manifests a balance between both a unilateral light stimulus and a gravity stimulus. This procedure has been routinely used in a number of different laboratories to classify the large number of *Phycomyces* behavioral mutants. The equilibrium angle is now known as the photogeotropic equilibrium angle and is the most sensitive measure of the sporangiophore's ability to respond to light.

In 1975, Cohen et al. described the rheotropic response, now better known as the anemotropic response, whereby a mature stage IVb sporangiophore grows into the wind with a bending rate that depends on the wind speed (Reynolds' number). The unanswered question in this work was whether the anemotropic response was truly a new response or just another manifestation of the avoidance

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response. Two laboratories have addressed this question using what is now known as the moving barrier technique (Gamow and Bottger, 1982*a*; Lafay and Matricon, 1982). A mature sporangiophore is placed next to a moving barrier and the kinetics of the response are measured in three dimensions. The moving barrier consists of a relatively large cylinder that can be rotated in either a clockwise or counterclockwise direction as viewed from above the sporangiophore. Placement of the moving barrier next to the sporangiophore should elicit two distinct responses. The sporangiophore should grow away from the barrier because of the avoidance response and should also grow into the wind because of the anemotropic response. Both laboratories indeed determined that, within the first 20 min after the moving barrier stimulus was given, the sporangiophore moved away from the barrier and into the wind when the barrier was moving in a clockwise direction. They also determined that *Phycomyces* moved toward the barrier and into the wind when the barrier was rotated in a counterclockwise direction. This last and apparently bizarre result was readily explained via an aiming error mechanism proposed by us (Gamow and Bottger, 1982*b*). The results from these experiments are entirely consistent with the original hypothesis that both the anemotropic response and the avoidance response are mediated by a gas that is released from the sporangiophore.

The anemotropic response and the moving barrier responses suggest that both responses are mediated in some way by a growth-stimulating or -inhibiting gas. In the avoidance response, the gas can be thought to accumulate in a higher concentration on the proximal side of the sporangiophore than on the distal side, thus causing positive growth away from the barrier. In the anemotropic response, the same gas accumulates on the leeward (downstream) side of the sporangiophore, once again causing the sporangiophore to grow into the wind.

The asymmetric accumulation of this gas emitted from the sporangiophore could result in asymmetric growth by one of two proposed mechanisms. One mechanism depends on a postulated emitter and receptor structure, whereby the sporangiophore senses the asymmetric gas concentration in an olfactory manner (Cohen et al., 1975). To date, the existence of such structures has not been reported. A second mechanism, called the mass transfer model (Gamow and Bottger, 1982*a*), proposes that the rate of release of the gas is governed by the concentration of the gas in the immediate vicinity of the cell wall (Pellegrino et al., 1983). An obvious candidate for the emitted gas is water, since it is released in relatively large quantities, several nanoliters per minute, from mature sporangiophores (Bergman et al., 1969). Recent numerical modeling confirms that steady state concentrations of water vapor are asymmetric around a sporangiophore placed both next to a stationary barrier and in a simulated wind. The numerical model assumes that a sporangiophore cross section transpires water vapor in two dimensions through a semipermeable cell wall with constant permeability. Even without modeling the system, it is intuitively obvious that the water vapor concentration profile and the rate of transpiration, as a function of position on the circumference of the cross section, would necessarily change as a result of exposing the sporangiophore to either a barrier or wind. The mass transfer model further postulates that the rate of release of gas from one region of the

cell wall is inversely proportional to the rate of growth in that same region. In support of this postulate, we (Gamow and Bottger, 1982a) have shown that hydration of the cell wall does result in cell wall softening.

When water is assumed to be the active species, the mass transfer model makes several predictions. First, it predicts that the avoidance response will be independent of the ambient relative humidity because the ratio of mass transfer from the two sides of the cell wall is not a function of relative humidity. Second, it predicts that the rate of growth will be a function of relative humidity. Third, it predicts that the anemotropic response will be greater at higher wind speeds and lower relative humidity. Although no quantitative experiments measuring the degree of avoidance response as a function of humidity have been reported, good avoidance responses have been seen at a wide range of humidities. Cohen et al. (1975) measured the growth rate of a mature sporangiophore while the relative humidity was changed from 68 to 96% and saw no measurable change in growth. This last result supports neither the mass transfer model nor the olfactory model, although it does argue against water being the active gas. The work presented here specifically addresses the third prediction of the mass transfer model by measuring the anemotropic response as a function of relative humidity and wind speed.

As discussed in the beginning of this introduction, equilibrium bend angles are well suited to determining sensory sensitivity in responses that are real but weak. In this work, the photogeotropic analysis was modified by substituting a unilateral wind for a unilateral light source. We have designated and constructed an appropriate apparatus in which wind and relative humidity can be defined over a number of hours. Using this apparatus and measuring what we have termed the anemogeotropic equilibrium angle, we have determined that the magnitude of this bend angle is a function of both wind speed and humidity. We thus conclude that an asymmetric distribution of water vapor around the growing zone could cause asymmetric growth. These data support the idea that water is the active gas in the anemotropic response, and by inference suggest that it is also the avoidance gas.

EXPERIMENTAL APPARATUS AND PROCEDURES

Wild-type *Phycomyces blakesleeanus* sporangiophores, NRRL555(-), originally obtained from M. Delbrück, California Institute of Technology, Pasadena, CA, were grown in shell vials containing 5.0% potato dextrose agar with 1.0% yeast extract. The shell vials were incubated under diffuse 25-W incandescent light in a high-humidity Warren/Sherer (Marshall, MI) incubator maintained between 22 and 27°C.

A Variable-Humidity Wind Tunnel

In order to measure dynamic and equilibrium anemotropic responses in *Phycomyces* sporangiophores as a function of wind velocity and relative humidity (RH), a small-scale wind tunnel and humidified wind generator were constructed. The wind tunnel consisted of several sections as shown in Fig. 1. The first section featured a diverging square cross section that reduced turbulent entrance effects in the flow. The final cross-sectional area was 58.1 cm² and matched the dimensions of the other wind tunnel sections. Following this nozzle, a second section contained fine mesh screens stretched perpendicular to the

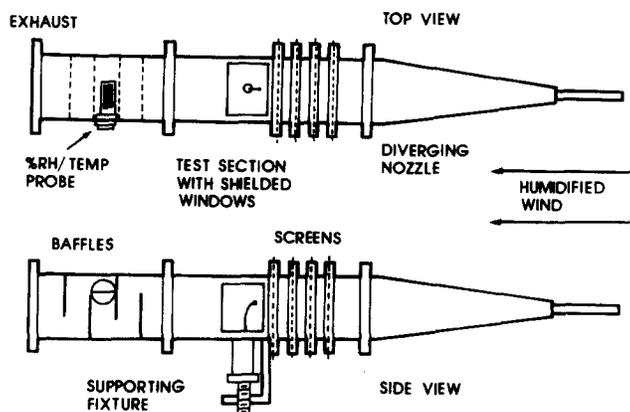


FIGURE 1. Top and side views of a wind tunnel constructed to measure anemogotropism in *Phycomyces* sporangiophores. Drawings are to scale. Total length is 79 cm. The wind tunnel is mounted on the movable carriage in front of the lens of the optical comparator (not shown).

flow to dampen velocity surges caused by upstream disturbances. Laminar flow was expected at all experimental velocities based on calculation of the nondimensional Reynolds' number for flows both through the tunnel and around the sporangiophore. Interpretation of the experimental results was not conditional on ideal laminar flow. The third section, containing the sporangiophore, featured windows on three sides, shielded by Kodak (Rochester, NY) No. 29 cellulose acetate gel filters, which admitted only light with wavelengths of >600 nm. Experimentally, *Phycomyces* was effectively blind to wavelengths of >600 nm. The filters prevented any phototropic interference during experimental observation.

A single *Phycomyces* sporangiophore, still in its shell vial, was placed upward through a small hole in the bottom of the wind tunnel. A fixture underneath this section surrounded the shell vial and was pressed against the outside bottom of the test section so as to seal out light. The shell vial itself remained outside the test section to ensure that the air flow was not disturbed by any large object within the test section. The test section was followed by baffles as shown in Fig. 1 to prevent light from entering the tunnel exhaust. A relative humidity and temperature probe was located near the tunnel exhaust rather than in the test section to minimize its disturbance of the flow around the sporangiophore. The relative humidity sensor employed a bifilar conductive grid on a sulfonated polystyrene substrate (Pope cell). Surface resistivity was measured and converted to relative humidity after compensation for temperature. The sensor responded fully within a few minutes to even a small change in humidity based on our observations. The accuracy of the probe was $\pm 3\%$ RH in the range 15–95% RH and was sufficient for our experiments.

The humidified wind generator is shown in Fig. 2 and was designed to meet the following specifications: (a) 0–5 ft³/min deliverability at standard conditions for 0–40 cm/s velocity in a 58.1 cm² cross section; (b) humidity adjustable from ambient to 95+% RH and controllable to within $\pm 3\%$ RH; (c) temperature maintained to within $\pm 1^\circ\text{C}$ of ambient.

During operation, a constant stream of air was first metered and then split into two fractions. One fraction was saturated or nearly saturated with water vapor; the other fraction was not treated. The two streams were remixed before entering the wind tunnel. Wind velocity depended on the volumetric flow rate of the air before splitting; wind

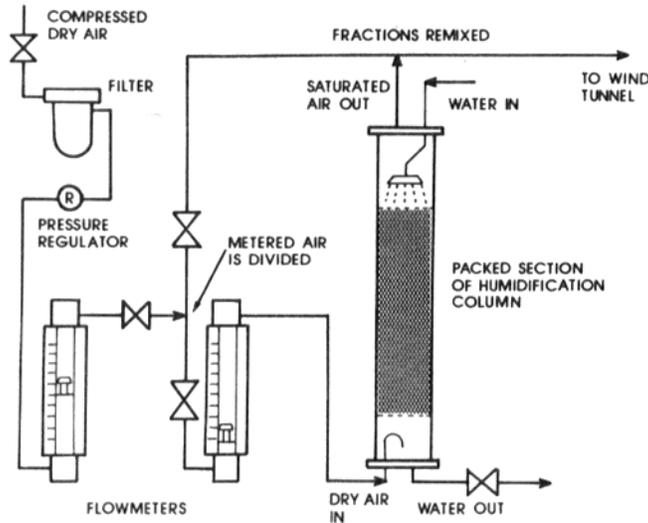


FIGURE 2. A schematic of the humidified wind generator that humidifies dry air to a desired degree of saturation at constant deliverability.

humidity depended on the fraction saturated and the ambient humidity of the metered air. In our case, the ambient humidity of the in-house compressed air was <10% RH. Successful design of this humidified wind generator required saturation, or near-saturation, of up to 5 standard ft³/min of air with no significant change in ambient temperature. This was accomplished with a countercurrent air/water humidification column. Water flowed downward and air flowed upward. The column had a 6.98-cm inside diameter and was filled with 0.76 m of 0.5-in. nominal ceramic Berl saddles, a commercially available packing. Selection of packing size, packed height, and column diameter was based on consideration of flood point and column efficiency. If either water or air flux was too high, the downward flow of water would be choked, resulting in column flooding. If air flux was too low, column efficiency would suffer and more packing would be required to reach saturation. More details concerning packed column design can be found in McCabe and Smith (1976) and Perry and Chilton (1973).

Column performance was highly satisfactory. Complete or nearly complete saturation of the air was suggested by sustained condensation of water vapor in the plenum above the packed section of the column. Low humidities were achieved by saturating only a small fraction of total metered air; intermediate and high humidities were achieved by saturating a larger fraction of total metered air. In actual experiments, relative humidity and temperature were controllable to within design specifications.

Measuring Anemogeotropism and Growth Rate

Before each experiment, a sporangiophore was first placed in the wind tunnel and allowed to grow in the absence of wind and light for at least 20 min. After this period of adaptation, the growth rate was measured. Before exposure to the wind stimulus and at every hour thereafter, a magnified image of the sporangiophore was traced on drawing paper placed over the image screen of an optical comparator. The optical comparator magnified the sporangiophore 30 times. Heating effects were minimized by illuminating the sporangiophore only long enough to trace its image on the screen before exposure to wind and once every hour.

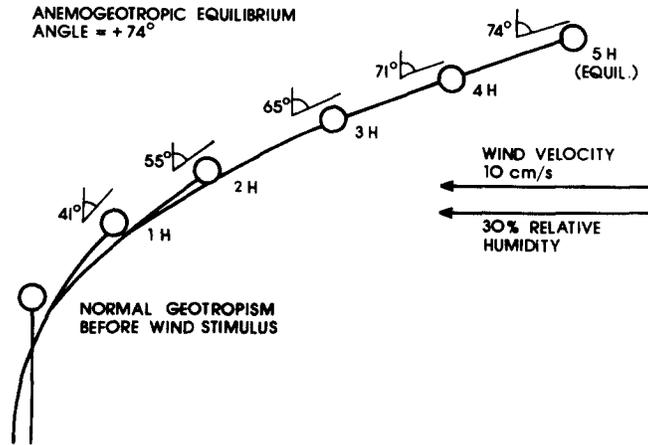


FIGURE 3. Sporangiophore growth and bending in an idealized anemogeotropic equilibrium experiment. Sporangiophore growth rate is typically 2.5 mm/h.

Each experiment yielded two measures of the anemogeotropic response. First, the dynamic anemogeotropic response was measured by noting the bend angle after the first hour of exposure to humidified wind. This single measurement, divided by 60 min, was the dynamic response of the sporangiophore to a humidified wind stimulus in degrees bending per minute. Second, the anemogeotropic equilibrium angle was measured after several hours of continuous exposure to humidified wind. For reasons discussed earlier, the equilibrium angle was considered a better measure of the anemogeotropic response. Fig. 3 shows an idealized anemogeotropic equilibrium experiment at 30% RH with a wind speed of 10 cm/s. The dynamic response is 41 degrees/60 min = 0.68 degrees/min, and the anemogeotropic equilibrium angle is 74 degrees. Bend angle was measured once every hour.

RESULTS

Effect of Wind Velocity and Relative Humidity on the Anemogeotropic Response

Fig. 4 shows the anemogeotropic response as a function of wind speed and relative humidity. Qualitative curves connecting the data points are drawn to indicate overall trends discernible from the data points. Curves are drawn to suggest the possibility of a threshold wind velocity below which no anemogeotropic response is observed. A threshold wind velocity was seen in some but not all of our early experiments. Error bars are plus or minus the square root of the standard deviation of the data at each experimental condition (standard error). For large data populations that are normally distributed, 1 SE above and below the mean encompasses 68% of the data. Typically, each equilibrium bending angle shown in Fig. 4 represents no less than five experiments. In all experiments, air temperatures were between 21 and 27°C. Notable features of these data are: (a) the sporangiophores grow into the wind at all experimental conditions of wind velocity and relative humidity; (b) equilibrium bending angles increase as a function of wind velocity and relative humidity; (c) average equilibrium angles of >90 degrees are not observed.

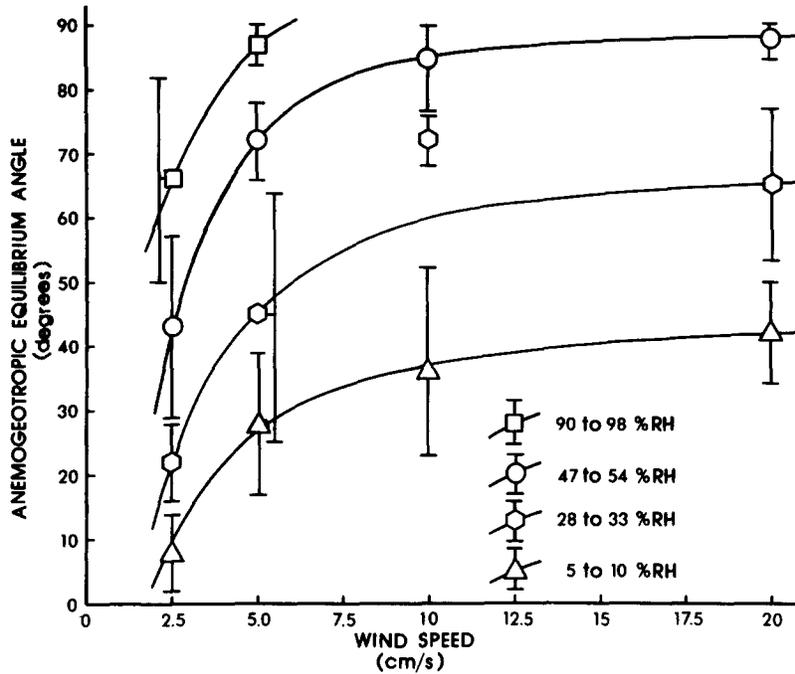


FIGURE 4. The anemogeotropic equilibrium angle observed in *Phycomyces* sporangiophores after 4–7 h vs. wind speed and percent relative humidity (% RH). Error bars represent the standard error.

The data in Fig. 4 are supported by the dynamic response data shown in Table I. These data show that average bending rates during the first hour of exposure to wind are generally higher for higher wind velocities and higher relative humidities.

Effect of Relative Humidity on the Growth Rate of Stage IVb Sporangiohores

Stage IVb sporangiophores were placed in the humidified wind tunnel in a manner identical in all respects to the procedure used to measure the anemogeotropic response.

TABLE I
Average Anemogeotropic Response in *Phycomyces* Measured During the First Hour of Stimulation (degrees bending/min)

Percent relative humidity	Velocity (cm/s)			
	2.5	5.0	10.0	20.0
5–10	0.15 (5)	0.20 (8)	0.18 (5)	0.25 (5)
28–33	0.25 (4)	0.38 (9)	0.42 (5)	0.78 (5)
47–54	0.28 (7)	0.44 (5)	0.90 (7)	0.83 (5)
90–98	0.70 (5)	0.70 (5)	—	—

The number of experiments is given in parentheses.

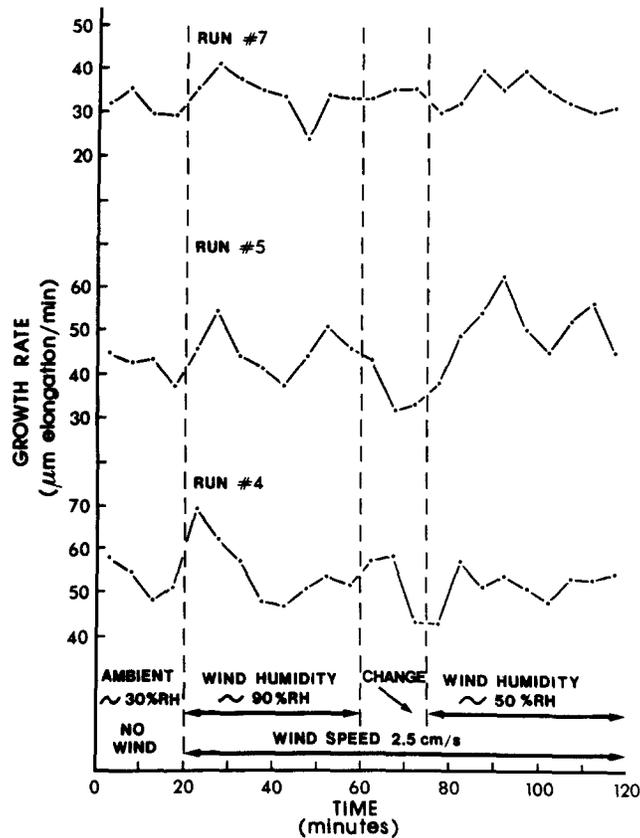


FIGURE 5. Growth rate of *Phycomyces* sporangiophores at 90% and 50% RH.

tropic equilibrium angle. In these experiments, step changes in humidity were made at constant wind velocity (2.5 cm/s). A minimal velocity was needed to effect changes in relative humidity in the wind tunnel in <15 min. The growth rate was measured directly from the optical comparator once every 5 min. Fig. 5 shows three such experiments in which the humidity was increased from ambient to ~90% and then decreased to ~50%. A total of six experiments failed to show a significant change in growth rate with changing relative humidity.

DISCUSSION

We (Gamow and Bottger, 1982) concluded from experimental data that the anemotropic response and the avoidance response were a result of a single transduction mechanism. We proposed that growth rate and growth direction were a function of the symmetry (with respect to the vertical axis of the sporangiophore) of mass transfer of at least one gas emitted from the sporangiophore. This suggestion that the primary site of transduction is based on a mass transfer mechanism rather than an olfactory mechanism eliminates the need to postulate the existence of one or more olfactory receptors. The data that have been published to date, the moving barrier experiments of Gamow

and Bottger (1982a) and Lafay and Matricon (1982), the house experiments of Cohen et al. (1975), and the double-barrier experiments of Ortega and Gamow (1970), all suggest that a gaseous mechanism is involved, but do not in themselves distinguish between a mass transfer model and the olfactory model.

To distinguish between these two models, Pellegrino et al. (1983) and Pellegrino (1983) mathematically simulated in two dimensions a sporangiophore exposed both to a humidified wind and a barrier, assuming that the gaseous species was water. This simulation confirmed quantitatively that either the presence of a barrier or a wind will cause a change in the symmetry and magnitude of water loss, i.e., transpiration of water from the cell wall. In addition, this mathematical analysis made three experimentally testable predictions. It predicted (a) that the growth rate of a stage IV sporangiophore would increase as a function of humidity, (b) that the anemotropic response would be inversely proportional to the relative humidity of the wind, and (c) that the anemogeotropic angle would increase with wind speed. We have tested all three predictions and have found that the first two have failed. We would like to discuss separately these two predictions and the possible reason that they failed.

Growth Rate as a Function of Humidity

Measuring growth rate as a function of a change in stimulus intensity is far less sensitive than measuring an equilibrium bend angle for several reasons. First, a bend angle is easier to measure than a change in length. Also, unless severe precautions are taken to ensure that no random air currents are present during the growth measurements, random fluctuations in growth occur that can obscure small growth responses (Gamow and Bottger, 1981; Gamow and Clough, 1983). Additionally, an equilibrium angle is continuously developed over many hours, whereas growth measurements are discrete measurements at instants of time. Thus, we did not expect to measure extremely small differences in growth rate or short-lived transient responses to changes in humidity. Rather, we expected to measure relatively large differences in average growth rate at different relative humidities. Consequently, we were surprised to find that the average growth rate of a mature sporangiophore is independent of humidity. In our laboratory, stage IV sporangiophores have grown equally well for many hours in virtually 0% humidity and at very high humidities. This last observation seems to dispel the idea that one needs to grow sporangiophores in high-humidity growth chambers, which is the common practice in all *Phycomyces* laboratories. High humidity, however, may still enhance mycelial growth or earlier stages of growth, or, at the very least, keep the growth agar from drying out.

Because of the problems concerning an assay based on growth rate, our experiments do not rule out the possibility that the sporangiophore may respond to a humidity pulse with a small, short-lived transient response and then adapt to the new humidity by resuming its previous growth rate. If in fact the sporangiophore does elicit such a transitory response, one may be able to experimentally verify this by a series of equally spaced humidity pulses with a time constant of ~10 min. This experiment is technically difficult and to date has not been performed. Failure to adapt to either an avoidance stimulus or to

an anemotropic stimulus does not argue against the suggestion that the sporangiophore can adapt to changes in humidity. The fact that a sporangiophore does show adaptation to symmetric stimuli, either a house stimulus (Cohen et al., 1975) or the double barrier (Ortega and Gamow, 1970), certainly argues favorably for an adaptation mechanism. The fact that the sporangiophore shows a well-documented aiming error during an avoidance response (Gamow and Bottger, 1982*b*) further argues in favor of humidity adaptation. Dennison and Foster (1977) have demonstrated that the ability of a sporangiophore to adapt to a unilateral light source occurs because of the phototropic aiming error. They found that when the sporangiophore is back-rotated, in order to compensate for the sporangiophore's innate growth rotation, the sporangiophore shows a decreased ability to adapt to a unilateral light source. Since the wind stimulus is also unilateral and the rotation of the sporangiophore is in only one direction, we surmise that failure to adapt to a wind stimulus is also based on the aiming error. Indeed, our results could allow for an undetectable transient growth response sandwiched between constant average growth rates at different humidities.

The Anemogeotropic Response as a Function of Humidity

The second prediction of the mass transfer model based on the mathematical stimulation was that the anemogeotropic response would be maximum at low relative humidities and minimum at high relative humidities. At low humidities, the asymmetry of mass transfer occurring around the periphery of the growing zone is maximal. This is because the windward side has the maximum mass transfer (it is directly subject to the dry wind), and the leeward side has the minimum mass transfer of water. As the relative humidity of the wind increases, the driving force for mass transfer—evaporation of water—from the windward side of the growing zone decreases, causing the ratio of the water vapor concentration of the windward side to the leeward side to decrease. Part of the humidity increase on the leeward side arises from the water vapor that is released from the windward side and then transported by convection to the leeward side. The other part of the humidity increase is due to reduced transport of water vapor away from the sporangiophore by diffusion simply because of higher overall ambient humidity. The mathematical simulation assumed that water vapor pressure on the surface of the cell was a function of external humidity. Consequently, at higher relative humidities, the driving force for mass transfer of water decreases, resulting in less asymmetry and a weaker response.

The data presented in this paper clearly argue against this prediction. Strong anemogeotropism, measured by the equilibrium angle, occurs at high humidities in contrast to low humidities. Even so, the anemotropic angle, the most sensitive indicator of *Phycomyces* stimulus-response behavior, is still a strong function of relative humidity. In other words, at constant wind speed, there is a clear humidity response.

We are clearly puzzled by this result. One possibility is that at high humidities the cell wall is so highly hydrated, and thus so highly extensible, that even a small asymmetry of water release would result in a full anemogeotropic response. We

have in fact shown that hydration of the cell wall of a stage IVb sporangiophore causes cell wall softening (Gamow and Bottger, 1982a). Recently, it has been shown that if a strain-hardened stage IVb *Phycomyces* sporangiophore is subject to a high-humidity stimulus, the cell wall does become more extensible (Chinn and Gamow, 1984). Additional support comes from our observation that in some instances when the sporangiophore is already bent 90 degrees as a result of a high-humidity stimulus, the sporangiophore falls below the horizontal. We cannot discount the possibility that this may be a result of excessive hunting, but it appears to us that in these cases, the sporangium has actually drooped as a result of its own weight. The effect is small and occurs only rarely. It has never been observed with a dry wind stimulus.

A second possibility is that one of the assumptions made in the mathematical simulation was wrong. We are now in the position to go back to the mathematical model and see which assumption must be changed in order to obtain the result that is compatible with our experimental findings. One critical assumption is that of constant cell wall permeability to water. This assumption demands that the flux of water through the cell be inversely proportional to the partial pressure of water vapor (relative humidity) at the surface of cell wall. In other words, the sporangiophore cannot actively regulate its rate of transpiration. A conceivable example of regulation might be that a fully hydrated cell wall in the high-humidity environment would become more permeable to water such that the rate of mass transfer would remain constant and would not decrease as we have assumed. This suggestion agrees with a recent experimental finding in our laboratory that a nongrowing sporangiophore transpires only ~20% of the water that is transpired from an actively growing sporangiophore. The inference is that the cell wall of an actively growing organism is more stretched and thus more permeable. Hydration of the cell wall would stretch it in a similar manner. In principle, it is easy to check whether the transpiration rate is or is not a function of the relative humidity. The qualitative rate of transpiration can be accurately determined by measuring the loss of weight of a growing sporangiophore over a number of hours as a function of relative humidity. We are presently conducting these experiments.

The fact that the mathematical simulation uses water as the gaseous molecule places no constraint on the analysis since the result would be the same for any other assumed gaseous molecule. However, our experimental discovery that the moisture content of the wind in our anemogeotropic experiments functions as a true sensory stimulus provides additional evidence that the gaseous molecule emitted from the sporangiophore, the gas that is responsible for both the anemotropic response and the avoidance response, is water.

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