TROPISMS IN THE MUSHROOM *PSilocybe cubensis*

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ABSTRACT

The growth of the mushroom *Psilocybe cubensis* was studied in a wind tunnel under controlled conditions of wind velocity, humidity, temperature, and light. The basidiocarp stipe grew into the wind up to the time of spore formation. When rotated with the long axis of the stipe perpendicular to the wind, fruitbodies grew upright. When spores began to be formed a negative geotropic curvature of the stipe occurred but no recurvation occurred in a sporeless mutant.

Key Words: mushroom, tropisms, wind tunnel.

The initiation and development of many mushrooms are controlled by environmental stimuli (Reijnders, 1963; Taber, 1973; Manachère, 1980). Studies of tropisms in mushrooms have generally been confined to photo- and geotropism (Plunkett, 1961; Carlile, 1970; Leach, 1971; Schwalb and Shanler, 1974). Different physiological stages of mushroom development have been described (Manachère, 1970) and several workers have postulated the existence of a mushroom hormone involved in tropisms (Gruen, 1963; Hagimoto, 1963). Decapitation experiments have linked these hormone(s) to the lamellae. Agar diffusates from the gills can partially replace the influence of the pileus (Hagimoto and Konishi, 1960). Some mushrooms contain the hormones of higher plants but so far no evidence suggests that these hormones regulate mushroom growth (Konishi and Hagimoto, 1961; Jeffereys and Greulach, 1956; Peg. 1973).

The anatomy of early development of *Psilocybe cubensis* (Earl.) Sing. has been described (Heim and Wasson, 1958). Apparently much of the cell division has taken place by the time the primordia are a few cm high. Further growth involves acropetal expansion of these cells (Heim and Wasson, 1958; Plunkett, 1961) and possibly some cell division at the upper part of the stipe (Craig, 1977). At least four different responses to light have been described for mushrooms (Eger-Hummel, 1980). *Psilocybe cubensis* is similar to *Coprinus concrementus* Bull. ex Fr. in this respect. During experiments designed to determine optimum growth conditions for *P. cubensis* the following observations were made. These observations are based on a study of approximately 100 developing basidiocarps.

MATERIALS AND METHODS

I inoculated an isolate used from a previous study (Badham, 1980) onto autoclaved brown rice (6 g/20 ml deionized water) in 50 mm Petri plates. A sterile mutant of this strain was also studied. After the hyphae covered the substrate, aseptic conditions were not necessary. The hyphal mass was placed in 13 cm diam pie tins with vermiculite and 25 ml of water. This was covered with glass and left under "cool white" fluorescent light (2685 lux) for 10 da or until primordia formed. The cultures were watered with distilled water when they had lost more than 10 ml of water (determined by weight loss). When the primordia were 15–25 mm high they were placed in a closed circuit wind tunnel (Fig. 1) with a working area of 43 × 30 × 20 cm and illuminated 12 h/da with "cool white" fluorescent light. Wind velocity was 9 ± 3 cm/sec (TSI hot wire anemometer Model 1650); humidity 94 ± 3% RH (wet and dry copper constantan thermocouples, the wet
one enclosed in a small cotton string and wicked to a bottle of distilled water); temperature $24.5 \pm 1.5$ C; light $0.002$ calories/cm$^2$/min (Eppley radiometer Model PSI). Generally the cultures were placed in the chamber when primordia were 2 cm high under various conditions (Fig. 2) and removed 72 h later at maturity.

For the purpose of this study I divide the development of *P. cubensis* into four different stages. Stage 1 is characterized by a slight swelling of the pileus (Fig. 2b, 0 h). At Stage 2 the pileus is nearly spherical (Fig. 2b, 24 h). Maturity (sporulation) or Stage 3 is indicated by an open hemispherical pileus (Fig. 2b, 48 h). Late maturity or Stage 4 occurs when the pileus becomes more or less plane (Fig. 2b, 72 h).

RESULTS

When mushroom primordia between Stage 1 and Stage 2 (Fig. 2) are placed in the wind tunnel the growth of the stipe is directed into the air flow (Fig. 2a, 0–24 h). If cultures are rotated perpendicular to the wind, growth is upward (Fig. 2b, 0–24 h). Such growth occurs in a 12 h photoperiod or in darkness, in fertile
FIG. 2. Growth of *Psilocybe cubensis* in a wind tunnel for 72 h. A. Growth of fertile basidiocarp with 12 h photoperiod, light incident from above or below, flow from the right, not rotated. B. Growth of fertile basidiocarp with 12 h photoperiod, light above, flow from the right, and rotated perpendicular to the air flow 3 rpm. C. Growth of sterile basidiocarp with 12 h photoperiod, light from above, airflow from the right, not rotated. D. Growth of a fertile basidiocarp with constant light from above, airflow from the right, rotated parallel to the flow 3 rpm.

and in sterile basidiocarps, and in cultures in which the basidiocarps were placed in the chamber with the stipes directed away from the wind. If upright fertile cultures were placed in the chamber at Stage 2 or later bending was not as pronounced.

Mushrooms in Stage 2 show a different tropic response. With the 12 h photoperiod a negative geotropism is expressed in fertile basidiocarps, i.e., the pileus turns upward from the direction of the wind and opens with the lamellae facing downwards (Fig. 2a, 24–48 h). This occurs when light is incident from above or below the cultures. Interestingly this recurvatum does not occur in sterile strains (Fig. 2c, 24–48 h) or in the absence of light (few spores formed). The rotation of basidiocarps into and parallel to the air flow results in stipe elongation and the pileus opening into the wind (Fig. 2d, 0–72 h).

**DISCUSSION**

One explanation of these results is that stipe elongation up to Stage 2 is influenced by a redistribution of the boundary layer so that it is thicker on the leeward side than on the windward side of the mushroom. Water vapor could be
one of the gases affected by this redistribution. The result of this could be that the windward side of the stipe would be exposed to a greater drying effect than the leeward side. This drying effect or evaporative demand is a function of at least four factors: wind, humidity, light, and temperature. Such a differential in evaporative demand could cause cells of the stipe to grow at different rates resulting in curvature.

*Phycomyces* shows an anemotropism in addition to an avoidance response (Cohen et al. 1975). Johnson and Gamow (1971) have demonstrated the necessity of wind and the importance of water vapor to these responses. The mechanism of stipe curvature in *Psilocybe cubensis* may be similar to that of *Phycomyces*. The wind could also cause a redistribution of gases other than water vapor. Russo et al. (1975) have suggested that ethylene may be involved in the avoidance response in *Phycomyces blakesleeanus* Burgeff.

An alternative explanation is that the mushroom is responding to the force of the wind. Studies on *Phycomyces blakesleeanus* (Dennison, 1961) have shown that the growth of the sporangiophore responds to gravity and centrifugal force.

At Stage 2 a second tropism masks the effect of the first tropism. This tropism occurs along with the production of spores and is a negative geotropic response. When mushrooms are rotated horizontally to equalize the effect of gravity under constant illumination, growth and pileus expansion are both horizontal. Some light is necessary for this negative geotropism but possibly only because it is necessary for spore production. The connection of geotropism to spore formation is reinforced by the fact that sporeless mutants did not exhibit this negative geotropism.

If the mechanism of stipe elongation involves a gradient of evaporative demand, light could have a substantial influence upon this tropism by heating the surface of the mushroom and increasing the evaporation of water or other gases. If strong in relation to wind and humidity, light could become the dominant factor of evaporative demand. This could be part of the mechanism of phototropism. If the effect of light is simply that of drying out the illuminated portion of the stipe, then it is unlikely that the light used in this experiment exerted significant effect since the flux density was approximately $1/50$ of what might be expected in the field. If, however, small quantities of light trigger hormonic responses, then the situation could be entirely different. Light is necessary in at least two phases of the life cycle of *P. cubensis*: initiation of basidiocarps (Badham, 1980), and spore formation and geotropic sensivity. Light exerts some inhibitory effect upon stipe elongation.

There are several possibilities for an adaptive role for anemotropism. It could be the mechanism by which mushrooms place their caps in the most favorable position for spore dispersal. Directed growth toward the evaporative demand could also serve to increase the spacing between the stipes of cespite fruiting bodies.

Plunkett (1961) suggests that the negative geotropic response is useful to lig-nicolous or coprophagous species since the habitat is unstable and effective spore dispersal demands a horizontal pileus. Possibly one of the functions of the veil is to protect the uppermost and unexpanded portion of the stipe from wind or light prior to final readjustment of the cap before spore release.

In summary, I suggest that there may be two phases of directed growth in *P. cubensis*. The first involves primary stipe elongation and is oriented toward the direction of greatest evaporative demand. The cells of the stipe may be responding to this stimulus individually. The second tropism is a negative geotropism. There is some relationship of this tropism to spore production. In this case, a substance produced in the gills probably modifies the first tropism causing the mushroom to respond primarily to gravity.
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LITERATURE CITED


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