The Removal of Helminthosporium maydis Spores by Wind

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ABSTRACT

Helminthosporium maydis spores were blown from maize leaves in proportion to the supply. Spores formed during four days of moisture were more easily removed than younger ones, spores near the leading edge were more easily removed than those near the center of the leaf, and spores between veins were slightly more easily removed than those on the veins of the leaves. In 15 sec, a wind of 3 m/s removed about 20% of the spores 5 mm from the leading edge and a wind of 7 m/s removed about 80%.

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Since the concentration of *Helminthosporium* spores in the air increases during the dry, breezy, daylight hours (7); and since spores are not airborne above wet leaves (5), it is reasonable to expect that *H. maydis*, the pathogen of southern corn leaf blight, is spread by the wind. The rapid spread of the blight across the United States in 1970 (8), and the removal of *H. maydis* spores by a puff from a syringe (9), confirm that expectation. When a calculation or simulation of the disease is attempted from weather observations, however, the critical relation between wind speed and removal turns out to be unknown. Our ignorance appears greater when we learn (1, 10), that surprisingly few spores are found in the air above or within a blighted crop. Observations were, therefore, made of the course of spore removal to determine whether a constant proportion of spores is removed in succeeding times; whether the susceptibility to removal changes with age, dryness, or location; and the effect of wind speed and airborne particles upon removal.

The difficulties of take-off facing the spore that is not propelled into the air by the parent fungus are considerable (4). A pathogenic fungus has sporophores of the order of only 100 microns tall and thus the spores are formed in the relatively still air near the leaf. For example, in a wind tunnel a flow of fully 5 m/s was required to remove more than half the spores deposited on a microscopic slide (3). One expects, therefore, that a brisk breeze will be required to remove many *H. maydis* spores from a maize leaf.

Some guidance as to the nature of spore removal can be found in studies of wind erosion of soil. The stress on the soil particles increases with the square of the wind speed, and a particle is often air-borne when struck by another (2). This observation concerning stress is the source of a rule in a simulator (9) that removal will increase with the square of the wind speed.

Another prediction about spore removal is derived from the fact that heat removal decreases across a leaf with distance from the leading edge (6). Thus, more spores (like more heat) will likely be removed near the leading edge than further along unless the spores released near the front of the leaf dislodge many spores and counteract the decreased ventilation further back.

MATERIALS AND METHODS.—Maize seeds (*Zea mays* 'Pa 602A' F_1 hybrid) were planted in cups of sand, and the plants grown for 3 to 5 weeks in the greenhouse. Plants were then inoculated with a spore suspension of race T of *H. maydis*, and they then were kept moist for 24 hr in a plastic bag. After 4 to 5 days incubation in dry air and the development of lesions, the leaves were excised and placed overnight in a moist chamber where sporulation occurred. The removal of spores by wind was then studied on 8.5- to 9-cm-long sections cut from these leaves and stretched between clamps in a wind from a centrifugal fan with a cylindrical outlet 6 cm long and 8 cm in diam. The air blew along a flat surface but was not otherwise confined. The underlying surface was 11 cm below the suspended leaf section. The leaf section was neither absolutely plane nor rigid, and the following edge particularly was apt to flap. Occasionally a leaf section was held in front of an ordinary propeller fan in the laboratory. Removal was estimated by observing the proportion of sporophores with attached spores before and after exposure to wind and the location of dislodged spores trapped on the leaf.

Lycopodium spores purchased as "*Lycopodium* N.F." were blown from a spatula and onto the leaf by wind from a fan.

RESULTS.—*Proportional removal of spores with time.*—To observe the relation between the number of spores removed and the duration of exposure, a leaf with a sporulating lesion was repeatedly exposed for 15 sec to a 3.6 or 6.0 m/s wind. Before and after each exposure, the number of spores removed was estimated by counting the number of spores still attached to a sample of 270 to 380 sporophores. The faster wind promptly removed nearly all spores, but the slower wind removed about half during each successive exposure until an unremovable eighth remained. The results are compared in Fig. 1 with a rule that says 88 percent of the spores are susceptible to removal and 60 percent of these are removed each 15 sec. There seems no reason to deny that the rate of spore removal by a given wind speed is a constant proportion of the supply.

Age and drying.—Sections cut from leaves inoculated four days earlier were placed in a moist chamber for 1 to 7 days and then promptly exposed for 15 sec to 3.6 or 6.0 m/s wind. Alternatively, they were removed from the chamber and allowed to dry for a day before exposure to the wind. Before and after exposure, the proportion of sporophores holding spores was observed; the proportion was estimated from a sample of 106 to 640 sporophores equidistant from the leading edge. The distance was the same in each experiment, either 2 or 5 mm. Since essentially all sporophores carried a spore before being exposed to wind, the percentages after blowing tell the story (Table 1).

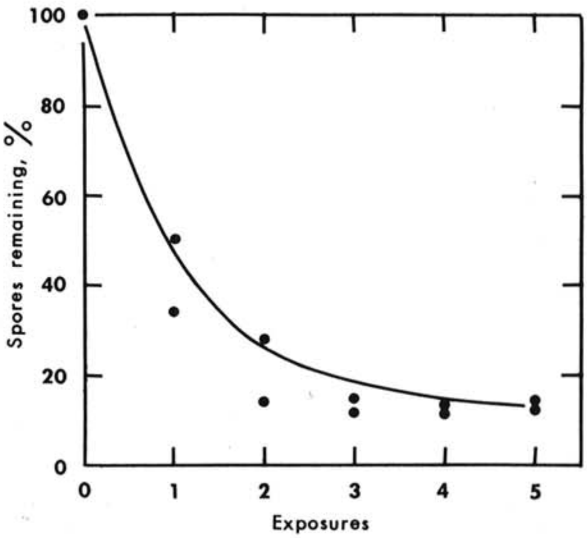

Fig. 1. The removal of *Helminthosporium maydis* spores by repeated 15-sec exposures to a wind of 3.6 m/s. The curve corresponds to a rule that 88% of the spores are susceptible to removal, and 60% of these are removed each 15 sec.

A comparison of the removal of the spores from moist vs. dried sporophores in experiments A, B, and C shows that the prolonged drying of 24 hr did not increase take-off. On the other hand, experiments C and D clearly show that spores formed during four or more days in the moist chamber were more easily removed than ones formed during shorter periods.

Location across the leaf.—The percentage of the spores removed from samples of 90 to 280 sporophores located at various distances from the leading edge was observed after leaf sections were exposed to the wind for 15 sec. More spores were blown off the leading and the following edges than off the middle of the leaf (Table 2).

To learn whether dislodged, flying, spores would increase the removal of spores downwind, a leaf section was first exposed to a 3.0 m/s wind from a

TABLE 1. The percentage of *Helminthosporium maydis* sporophores without spores after moist and dry spores of different ages were exposed to wind

Exp.	Wind (m/s)	Age (days) 1	2	3	4	7
				Moist		
A	6.0	84	95	96	94	
B	3.6	54	45	34		
C	3.6	38	60	23	85	
D	3.6	22	22	30	79	78
				Dry		
A	6.0	74	46	95		
B	3.6		46			
C	3.6	50	7	42		

TABLE 2. Spore removal by wind related to distance from the leading edge of a 20-mm wide leaf. The table shows the percentage of *Helminthosporium maydis* sporophores without spores after exposure to winds of 6.0 to 7.2 m/s for 15 sec. Each line describes a different leaf and exposure to wind

Wind velocity (m/s)	Distance from leading edge (mm)					
	3 to 5	10	12	13	14	20
6.0	84	0				
7.2	88		10			
7.2	50		0			
7.2	84			15		
7.2	88				30	98

propeller fan. None or few spores were removed from two leaves after 15 sec. Then *Lycopodium* spores were caused to strike the leaf for 15 sec by holding *Lycopodium* powder on a spatula between the fan and leaf section. After this bombardment, 80 and 71% of *H. maydis* spores were removed from lesions 3 and 9 mm, respectively, from the leading edge of one leaf and 86 and 91% from two lesions 4 mm from the leading edge of a second leaf. There seems little doubt that *Lycopodium* projectiles dislodged *H. maydis* spores.

Veins of the leaf.—The veins of the leaf other than the large middle vein are ridges about 60 μm tall that lie across the wind. Sporophores grow on veins as well as in the intercostal valleys. The horizontal widths of 66 valleys and intervening veins on four leaves were measured. The veins averaged 2.5% the width of the valleys. A sample of 23 sporophores and spores on the ridges of five leaves had average lengths of 110 and 70 μm; an erect sporophore and spore on a ridge thus rose about 240 μm above the floor of the valley. A sample of 33 from the valley had average lengths of 120 and 100 μm; an erect sporophore and spore rose about 220 μm or slightly less than the same structure on a vein. This was confirmed at another time when a microscope was moved toward the leaf, and a few spores on the veins came into focus before those in the valleys.

A leaf was fastened to a thin sheet of metal and the sheet was elevated about 3 cm above a microscope stage, air was blown across it, and the fungus observed to see whether some part of the fungus moved more in the wind than others. Mycelium that reached well above other parts did move in the wind, but no greater movement of spores could be seen on the ridges than in the valleys.

The next step was to observe the susceptibility to removal of spores on the ridges and veins. When day-old spores were blown by a 1.5 to 3 m/s wind across three 4- to 5-day-old lesions, more spores were blown from the sporophores in the valleys than on the ridges. In a larger experiment, this effect was confirmed, but the greater susceptibility to removal in the valleys than on the veins was not significant. In this experiment a wind of 3.6 m/s blew across or along leaf sections and the removal of spores was observed 5 mm from the leading edge. The removal on the veins was an insignificant 15% less than in the valleys, and the outcome was unchanged whether the wind blew across or along the veins.

Wind speed.—Eighteen leaf sections with *H. maydis* spores 1 or 2 days old were exposed for 15 sec to winds of 3.1 to 7.2 m/s, which were varied by holding the leaf sections at different distances from the centrifugal fan. Spore removal was estimated by counting the number of sporophores with spores in samples containing 220 to 420 sporophores on lesions 5 mm from the leading edge. The percentages of the spores removed are plotted on Fig. 2 as a function of the square of the wind speed, which is assumed to be proportional to the stress on the spores. The removal increased from approximately a fifth in a wind of 3 m/s for 15 sec to four-fifths in one of 7 m/s.

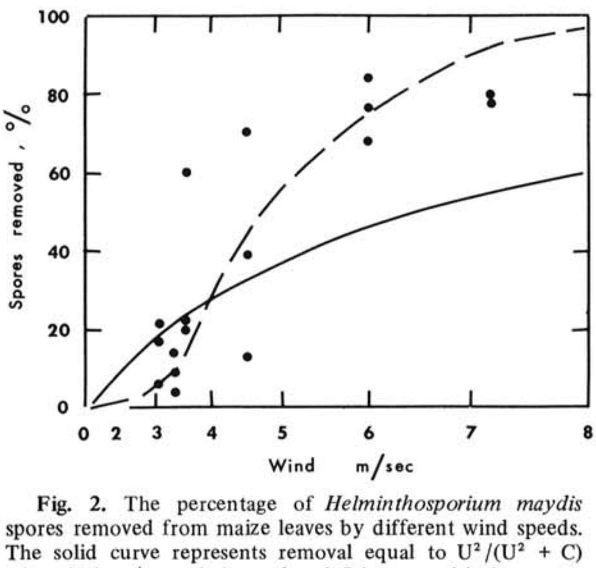

Fig. 2. The percentage of *Helminthosporium maydis* spores removed from maize leaves by different wind speeds. The solid curve represents removal equal to $U^2/(U^2 + C)$ where U is m/s wind speed and C is an empirical constant equal to 40. The dashed curve is the log-probit relation between wind speed and removal.

DISCUSSION.—A rule for calculating spore removal is simply that removal is proportional to the supply remaining. This is confirmed by Fig. 1. Two exceptions complicate matters. The first complication is the residuum that sticks to the leaf and is likely a function of wind speed. It must be entered in any rule for calculation, as in the curve of Fig. 1. The second complication is that older spores are more easily removed than younger ones. This second exception is demonstrated by Table 1, where one sees that spores become easier to detach after they have grown for 100 hr in moist air. This is an unnaturally long wet period, however, and one cannot say whether a natural alteration of wetting and drying would eventually produce such easily removed spores. Although *Helminthosporium* spores are not blown from wet leaves in the field (5), Table 1 shows that a brief drying between the moist chamber and blowing makes the spores as liable to removal as a long desiccation.

Spores near the leading edge of a leaf are more liable to removal than those further back, at least until the rear edge is approached. This decreasing spore removal is obviously caused by the same thickening in the boundary layer of air that decreases the exchange of heat or water with distance across a leaf and perhaps by flapping of the edge. The increased rate of removal near the rear seems to be caused by spores that are released upwind and then strike those further along and by the flapping of the rear of the ruffled leaves. The easier removal of spores from valley than from veins is suggested but not clearly established. Since the difference appears whether the wind blows across or along the veins, it is evidently caused by the tenacity of the spore-sporophore connection and not by ventilation differences.

Finally, one must test some rule for calculating spore removal. In a simulator (9) it was proposed that removal would be the number of spores present multiplied by

$$\frac{U^2}{U^2 + C}$$

where U^2 is the square of the wind speed and C was assigned the value 200 mi^2/hr^2 or 40 m^2/sec^2. The validity of multiplying by the number of spores is confirmed by Fig. 1, as long as an ample supply remains. The validity of the relation between the square of the wind speed and the proportion removed is tested by the fit of the curve in Fig. 2. Apparently somewhat fewer spores are removed by slow winds and more by fast winds than predicted by the rule with C equal to 40 m^2/sec^2. Decreasing C to make the curve fit the observations at faster speeds will cause poorer fit at the slow speeds. One is led, therefore, to the device often used in biology of saying that the susceptibility is distributed normally if some transformation of the treatment quantity is made; the dashed curve on Fig. 2 is the log-probit relation between wind speed and removal. The conclusion is, however, that either the rule of the simulator or the log-probit rule will cause the calculation of the rather small concentrations of spores in the air that have been observed (1, 10).

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LITERATURE CITED

1. BELL, N. L., & J. R. BURLEIGH. 1973. Atmospheric dispersal of southern corn leaf blight spores over the Midwest in 1971. p. 65-76. *In* R. L. Edmonds, & W. S. Benninghoff [ed.]. Ecological systems approaches to aerobiology. II. Development, demonstration, and evaluation of models. US/IBP Aerobiology, University of Michigan, Ann Arbor.
2. CHEPIL, W. S. 1965. Transport of soil and snow by wind. Meteorol. Monogr. 28(6):123-132.
3. GREGORY, P. H., & O. J. STEDMAN. 1953. Deposition of air-borne Lycopodium spores on plane surfaces. Ann. Appl. Biol. 40:651-674.
4. HIRST, J. M. 1959. Spore liberation and dispersal. p. 529-538. *In* C. S. Holton et al. [ed.]. Plant Pathology: Problems and Progress, 1908-1958. Univ. Wis. Press, Madison.
5. MEREDITH, D. S. 1966. Airborne conidia of Helminthosporium turcicum in Nebraska. Phytopathology 56:949-952.
6. PARLANGE, J-Y., P. E. WAGGONER, & G. H. HEICHEL. 1971. Boundary layer resistance and temperature distribution on still and flapping leaves. I. Theory and laboratory experiments. Plant Physiol. 48:437-442.
7. SREERAMULU, T., & A. RAMALINGAM. 1966. Two-year study of the air-spora of a paddy field near Visakhapatnam. Indian J. Agric. Sci. 36:111-132.
8. TATUM, L. A. 1971. The southern corn leaf blight epidemic. Science 171:1113-1116.
9. WAGGONER, P. E., J. G. HORSFALL, & R. J. LUKENS. 1972. EPIMAY, a simulator of southern corn leaf blight. Conn. Agric. Exp. Stn. Bull. 729. 84 p.
10. WALLIN, J. R. 1973. Spore sampling of Helminthosporium maydis race T in 1971. Plant Dis. Reptr. 57:298-299.