Escape of *Peronospora tabacina* Spores from a Field of Diseased Tobacco Plants

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ABSTRACT

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Blue mold disease of tobacco is spread from field to field by wind-blown spores of the fungal pathogen, *Peronospora tabacina*. Estimation of the number of spores likely to reach a distant field requires knowledge of the rate at which spores escape from an infected crop. Vertical profiles of spore concentration and wind speed above a small field of tobacco plants severely diseased with blue mold were measured on several days during the hours of peak spore release. The rate of spore escape derived from these measurements ranged from one to seven spores per square meter per second. By means of a mathematical model, these results were used to estimate spore escape from more extensive plantings.

Peronospora tabacina Adam, the fungus that causes tobacco blue mold, is spread primarily by airborne spores. The danger to other tobacco plantings posed by spores escaping from an infected crop depends on distance between the fields, wind velocity, and the time rate of spore release from the diseased plants. If the number of spores escaping were known, then the numbers reaching nearby fields could be calculated using meteorological methods (1,4,12).

In this paper we report measured fluxes of *P. tabacina* spores leaving a field of severely diseased tobacco and relate these measurements to wind speed, turbulence, and the amount of disease in the field. With the help of a mathematical model, we use these measurements to estimate escape of spores from an extensive area of diseased tobacco.

MATERIALS AND METHODS

Disease severity, concentration of spores in the air, and the speed and turbulence of the wind were observed in and near a tobacco field at the Valley Laboratory of the Connecticut Agricultural Experiment Station in Windsor, CT, during 1981. The observed field was a 50 × 50-m area transplanted to broadleaf tobacco on three successive dates: 10 June (area A, Fig. 1), 2 July (area B, Fig. 1), and 23 July (area C, Fig. 1). The rows were oriented NW-SE, spaced 1 m apart, and the plants were spaced 0.6 m in the row. Crop height in area C where the spores were trapped was about 0.7 m during the first experiments and about 1.0 m during the last experiments. Spore production and disease spread in the observed field was encouraged by weekly irrigation of the second and third planting beginning 20 August. The observations began 2 September and continued through 22 September on certain days judged to be favorable for the release of substantial numbers of spores.

Disease severity assessment. On 4 September, the number of lesions per plant was determined for each of 1,200 plants including the last three rows of the 2 July planting and all 12 rows of the 23 July planting. Disease in each plant was estimated on a scale of 0 to 6 in which 0 = no lesions, 1 = 1 lesion, 2 = 2–3 lesions, 3 = 3–10 lesions, 4 = 10–20 lesions, 5 = 20–50 lesions, and 6 = >50 lesions per plant.

On 10 September, and again on 17 September, we harvested three plants each to represent the least, moderate, and most severely diseased plants present at that time, counted the number of lesions on each leaf, and measured the location, length, and width of each leaf on the stalk. From these data we derived estimates for the vertical distribution of lesions in the canopy, the number of lesions per plant, the leaf area per unit ground area in the field, and the vertical distribution of leaf area in the canopy.

The number of spores per square centimeter of freshly sporulating lesion was determined on 9 September 1981. The spores were counted with a microscope at ×400 after a coverslip was placed on the lesion and pressed down lightly. A total of 100 counts were made choosing 10 different areas from each of 10 lesions.

Time of peak spore release. To determine the optimum time to sample spore concentration, we operated rotoslide impaction samplers (7) throughout the day on several occasions, some in 1979 and some in 1981, in fields of tobacco diseased with blue mold. We also interpreted data published by Waggoner and Taylor (13) and by Hill (5).

Concentration of spores in the air. Spores were trapped on the greased edge of microscope slides whirling at about 1,600 rpm in rotoslide impaction samplers (7). Each trap contained two slides. Five traps were placed at either 0.75 or 1.0 and at 1.5, 2.0, 3.0, and 4.0 m above the ground near the middle of the infected plot at location 4 in Fig. 1. For some experiments an additional trap was placed 2 m above ground level at location 4.

Traps were operated for either 2 or 3 hr between 900 and 1300 hours Eastern Standard Time (EST), the time when peak spore release was expected. The number of spores caught on the middle 50 mm of a slide edge was counted at ×100. Spores of *P. tabacina* are about 20 μm in diameter and settle in still air at about 0.01 $m \cdot s^{-1}$; thus, we used a collection efficiency of 64% (7) to convert the number of trapped spores to the concentration (C) of spores per cubic meter of air. Traps were operated for specified periods of time and the average concentrations of airborne spores during the period were calculated.

The greased slides used in the field were taken from and returned to a covered plastic slide box also containing two or more slides, which were not exposed in traps and which served as controls to assess inadvertent contamination. To obtain an estimate of uncertainty due to nonuniform slide greasing and counting errors we used the catches on the two slides in each trap to calculate an average coefficient of variation for each experiment. Variation in sampling rate between individual traps was minimized by calibrating rotation rates with a stroboscope. The uncertainty in sampling rate was about 3%. Reported coefficients of variation combine the effects of greasing, counting, and sampling rate. Uncertainty due to nonhomogeneity of disease in the horizontal plane is difficult to assess and is not included in the reported

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coefficients of variation.

Meteorological conditions. Wind speed was measured at 1.2, 2.3, 3.1, and 4.2 m above ground level by Thornthwaite sensitive cup anemometers at location 1 in Fig. 1, and at 3.5 m height with three mutually perpendicular Gill propeller anemometers at location 2. Wind direction was measured at 2 m height with a sensitive vane at location 3. Measurements obtained with the propeller anemometers and the vane were recorded about every 3 sec on a Fluke data logger during selected 10-min periods when other measurements were being made. The indication of the totalizing cup anemometers was recorded every 10 min. Solar irradiance was measured with a LI-COR pyranometer and relative humidity was measured outside the crop with a forced-ventilated psychrometer.

Escape of spores. In calculating the number of spores that escape from the crop per unit area and time, we assumed that the vertical diffusion of spores is controlled by the vertical diffusivity of the air (10) and set the diffusivity of spores K_s equal to the diffusivity of momentum K_m. The K_m was calculated as the friction velocity

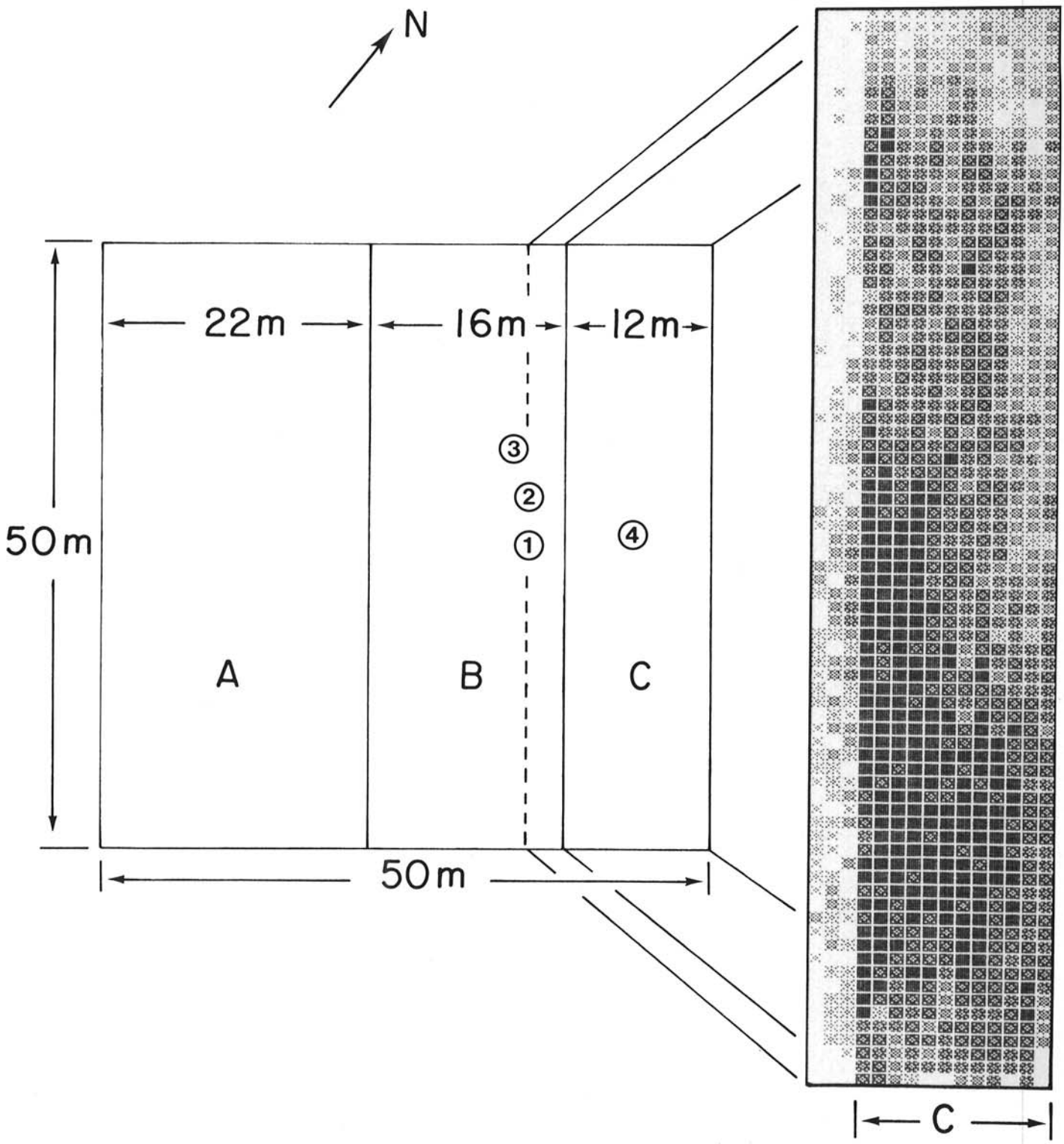

Fig. 1. Diagram of tobacco field showing the location of spore traps and wind instruments. Areas **A, B,** and **C** received transplants of broadleaf tobacco on 10 June, 2 July, and 23 July, respectively. Also shown is the level of disease on each plant in the 15 easternmost rows of tobacco on 4 September 1981. Absence of shading stands for no disease and six levels of shading are used that represent the disease severity rating scale of 0 to 6.

squared divided by the rate of change of the average horizontal wind speed (11), ie,

$$K_s = K_m = u_*^2/(\mathrm{d}u/\mathrm{d}z) \quad (1)$$

in which u_* is the friction velocity, u is the average horizontal wind speed and z is the vertical direction. The u_* was obtained directly from the wind profile measurements of the cup anemometers with the assumption that the zero-plane displacement height was 0.7 of crop height. The u_* is also equal to $\sqrt{|[u'w']|}$ (Ref. 11), in which u' and w′ are the deviations from the mean horizontal and mean vertical wind speed and are measured by the propeller anemometers. The bold face square brackets signify an average over time and the vertical lines signify the absolute value. We used the measurements of the propellers to check the value of u_* obtained from the cup anemometers.

The vertical flux of spores F_s (spores per square meter per second) was calculated as

$$F_s = -K_s\,(\partial C/\partial z) \quad (2)$$

in which the vertical gradient of spore concentration $\partial C/\partial z$ was determined from the measurements of spore concentration at various heights. Equation 2 is applied above the crop and we have ignored sedimentation under gravity which, at 1–2 m above the crop, reduces F_s by only about 10%.

Far from the edge of and just above an extensive and uniformly diseased crop, the vertical variation of both wind speed and spore concentration is approximately logarithmic, ie,

$$u = (u_*/k)\ln[(z-D)/z_0] \quad (3)$$

and

$$C = A + B\ln(z-D) \quad (4)$$

in which D is displacement height, u_* is friction velocity, $k = 0.4$ is von Karman's constant, and A and B are constants determined by fitting equation 4 to the data by least squares regression. In general, the D for spore concentration may not be the same as the D for wind speed; nevertheless, by using the same D we obtained good fits (r^2 between 0.93 and 0.99) to the data. In this case, F_s is constant with height in the first few meters above the crop and is calculated simply by

$$F_s = -k\,u_*\,B. \quad (5)$$

Equation 5 contains the product of the slopes of regression lines for u and C. The uncertainty in F_s was calculated as the sum of the relative errors at the 95% level of confidence of the standard error of these slopes (3). In one case, the spore concentration profile was better described by a power law and for this case, F_s was calculated by both equations 2 and 5. By comparing the two methods of calculation, we obtained another estimate of the uncertainty in our determination of F_s in that case.

Mathematical model. To extend the generality of our observations we also calculated spore transport among and above tobacco plants by using a mathematical model whose main elements have been described previously (2,6). The escape of spores from a crop was calculated by using an equation that balances horizontal and vertical transport of spores by the wind, deposition to the crop and ground, and the release of spores to the air by the diseased crop. For a large, uniformly diseased field, this balance can be expressed as

$$u\,(\partial C/\partial x) = \partial[K_s(\partial C/\partial z) + \mathrm{v}C]/\partial z - DC + Q \quad (6)$$

in which v (meters per second) is the settling speed of a spore in still air and D is the rate (per second) of particle deposition per unit volume of canopy. $Q(z)$ is the number of spores released per unit time into the air per unit volume of standing diseased crop plants where the dependence of Q on the vertical coordinate z takes into account the vertical variation in numbers of sporulating lesions on the plants. Above the crop, both D and Q are zero. The direction of x is downwind and u, C, and K_s have the same meanings as before.

We approximated the derivatives in equation 6 by finite differences and integrated numerically. Starting with zero concentrations at $x = 0$, we estimated the right side of equation 6 at x from the concentrations at the previous x (9). We assumed that the rate of deposition of spores on the ground was $\mathrm{v}C(x,0)$. At the top of the integration grid we assumed that the change in flux of spores with height divided by the flux was a constant. The diffusivity K_s and the wind speed u were taken to be constant below 0.4 of crop height and to increase linearly from there to the top of the crop. Above the crop we took K_s to increase linearly and u to increase logarithmically with height (6). Deposition to the crop was by sedimentation and impaction (2).

RESULTS

Disease severity. Blue mold first appeared in mid-August. The disease developed hardly at all in the first two plantings (areas A and B, Fig. 1), but developed extensively in the latest planting (area C, Fig. 1) where the still expanding leaves were more susceptible. By 25 August the disease had spread to approximately 25% of the plants in area C, mostly at its southwesterly end with only 10 lesions on the most severely diseased plants. By 4 September, lesions were present throughout area C of the field and disease severity, expressed on a scale of 0 to 6 for each plant, is shown in Fig. 1 by level of shading. After 4 September, the general distribution of disease was little changed although the number of lesions increased on plants throughout area C. On 10 September most of these plants were at or above the 4 rating. Individual plants, selected by eye to represent the least, moderate, and severest disease present at that time, had 19, 119, and 127 lesions, respectively. On 17 September most plants had many more than 50 lesions, and individual plants, again selected to represent the least, moderate, and most severe disease incidence at that time, had 143, 200, and 399 lesions, respectively. By 22 September, disease had not increased further and new lesions were not appearing, indicating that sporulation was near an end. This assessment shows that there was a high level of disease throughout our spore trapping period.

Over the entire period of 4 September to 22 September the greatest number of lesions occurred in the lower part of the crop canopy. Plants were about 0.7 m tall on 4 September, and by 9 September had reached their full height of about 1 m. About 80% of the lesions occurred in the bottom two-fifths of the canopy. Only about 2% of the lesions were in the top two-fifths of the canopy and the remaining 18% of the lesions were in the middle fifth of the canopy.

The number of spores per freshly sporulating lesion determined on 9 September was 196,000 ± 39,000 or about 62,000 spores per square centimeter of lesion. We tried to conduct our experiments on days when weather conditions suggested that sporulation would be near this level and avoided days when sporulation was likely to be poor.

Time of peak spore release. Peak spore concentrations occurred around 1000 hours EST on two occasions, one over volunteer seedlings on 24 June 1981, and one inside a shade tent on 28 August 1979. On another occasion inside a shade tent on 27 August 1979, the peak concentration occurred between 1200 and 1300 hours EST. The hour of peak spore concentration in 1979 and 1981 occurred much later in the day than in seedbeds in June 1955 (13). Others have shown that conidia of *P. tabacina* are released when the relative humidity drops (5,8). In Fig. 2, we show the relative humidities for a given level of relative spore concentration (based on the maximum for the day) on different days, including our data from 24 June 1981, 27 and 28 August 1979, and Waggoner and Taylor's (13) data from 2 and 8 June 1955. In all three years the maximum concentration occurred at 61 ± 5% RH with only about 10% of this maximum occurring at 77 ± 8%. In general, because of dilution proportional to wind speed, maximum spore concentration does not necessarily coincide with peak spore release. For *P.*

TABLE 1. Summary of meteorological data in the field during the spore trapping experiments

Expt. no.	Date (Sept.)	Time[a] (hr)	D[b] (m)	z_0[b] (m)	u_*[b] ($m \cdot s^{-1}$)	r^2	$\sqrt{\lvert[u'w']\rvert}$[c] ($m \cdot s^{-1}$)	$u_{4.2}$[c] ($m \cdot s^{-1}$)	Wind direction[d] (degrees)	Irradiance ($W \cdot m^{-2}$)
1	2	1125–1305	0.45	0.03	0.12	0.9999	...	1.5	101	...
2	4	0848–1048	0.45	0.06	0.20	0.9987	0.20	2.0	82	210 ± 70
3	4	1100–1300	0.45	0.05	0.18	0.9996	0.22–0.32	2.0	99	490 ± 280
4	9	1100–1300	0.70	0.03	0.33	0.9998	0.26–0.35	3.7	337	770 ± 210
5	17	1000–1300	0.70	0.02	0.12	0.9915	0.12	1.2	335	630 ± 280
6	22	1000–1300	0.70	0.01	0.19	0.9993	0.37	2.7	216	490 ± 210

[a] Time (24-hour clock, Eastern Standard Time) during which spores were trapped.
[b] D is zero-plane displacement height, z_0 is the roughness height, and u_* is the friction velocity of equation 3 for the vertical variation of horizontal wind speed. D was set at 0.7 of crop height and z_0 and u_* were obtained by regression analysis.
[c] $\sqrt{\lvert[u'w']\rvert}$ is an independent measure of u_* obtained from the Gill anemometers and $u_{4.2}$ is the average horizontal wind speed at 4.2 m height.
[d] Wind direction was measured clockwise from 0° at the top of Fig. 1.

TABLE 2. Summary of spore concentration profiles and the vertical flux of spores F_s estimated by equation 5

Height (m)	Spore concentration (spores per cubic meter)					
	Expt 1	Expt 2	Expt 3	Expt 4	Expt 5	Expt 6
0.75	384.6	75.3	248.3	...	...	...
1.0	...	...	...	130.7	181.7	23.2
1.5	128.0	42.2	131.7	71.5	115.3	10.8
2.0	69.3	16.3	95.8	34.7	84.8	3.7
3.0	54.0	11.7	67.9	16.9	51.1	1.2
4.0	32.1	8.3	35.5	13.8	46.1	0.9
cv(%)[a]	10	15	8	9	12	32
$B(m^{-3})$[b]	−141.5	−28.7	−85.3	−41.3	−58.6	−9.7
r^2	0.93	0.95	0.99	0.97	0.98	0.93
F_s(spores $m^{-2} \cdot s^{-1}$)[c]	6.9 ± 1.5	2.3 ± 1.2	6.1 ± 0.7	4.3 ± 0.9	2.8 ± 1.3	0.8 ± 0.2

[a] Coefficient of variation.
[b] B is a constant describing the spore concentration profiles defined by equation 4.
[c] Estimate ±95% confidence limits.

tabacina spores, however, they seem to be strongly correlated; in our measurements, spore concentrations increased with decreasing RH even though wind speed increased. In Australia, Hill (5) also compared the time of day and relative humidity with concentration of spores in the air. Using data taken from the graphs in his paper, it appears to us that maximum release in his experiments also occurred when RH was about 62 ± 8%. Thus, in our observations in Connecticut in 1979 and 1981, in Waggoner and Taylor's (13) observations in Connecticut in 1955 and in Australia (5) spore release seems to be synchronized with changes in RH.

Meteorological conditions. The variation of the average horizontal wind speed with height followed the logarithmic law given by equation 3. With D set at 0.7 of crop height, the parameters z_0 and u_* were obtained by fitting equation 3 to the data. These are shown in Table 1 with the resulting coefficients of determination r^2. For comparison with u_* we have shown $\sqrt{\lvert[u'w']\rvert}$ obtained from the propeller anemometer data during selected 10-min intervals. Considering that u_* was determined over 120 min while $\sqrt{\lvert[u'w']\rvert}$ was determined over 10 min, the overall agreement between them is quite good. Also shown in Table 1 is the mean wind direction, the average speed at 4.2 m above ground level, $u_{4.2}$, and the average solar irradiance during the experiment.

Concentration of spores and numbers escaping. Spores were trapped between 0900 and 1300 hours when RH was favorable for peak spore release. The concentration of spores trapped near the top of and above the tobacco canopy during six experiments are shown in Table 2. The concentration of spores ranged from 384.6 m^{-3} at 0.75 m above ground level to 0.9 m^{-3} at 4.0 m above ground level. The data from these experiments were used to calculate spore escape. The concentration data, when fitted to equation 4 by regression using the corresponding D values from Table 1, yielded Bs ranging between about −10 and −140 spores per cubic meter and r^2s between 0.93 and 0.99 (Table 2). The vertical flux of spores calculated by equation 5 ranged from about one to seven spores per square meter per second.

Escape of spores calculated by the mathematical model. Calculations of spore concentration were made using equation 6 for values of u_* of 0.13, 0.26, and 0.39 $m \cdot s^{-1}$ corresponding to wind speeds at 1 m above the canopy (u_1) of 1, 2, and 3 $m \cdot s^{-1}$. Downwind from the windward edge of the diseased crop, spores are contained in a boundary layer whose thickness increases with distance (11). By 50 m downwind, the growth of the boundary layer has slowed considerably and the vertical flux of spores at 1 m above the crop has approached a nearly constant value representative of an extensive crop. By assuming that about 290 spores per square meter per second (see Discussion) were released inside the crop we calculated spore concentration profiles and vertical fluxes above the crop at 20 m downwind that were in reasonably good agreement with those found in experiments 1, 3, and 5. At 50 m and beyond the calculated flux at 1 m above the crop for this amount of spore release approached the constant values of 9, 15, and 18 spores per square meter per second for u_1 = 1, 2, and 3 $m \cdot s^{-1}$, respectively.

DISCUSSION

The vertical flux of spores escaping the crop, F_s, depends both on turbulence and on the rate of spore release, Q. The effect of Q on F_s is most clearly seen by comparing experiments 2 and 3. Since both were conducted on 4 September, the amount of sporulation is not a variable. Moreover, the average wind speed and turbulence, as measured by u_* were essentially the same during both experiments (Table 1). In experiment 2, spores were trapped between 0848 and 1048 hours EST when the RH decreased from 78 to 66%, dropping below 70% only during the last half hour of trapping. In experiment 3, spores were trapped between 1100 and 1300 hours EST when the RH was about 64% for most of the trapping period, dropping to 57% during the last quarter hour of trapping. Despite the wind speed and turbulence being essentially the same, the F_s in experiment 3 was about 2.7 times greater than F_s in experiment 2. Reference to Fig. 2 suggests that this difference was due to more spores being released during experiment 3 when the RH was lower. A low value of F_s also can be due to poor sporulation as in experiment 6 in which RH was a favorable 65 to 61%, but the disease had nearly run its course and sporulation was declining.

Our method of calculating F_s by using equation 5 requires that the measurements of wind and spore concentration be made far from the upwind edge of a uniformly diseased crop. Ideally, for the height of our anemometers, the distance from the upwind edge of the crop should be ~200–400 m. Such large distances were not available in our crop (Fig. 1); nevertheless, wind data were fitted quite well by equation 3. This is probably because the average roughness of the surrounding vegetation and obstacles—a 1-m-tall tobacco crop to the southeast; a 1.5–2.0-m-tall, widely spaced, evergreen tree plantation to the east; a slight grass-covered knoll with a 1.5–2.0-m-tall structure to the northwest—may not have been greatly different from the roughness of the experimental

tobacco. Thus, changes in the momentum boundary layer as the wind passed over the experimental field may have been small, accounting for the good agreement between the wind profile data and equation 3. There did not seem to be any systematic effect of wind direction on the goodness of fit (Table 1). Moreover, at a height of 3.5 m the average vertical velocity was usually less than ±1% of the average horizontal velocity and did not indicate any substantial or systematic divergence in the flow. Changes in surface roughness may partly account for the discrepancies between u_* estimated from mean wind profiles and from the Gill anemometers.

Although the presence of the surrounding vegetation apparently lessened the change in the momentum boundary layer as the wind blew over the tobacco, there was no sizeable source of spores of *P. tabacina* outside our field (Fig. 1), and the spore concentration boundary layer should have started abruptly at the edge of the crop. Our model of spore transport, equation 6, indicates that, within 2–3 m above the crop, the vertical spore concentration will gradually approach the logarithmic profile of equation 4 ($r^2 = 0.96$) after a downwind distance of 40–60 m. In our experiments, the edge of the diseased crop was at most 25 m, and sometimes was only about 6–8 m, upwind of the spore traps. Furthermore, disease severity was not entirely uniform (Fig. 1) as required by the model. Nevertheless, the C profiles were fitted quite well by equation 4.

In one case (experiment 1), the C profile was fitted better ($r^2 = 0.97$) by $C = Az^B$ than by the logarithmic law (see equation 4). In this case F_s, calculated by equations 1 and 2, decreased with height above the canopy from about 10 spores per square meter per second at the top of the canopy, to about five spores per square meter per second at 1 m above, and to about three spores per square meter per second at 2 m above the canopy. This comparison suggests that F_s for experiment 1 might be some 30% greater than the value given in Table 1. The concentration of spores in the air increases steadily downwind from the leading edge of disease as more and more spores are put into the air. Theoretically, F_s should increase indefinitely with downwind distance x, but for practical purposes the increase in F_s slows markedly, and by $x \cong 50$ m, the flux of spores above the crop approaches a constant value that depends on wind speed and turbulence. We calculated this F_s by letting the integral of $Q(z)$ over the height of the crop be 290 spores per square meter per second, a value that gave aerial concentrations in reasonable agreement with our measurements. Assuming 2×10^5 spores per lesion and 50 lesions per plant, a release of 290 spores per square meter per second corresponds to a release of about half of the available spores in 7 hr. Only a small fraction of these spores escape from the crop. For u_1s of 1, 2, and 3 $m \cdot s^{-1}$, some 97, 95, and 93%, respectively, of the spores released never leave the crop. Fewer spores leave the crop at lower wind speed because turbulence is less and settling under gravity is more important. We have only considered spore transport in neutral (11) atmospheric conditions. During conditions of high solar irradiance and light winds, buoyancy of the air could increase vertical spore transport beyond what we have calculated.

In summary, we measured maximum rates of escape of *P. tabacina* conidia from a small field of severely diseased tobacco of seven to 10 spores per square meter per second. We calculated that, for the same sporulation and spore release, the maximum rate of escape from an extensive area of diseased crop would be about 20 spores per square meter per second when wind speed 1 m above the crop is 3 $m \cdot s^{-1}$. In view of our simplifying assumptions concerning the spatial uniformity of wind and disease, this calculation should only be considered correct to within an order of magnitude. Nevertheless, this approximate value of spore escape seems a reasonable one for estimating the number of spores reaching uninfected fields.

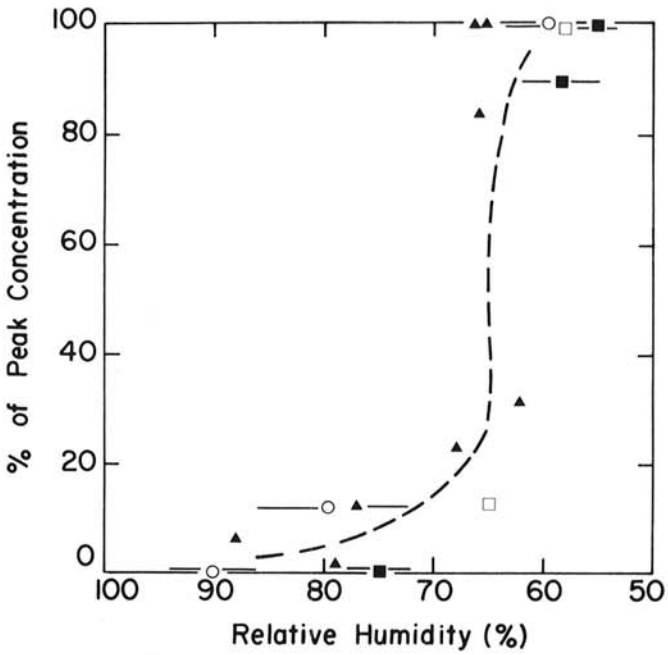

Fig. 2. Percent of peak spore concentration vs the average relative humidity when spores were trapped in the field. Data are from 24 June 1981 (O), 27 August 1979 (■) and 28 August 1979 (□). Also shown are data from Waggoner and Taylor (13) for spores trapped on 2 June and 8 June 1955 (▲). The horizontal bars indicate the change in RH during the trapping period. The dashed line was visually fitted to the data points.

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