Release of *Venturia inaequalis* Ascospores During Unsteady Rain: Relationship to Spore Transport and Deposition

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We thank Ray Pope, John Nardacci, and Gene Klimstra for help in collecting the samples and counting spores.

Accepted for publication 7 January 1992 (submitted for electronic processing).

ABSTRACT

Aylor, D. E., and Sutton, T. B. 1992. Release of *Venturia inaequalis* ascospores during unsteady rain: Relationship to spore transport and deposition. Phytopathology 82:532-540.

Aerial concentrations of ascospores of *Venturia inaequalis* were measured by using Burkard spore traps located in several orchards in North Carolina during 1977–1980. Rainfall amounts were recorded continuously with rain gages located either next to the spore traps or at nearby locations. During the course of 20 separate events, for which significant ascospore release occurred, rainfall rates, R, ranged from 0 to 19.6 mm h^{-1}, and 1-h average aerial ascospore concentrations ranged from 2 to 488 spores per cubic meter of air. A significant portion of the total ascospores (approx. 44%) were collected during hours when R was less than 0.25 mm h^{-1}. A model of spore transport and deposition was developed that accounts for deposition of ascospores as a function of R. This model was used to calculate spore deposition for the temporal values of R and aerial ascospore concentration, C, observed for each spore release event. Deposition was also calculated by using the average rainfall rate, R_{avg}, for each event. These two methods of calculation were compared by using the ratio of spore deposition calculated with R_{avg} to that calculated with the time history of R. This ratio ranged from 0.6 to 5.1 (mean = 1.5) at 0.5 km and from 1.0 to 10.6 (mean = 3.2) at 10 km downwind from a source. Our model presents a method for estimating deposition of spores released during rain and for estimating the range of error likely to occur in predicted spore deposition rates if average rainfall rates are used in lieu of actual time courses of rainfall in the calculation.

Additional keywords: apple scab, spore dispersal, washout of spores, wet deposition.

The ability to calculate deposition of pathogenic spores on susceptible tissue is of primary importance for calculating the potential number of disease infections on any crop. Ascospores of *Venturia inaequalis* (Cooke) G. Wint. are removed from the air and deposited on apple tissue by a combination of wet and dry deposition processes. Because of the relatively small settling speed (15) of *V. inaequalis* ascospores and the fact that they are released primarily during rain, washout of the spores from the air by rain is expected to contribute substantially to their deposition on the ground (2,7,9). Wet deposition becomes relatively more important as the distance from a source of spores increases, because dry deposition tends to be limited to the removal of spores near the ground, whereas wet deposition can remove spores from the entire depth of the spore cloud (7,11,32).

The major proportion of *V. inaequalis* ascospores becomes airborne during releases that are triggered by rain (6,16,20,21). Relatively few releases are triggered by dew (16), and some releases have been recorded during fair weather (16,27). Once release is initiated by rain, however, ascospores can continue to be released for some time after the rain has stopped (16).

The rate of deposition of particles to the ground depends strongly on the rate of rainfall (7,9,11,32). Therefore, in the calculation of the deposition of ascospores, it is important to account for the rate of rainfall (or lack of rain) during the period of spore release. Often, the only information available about rainfall for a site are the total amount and the duration of rain, which allow for only the average rate of rainfall for the entire period to be estimated. In this paper, we examine the time courses of ascospore release and rainfall. A model of spore transport and deposition is also presented; we use the model to estimate the number of ascospores that would be expected to be deposited in orchards located downwind from a source of ascospores for various time courses of rainfall and ascospore release. Finally, we use this model to assess the error likely to occur in estimating deposition when the actual time course of rainfall is replaced in the calculation by the average rainfall rate.

MATERIALS AND METHODS

Orchards and weather measurements. Orchards used in this study were included in the Integrated Pest and Orchard Management Systems (IPOMS) project established in 1976 in Henderson Co., NC (30). Orchards were selected for our study based on the presence of abundant apple scab inoculum in the overwintered leaves. The following are the orchards and the years they were monitored for the present study: 12 (Nielsen) in 1980; 22 (Jones) in 1979 and 1980; 27 (Pace) in 1977 and 1978; 47 (Stepp) in 1980; and Hill in 1979. The Hill orchard was not part of the IPOMS project but was an abandoned orchard adjacent to the Mountain Horticultural Crops Research Station in Fletcher, NC (MHCRS). Orchards 12, 22, 27, 47, and Hill were approximately 6.9, 2.0, 4.4, 3.9, and 1.0 ha in size, respectively.

Spore traps and rain gages were placed in orchards during March–May of 1977–1980. Rainfall was measured with a continuously recording, top-weighing, rain gage (Belfort Universal Rain Gage, Model 5-780, Belfort Instruments Co., Baltimore, MD). The sensitivity of these gages was to 0.25 mm of rain. Hourly average rainfall rates, R (millimeters per hour) were derived graphically from these recordings. Rain gages were located in orchards 27 and 47. Rainfall data for Hill orchard were obtained from MHCRS, approximately 200 m away; data for orchard 12 were obtained from an IPOMS station 1.8 km away; and data for orchard 22 came from an IPOMS station 3.8 km away.

Wind speed data for the following orchards were obtained from other nearby IPOMS weather stations (using a wind speed and direction sensor [Belfort Model 5-4857-B]) or the Asheville airport (approximate distance from the wind monitor in parentheses after the orchard number): 27 (5.0 km); 12 (1.8 km); 22 (3.8 km); 47 (12.1 km); and Hill (0.6 km). DeWit leaf wetness recorders (Valley Stream Farm, Orono, Ontario) were employed in some orchards and were used to help validate the start of rain, when amounts were less than the sensitivity of the rain gage. The weather-monitoring equipment and its deployment are described in more detail elsewhere (31).

Spore-trapping. The aerial concentration, C (ascospores per cubic meter), of *V. inaequalis* ascospores was measured approximately 0.45 m above the ground with Burkard volumetric spore traps (Burkard Scientific Sales, Lts., Rickmansworth, Hertfordshire, England). Traps were placed in representative areas in the orchards, usually near the weather stations or in the center of the blocks. Traps were adjusted to sample air at 10 L min^{-1}. We made a time mark through the trap orifice at both the start and end of the spore trap tape to precisely identify the beginning and end of the sampling period. The clocks for both the spore traps and the rain gages kept time accurate to within 30 min or less during the 7-day sampling periods. The trapping surface on the tapes was prepared by first coating the tape with 10% Gelvatol, allowing it to dry, and then overlaying this with an adhesive mixture of vaseline and paraffin wax to which a small amount of phenol was added. Tapes from the traps were cut into daily segments (48 mm), mounted on a glass slide, and ascospores were counted at ×250 by making one traverse through the center of each hourly exposure. Hourly counts were converted to hourly aerial concentrations by accounting for the proportion of the tape counted and the volume of air sampled.

Model. We restrict our examination of the effect of rainfall rate on spore deposition to transport distances of 0.5–15 km from a source. For this range of distances and for release periods lasting 1 h or more, it is reasonable to model spore transport as a continuous plume (1,10,14). Symbols used are listed in Table 1. In this case, the deposition flux D_F (x) (spores per square meter per second) of spores to the ground at downwind distance, x, can be expressed as the product of a deposition rate v_T (meters per second) and the aerial concentration $C(x)$ (spores per cubic meter) of spores at distance x (i.e, 1,2,5,7,9):

$$D_F = v_T \cdot C = v_T \cdot f \cdot Q_0 \cdot T \tag{1}$$

Here, v_T includes the effects of both wet (v_w) and dry (v_d) deposition processes (7); Q_0 (spores per second) is the rate of release of spores at the source; $f(x)$ is the fraction of Q_0 remaining airborne at x; and T (seconds per cubic meter) is a transport function that incorporates dilution of C by turbulent mixing and wind shear in the atmosphere (1,2,10). The total number of spores deposited per area of ground during a transport event, D (spores per square meter), is obtained by integrating D_F for the duration that the plume of spores is over a location. We assumed that spore release and rainfall rate remained constant for each hour during a spore release event and that the average wind direction remained constant during an entire release event. Thus, we obtained D by adding the contributions from D_F (× 3,600 s) for each hour to obtain a total for each event. We then compared these totals to assess the effect of variable spore release and rainfall rate on estimates of spore deposition as a function of distance.

Spore release vs. rate of rainfall. Because D is directly proportional to Q_0 and because we intend to use our model to estimate the effect of rainfall rate, R, on the deposit of ascospores, we need to examine how, if at all, Q_0 varies with R. Q_0 was not measured directly. However, the airborne flux of ascospores, F (spores per square meter per second), which, for a given source, is directly proportional to Q_0 (= q_0·source area; ref. 3), can be estimated by using our measurements. Therefore, for the purpose of examining the relationship between Q_0 and R, we used F as a surrogate measure of Q_0. F was calculated from the 1-h average wind speeds, U, and the corresponding 1-h ascospore concentrations, C, measured in several orchards, by multiplying the values of C and U (3). Values of F were matched with measured values of R, and the relationship between F and R was examined by using regression analysis.

Dilution. The concentration $C(x,y,z,t)$ for a Gaussian plume for spores released at ground level can be expressed as (1,7, 10,14,28,34):

$$C = [f(x)\, Q_0/(\pi\, U\, \sigma_y\, \sigma_z)] \exp(-y^2/2\sigma_y{}^2) \exp(-z^2/2\sigma_z{}^2) \tag{2a}$$

in which $\sigma_y(x)$ and $\sigma_z(x)$ are functions of x and are the standard deviations of the spore plume in the crosswind (y) and vertical (z) directions, respectively. U is the average wind speed in the x direction. The two exponential factors account for reductions in C away from the center of the plume. In examining the effect of rate of rainfall on spore deposition, we limit our attention to points in space where $y = z = 0$, for which the maximum of C is given by:

$$C_{\max} = C(x,0,0) = f(x)\, Q_0/[\pi\, \sigma_y\, \sigma_z\, U] \tag{2b}$$

TABLE 1. List of symbols used in this study

Symbol	Explanation (units)[a]
C	Aerial spore concentration (m^{-3})
d_D	Diameter of raindrops (mm)
d_s	Diameter of spores (mm)
D_F	Spore deposition flux at distance x downwind from a source (m^{-2} s^{-1})
D	Total number of spores deposited per ground area at distance x during a transport event (m^{-2})
E	Efficiency of impaction of spores on raindrops
f	Fraction of spores released at the source that remain airborne at x
F	Airborne horizontal flux of spores in the downwind direction (m^{-2} s^{-1})
g	Acceleration of gravity (m s^{-2})
h	Effective height of spore plume subject to precipitation scavenging (a function of x) (m)
H	Height of the top of the atmosphere's mixed layer (m)
H_P	Height of the bottom of the precipitation layer (m)
LAI	Leaf area index
N	Number of raindrops per unit volume of air with diameters between d_D and $d_D + d(d_D)$ (m^{-3}mm^{-1})
N_0	Parameter of Marshall-Palmer distribution (m^{-3} mm^{-1})
Q_0	Rate of release of spores by a source region (s^{-1})
q_0	Rate of release of spores per unit ground area within a source region (m^{-2} s^{-1})
r	Correlation coefficient
R	Rainfall rate (mm h^{-1})
S	Stokes' number (= $V_s\, V_D\, /\, g\, d_D$)
T	Atmospheric transport and dilution function (s m^{-3})
U	Mean horizontal speed of spores in the transport layer (m s^{-1})
V_s	Fall speed of a spore in still air (m s^{-1})
V_D	Fall speed of a raindrop in still air (m s^{-1})
v_d	Dry deposition velocity (m s^{-1})
v_w	Wet deposition velocity (m s^{-1})
v_T	Combined (dry + wet) spore deposition velocity (m s^{-1})
W	Crosswind width of the source region (m)
x, y, z	Coordinates of a Cartesian coordinate system in the downwind, crosswind, and vertical directions, respectively
x_0	A virtual upwind location of an area source that accounts for the finite size of the source in the Gaussian plume model (m)
X	Effective downwind distance equal to $x + x_0$ (m)
β	Parameter of the Marshall-Palmer distribution for raindrop size distribution (mm^{-1})
Γ	Washout coefficient for removal of spores from air by rain (s^{-1})
π	The constant, pi = 3.14159 . . .
σ_y, σ_z	The standard deviations of the spore plume in the crosswind (y) and vertical (z) directions, respectively (m)

Equation 2b shows that C_{max} decreases as the spore plume expands into an ever-increasing volume of air, characterized by the product of the standard deviations σ_y and σ_z. These measures of plume width and depth can be expressed as:

$$\sigma_y = a_1 \cdot X^{b_1} \qquad \text{(3a)}$$
$$\sigma_z = a_2 \cdot X^{b_2}$$

in which (35)

$$X = x_0 + x \qquad \text{(3b)}$$
$$x_0 = (W/4.3\ a_1)^{(1/b_1)}$$

W is the crosswind width of the source region. In the calculations presented here, we assumed that the atmosphere is neutrally stable (i.e., Pasquill stability class D [28]), so that $a_1 = 1.43 \times 0.1755$, $b_1 = 0.875$; $a_2 = 0.32$, $b_2 = 0.674$ (14,28,35). The factor 1.43 included in a_1 accounts for the added variance due to lateral swings of the plume that generally occur during 1 h (compared to 10 min for which the premultipliers and exponents given above were derived [14,35]). We found distance x_0 by treating an area source as a virtual point source located at an upwind distance determined by the size of the source (17,35). The distance accounts for the added variance in the cross-plume width due to W. In the calculations presented here, we took the source to be a square area 5 ha in size; thus W was 224 m.

Depletion of the spore cloud: The airborne fraction $f(x)$. The loss of spores from the spore cloud is directly proportional to aerial spore concentration C. This loss is due to both dry and wet deposition processes.

Dry deposition. If the atmospheric layer containing the spores is well mixed, then the fraction of the released spores that remain airborne after traveling a distance x (during a travel time $t = x/U$) during dry conditions is given by the source-depletion model of Chamberlain (1,2,5,7,19):

$$f(x) = Q(x)/Q_0 = \exp\{-(2/\pi)^{1/2}\,(v_d/U) \int_{x_0}^{x} [dx/\sigma_z(x)]\} \qquad (4)$$

in which the distance x_0 is such that $\sigma_z(x_0)$ specifies the initial growth of the plume of spores while air is passing over the source. In arriving at Equation 4, we carried out a crosswind integration over y from $-\infty$ to ∞ (19,36).

The degree of vertical atmospheric mixing, represented by $\sigma_z(x)$ in Equation 4, depends on the stability of the atmosphere, on surface roughness, and on wind speed. During rainfall, we expect the atmosphere near the ground to be neutral to slightly stable (28,33), as represented by the Pasquill stability classes D and E (14,28). The calculations given here are for stability class D. The mixing layer depth, H, is usually limited by a temperature inversion that marks the top of the atmospheric mixing layer. This may be as low as 100 m at night and as high as 2–3 km during the day (18). During springtime rains, it is reasonable for average values of H to be about 1,000 m and for average wind speeds in the mixed layer to be 10–20 km h^{-1} (D. E. Aylor, unpublished analysis of mixing height data for Albany, NY, supplied by the National Center for Climatic Data, National Weather Service, Asheville, NC). For the transport distances considered here, the vertical extent of the spore cloud should, for the most part, remain below H, and spores should travel from the source region to a distance of 10 km in 30 min to 1 h.

In deriving Equation 4, we assumed that spores are removed uniformly from all heights in the atmosphere. In the absence of rain, spores are removed mainly from air near the ground. Nevertheless, Horst (19) has shown that Equation 4 remains approximately correct as long as $v_d/U < 0.01$, and the stability of the atmosphere is nearly neutral. During dry conditions, the value of v_d is expected to range approximately between V_S and (2,8,12,26):

$$v_d = (1 + \text{LAI}) \cdot V_S \qquad (5)$$

in which LAI is the amount of leaf area per ground area, and V_S is the settling speed of an ascospore in still air. Thus, v_d for dry deposition on apple trees is expected to be about one to three times V_S (i.e., 0.002–0.006 m s^{-1} for *V. inaequalis* ascospores). For the calculations presented here, $v_d = V_S$.

Wet deposition. The rate of removal of spores from the air by washout during rain can be formulated in terms of a washout coefficient, Γ (s^{-1}), which depends on the efficiency of inertial impaction of spores on raindrops and on the rate that these raindrops sweep through the air (11,29,32). Γ can be expressed as (7,24,29):

$$\Gamma = \int (\pi/4)\, d_D^2\, V_D(d_D)\, E(d_S,d_D)\, N(d_D)\, d(d_D) \qquad (6)$$

in which E is the efficiency of impaction of spores on raindrops, and d_D and d_S are the diameter of raindrop and spore, respectively. V_D is terminal fall speed of a raindrop of diameter d_D, and $N(d_D)\ d(d_D)$ is the number of raindrops present per cubic meter of air with diameters between d_D and $d_D + d(d_D)$. In the following paragraphs, we use Equation 6 to arrive at an expression for Γ as a function of rainfall rate R (millimeters per hour), which will be used with Equations 1–5 to evaluate spore deposition in terms of R.

To evaluate Equation 6, we need to obtain expressions for $V_D(d_D)$, $E(d_S,d_D)$, and $N(d_D)$. We used nonlinear regression analysis to fit data for V_D vs. d_D presented by Englemann (11). We obtained the following expression ($r^2 = 0.998$):

$$V_D = 9 \cdot (1 - \exp[-0.5796 \cdot d_D^{1.234}]) \qquad (7)$$

in which the units of V_D and d_D are in meters per second and millimeters, respectively.

We assumed that all spores that impact on a raindrop are retained by the drop and, thus, E is equal to the collection efficiency of spores on raindrops. E is a function of the size of the spores and raindrops, which are combined in a dimensionless Stokes number, $S = V_S V_D/(g d_D)$, in which g is the acceleration of gravity. V_S of *V. inaequalis* ascospores is 2 mm s^{-1} (15). Thus, an effective "Stokes" particle diameter is 8.16 μm. We fitted the results of May and Clifford (25) for the efficiency of impaction on a sphere by nonlinear regression to yield ($r^2 = 0.998$):

$$E = 0.9/(1 + 0.51 \cdot S^{-1.26}) \qquad (8)$$

Finally, to evaluate the integral in Equation 6 in terms of R, we need to find a relationship between N and d_D as a function of R. For our calculations, we used the Marshall-Palmer distribution for raindrop sizes, which can be expressed as (23,29):

$$N = N_0 \exp(-\beta d_D) \qquad (9)$$
$$N_0(\text{m}^{-3}/\text{mm}) = 8{,}000$$
$$\beta\ (\text{mm}^{-1}) = 4.1\ R^{-0.21}$$

Equations 6–9 were used to calculate Γ for a range of values of R. These results were examined by using regression analysis to yield ($r^2 = 0.9998$):

$$\Gamma = 0.000272\ R^{0.7873} \qquad (10)$$

This equation has essentially the same functional dependence of Γ on R as the results calculated by May (24) and Chamberlain (7). When the diameter and the settling speed of a *Lycopodium* spore are substituted into Equations 6–9, the resulting equation for Γ agrees well ($r^2 = 0.967$; excluding one high intensity thunder shower) with the results of May's washout experiments using *Lycopodium* spores during frontal rain (24). It does overpredict substantially the washout coefficient observed during a high intensity (R = 23 mm h^{-1}) thunder shower (24); however, such a high value of R is well above those generally observed in this study. For a reasonable range of R of 1–15 mm h^{-1}, Equation 10 gives a range of 2.7×10^{-4}–2.2×10^{-3} s^{-1}. For these values of Γ, the concentration of *V. inaequalis* ascospores in the air would be expected to be depleted by 63% in 1.0–0.1 h (9).

Combined dry and wet depositions. Finally, because both dry and wet depositions are relatively small, we assume that they act independently and that their effects can be combined as a product of the individual probabilities of removal by wet and dry depositions to yield:

$$f(x) = \exp(-\Gamma x/U) \exp\{-\sqrt{(2/\pi)}\,(v_d/U)\int_{x_0}^{x} [dx/\sigma_z(x)]\} \quad (11)$$

For comparing wet and dry depositions, we found it convenient to rewrite Equation 11 as:

$$f(x) = \exp\{-(x/U)\cdot[\Gamma + \Gamma_d]\} \quad (12a)$$

in which

$$\Gamma_d = \sqrt{(2/\pi)}\,(v_d/x)\int_{x_0}^{x} [dx/\sigma_z(x)] \quad (12b)$$

is a time scale for dry deposition analogous to Γ for wet deposition. Whereas Γ is a constant, Γ_d is a decreasing function of x.

By analogy to a dry deposition velocity, Chamberlain (9) also defined a wet deposition velocity, v_w (meters per second), as:

$$v_w = \Gamma\, h \quad (13a)$$

in which

$$h = [1/C(x,0,0)]\int_0^{\infty} C(z)\, dz \quad (13b)$$

Finally, if we approximate σ_z by a "top hat" distribution (34) approximation to a Gaussian distribution so that $h = 0.5\sqrt{(2\,\pi)}$ $\sigma_z = 1.25\,\sigma_z$, we obtain:

$$v_w = 1.25\,\Gamma\,\sigma_z \quad (14)$$

Here, we have assumed that the depth of the precipitation layer H_P is greater than the vertical extent of the spore plume. Inspection of Equations 12 and 13 shows that the relative importance of wet compared to dry deposition increases with increasing distance from a source.

Calculated spore deposition. The relative contributions of dry and wet depositions during an ascospore release depend on the respective durations of these processes. We used the hourly values of C and R measured in orchards (cf. Materials and Methods) with our model (Eqs. 1–14) to examine how deposition might be expected to vary for observed, variable ascospore release and rainfall events. The observed values of R were used directly in the calculations, whereas the observed values of C were used to estimate values for the relative release of ascospores, Q_0, as a function of time; Q_0 for a particular hour was taken to be directly proportional to the fraction of the cumulative C trapped during that hour (Fig. 1). To facilitate our examination of the effect of rainfall on deposition, we kept the total release at the same value for all calculations and apportioned this total over the duration of a release in proportion to the observed time course of C. For each calculation, U was equal to 10 km h^{-1}, and the total release was taken to be 5,500 ascospores per square meter of orchard floor, which is within the range of values to be expected in moderately to heavily diseased orchards (13). Thus, D was calculated as the sum of individual 1-h values, each obtained by using the corresponding hourly values of R and a proportional part of Q_0 as described above. The transport portion of the model has not been validated for *V. inaequalis* ascospores. Nevertheless, the model is based on generally accepted principles of atmospheric

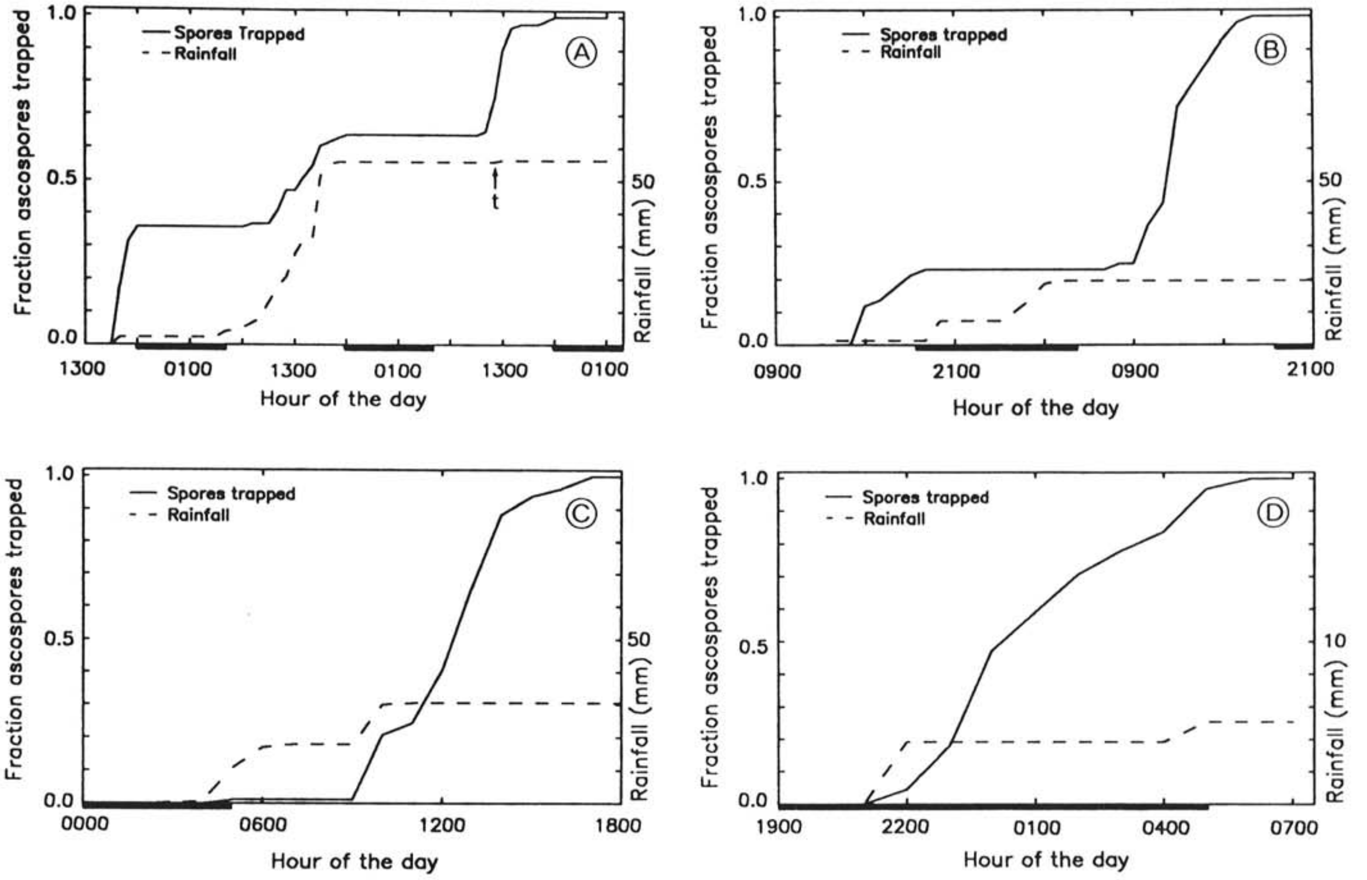

Fig. 1. Selected time courses of the cumulative 1-h average aerial concentrations of *Venturia inaequalis* ascospores and the cumulative amount of rainfall measured in this study. Periods of darkness are indicated by a bar just below the x-axis. t = Trace of rain (<0.25 mm). Measurements were made in the Pace orchard on **A,** 3–5 May 1978; **B,** 18–19 April 1978; **C,** 13 May 1978; and **D,** 30 April 1977.

transport processes (2,7,9-11,17,19,24,28,32) and does give a reasonable framework for estimating the effect of unsteady rainfall and ascospore release on ascospore transport and deposition.

We also calculated the deposition that would be expected to occur if R was assumed to be constant and equal to the average rainfall rate, R_{avg}, for the entire release period. Thus, we used values of C and R observed in practice to examine the uncertainty that this assumption could introduce into estimates of spore deposition.

RESULTS

Observed patterns of ascospore release. Temporal patterns of the cumulative hourly aerial spore concentrations, C, and the corresponding cumulative rainfall amounts for four ascospore release events are shown in Figure 1. The data for the other 16 events analyzed are shown in Table 2. In general, there was a good temporal correspondence between ascospores in the air and the occurrence of rain during the daylight hours (Fig. 1A–C;

TABLE 2. Hourly values of the percentage, P (%), of the total number of *Venturia inaequalis* ascospores collected for a spore release event by the Burkard spore traps and the corresponding rainfall rates, R (mm h^{-1}), measured in apple orchards for 16 of the 20 individual spore release events analyzed (the other four events that were analyzed are shown in Fig. 1)

	Pace[a] 23 Apr 1977		Pace 24 Apr 1977		Pace 26 Apr 1978		Stepp 23 Apr 1980	
Hour[b]	P[c]	R[d]	P	R	P	R	P	R
0100	0.3	0.00	1.1	7.37	0	0.00	...	...
0200	5.5	0.00	0.6	0.25	0	0.25	0	0.00
0300	1.3	0.25	0.8	0.51	1.6	0.51	0	0.25
0400	1.1	0.25	0.6	0.00	7.7	0.51	0	0.00
0500	1.3	0.00	0.6	0.00	6.0	0.25	0	1.02
0600	1.4	3.30	0.2	0.00	20.2	1.52	0	3.05
0700	0.9	5.08	0.6	0.00	7.7	1.02	0	3.30
0800	4.1	7.62	4.4	0.00	3.3	1.02	0	3.81
0900	3.3	2.54	7.9	0.00	7.7	0.76	3.6	2.54
1000	2.8	0.51	8.8	0.00	14.2	1.78	3.6	5.84
1100	8.2	0.00	8.5	0.00	15.8	1.27	14.3	1.78
1200	2.2	1.27	6.3	0.00	12.6	1.27	14.3	4.83
1300	14.5	0.00	2.2	0.25	3.3	1.27	0	3.30
1400	3.8	6.10	1.9	0.00	...	...	0	2.79
1500	1.6	0.51	1.1	0.00			21.4	1.78
1600	1.4	0.25	...	...			17.9	1.02
1700	0	0.25					10.7	1.02
1800	0	0.25					7.1	0.51
1900	0	0.25					3.5	1.27
2000	0	0.00					0	0.00
2100	0	0.00					0	0.00
2200	0.2	0.00					3.5	0.00
2300	0	0.25					...	...
2400	0.6	0.00						

	Stepp[a] 11 Apr 1980		Stepp 12 Apr 1980		Hill 2 Apr 1979		Hill 3 Apr 1979	
Hour[b]	P[c]	R[d]	P	R	P	R	P	R
0100			0	0.00			0.6	3.05
0200			0	0.00			0	2.29
0300	...	...	0	0.00			0	0.76
0400	0	0.00	0	0.00			0.6	3.30
0500	0	1.27	0	0.00			7.9	1.27
0600	0	1.27	0	0.76			18.5	3.30
0700	0	1.02	0	0.51			21.3	4.32
0800	1.7	0.25	0	0.00			6.7	3.30
0900	1.2	0.76	0	0.00			5.1	4.83
1000	1.2	3.05	0	0.00			1.1	9.65
1100	0.6	3.81	0	0.00			0	2.79
1200	5.2	6.35	1.7	0.51			2.2	0.00
1300	57.5	5.08	1.7	2.54			2.8	0.00
1400	6.3	2.03	1.1	1.78	...	...	0	0.00
1500	1.7	0.25	5.7	0.00	0	0.00	0	0.00
1600	2.9	0.00	7.5	0.00	6.2	0.00	0.6	0.00
1700	2.9	0.00	...	...	19.7	0.00	...	...
1800	0	0.00			2.3	0.25		
1900	0.6	0.00			0.0	0.00		
2000	0.6	0.00			0.6	0.00		
2100	0	0.00			0	0.00		
2200	0	0.00			1.1	0.76		
2300	0	0.00			1.1	1.02		
2400	0	0.00			1.7	2.54		

	Hill[a] 4 Apr 1979		Hill 11 Apr 1979		Hill 12 Apr 1979		Hill 13 Apr 1979	
Hour[b]	P[c]	R[d]	P	R	P	R	P	R
0100	...	...			0	0.76	0	5.08
0200	0	0.00			0	0.76	0	5.08
0300	1.0	0.00			0	1.27	0	1.78
0400	2.1	2.54			0	1.52	0	1.27
0500	3.1	3.81			0	1.02	0.3	1.02
0600	2.9	4.32			0	0.25	0.8	0.25
0700	4.4	5.84			1.1	1.02	0.3	0.00
0800	31.9	2.54			7.3	0.51	4.2	0.51
0900	16.2	1.78			8.9	0.51	10.5	0.51
1000	23.5	0.00			9.2	0.00	8.9	1.02
1100	9.1	0.25			18.1	0.00	10.7	0.00
1200	2.9	0.25			3.1	0.00	0.8	2.54
1300	1.0	0.25			2.9	0.51	1.1	3.81
1400	1.8	0.00	...	...	0.3	1.27	0	2.54
1500	...	...	0	0.00	0	2.03	0.3	0.00
1600			0.8	0.00	0	1.27	0.5	0.00
1700			1.6	0.25	0	0.00	0.3	0.00
1800			1.3	0.25	1.6	0.00	...	...
1900			0.5	0.25	1.1	0.00		
2000			0.3	0.25	0.5	0.00		
2100			2.1	0.25	0	0.00		
2200			0	0.51	0.3	3.81		
2300			0	0.25	0.5	3.81		
2400			0.3	0.51	0	6.35		

	Hill[a] 25 Apr 1979		Hill 26 Apr 1979		Hill 27 Apr 1979		Jones 3 Apr 1979	
Hour[b]	P[c]	R[d]	P	R	P	R	P	R
0100			0	3.05	0.2	0.00	0	3.81
0200			0	0.76	0.3	0.00	0	0.00
0300			0	0.00	0.4	0.00	0	0.25
0400			0	1.27	0.2	0.00	0.5	1.02
0500			0	1.78	0	0.00	0.5	2.54
0600			0	0.51	0.2	0.00	0.3	3.81
0700			0	0.25	0	0.00	1.9	3.05
0800	...	...	0	0.25	0.2	0.00	14.8	2.79
0900	0	0.00	0.5	2.29	...	...	27.3	5.59
1000	0.2	0.00	0	0.00			12.5	8.13
1100	11.6	0.00	0.5	0.00			1.3	2.03
1200	19.6	0.00	1.3	0.00			1.3	0.51
1300	20.9	0.00	0.7	0.00			4.5	0.51
1400	13.8	0.25	1.3	1.52			3.3	0.25
1500	16.7	1.02	1.5	13.46			1.8	0.00
1600	3.3	0.25	0.4	0.00			0.3	0.00
1700	0.4	0.51	0.2	0.00			0	0.00
1800	2.9	1.02	0.4	0.00			0	0.00
1900	0	1.27	0.4	0.00			0	0.00
2000	0.2	1.27	0.4	0.00			0	0.00
2100	0	3.30	0.3	0.00			0	0.00
2200	0	0.51	0.2	0.00			0	0.00
2300	0	0.25	0.9	0.00			0	0.00
2400	0	5.59	0	0.00			0	0.00

[a] Name of the apple orchard and the date on which data were recorded.

[b] Hour of the day (Eastern Standard Time) based on a 24-h clock.

[c] P was derived from hourly values of aerial spore concentration measured by Burkard spore traps. The model calculations use the fractional value (i.e., $P/100$).

[d] R was derived from traces of rainfall amount measured by a recording rain gage with a minimum sensitivity of 0.25 mm.

Table 2). Ascospore release generally ceased during darkness and often resumed during the next daylight period. Only in one out of the 20 events examined did a significant proportion of a spore release occur during darkness (Fig. 1D). On several occasions, spore release continued for several hours after rain had stopped falling (e.g., Fig. 1B,C). On one occasion (Table 2, Hill orchard, 25 April 1979), ascospore release appeared to start several hours before the start of rain. Although our rain gage did not indicate rain before 1400 h, the nearby (3 km) Asheville airport indicated that conditions were foggy and that a trace of rain occurred during each hour between 1000 and 1300 h, with measurable rain starting at 1400 h. Apparently, these traces of rain triggered the ascospore release.

Spore release vs. rate of rainfall. About 44% of the total number of ascospores sampled were deposited during hours when R was less than 0.25 mm (Fig. 2). R was less than 0.25 mm during 45% of the 1-h periods in which ascospores were trapped ($n =$ 345 events). No significant relationship was found between F and R ($F = 0.185 + 0.0042\ R$; $r^2 = 1.5E - .05$; $n = 170$); therefore, the assumption used in our model that Q_0 and R can be treated

TABLE 2. *Continued*

Hour[b]	Jones[a] 4 Apr 1979		Jones 11 Apr 1979		Jones 12 Apr 1979		Jones 13 Apr 1979	
	P[c]	*R*[d]	*P*	*R*	*P*	*R*	*P*	*R*
0100	0	0.00			0	0.25	0.9	5.08
0200	0	0.00			0	0.76	2.7	3.81
0300	0	0.00			0	0.25	2.2	3.81
0400	0	0.64			0	0.25	0.9	0.76
0500	0	3.18			0	0.00	0	1.02
0600	0.3	5.33			0	0.25	0	0.25
0700	0.5	3.56			0	0.25	0	0.25
0800	1.6	2.54			2.2	0.25	0	0.25
0900	2.7	2.54			0	0.25	0.4	1.02
1000	6.1	1.78			0	0.51	7.1	0.00
1100	2.4	0.25			0.9	0.25	2.6	2.79
1200	4.2	0.00			3.6	0.00	19.6	6.35
1300	1.6	0.51			10.7	0.51	12.4	5.08
1400	2.6	0.25	...	...	2.7	0.25	1.8	5.08
1500	4.8	0.25	0	0.00	0.4	3.30	9.8	0.00
1600	1.6	0.00	11.1	0.00	0	0.51	0.9	0.00
1700	0.8	0.00	2.2	0.25	0	2.54	0.9	0.00
1800	0.5	0.00	0	0.25	0	0.00	0.9	0.00
1900	...	...	0	0.00	0.9	0.00	0	0.00
2000			0	0.00	0	0.00	0	0.00
2100			0	0.13	1.3	7.11	0.4	0.00
2200			0	0.89	0	1.27	0	0.00
2300			0	1.02	0	5.08	0	0.00
2400			0	0.25	0	11.43	0.4	0.00

Hour[b]	Jones[a] 12 Apr 1980		Jones 13 Apr 1980		Jones 14 Apr 1980		Nielsen 28 Mar 1980	
	P[c]	*R*[d]	*P*	*R*	*P*	*R*	*P*	*R*
0100			0	0.00	0	0.00		
0200			0	0.00	0	0.00		
0300			0	0.00	0.8	0.00		
0400	...	...	0	0.51	0	0.51	...	...
0500	0	0.25	0	0.76	0.7	0.00	0	0.00
0600	0	0.25	0	0.51	0	2.54	0	2.29
0700	0	0.13	0	0.25	0.8	0.00	0	2.29
0800	0.8	1.40	0.8	0.25	0	0.00	3.9	3.05
0900	0.8	3.05	0	0.00	0	0.00	5.9	2.29
1000	0.8	5.08	0	0.00	3.2	0.00	9.8	2.79
1100	15.1	6.35	1.6	0.25	12.7	0.00	7.8	3.81
1200	8.7	6.86	0.8	1.78	16.7	0.00	7.8	3.81
1300	11.9	2.29	3.2	1.02	8.7	0.00	31.4	3.81
1400	3.2	0.00	2.3	0.00	...	...	9.8	1.27
1500	0	0.00	3.1	0.00			7.8	1.27
1600	2.4	0.00	0	0.00			9.8	1.27
1700	0.8	0.00	0	0.51			3.9	2.79
1800	0	0.00	0	8.64			2.0	0.00
1900	0	0.00	0	7.62			...	...
2000	0	0.00	0	4.32				
2100	0	0.00	0	0.25				
2200	0	0.00	0	7.11				
2300	0	0.00	0	3.05				
2400	0	0.00	0	6.35				

Hour[b]	Nielsen[a] 30 Mar 1980		Nielsen 12 Apr 1980		Nielsen 13 Apr 1980	
	P[c]	*R*[d]	*P*	*R*	*P*	*R*
0100	...	...	0.1	0.00	0	0.00
0200	0	0.00	0	0.00	0	0.00
0300	0	1.78	0.3	0.00	0	0.00
0400	0	0.51	0.1	0.00	0	0.00
0500	0	0.25	0.2	0.76	0.2	0.25
0600	0	0.00	1.7	1.27	0.6	0.76
0700	0	0.51	17.6	1.02	1.8	0.25
0800	1.7	2.03	10.2	0.25	6.2	0.25
0900	17.2	0.25	2.1	1.02	2.4	0.00
1000	18.9	0.25	0.3	3.30	33.5	0.00
1100	20.7	0.76	0	2.54	18.0	0.00
1200	27.6	0.00	0	6.35	0.8	0.76
1300	5.2	0.00	0	5.33	0.8	1.52
1400	5.2	0.00	0	1.02	2.3	1.27
1500	1.7	0.00	0	0.00	0.9	0.00
1600	1.7	0.00	0	0.00	...	...
1700	...	...	0	0.00		
1800			0	0.00		
1900			0	0.00		
2000			0	0.00		
2100			0	0.00		
2200			0	0.00		
2300			0	0.00		
2400			0	0.00		

Hour[b]	Nielsen[a] 26 Apr 1980		Nielsen 29 Apr 1980	
	P[c]	*R*[d]	*P*	*R*
0100	0	0.25		
0200	0	0.25		
0300	0	0.00		
0400	3.6	0.25		
0500	1.8	1.78		
0600	5.4	4.32	...	...
0700	1.8	1.02	0	0.25
0800	7.1	0.00	8.0	0.25
0900	25.0	0.00	38.0	0.51
1000	19.6	0.00	18.0	0.00
1100	3.6	0.00	19.0	0.00
1200	17.8	0.00	14.0	0.00
1300	14.3	0.00	3.0	0.00
1400	...	...	0.0	0.00
1500			0.0	0.00
1600			...	...
1700				
1800				
1900				
2000				
2100				
2200				
2300				
2400				

[a] Name of the apple orchard and the date on which data were recorded.

[b] Hour of the day (Eastern Standard Time) based on a 24-h clock.

[c] P was derived from hourly values of aerial spore concentration measured by Burkard spore traps. The model calculations use the fractional value (i.e., $P/100$).

[d] R was derived from traces of rainfall amount measured by a recording rain gage with a minimum sensitivity of 0.25 mm.

as independent variables seems to be justified. Considering all periods when ascospores were trapped, we found that the average value of R was 1.2 mm h^{-1}, and considering only those release events that occurred while it was raining, we found that the average R was 2.5 mm h^{-1}. Generally, R was below 15 mm h^{-1}. The maximum R, which was observed once for 1 h in our study, was 19.6 mm h^{-1}.

Calculated patterns of spore deposition. We calculated spore deposition, D, at several distances downwind from a source by using the model Equations 1–14. Generally speaking, when the value of R was high, the higher D was near the source and the lower D was far from the source (Fig. 3). The main exception to this is that D during dry conditions ($R = 0$) tended to be less than D calculated for rates of rainfall as high as 10 mm h^{-1} up to distances of 8–9 km from a source. As a further illustration of the model, two additional calculations are shown for the cumulative spore deposit. In the first, equal contributions (20%) to the aerial spore load are assumed to be released at each value of R (i.e., 0, 1, 2, 5, 10 mm h^{-1}; each lasting 20% of the total time). In the second, the entire deposit is assumed to occur during a steady rain with R equal to the average of the five values of R used in the previous calculation (i.e., $R = 3.6$ mm h^{-1}).

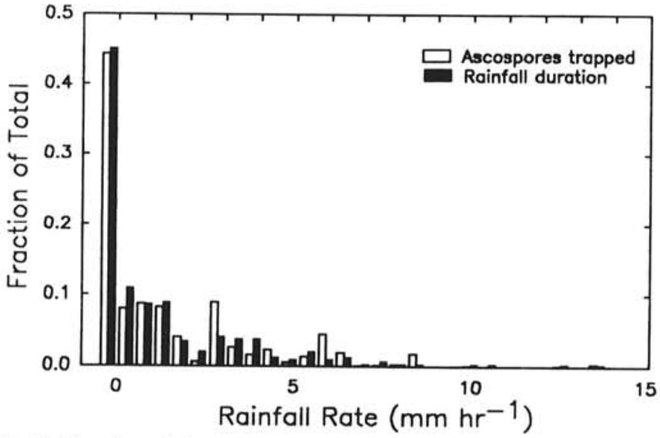

Fig. 2. Fraction of the ascospores caught by Burkard spore samplers in orchards and the fraction of the time (during periods when ascospores were caught) that the value of rainfall rate, R, was in a particular range; both are plotted as a function of rainfall rate (class interval = 0.5 mm h^{-1}). One 1-h period of rainfall (fraction = 1/345) at $R = 19.6$ mm h^{-1} with few ascospores trapped (fraction = 0.0004) is not shown.

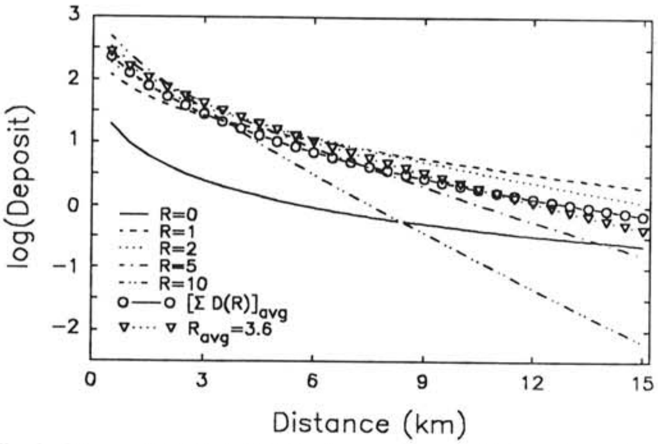

Fig. 3. Calculated relative deposit of ascospores vs. distance downwind from a 5-ha source using the model equations with an average wind speed of 10 m s^{-1} and steady rainfall rates, R, of 0, 1, 2, 5, and 10 mm h^{-1}. Also shown are the relative amounts of spore deposit calculated by adding equal contributions (one-fifth of the amount calculated for each of the five Rs) for each of these Rs (labeled as $[\Sigma D(R)]_{avg}$) and by assuming that the entire spore release event is subject to a rainfall with $R = 3.6$ mm h^{-1} (i.e., the average of five values of R given above).

The model was used to compare relative amounts of spore deposition calculated for the observed patterns of spore release (Fig. 1; Table 2). Two methods were used. To calculate relative spore deposition, we first calculated a spore release pattern by adding the hourly values of C for a release event and then converting each hourly value to a fraction of this total. In one method, we calculated $D(R[t])$ by using hourly values of R and fractional spore releases (taken to be proportional to C; see Model) obtained from our observations. In the second method, we calculated $D(R_{avg})$ by using the average value of R for the entire spore release period. Including the results for all 20 events, the two methods of calculation differed by a factor that ranged from 0.6 to 10.7 (the standard deviations of the mean values of the ratio ranged from 0.5 to 5.5; Fig. 4) over the distances studied. The ratio of $D(R_{avg})/D(R[t])$ ranged from 0.6 to 5.1 (mean = 1.5) at 0.5 km and from 1.0 to 10.6 (mean = 3.2) at 10 km downwind from the source. Calculations were also done in which rain that occurred at night was excluded from the calculation of R_{avg} (Fig. 4, lower panel). In this case, the range of values calculated was reduced only slightly (0.3–9.5); however, the mean ratios of $D(R_{avg})/D(R[t])$ and their standard deviations were reduced more substantially, especially when nearer to the source.

DISCUSSION

The release of *V. inaequalis* ascospores is tied very closely to the occurrence of rain (6,16,20,21). Although rainfall is important

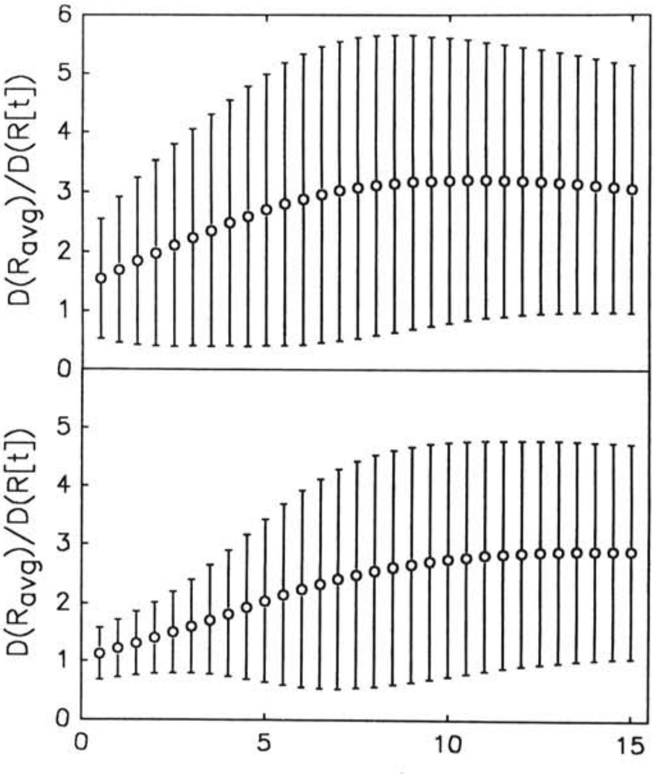

Fig. 4. The ratio of two calculated amounts of spore deposition, $D(R_{avg})/D(R[t])$ vs. distance downwind from a source. $D(R_{avg})$ was calculated by assuming that the rainfall rate was steady and equal to the average value, R_{avg}, for the entire spore release period. $D(R[t])$ is the sum of the deposition values calculated by using observed hourly values of R and fractional spore releases in proportion to observed values of hourly averaged spore concentrations, C (see text) (top panel). Circles and I-bars are the means and standard deviations of values of the ratio calculated for 20 separate ascospore release events. Also shown are results of similar calculations, modified to exclude rainfall occurring at night from the calculation of R_{avg} (bottom panel).

to initiate ascospore release, continued rain is not absolutely necessary for continued release (Fig. 1). In our study, about 44% of the total number of ascospores sampled were collected during hours when R was not detected. This is similar to the findings of Hirst and Stedman (16), who observed that on the average for rains lasting not longer than 2 h about 40% of the release occurred after rain had stopped. Because mature ascospores can be released once scabbed leaves are sufficiently wetted (for example by misting them with water in the laboratory), it is reasonable to assume that Q_0 should, in general, be independent of R. We found this to be the case in our study; we could find no significant relationship between R and the flux of spores, F, in the air. Of course, there are likely to be exceptions to this (e.g., high values of R might cause water to temporarily pond in some areas, and the resulting layer of water over the leaves could stop ascospores from being discharged into the air) (4).

The rate of washout of particles from the air depends strongly on the rate of rainfall (7,9,11,29,32). Therefore, it is reasonable to expect that the time course of rainfall during the release of *V. inaequalis* ascospores will be important for determining the number of ascospores deposited away from a source. We developed a mathematical model that allows the effect of R on D to be estimated. The model indicates that D, at downwind distances of 15 km, can differ by two to three orders of magnitude depending on if R during a transport event is 1 or 10 mm h^{-1}. It also indicates that a slight rain of 1 mm h^{-1} is more likely to deposit spores at some distance from a source than is a heavy rain or no rain at all (Fig. 3).

Often, in real situations, access to continuous recordings of rainfall (or of C for that matter) may not be available. We used the model to examine the uncertainty that might occur in calculations of D, if the average rainfall rate during the release event was used in the calculation. Clearly, this simplification introduces a substantial amount of uncertainty (Fig. 4) into estimates of deposition. However, if there is enough information available to exclude rainfall occurring at night from the calculation of the average R, then, on average, this uncertainty can be substantially reduced (Fig. 4). This can be done largely because relatively few ascospores are released at night (6,21,22). For example, for the spore release illustrated in Figure 1B, the range of values of $D(R_{avg})/D(R[t])$ decreased from 5.1–10.7 to 1.6–4.1 when rain at night was excluded from the calculation. In our study, there was only one occasion with a substantial nighttime ascospore release. However, this possibility should be kept in mind when considering whether or not to exclude nighttime rains in model calculations.

Much of the variance that remains in $D(R_{avg})/D(R[t])$ after excluding nighttime rains is the result of patterns of spore release such as that pictured in Figure 1C. Here most of the rain occurred during daylight but before the major part of the spore release. Thus, the average R calculated was not representative of the period of major spore release. In view of cases like this and of the possibility of nighttime ascospore releases, it is obviously better to use $R(t)$ in calculations whenever possible. However, when rainfall is steady, R_{avg} can be used in the model with little error. When rainfall is intermittent, use of R_{avg} is generally likely to produce conservative estimates of deposit (in the sense of apple scab management), because ascospore deposit will generally be overpredicted by using R_{avg}. A notable exception to this is for releases during which rainfall is generally light but punctuated with one or more short periods of intense rain; for such cases, use of R_{avg} in the model will not generally be conservative in the above sense.

Our model of ascospore transport offers a reasonable means of assessing the interaction of temporal patterns of rainfall and ascospore discharge. To use it to quantitatively predict deposition for particular situations, we need to improve substantially our ability to specify the strength, Q_0, of an ascospore source. Because ascospores are expected to survive well in the length of time it takes for them to be transported 10–15 km by wind (20), uncertainty in Q_0 for a specific event is most likely the largest uncertainty in the model (2). Methods to quantify ascospore source strength continue to be improved (4,13,21,22). The framework we have developed for estimating D can directly use improved estimates of Q_0 as they become available and thus can give good working estimates of the likelihood of transmission of scab between orchards.

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