Vertical Variation of Aerial Concentration of *Venturia inaequalis* Ascospores in an Apple Orchard

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I thank P. Thiel, A. Moore, S. Massimo, and S. Moulton for able technical assistance. This material is based upon work supported in part by the Cooperative State Research Service, U. S. Department of Agriculture, under Agreement No. 93-37303-9134.
Accepted for publication 15 November 1994.

ABSTRACT

Aylor, D. E. 1995. Vertical variation of aerial concentration of *Venturia inaequalis* ascospores in an apple orchard. Phytopathology 85:175-181.

The ability to determine the concentration of pathogenic spores in the air surrounding host plants is fundamental to the development of models for predicting airborne spread of disease. The aerial concentration of *Venturia inaequalis* ascospores, C (ascospores m^{-3}), was monitored during two seasons using Rotorod samplers deployed at several heights above the ground in a young orchard of dwarf apple trees. C decreased rapidly with height above the ground, and, on average, values of C at 3.0 m height were only about 6% of C measured at 0.15 m. A spore dispersal model is presented that suggests that this rapid decrease of C with height was due mainly to a rapid increase of wind speed and turbulent eddy diffusivity with height above the ground. The model described adequately the general shape of the vertical variation of C. During conditions of light wind, however, the model tended to underpredict relative values of C both near the ground and near the top of the trees. Improved model performance during light wind and rain will require better methods for measuring and modeling wind speed and turbulent eddy diffusivity under these conditions.

Additional keywords: aerial spore dispersal, spore deposition, apple scab, turbulence, rain.

The aerial concentration of spores is the physical link between the number of spores that are released at a source and the number of spores deposited on host plants at various distances from the source (3–5). In particular, the aerial concentration of ascospores of *Venturia inaequalis* (Cooke) G. Wint., C (ascospores m^{-3}), links ascospore inoculum overwintering in leaves on the ground and its potential for initiating apple scab infections. The probability of scab infections can be estimated from a knowledge of the number of deposited ascospores and the infection efficiency of ascospores (10). The number of ascospores deposited on apple tissue is proportional to C in the air surrounding that tissue. Therefore, the ability to predict C is a crucial step in the development of a model for predicting the aerial dispersal of apple scab.

In this paper, measurements of C at various heights above the ground in a small orchard of dwarf apple trees are presented. The characteristic shape of these C profiles is interpreted using a model for the aerial transport of spores and the diffusive characteristics of the wind in the orchard.

MATERIALS AND METHODS

Measurement site. Airborne *V. inaequalis* ascospores were collected during the 1992 and 1993 ascospore release seasons. Spore samplers were placed near the center of a 0.2-ha orchard of 5- to 6-yr-old dwarf apple trees in Mt. Carmel, Connecticut, and were operated during periods of rain. The trees in the orchard (including cvs. McIntosh, Empire, Liberty, Ida Red, and experimental scab-resistant cultivars, grafted on dwarfing rootstocks Mark and M9) were trained to a single spindle and spaced at 2.1 m within rows and 4.0 m between rows. The ground surface was bare within 1.6-m-wide strips centered on the rows and was covered with grass in 2.4-m-wide aisles centered between the rows. During the 1992 and 1993 measurement periods, the trees were about 2.0 and 2.3 m tall, respectively. Interrow spacing between branches on adjacent trees was about 1 m, and branch spacing between adjacent rows was about 2.4 m.

Measurements were made during periods when the phenological development of the trees advanced from green tip to petal fall and there was little foliage on the trees. The projected cross-sectional area of the tree stems and branches in the orchard was estimated from measurements of the lengths and diameters of individual stems and branches on individual trees. The average stem and branch area per tree was divided by the average ground area per tree to obtain a Stem Area Index, SAI, for the orchard of about 0.03 m^2 per m^2. Dividing this number by the height of the trees gave an estimate of the average stem area density per unit ground area of about 0.01 m^{-1}.

Ascospore source. The ground surface in the orchard within the grass strips was "seeded" uniformly with apple leaves with scab lesions. The scabbed leaves were collected from another orchard planted to cv. McIntosh and were placed on the floor of the test orchard in early December of 1991 and 1992 for the 1992 and 1993 tests, respectively. At the time of the tests, almost all of the scabbed apple leaves were contained in the grass strips, and virtually none were on the bare ground.

The spatial distribution of the leaf litter density of scabbed apple leaves, N_L (number of leaves per m^2 of ground surface), was determined in late March of each year by counting the number of apple leaves in 3.0 m × 0.1 m strips at 26–28 locations in the orchard.

The pseudothecial density on the diseased leaves, P_D, (pseudothecia cm^{-2}) was estimated by counting the pseudothecia at 50× magnification in 15 randomly selected 5-mm-diameter fields per leaf on each of 61 leaves in 1992 and 150 leaves in 1993 randomly selected from the orchard floor during the ascospore release season. The average number of pseudothecia per leaf was calculated as the product $P_D \times A_L$, with A_L, the average area of the sampled leaves, determined to be about 24.1 cm^2. The potential ascospore dose, PAD (i.e., the potential number of ascospores released m^{-2} for the entire season, defined by Gadoury and MacHardy) (16) was estimated as the product of $8 \cdot N_A \cdot N_L \cdot P_D \cdot A_L$, where N_A is the average number of asci per pseudothecium, which was taken to be $N_A = 122$ (16).

Aerial ascospore concentrations. The airborne concentration of *V. inaequalis* ascospores, C (ascospores m^{-3}), was measured with Rotorod spore samplers (Model 82, Sampling Technologies, Inc., Los Altos Hills, CA). The rotorods were deployed under rain shields (21) and were located near the center of the orchard in the middle of one of the grass strips. Two duplicate towers with one rotorod sampler at each of five (1992) or six (1993) heights were located next to one another, approximately 1.5 m apart. The length of the run of wind over the source leaves between the upwind edge of the source and the rotorod sampler towers depended on wind direction: approximately 16 m for winds from the north or the south (0 or 180°), 30 m for winds from the northeast, northwest, southeast, or southwest (45, 315, 135, or 225°), and 25 m for winds from the east or west (90 or 270°). In 1992, the centers of the spore collection rods of the rotorod spore samplers were placed at heights of 0.15, 0.40, 0.60, 0.90, and 2.10 m above the ground. In 1993, the spore collection rods were at heights of 0.15, 0.30, 0.50, 0.80, 1.50, and 3.00 m above the ground.

The rotorod samplers rotate the sampling head and the spore collection rods at about 2,400 rpm. This motion stirs the air and tends to draw air into the sampling rods from a region of vertical extent that exceeds the length (25 mm) of the rod's sampling surface. The vertical extent of the region of induced airflow was examined qualitatively by visually inspecting the motion of smoke released from smoldering incense sticks (California Fragrance Co., Watsonville, CA) placed at various distances from the rotating sampling head. The smoke was viewed in a partially darkened room using the light from a stroboscopic light operating at about 2,400 flashes per minute, so that the rotation of the sampling head appeared to be stopped. In nearly still air in a closed room with air currents typically less than 0.05–0.10 m s^{-1}, the smoke was simultaneously drawn downward from about 9 cm above and upward from about 13 cm below the rotating sampling rods. In a light breeze generated by a fan (average air speed 0.8–1.1 m s^{-1}), the vertical extent of the disturbed airflow was only about 2 cm above and below the sampling head.

The first set of rotorods generally operated for 2 h following the start of rain during daylight hours and then switched off. The duplicate set was then activated and operated for an additional 2 h. During long periods of continuous rain, the rotorod sampling rods were changed and the sampling sequence was begun again. For some sampling periods when the rain stopped and the wetness sensor (described below) became dry, the rotorods operated for a period that was less than 2 h. The catches of ascospores by the rotorods were used to determine the vertical variation of airborne ascospore concentration.

The sampling surfaces of the rotorods were made sticky by applying a thin layer of high vacuum grease (Dow Corning Corp., Midland, MI), which was thinned with hexane before application. *Venturia inaequalis* ascospores deposited on sampling surfaces were counted using a microscope at 200× magnification. The counts on the rotorods were converted to values of C by accounting for the proportion of the sample surface that was counted, the sampling rate (≈38 l min^{-1}), the duration of the sampling period, and the sampler efficiency (7).

Meteorological measurements. Wind speed and direction were monitored at the center of the orchard using a data logger (Model 21X, Campbell Scientific, Inc., Logan, UT). Wind speed was measured using three cup anemometers (Model 014A, Met-One, Inc., Grants Pass, OR) located at heights of 0.6, 1.5, and 3.2 m above the ground, and wind direction was measured using a vane (Model 024A, Met-One) placed 3.2 m above the ground. The instruments were sampled every 10 s and 720 readings were averaged to yield two-hourly values of mean wind speed, mean wind direction, the standard deviations of wind speed and direction, and cumulative rainfall. A leaf wetness resistance grid (Model 731, Campbell Scientific), was used to trigger the rotorods to start sampling at the beginning of rainfall. Rainfall amounts were measured near the center of the orchard using a tipping bucket rain gauge (Model RG2501, Sierra Misco, Inc., Sacramento, CA, in 1992, and Model TR-525, Texas Electronics, Dallas, TX, in 1993).

Model description. *Venturia inaequalis* ascospores are released into the air from diseased apple leaves on the ground during periods of leaf wetting, primarily by rain (11,16,19). It is the release of ascospores that causes the aerial concentration of ascospores to increase above the source. After ascospores are released into the air, they are simultaneously transported in the downwind direction by the horizontal motion of the wind and diffused in the vertical direction by the turbulent fluctuations of the wind. As a result of these diluting actions of the wind, the aerial concentration of ascospores, C (ascospores m^{-3}), decreases with downwind distance, x, and vertical distance, z, from their point of release. Thus, C is a function of x and z, i.e., $C(x,z)$, however, for economy of notation it will be represented in the text simply by C. The change of C with downwind distance and height above the ground can be described by an equation that expresses the conservation of the numbers of airborne ascospores. Assuming that the source extends infinitely far in the cross-wind direction and that conditions are steady, this conservation equation can be written as (9,12,14)

$$U(z)\frac{\partial C(x,z)}{\partial x} = \frac{\partial}{\partial z}\left[K(z)\frac{\partial C(x,z)}{\partial z} + v_S \cdot C(x,z)\right] - G(z) \cdot C(x,z) \quad (1)$$

In this equation, x is downwind distance, z is the vertical distance above the ground, and the $(\partial/\partial x)$ and $(\partial/\partial z)$ represent partial differentiation with respect to x and z, respectively. $U(z)$ (m s^{-1}) is the time-averaged horizontal wind speed, $K(z)$ (m^2 s^{-1}) is the turbulent diffusivity of ascospores in the vertical direction, and $G(z)$ (s^{-1}) is the rate of removal of ascospores per unit volume of air by deposition processes. All three parameters are functions of z, but for simplicity of notation they will be written as U, K, and G. The settling speed of *V. inaequalis* ascospores in still air (≈0.002 m s^{-1}) (17) is v_S (m s^{-1}).

The rate of removal of ascospores from the air (G) is influenced by washout from rain (11) and by deposition of ascospores on plants and on the ground (3,6,9). Ascospores can be deposited onto plant surfaces by ascospore-containing raindrops and by impaction and sedimentation of ascospores that are contained in the air but not in raindrops (3,9,10). Ignoring the negligibly small (for purposes of calculating aerial ascospore concentration) area of the developing leaf and flower buds during the present measurements, G can be expressed as

$$G(z) = \Gamma + \left[v_S \cdot f_X + U(z) \cdot E_S \cdot f_Z\right] \cdot a_s \qquad \text{for } z \le H \qquad (2a)$$

and

$$G(z) = \Gamma \qquad \text{for } z > H \qquad (2b)$$

where Γ (s^{-1}) is the washout coefficient for wet removal of ascospores by rain (11), f_X and f_Z are the fractions of the plant area projected onto the horizontal and vertical planes, respectively, E_S is the efficiency of inertial impaction of ascospores in the air onto stems, a_s (m^{-1}) is the density of projected stem area per ground area and H is the height of the trees. The first and second terms in the square brackets in equation 2a represent, respectively, the contribution of gravitational settling and inertial impaction of spores onto the stem area of the trees.

The stem area density, a_s, was assumed to be uniform in the vertical direction and was set equal to the average stem area density, SAI/H, a constant that was about 0.01 m^{-1}. The magnitude of the entire term in square brackets following the first + sign in equation 2a was of the order of 10^{-5}. The rate of spore removal from the air by rain, Γ, was about 0.0003–0.0018 s^{-1} (calculated with equation 10 in reference 11) for the rainfall rates that occurred during the ascospore collection periods (Table 1). In view of the above, the magnitude of the ascospore removal rate $G \cdot C$ was small relative to the other terms in equation 1 and had little effect on the calculation of the shape of the aerial ascospore concentration profiles.

Wind speed and diffusivity. Mathematical descriptions for U and K are required in order to evaluate equation 1. These functions were estimated from the values of wind speed measured in the orchard with the cup anemometers. Plant surfaces in the orchard canopy air space were sparse (very little foliage or branch area) during the experiments, and wind was impeded relatively little by the essentially bare branches. Under these conditions, the cup anemometers give a good indication of U (9).

An equation describing the vertical variation of wind speed U was obtained using nonlinear regression to fit the measured values to a power law (2,14). At the ground surface, $U(z = 0)$ is equal to zero due to physical constraints (2,14). This boundary condition was used to obtain an additional point for fitting the profiles. Therefore, U and K, both functions of z, were modeled using the so-called conjugate power law equations (2)

$$U(z) = U_0 \cdot z^{a_1} \quad (3a)$$

$$K(z) = K_0 \cdot z^{(1-a_1)} \quad (3b)$$

where U_0 and a_1 are parameters derived from the fitted wind speed profiles. K_0 was estimated using $K(z = z_{ref}) = 0.04 \cdot U(z = z_{ref}) \cdot z_{ref}$, where z_{ref} is the height of the highest cup anemometer (i.e., $z_{ref} = 3.2$ m). This approximate equation was derived using the known linear relationship between K and height above the ground under neutral atmospheric conditions (equation 11.5 in reference 2) and by setting the friction velocity equal to $0.1 \cdot U(z = z_{ref})$. Equations 3a and 3b are based on the assumption that the small plant area density in the orchard removes a negligible amount of momentum from the wind (2).

During the sampling periods, the height of the grass in the orchard was 10–25 cm tall. Therefore, equations 3a and 3b are not a good description of U and K close to the ground. Since the cup anemometers have a threshold of about 0.45 m s^{-1}, they could not be used to measure U near the ground. For purposes of illustrating the potential effect of the grass on ascospore concentrations at the lowest measurement height, U and K were assumed to decrease exponentially with depth in the grass canopy, as described elsewhere (9,13,22). Two sets of model calculations were done for comparison. In one case, equations 3a and 3b

TABLE 1. Dates, meteorological conditions, and aerial concentrations of *Venturia inaequalis* ascospores, C_1 (ascospores m^{-3}), measured in an orchard at a height above the ground $z = 0.40$ m in 1992 and $z = 0.30$ m in 1993

Year DOY[a]	m s^{-1}							
	U_1[b]	U_2[b]	U_3[b]	σ_{U_3}[b]	a_1[c]	$\theta \pm \sigma_\theta$[b] (°)	Rain (mm)	C_1[d] (ascospores m^{-3})
1992								
113.1	0.72	0.88	0.97	0.43	0.18	142 ± 40	0.9	113
113.2	0.83	1.05	1.13	0.47	0.18	151 ± 50	0.3[e]	144
113.3	0.83	1.03	1.11	0.46	0.17	144 ± 49	0.5	88
113.4	0.81	0.99	1.08	0.40	0.17	143 ± 43	1.0	144
116.1	1.95	2.44	2.81	0.87	0.22	20 ± 25	*t*[e]	534
116.2	1.36	1.74	1.99	0.63	0.22	45 ± 23	0.7	2,799
116.3	1.58	1.99	2.29	0.81	0.22	49 ± 21	0.3	190
124.1	2.95	3.97	4.63	1.27	0.26	289 ± 21	*t*[e]	130
129.1	2.29	2.95	3.45	0.89	0.24	53 ± 22	0.5[e]	1,637
129.2	2.34	2.57	2.97	0.82	0.14	46 ± 23	2.0	310
131.1	0.54	0.75	0.74	0.33	0.17	218 ± 73	0.3[e]	336
137.1	0.83	1.34	1.52	0.56	0.33	42 ± 33	3.0	205
137.2	0.81	1.33	1.53	0.40	0.35	46 ± 26	1.0	366
137.3	0.79	1.22	1.37	0.35	0.30	40 ± 28	0.5[e]	349
147.1	0.46	0.54	0.58	0.20	0.17	200 ± 49	0.7	402
1993								
101.1	2.29	2.85	3.19	1.05	0.19	345 ± 25	2.9	161
101.2	1.75	2.11	2.40	0.82	0.19	354 ± 28	1.4	783
107.1	1.04	...[f]	1.25	0.63	0.11[f]	160 ± 52	0.1	180
107.2	1.24	...	1.59	1.05	0.15[f]	215 ± 60	0.0	385
112.1	1.10	1.46	1.68	0.77	0.25	92 ± 37	7.9	1,195
112.2	1.59	2.02	2.30	0.85	0.22	115 ± 31	11.2	7,013
112.3	1.21	1.61	1.74	0.81	0.21	114 ± 35	0.5	13,975
112.4	1.64	1.95	2.25	0.97	0.19	132 ± 37	3.1	5,220
112.5	1.27	1.62	1.85	0.80	0.22	122 ± 34	5.8	4,816
112.6	0.95	1.24	1.38	0.74	0.22	129 ± 44	1.9	249
116.1	2.22	2.85	3.41	1.16	0.25	9 ± 35	1.7	1,976
116.2	3.00	3.87	4.59	1.61	0.25	24 ± 29	0.6	469
125.1	0.94	1.04	1.20	0.51	0.15	168 ± 58	5.1	3,128
125.2	0.80	0.96	1.08	0.49	0.18	175 ± 62	1.1	1,373
133.1	0.81	0.86	1.35	0.64	...[g]	318 ± 41	0.1	3,305
136.1	0.47	0.50	0.69	0.36	...[g]	240 ± 47	1.3	1,149
136.2	0.87	0.97	1.60	0.70	...[g]	322 ± 27	0.4	360

[a] DOY is Day of the Year from January 1; added decimals indicate individual sampling periods on same day. Temporal development of apple trees in test orchard during spore sampling periods is indicated by date of occurrence of specific phenological stages (i.e., stage, DOY). In 1992 these were: (green tip, 103), (tight cluster, 124), (pink, 131), (bloom, 137), (petal fall, 147). In 1993 these were: (silver tip, 101), (green tip, 107), (tight cluster, 116), (pink, 125), (bloom, 130), (petal fall, 136).

[b] U_1, U_2, U_3 (m s^{-1}), are 2-h average values of wind speed at heights of 0.6, 1.5, and 3.2 m above the ground, respectively. σ_{U_3} (m s^{-1}) is standard deviation of U_3, θ is average wind direction (0° = north), and σ_θ is standard deviation of θ, all at height of 3.2 m.

[c] Wind speed profile parameter a_1 (see equation 3a) derived from wind speed measurements using nonlinear regression.

[d] Concentrations are average values measured during 120-min sampling periods except as follows: In 1992, exceptions were 129.1 (54 min) and 131.1 (106 min); in 1993, exceptions were 107.2 (111 min), 112.3 (59 min), 112.4 (57 min), 116.1 (92 min) and 133.1 (68 min).

[e] Rainfall amount (mm) during these sampling periods was less than sensitivity of rain gauge (1 mm in 1992 and 0.1 mm in 1993) and was estimated using records from a standard weather station adjacent to orchard and from airport weather stations at Bridgeport and Hartford, Connecticut. A trace amount of rain (<0.25 mm) is designated by *t*.

[f] Anemometer at this height malfunctioned on this date. Missing values of wind speed replaced by linearly interpolated values before nonlinear regression carried out.

[g] These profiles exhibited an inflection point and were not fitted to equation 3a.

were employed for all heights above the ground. In the second case, equations 3a and 3b were used for heights above 0.25 m, while U and K were assumed to decrease exponentially for $z \leq 0.25$ m.

Calculation of C. Equation 1 was solved numerically for $C(x,z)$ on a PC computer using a finite difference approximation for the derivatives (12). Values of C at the upwind edge of the source, i.e., $C(x=0,z)$, were set equal to zero. Ascospores were introduced at the ground ($z = 0$) at a rate Q (ascospores m^{-2} s^{-1}) per unit area, which was assumed to be constant during a spore sampling period and to be spatially uniform over the extent of the source. Without the influx Q at $z = 0$, C would remain zero everywhere, i.e., the release of ascospores at $z = 0$ is the reason for the increase in C with x at each height above the ground. Actual values of Q were not known. Q was arbitrarily set equal to the same constant value in all calculations. The numerical integration was conducted over a region starting at the upwind edge of the source at $x = 0$ and extending downwind to the location of the rotorod spore sampler tower at a distance $x = X$ from the upwind edge of the source. The top of the integration grid was at 6.0 m. For the downwind distances used in the calculations (limited to 32 m), the results were insensitive to the choice of top boundary condition. At downwind location of the spore sampling tower, $x = X$, the numerical integration of equation 1 yielded $C(X,z)$.

Normalization of the concentration profiles. The release rate of ascospores per ground area, Q (ascospores m^{-2} s^{-1}), varies considerably with time during a release event (11) and during the season due to the time-dependent maturation of the ascospores (15,16). It is not now possible to specify Q during a specific ascospore release event. Thus, without knowing Q, we are unable to predict absolute values of concentration. However, because C varies linearly with Q (i.e., doubling Q will double C at all heights) (14), it is possible to compare C profiles measured on different days by adjusting them to a common point of reference. To allow comparison between collection periods, the values $C(z)$ for each profile were divided by the value, C_1, which was the concentration measured at $z = 0.40$ m in 1992 and at $z = 0.30$ m in 1993.

RESULTS

Ascospore source. The average density of scabbed apple leaves in the grass strips was 148.9 (SD = 52.7) and 232.6 (SD = 51.0) leaves m^{-2} in 1992 and 1993, respectively (Fig. 1). Because the grass strips composed about 60% of the orchard floor, and there were essentially no leaves in the bare strips, the overall average number of leaves per unit ground area for the entire orchard, N_L, was about 0.6 times the values given above, or, about 89.3 and 139.6 leaves m^{-2} in 1992 and 1993, respectively. The average value of P_D was 38.3±29.2 in 1992 and 45.6±19.7 in 1993. Multiplying these values by the average area of the sampled leaves (24.1 cm^2) yielded about 920–1,100 pseudothecia per leaf in 1992 and 1993, respectively. These numbers were combined to yield an estimate of the potential seasonal release of ascospores, or potential ascospore dose, PAD (see Materials and Methods) (16), which in 1992 was estimated to be about 8.0×10^7 and in 1993 PAD about 1.5×10^8 ascospores m^{-2}.

Wind speed. Throughout most of the ascospore release season in both years, the measured wind speeds (Table 1) were described well by equation 3a (Fig. 2, left panel). Late in the 1993 ascospore release season (days of the year, from 1 January, 133 and 136) when the wind was very light (Fig. 2, right panel, and Table 1), the profiles exhibited a point of inflection and were not described well by equation 3a.

Shape of the ascospore concentration profiles. Ascospore concentrations typically decreased rapidly with height above the ground (Fig. 3). C profiles for a wide range of conditions can be more readily compared by plotting normalized concentration profiles. The shape of these profiles was very similar in both years (Figs. 4 and 5). Ascospore concentrations decreased by some 40–97% between 0.15 m and 0.40 m above the ground in 1992 (Fig. 4) and by 22–90% between 0.15 m and 0.30 m in 1993 (Fig. 5). The decrease of C above a height of 0.3 m was relatively small. The rapid vertical variation of C near the ground is mainly a reflection of the rapid increase of wind speed and turbulent diffusivity with height near the ground (equation 3, Fig. 2).

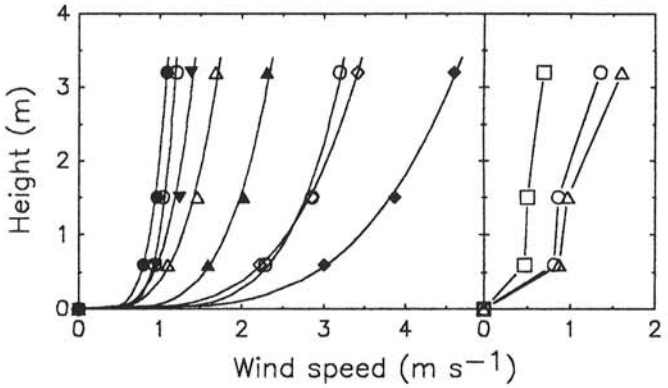

Fig. 2. Examples of average horizontal wind speed, U, at various heights during periods when *V. inaequalis* ascospores were sampled in apple orchard. Profiles were fitted well by equation 3a (left panel, lines) for most of sampling dates when there was little foliage on trees (see phenology, Table 1). Late in 1993 season (right panel) wind speed profiles exhibited a point of inflection.

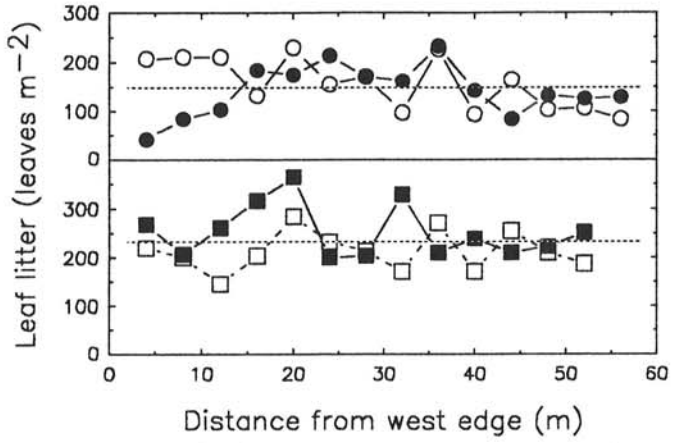

Fig. 1. Number density of scabbed apple leaves on the ground in the grass strips in the test orchard in 1992 (upper panel) and 1993 (lower panel). Individual measurements made along lines approximately 9 m from north edge (open symbols) and 9 m from south edge (filled symbols). Dashed lines represent overall mean density: 148.9 leaves m^{-2} in 1992 and 232.6 leaves m^{-2} in 1993.

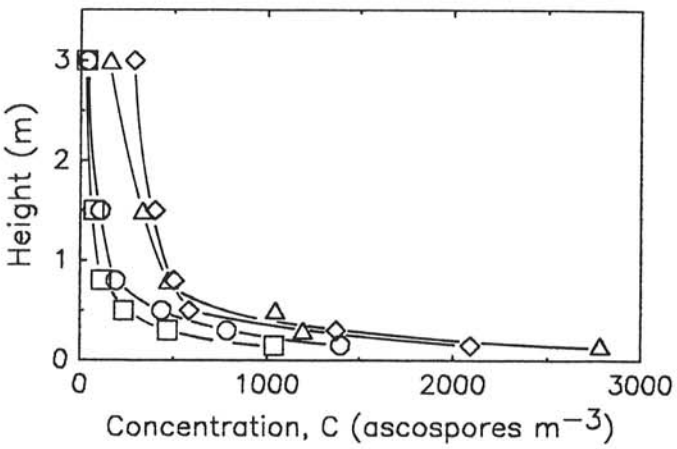

Fig. 3. Vertical profiles of aerial concentration of *V. inaequalis* ascospores measured in apple orchard in 1993 during sampling period (Table 1): 101.2 (circle), 112.1 (triangle), 116.2 (square) and 125.2 (diamond). Lines through data points are fitted by eye.

The general shape of the vertical profiles of C observed in both years was described well by the model. There was a noted tendency for the model to underpredict values of C that were measured by the rotorods at a height of 0.15 m, and this was especially true for measurements made during conditions of lower wind speeds (panel B of Figs. 4 and 5). For purposes of clarity of presentation, calculated profiles have been shown for only one sampling period in a year (period 113.2 in 1992 and period 101.1 in 1993, Table 1). Two calculated lines are presented in each case. The main differences in the two calculations (see Materials and Methods) appear below a height of 0.25 m, at which the values of U and K were much smaller in one case (dashed line) than in the other (solid line). Above this height, there was almost no difference in the two calculations. The variation in calculated profile shapes over a season was not large (Fig. 6).

DISCUSSION

The aerial concentration of *V. inaequalis* ascospores was highest at $z = 0$ and decreased with increasing height as expected (3,14) for spores released from a ground level source (1,8,10,16,18,19). The rapid decrease of C with height near the ground (Figs. 3, 4, and 5) reflects the rapid change in wind speed and turbulent diffusivity near the ground. The model described the shape of the observed concentration profiles of *V. inaequalis* ascospores (Figs. 4, 5, and 6) reasonably well, because it accounted for the main variation of U and K above the ground. The general shape of the C profiles was similar between sampling periods within a year as well as between years, reflecting an underlying generality in the physical laws governing the transport and dilution of airborne ascospores.

Ascospore concentration values were generally higher in 1993 than in 1992 (see C_1 values in Table 1). These differences are in accord with the larger value of PAD (and presumably larger values of Q) in 1993 than in 1992 (8.0×10^7 in 1992 compared with 1.5×10^8 in 1993). In addition, everything else being equal,

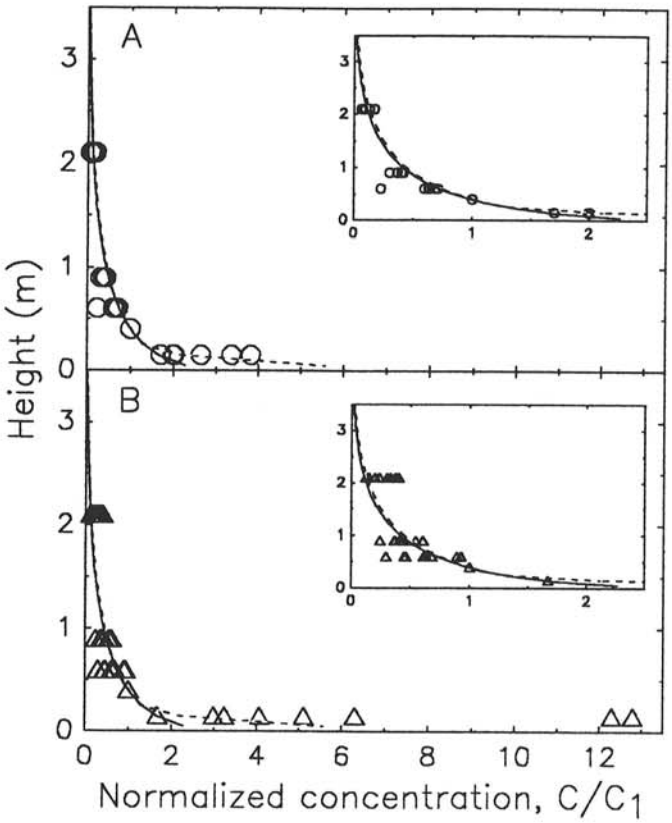

Fig. 4. Vertical profiles of normalized aerial concentrations of *V. inaequalis* ascospores measured in apple orchard in 1992. Concentration values have been normalized by value of C (ascospores m^{-3}) measured at height of 0.40 m. Data are shown for all sampling periods (see Table 1) when $U_3 > 1.8$ m s^{-1} (panel A) and when the average wind speed U_3 was < 1.8 m s^{-1} (panel B). One data point, located at $z = 0.15$ m and a normalized concentration equal to 38.8, has not been plotted to avoid compression of the X-axis values. Lines calculated for period 113.2 (Table 1) using model described in text, wherein U and K were assumed to vary according to equations 3a and 3b for all $z > 0$ (solid line) or to follow equations 3a and 3b for $z > 0.25$ m, and were assumed to decrease exponentially with depth in grass canopy (13) for $z \leq 0.25$ m (dashed line). A portion of the range has been expanded (inset).

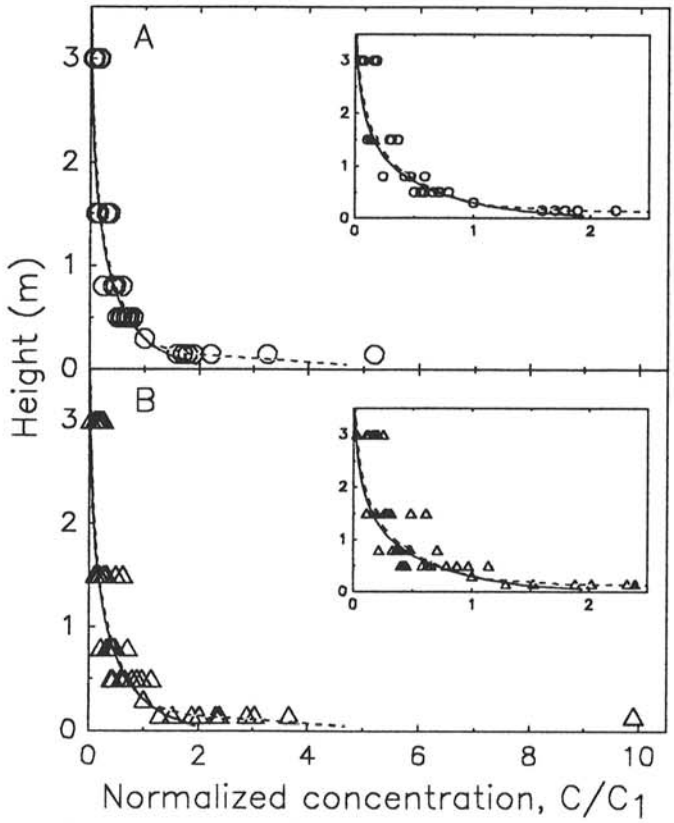

Fig. 5. Vertical profiles of normalized aerial concentrations of *V. inaequalis* ascospores measured in apple orchard in 1993. Concentration values have been normalized by value of C measured by spore sampler at height of 0.30 m. Data are shown for all sampling periods (see Table 1) when $U_3 > 1.8$ m s^{-1} (panel A) and average wind speed U_3 was < 1.8 m s^{-1} (panel B). Lines calculated for period 101.1 (Table 1) using model described in text, wherein U and K were assumed to vary according to equations 3a and 3b for all $z > 0$ (solid line) or to follow equations 3a and 3b for $z > 0.25$ m, and were assumed to decrease exponentially with depth in grass canopy (9) for $z \leq 0.25$ m (dashed line). A portion of the range has been expanded (inset).

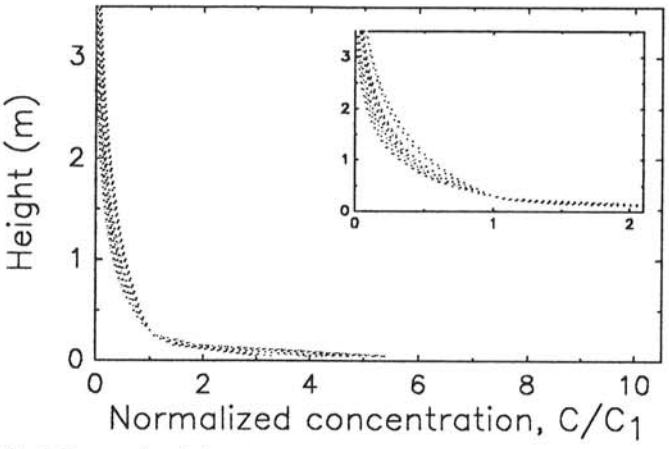

Fig. 6. Range of variation in the predicted normalized ascospore concentration profile shapes for 1993 sampling periods given in Table 1.

the normalized concentration values for 1992 are expected to be about 20% larger than those for 1993 simply because of the difference in sampling heights used for normalization in the two years. Model calculations indicate that C should decrease by about 20% between the heights of 0.3 and 0.4 m.

A major reason for the success of the model and the relatively simple descriptions of wind speed and eddy diffusivity used here was that both the foliage and stem area density were sparse in the canopy air space during the ascospore releases. The average stem and branch area density of these trees (0.01 m^{-1}) was less than 1% of typical values of the leaf area density of a row crop such as wheat or corn (20). Because of this low density of plant elements in the tree canopy volume, the tree stems presented relatively little resistance to air movement. In both years, the majority of the season's ascospore supply was released before apple foliage development was advanced (i.e., soon after petal fall, Table 1). It is certainly possible for a sizeable ascospore release to occur later in the season when the foliage on the trees is more fully developed. To accurately describe C profiles in foliated canopies will probably require different and more complex descriptions of U and K than were used here. Such new formulations are a challenge for biometeorologists and remain to be determined.

In several cases, the observed values of C at the lowest measurement height (0.15 m) were considerably higher than would be expected from the model calculations (Figs. 4 and 5). It was noted, in most cases where this occurred, that the wind speed was relatively low ($U_3 < 1.8$ m s^{-1}, panel B of Figs. 4 and 5). Because C changes rapidly near the ground, a relatively small uncertainty in measurement height could result in a relatively large uncertainty in predicted C at the lowest measurement height. The laboratory observations of smoke movement induced by the rotation of the rotorod samplers indicated that, in nearly still air, light particles could be drawn into the region of the sample collection rods from a distance about 13 cm below the rods. The model indicates that, in the presence of a grass ground cover, C could increase by about a factor of 2.5 in going from a height of 0.15 m to a height of 0.05 m above the ground. Thus, it is feasible that at least some of the discrepancies between the model and observations noted for the lowest sampling height could be because the rotorod sampled spore-laden air from a height less than 0.15 m.

Laboratory tests indicated that induced vertical inflow of air toward the rotorods tends to be minimized in the presence of moderate wind (0.8–1.1 m s^{-1}). Therefore, better agreement between the model and observations should be expected when the wind speed is higher. This was found to be true in most cases (compare panel A [$U_3 > 1.8$ m s^{-1}] with panel B [$U_3 <$ 1.8 m s^{-1}] in Figs. 4 and 5). Finally, uncertainty in sampling height due to inflow induced by the sampler is expected to be small for heights well above the ground where wind speed is generally higher than 0.8 m s^{-1} and the variation of C is relatively small.

There were a few "outlying" points at $z = 0.15$ m that cannot be explained easily. In 1992 there were three such points, viz., $C/C_1 = 12.3$, 12.8, and 38.8 (not plotted), while in 1993 there was only one such point at $C/C_1 = 9.9$. An assumption of the model is that the release of ascospores was distributed uniformly over the ground in the test orchard. It is possible that ascospore concentrations at the lowest sampling height could be enhanced if there had been a disproportionately large release of ascospores right next to the sampling towers. If such a spatially patchy source distribution existed, this could help to account for these outlying points. There was a degree of spatial nonuniformity in the distribution of scabby leaves on the ground (Fig. 1). It is not known, however, whether or not there were spatial differences in the maturation and release of ascospores over the extent of the source. Thus, patchiness of the source could be partly responsible for these apparent outliers.

Most, but not all, of the largest values of normalized C at $z = 0.15$ m) occurred during low wind conditions when the model equations (equations 3a and 3b) are not expected to describe the physics governing U and K very well. The atmospheric diffusivity, in particular, is not well defined during these conditions. Currently, there are no anemometers that are both rugged enough to work continuously and reliably in the rain and still sensitive enough to measure the very low wind speeds and turbulent fluctuations just above the ground surface needed to characterize turbulent diffusion under these conditions. Improved micrometeorological techniques to better define turbulence under conditions of light wind and rain should directly lead to improvements in models of aerial transport of *V. inaequalis* ascospores, which appear to be released frequently under these conditions (Table 1).

The measurements and the model presented here describe the vertical variation of the aerial concentration of *V. inaequalis* ascospores released from a ground-level source in an orchard. The model suggests that aerial spore concentration depends mainly on two factors: *(1)* the rate of release of spores, Q, by the source, and *(2)* the physical transport and dilution of airborne spores by the wind. It is not presently possible to quantify the release rate of ascospores, Q. Therefore, the present study focused on describing the physical transport of airborne spores. Profiles of C on different days or at different times on the same day result from different ascospore release rates. Nevertheless, these profiles can be directly compared because C depends linearly on Q (14). In view of this, values of C at various heights have been divided by a value measured at a reference height. This normalization procedure removes the effect of differences in Q between sampling periods and allows the shape of C profiles from all sampling periods to be readily compared.

This study presents measured profiles of airborne ascospore concentrations and has advanced a model for describing the effect of wind speed and turbulence on the vertical variation of C for naturally released *V. inaequalis* ascospores. Unfortunately, it is not presently possible to predict absolute values of C from first principles. In order to do this it will first be necessary to develop methods for predicting the rate of release of ascospores into the air. Once this has been done, this information can be used directly with the model presented here to predict C. Knowing C is important for estimating the potential number of apple scab infections from a given ascospore release (10). Thus, the present study is an important step in the development of a framework within which to estimate the potential number of scab infections from a knowledge of the amount of inoculum present, and could be useful, for example, in evaluating effectiveness of sanitation practices in disease management.

LITERATURE CITED

1. Agrios, G. N. 1988. Plant Pathology, 3rd edition. Academic Press, Inc., San Diego, CA.
2. Arya, S. P. 1988. Introduction to Micrometeorology. Academic Press, San Diego, CA.
3. Aylor, D. E. 1978. Dispersal in Time and Space: Aerial Pathogens. Pages 159-180 in: Plant Disease: An Advanced Treatise. II, J. G. Horsfall and E. B. Cowling, eds. Academic Press, Inc., New York.
4. Aylor, D. E. 1986. A framework for examining inter-regional aerial transport of fungal spores. Agric. For. Meteorol. 38:263-288.
5. Aylor, D. E. 1989. Aerial spore dispersal close to a focus of disease. Agric. For. Meteorol. 47:109-122.
6. Aylor, D. E. 1990. The role of intermittent wind in the dispersal of fungal pathogens. Annu. Rev. Phytopathol. 28:73-92.
7. Aylor, D. E. 1993. Relative collection efficiency of Rotorod and Burkard spore samplers for airborne *Venturia inaequalis* ascospores. Phytopathology 83:1116-1119.
8. Aylor, D. E., and Anagnostakis, S. L. 1991. Active discharge distance of ascospores of *Venturia inaequalis*. Phytopathology 81:548-551.
9. Aylor, D. E., and Ferrandino, F. J. 1989. Dispersion of spores released from an elevated line source within a wheat canopy. Boundary-Layer Meteorol. 46:251-273.
10. Aylor, D. E., and Kiyomoto, R. K. 1993. Relationship between aerial concentration of *Venturia inaequalis* ascospores and development of apple scab. Agric. For. Meteorol. 63:133-147.
11. 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.

12. Aylor, D. E., and Taylor, G. S. 1982. Aerial dispersal and drying of *Peronospora tabacina* conidia in tobacco shade tents. Proc. Natl. Acad. Sci. U.S.A. 79:697-700.
13. Aylor, D. E., Wang, Y. S., and Miller, D. R. 1993. Intermittent wind close to the ground within a grass canopy. Boundary-Layer Meteorol. 66:427-448.
14. Csanady, G. T. 1973. Turbulent Diffusion in the Environment. Reidel Publ. Co., Dordrecht, Holland.
15. Gadoury, D. M., and MacHardy, W. E. 1982. A model to estimate the maturity of ascospores of *Venturia inaequalis*. Phytopathology 72:901-905.
16. Gadoury, D. M., and MacHardy, W. E. 1986. Forecasting ascospore dose of *Venturia inaequalis* in commercial apple orchards. Phytopathology 76:112-118.
17. Gregory, P. H. 1973. The Microbiology of the Atmosphere. John Wiley and Sons, New York.
18. Hirst, J. M., and Stedman, O. J. 1962. The epidemiology of apple scab (*Venturia inaequalis* (Cke.) Wint.). III. The supply of ascospores. Ann. Appl. Biol. 50:551-567.
19. MacHardy, W. E., and Jeger, M. J. 1983. Integrating control measures for the management of primary apple scab, *Venturia inaequalis* (Cke.) Wint. Prot. Ecol. 5:103-125.
20. Monteith, J. L. 1976. Vegetation and the Atmosphere. Vol. 2, Case Studies. Academic Press, New York.
21. Sutton, T. B., and Jones, A. L. 1976. Evaluation of four spore traps for monitoring discharge of ascospores of *Venturia inaequalis*. Phytopathology 66:453-456.
22. Thom, A. S. 1975. Momentum, mass and heat exchange of plant communities. Pages 57-109 in: Vegetation and the Atmosphere: Vol. 1. J. L. Monteith, ed. Academic Press, London.