Dispersion and Deposition of Spores of Fomes Annosus and Fluorescent Particles

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ABSTRACT

Fomes annosus, spread by airborne spores is an important pathogen in intensively managed conifer forests. This study examined dispersion and deposition patterns of conidia and fluorescent particles in relation to meteorological conditions. Experiments were conducted on 60 × 60 m sampling grids in a cleared area, at the edge of a 20-m-high Douglas-fir forest, and in the forest. Particles and spores were trapped with Rotorod samplers at heights of 1, 5, 10, 15, and 20 m. Deposition of fluorescent particles was determined on petri plates set 30 cm above the forest floor, simulating major infection courts. Wind speed and direction and temp were measured. Fluorescent particles generally dispersed in a similar manner to conidia. Horizontal and vertical dispersion was greater at night in the forest than in the cleared area, but this was reversed during the day. Dispersion was also affected by vegetation density with plumes being moved around areas of high density. Deposition in the forest was lower at night and higher during the day than deposition in the cleared area. At the forest edge at night, deposition was heavy due to local turbulence. Airborne concns were predicted with a dispersion model within a factor of two of observed, but deposition patterns were not reliably predicted. Natural spore deposition rates ranged from 0.0003 to 0.007 spores per cm^2 per h with the maximum occurring at night on a sampler close to the forest edge.

Additional key word: epidemiology.

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One of the most economically important diseases of conifers in the North Temperate Zone is the root- and butt-rot caused by *Fomes annosus* (Fr.) Karst. Spread of *F. annosus* to new infection centers is primarily by airborne spores which are deposited on freshly cut stump surfaces, or on other infection courts. After spore germination, hyphae are able to penetrate the stumps and their root systems. Adjacent living trees are infected by hyphae passing through natural root grafts or across root contacts. This fungus is a problem in intensively managed conifer forests where thinning occurs routinely.

Basidiospores and conidia produced by *F. annosus* are hyaline and approximately 5 μm in diam. Little is known of the dispersion and deposition of these spores within a forest in relation to meteorological conditions.

In a forest environment, there is a highly variable distribution of wind speed, wind direction, and temp (7, 14); thus, spore dispersion is expected to be complicated. There are few experiments involving spore dispersion in forests. Wind velocity affected dispersion patterns of *Hypoxylon pruinatum* in a deciduous forest (6). Winds exceeding 5 m/s outside the stand resulted in little vertical and horizontal dispersion of both spores and smoke tracers. Spores and smoke rapidly gained altitude with slower wind speeds. Nocturnal diffusion experiments using smoke to trace the path of *Cronartium ribicola* basidiospores by Van Arsdel (22), revealed that under cold air drainage conditions, smoke drained downslope to valley bottoms, rose through the trees and returned upslope at the level of the top of the canopy, enabling infection patterns to be understood.

Quantitative studies involving dispersion and deposition of fluorescent particle tracers have been conducted in a jungle forest (11) and in a deciduous forest (21). As a result of these studies, Brown et al. (1) concluded that: (i) an aerosol cloud within a forest was influenced by meteorological conditions and the vegetation character; (ii) tree crowns were physical barriers to vertical dispersion; (iii) wide differences in aerosol concn between locations within a stand were due to the irregular distribution of the canopy; (iv) aerosol concn and deposition below the measurement point were poorly correlated; and (v) diffusing materials may behave differently in the canopy, crown space, trunk space, and undergrowth. Similar conclusions were reached by Raynor et al. (13) in studying particulate dispersion into and within a pine forest.

Predicting particle dispersion in forests has generally been disappointing (12, 21). Sutton's (20) theory failed to predict dispersal of *Hypoxylon pruinatum* spores in a deciduous forest (6). Most dispersion models assume that the plume has a Gaussian distribution in both horizontal and vertical planes with uniform turbulence. These assumptions rarely apply in forests because of the complex nature of the wind fields.

The time of maximum deposition of spores of *F. annosus* is variable (9, 16, 18, 19), although maximum spore discharge occurs at night (17, 23, 24). The work reported here involves an examination of spatial dispersion and deposition patterns of conidia of *F. annosus* and ZnCdS fluorescent particles in a coniferous forest and a cleared area, and comparison with predicted results. Fluorescent particles were used because of their ease of availability and size similarity to spores of *F. annosus*. Natural spore deposition was also examined.

MATERIALS AND METHODS.—*Released materials.*—Cultures of *F. annosus* were grown on 2% malt agar in petri plates at 20 C for 7-14 days. The 4.5 - 7.5

TABLE 1. Details of releases of spores of *Fomes annosus* and fluorescent particles (FP) at 1 m height, within, at the edge of, and outside a Douglas-fir forest in a clearcut at Pack Forest, Washington

Date		Time (h)			Amount released			Sky	Sampling time
Year	Day mo	Begin	End	Location[a]	FP × 10^{10}	Spores × 10^{8}	Wind speed[b]	condition	(min)
1969									
	14 Aug[c]	1540	1545	F3	1.04	1.58	1.95	Clear	10
		1635	1640	F3	1.28	0.58	1.43	Clear	10
	29 Aug.[c]	1156	1202	F3	1.25	4.90	2.46	Clear	10
		1241	1246	F3	1.23	2.20	2.44	Clear	10
		1517	1523	G3	1.18	4.90	1.52	Clear	11
	4 Sept.[c]	1730	1737	Midway K3-L3	1.17	2.40	0.25	Overcast	12
		2249	2257	O3	1.19	2.40	0.05	Clear	18
	5 Sept.[c]	0931	0938	Midway K3-L3	1.11	2.40	0.15	Partly cloudy	12
		1141	1146	M1	1.24	2.40	0.30	Clear	10
1970									
	2 July[d]	2303	2308	E4	1.35		0.90	Clear	10
		2336	2341	O3	1.35		0.05	Clear	10
	3 July[d]	0726	0731	E3	1.35		0.30	Clear	10
		0744	0749	M3	1.35		0.05	Clear	10
		1240	1245	C1	1.35		2.20	Clear	10
		1255	1300	Midway M1-M2	1.35		1.15	Clear	10

[a]Grid location given in Fig. 2.
[b]Average wind speed at release point over release time.
[c]Spores and fluorescent particles atomized.
[d]Only fluorescent particles with 1% hydrophobic silica released.

× 3.0 - 6.0 μm (approximately 5-μm diam) conidia were washed from the mycelial mat with distilled water and filtered through a glass-wool filter to remove the mycelia. The conidia were concd on a 0.5-μm pore size filter and washed into a small amount of distilled water. Concentrations of spores were determined with a haemocytometer. Conidia were stained pink with 0.5% "Phloxine." The "Helecon" ZnCdS fluorescent particles (U.S. Radium) have a mean diam of 3.3 μm (1-7 μm range), a specific gravity of 4.0 g/cm^3, an irregular shape, and have green fluorescence. Particles per gram were 1.35 × 10^{10} (Lot No. 2210, H775), and 1.45 × 10^{10} (Lot No. 3206, H848). Concurrent releases of spores and fluorescent particles from a point source 1.0 m above the ground were made by atomizing a suspension of spores and fluorescent particles (1.0 g) in water through a common throat-type atomizer using a regulated compressed air source at 2.9 kg/cm^2. Fluorescent particles without spores were released from a Hudson commercial garden duster. Release details are shown in Table 1. Sampling times were longer than release times to allow dispersion of all spores and particles through the sampling grids.

Sampling instruments.—H-shaped Rotorods® (Metronics Assoc., Inc., 3201 Porter Drive, Palo Alto, Calif.), with 0.38 × 66 mm frontal area collecting surfaces, were used to sample fluorescent particles. The sampling surfaces were thinly coated with silicone grease by finger application.

Rotorods were first scanned under ultraviolet light with a ×30 dissecting microscope to determine the presence or absence of particles. Counts were made with a compound binocular microscope (×100 magnification).

Due to the lower specific gravity of the spores in comparison to the fluorescent particles, the H-shaped Rotorod was modified to increase sampling efficiency (4) with the width of the sampling surface being reduced to 0.15 mm. Sampling efficiencies for the fluorescent particles and conidia were 66% and 85%, respectively. The modified Rotorods were coated with 1:2 rubber cement: xylene mixture (6). The H-shaped, and modified H-shaped, samplers were placed 30 cm apart in the field.

Spores were removed from the Rotorods by pressing transparent tape against their surfaces. The tape was placed on a standard microscope slide and evaluated under a compound microscope at ×250 magnification. The total number of "tagged" spores on each arm of the Rotorod was counted, and adjusted to take into account the different sampling efficiencies and rates to compare the results of the two samplers. Deposition of spores was not determined because of the difficulty in locating and identifying the spores on the plates.

Deposition samplers for fluorescent particles were designed to simulate stump surfaces. The bottom surfaces of petri plates were coated with silicone grease and placed in an inverted position on the top of 10 cm (outside diam) PVC (polyvinylchloride) pipes. The collecting surface was 30 cm above the ground. The deposition plates were evaluated by counting the number of fluorescent particles in eight microscope fields (×100) across the surface of the plates. Counts were expressed as number of particles/m^2.

The spore deposition sampler (Fig. 1) consisted of 16, 15 cm high, 10 cm diam PVC pipes mounted on a circular

Fig. 1. Propeller anemometer and spore deposition sampler at Marckworth Forest. Two petri plates containing selective media were exposed at one time.

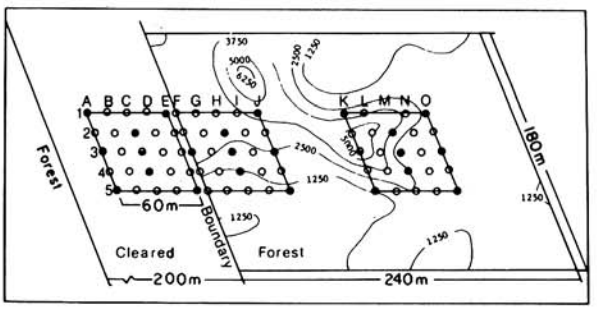

Fig. 2. Location of three 60 × 60 m sampling grids at Pack Forest. Grid columns are lettered and rows are numbered. Rotorod sampler heights are shown (o) 1 m, (•) 1 and 5 m, and (⊛) 1, 5, 10, 15, and 20 m. Vegetation density isopleths are shown as stems/ha.

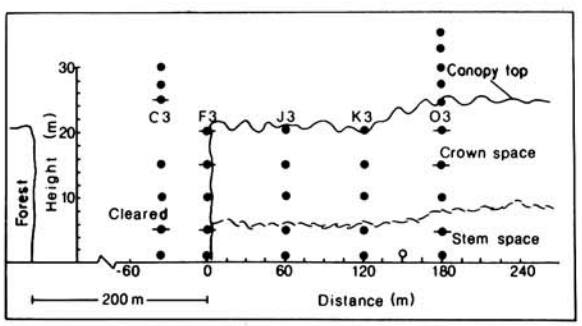

Fig. 3. Location of meteorological sensors within, at the edge, and outside a Douglas-fir forest along Row 3 (Fig. 1); wind vanes (—), temp sensors and cup anemometers (•), and propeller anemometer (o).

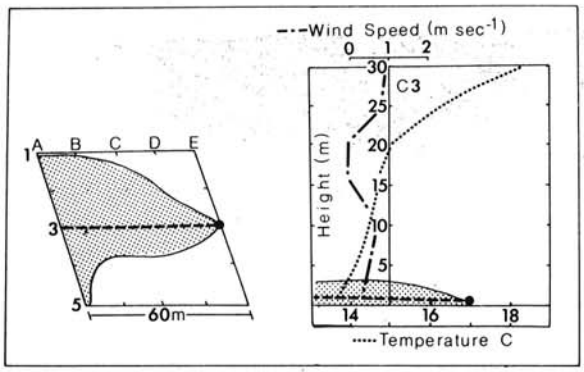

Fig. 4. Horizontal (at 1 m) and vertical extent of the fluorescent particle plume in the cleared area grid to 5% of maximum values (shaded). Line linking points of maximum value is shown (- -). Wind speed and temp profiles at C3 are shown. Release point was E3 at 0726 hours on 3 July 1970.

6.3 mm thick "Plexiglas" sheet. Petri plates (100 × 15 mm) were filled to the top, to avoid the "edge effect," with selective media [K and H with 1:30,000 rose bengal (10)]. The plates were taped to the top of the PVC pipes. The top of the sampler was covered so that only two of the plates were exposed at any one time. The 16 pipes were in groups of two for replication purposes. Every three hours the "Plexiglas" sheet moved to a new position by means of an electric motor coupled to a timing mechanism, exposing two fresh plates.

Each plate was identified as to the time period of exposure, transported to the laboratory and incubated at 25 C. After seven days, they were examined for the presence of the Oedocephalum stage of *F. annosus*. Each colony was assumed to have originated from a single spore.

This sampler was located 25 m from the forest edge in steep terrain (30-degree slope), in a 40-yr-old western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) stand infected with *F. annosus* at Marckworth Forest, which is approximately 50 km northeast of Seattle.

Sampling grids.—Sampling grids, location of samplers on towers, and vegetation density at Pack Forest are shown in Fig. 2. Pack Forest is located 100 km south of Seattle, Washington. The site is rather level (±2.5 m). Three (five columns × five rows) sampling grids were utilized, each grid being 60 × 60 m. Grids were situated in a second-growth Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) forest 20-30 m high, at the forest edge, and in a 200 × 600 m cleared area which was cut in 1968. Rotorod samplers (at 1 m height) and deposition plates (at 30 cm ht) were placed at each of the 25 grid points in each grid. Additional Rotorods were placed 5, 10, 15, and 20 m above the forest floor.

Meterological observations.—Wind speed and direction and air temp were monitored. Air temp was determined by measuring the forward voltage drop across a silicone diode "Fairchild No. FD. 300." Wind speed was measured on the towers with sensitive cup-type anemometers (5). In addition, a propeller-type anemometer measured the three windspeed components at right angles to each other (See Fig. 1). Wind direction was determined with wind vanes consisting of counter-weighted balsa wood tails mounted on brass tubes. The location of these sensors at Pack Forest is shown in Fig. 3. Signals from the instruments were recorded in a mobile laboratory at the forest edge. Data were recorded every two min.

Dispersion model.—The dispersion model used was that of Chamberlain (2) for a continuous ground-level point source modified for deposition:

$$\chi(x,y,z) = \frac{Q}{\pi C_y C_z u x^{2-n}} \text{EXP}\left[-\frac{y^2}{C_y^2 x^{2-n}}\right] \text{EXP}\left[-\frac{z^2}{C_z^2 x^{2-n}}\right] \text{EXP}\left[-\frac{4V_g x^{n/2}}{nu\pi^{1/2}C_z}\right]$$

in which

χ = concn (particles/m^3)
π = 3.14
Q = source strength (particles/s)
C_y = virtual diffusion coefficient in horizontal plane (m$^{1/8}$)
C_z = virtual diffusion coefficient in vertical plane (m$^{1/8}$)
u = wind speed (m/s)
n = constant depending on stability conditions (range 1-0; highly unstable as n approaches 0)
V_g = deposition velocity (m/s)
x,y,z = grid coordinates in direction of mean wind, horizontal to mean wind, and vertical to mean wind (m), respectively.

Chamberlain's (2) original model included the source strength (Q) multiplied by a factor of two. This was done to allow for reflection of the plume at the ground. With the amount of deposition anticipated with the fluorescent particles and spores, it was deemed better to delete the factor of two from the model. The model for a ground-level release was used because the release height was only 1 m, the topography varied 1.0 m or so in each grid, and ground vegetation often projected up to a height of 1.0 m. Had the release point been higher, then it may have been better to use the model which takes source height into account.

RESULTS.—*Comparison of disperison of spores of F. annosus and fluorescent particles.*—In some releases there was no difference between spore and fluorescent particle concns, but in other releases there were differences (Table 2).

Dispersion patterns.—Horizontal and vertical plume dimensions for five selected examples are shown in Fig. 4-8, along with vertical wind speed and temp profiles. Complete details of all releases were presented by Edmonds (3). Actual and predicted concns for fluorescent particles are shown in Fig. 9 for the five releases. Plume widths as indicated by standard deviations O_y (horizontal) and O_z (vertical) are shown in Table 3.

Typical nighttime or very early morning cold air drainage releases are shown in Fig. 4 and 5. Fig. 4 shows a release in the cleared area and Fig. 5, a release in the forest. Particles released in the cleared area are dispersed less in the horizontal and vertical planes compared to particles released in the forest under similar conditions. Table 3 also shows this trend. Note that the steep temp

inversion which is formed in the cleared area (Fig. 4) inhibits vertical mixing.

Typical daytime releases under clear unstable conditions are shown in Fig. 6, 7, and 8. In the cleared area grid under these conditions, horizontal dispersion (Fig. 6) was greater than at night (Fig. 4) due to increased wind speed and turbulence, both mechanical and thermal. During the day, horizontal dispersion close to the forest edge (Fig. 7) was greater than that in the forest (Fig. 8). Horizontal dispersion in the clearcut (Fig. 6) is greater than that in the forest (Fig. 8). These differences are also shown in Table 3. The values of the standard deviations increase irregularly with distance from the source because the plumes did not have regular Gaussian distributions. The particles tended to channel around or between areas of high vegetation density.

Vertical dispersion in the cleared area close to the source is greater (Fig. 6) than in the forest (Fig. 7, 8), due to rapid thermal mixing. The temp profile shows that unstable conditions existed in the cleared area (Fig. 6). In the forest this temp profile is reversed (Fig. 7, 8) indicating that stable conditions occurred in the forest. There is more vertical dispersion close to the forest edge than in the forest proper, where a well-developed inversion inhibited vertical spread (Fig. 8).

TABLE 2. Comparison of concns of spores of *Fomes annosus* and ZnCdS fluorescent particles sampled at the same location

Date	Release time (h)	Significance of differences between sample means as determined by paired *t*-tests: 1 m samplers	Tower samplers	All samplers
14 Aug. 1969	1540	NS[a]	---	NS
	1635	NS	---	NS
29 Aug. 1969	1156	NS	*	*
	1241	NS	NS	NS
	1517	*[b]	*	**
4 Sept. 1969	1730	*	NS	*
	2249	NS	NS	NS
5 Sept. 1969	0931	*	NS	*
	1141	**[c]	NS	**

[a]NS = No significant difference.
[b]* = difference significant, $P = 0.05$.
[c]** = difference significant, $P = 0.01$.

Isothermal temp profiles occurred in the forest under cloudy, or neutral stability conditions (3). In this situation, there was no sharp temp discontinuity at the

TABLE 3. Plume width (σ_y) at a height of 1.0 m and plume height (σ_z) along the centerline for the releases of ZnCdS fluorescent particles illustrated in Fig. 4 to 8

Date	Release time (h)	Fig. no.	Grid location	σ_y (m)[a] Distance from source (m): 15	30	45	60	σ_z (m)[b] Distance from source (m): 15	30	45	60
3 July 1970	0726	4	Cleared area	4.8	5.6	4.9	5.7	---	1.3	---	1.3
4 Sept. 1969	2249	5	Forest	5.0	9.9	10.4	---	---	1.4	---	5.0
3 July 1970	1240	6	Cleared area	10.1	12.4	---	---	---	2.4	---	---
29 Aug. 1969	1517	7	Forest edge	5.6	9.3	12.3	---	1.4	---	3.1	---
5 Sept. 1969	1141	8	Forest	8.8	9.0	6.0	7.1	---	---	2.9	---

[a]σ_y = horizontal distance perpendicular to plume axis to 68% of maximum value (m).
[b]σ_z = vertical distance perpendicular to plume axis to 68% of maximum value (m).

TABLE 4. Percentage of fluorescent particles [ZnCdS, avg diam 3.3 μm (range 1.0-7.0 μm)] deposited as a function of distance from source in releases in the forest, at the forest edge, and outside the forest in the cleared area

Type of site	Date	Release time (h)	Percent deposited (m from source): 5	10	15	30	60	Relative deposition[a]
Forest								
	3 July 1970	0744	0.07	0.19	0.34	1.71	4.19	6
	5 Sept. 1969	0931	0.85	2.58	5.79	14.23	31.71	1
	5 Sept. 1969	1141	0.03	0.10	0.21	0.69	1.66	7
	3 July 1970	1255	0.02	0.07	0.17	0.52	1.15	9
	4 Sept. 1969	1730	0.38	1.39	2.88	5.80	12.99	2
	4 Sept. 1969	2249	0.003	0.01	0.02	0.06	0.12	13
	2 July 1970	2336	0.01	0.04	0.06	0.14	0.28	11
Forest edge								
	29 Aug. 1969	1156	0.03	0.08	0.16	0.49	1.19	8
	29 Aug. 1969	1241	0.003	0.009	0.02	0.07	0.19	12
	29 Aug. 1969	1517	0.01	0.047	0.09	0.29	0.64	10
Cleared area								
	3 July 1970	0726	0.09	0.34	0.66	3.30	6.90	3
	3 July 1970	1240	0.17	0.63	1.22	2.89	6.04	5
	2 July 1970	2303	0.11	0.44	0.91	2.70	6.58	4

[a]1 = heaviest, 13 = lightest deposition of fluorescent particles.

TABLE 5. Relation between Rotorod samples at 1.0 m and deposition samples at 30 cm as shown by correlation coefficients

Date	Release time (h)	Correlation coefficient	Sampling grid location
14 Aug. 1969	1540	0.19 NS[a]	Forest edge
14 Aug. 1969	1635	0.20 NS	Forest edge
29 Aug. 1969	1156	0.69 **[c]	Forest edge
29 Aug. 1969	1241	0.90 **	Forest edge
29 Aug. 1969	1517	0.57 **	Forest edge
4 Sept. 1969	1730	0.85 **	Forest
4 Sept. 1969	2249	0.59 **	Forest
5 Sept. 1969	0931	0.62 **	Forest
5 Sept. 1969	1141	0.03 NS	Forest
2 July 1970	2303	0.17 NS	Cleared area
3 July 1970	0726	0.47 *[b]	Cleared area
3 July 1970	1240	0.38 NS	Cleared area

[a]NS = no significant difference.
[b]* = significant difference, $P = 0.05$.
[c]** = significant difference, $P = 0.01$.

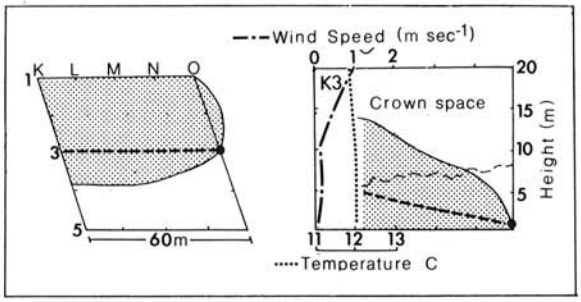

Fig. 5. Horizontal (at 1 m) and vertical extent of the fluorescent particle plume in the forest grid to 5% of maximum values (shaded). Line linking points of maximum value is shown (- -). Wind speed and temp profiles at K3 are shown. Release point was O3 at 2249 hours on 4 Sept. 1969.

top of the forest and the only barrier to vertical dispersion was the physical barrier of the tree crowns.

Deposition patterns.—Table 4 shows the percentage of particles deposited at various distances from the source. Particles deposition was light at night in the forest. Even when wind speeds were less than 6 cm/s, 99.88% of the particles were still airborne 60 m from the source in a nighttime release on 4 Sept. 1969 at 2249 hours.

Deposition in the cleared area at night, however, under similar conditions was much heavier than in the forest. In this case, vertical dispersion was inhibited by a strong inversion and particles settled out.

Deposition during the day in the cleared area was about the same as it was at night (Table 4). However, deposition in the forest was complicated by the variable vertical dispersion patterns. Close to the forest edge deposition was light when the wind was blowing directly into the forest (29 Aug. 1969 at 1241 hours). However, it tended to increase at the edge when the wind was blowing along the forest edge (29 Aug. 1969 at 1156 hours). Deposition was extremely variable in the forest. Vertical velocities were measured with the propeller anemometer on 3 July 1970 at 1255 hours. Average velocities of 10.7 cm/s in the

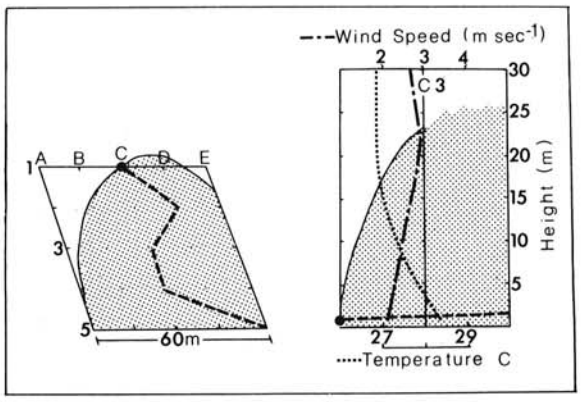

Fig. 6. Horizontal (at 1 m) and vertical extent of the fluorescent particle plume in the cleared area grid to 5% of maximum values (shaded). Line linking points of maximum value is shown (- -). Wind speed and temp profiles at C3 are shown. Release point was C1 and 1240 hours on 3 July 1970.

downwards direction were recorded. These velocities are considerably higher than the settling velocities of the spores or particles (0.0748 and 0.1315 cm/s, respectively) resulting in more deposition than expected from settling alone.

Vertical velocities were not recorded at night in the forest because the threshold of detection of the anemometer was higher than the high-frequency turbulent movements that apparently were effective in keeping spores aloft.

Relationships between deposition and atmospheric concentration at the same location.—The relationship between particle concn at 1 m deposition onto a horizontal surface 30 cm above the forest floor is poorly defined. Correlation coefficients relating these two variables vary from 0.90 and 0.03 (Table 5). The correlation coefficients are generally higher in the forest in comparison to the cleared area, but this was not consistent.

Prediction of dispersion and deposition.—Predicted and observed fluorescent particle concns horizontally 1 m above the ground surface and vertically along the center line of the plume, and deposition 30 cm above the forest floor are shown in Fig. 9.

The values of the model variables which give best fits to the observed data are shown in Table 6. These values are similar to those used by Gregory (8) in spore dispersion experiments. Values for the deposition velocity (V_g) were not constant (Table 7), but varied spatially and tended to decrease with distance from the source. Average values were used in the model.

Predicted concn values within 60 m of the source differed from the observed values by less than a factor of two (Fig. 9). The mean wind directions available from wind vane data were used to determine predicted plume directions. However, on occasions when wind vanes stalled due to low wind speeds, plume directions were determined from observed concn data.

The observed dispersion patterns generally are not Gaussian due to the irregular vegetation density. The plumes moved preferentially into areas of lower vegetation density. Dispersion patterns in Fig. 9 should

be compared with vegetation density in Fig. 2. Changes in topography also cause plume distortion. Agreement between observed and predicted values of concn was best in early morning and night releases, both in the cleared area and forest (Fig. 9-a and 9-b) and in the daytime release in the cleared area (Fig. 9-c). Plumes are more distorted in the daytime release near the forest edge (Fig. 9-d) and in the forest (Fig. 9-e). Observed vertical concn values tend to be greater than predicted in these releases.

We were primarily interested in predicting deposition, which was not as well predicted as concn. The predicted values of deposition were determined by multiplying V_g by the concn. That is, a direct relationship between concn and deposition was assumed. We have already determined that a poor relationship exists between these two variables (Table 5), mainly due to the complicated vertical dispersion and deposition regimes. Best prediction of deposition occurred in the early morning and night releases (Fig. 9-a and -b), and at the edge of the forest (Fig. 9-e) during the day.

Natural deposition of spores of Fomes annosus.—Deposition of spore of *F. annosus* was determined in July and August, 1970, in a western hemlock forest at the Marckworth Forest site infected with *F. annosus*. Very few spores of *F. annosus* were deposited, but deposition of these spores occurred at night or early in the morning. Spore deposition rates varied from 0.0003 to 0.007 spores per cm^2 per hr during 24 h.

DISCUSSION.—*Fomes annosus* conidia were dispersed in a similar manner to fluorescent particles of similar size in some releases, but not in others. Sampling errors may have caused this difference. The samplers at each location were separated by 30 cm and thus, were not sampling exactly the same volume of air. Also, the efficiencies of the samplers were only averages and did not take into account variability in size and shape of spores and fluorescent particles.

The most important factors influencing dispersion of spores and fluorescent particles were atmospheric stability, release time, and the presence and density of vegetation. The vertical dispersion regime, in particular, was markedly influenced by the presence of the forest canopy. During sunny days the upper part of the canopy was heated, which in turn heated the air in this region producing an inversion under the canopy. Particles or spores were unable to escape from the forest in these conditions, except when they reached large openings in the forest where thermal chimneys carried them aloft (3). Under cloudy conditions, the inversion under the canopy was not well developed, and dispersion through the canopy was limited only by the obstruction of the canopy (3). On clear nights particles were unable to break through the temp inversion which forms above the tree tops (3).

Dispersion patterns in the cleared area differed markedly from those in the forest, particularly at night or early in the morning where there was little dispersion in the cleared area and great dispersion in the forest. The greater dispersion in the forest was due to the presence of trees in the laminar cold air flow which produced high frequency turbulence and enhanced mixing, resulting in

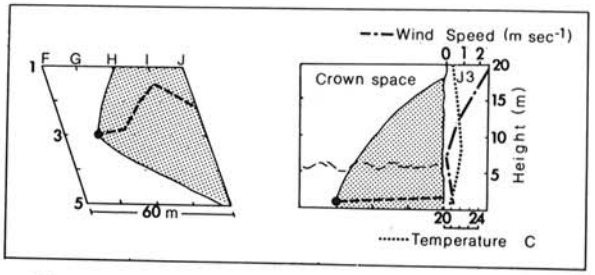

Fig. 7. Horizontal (at 1 m) and vertical extent of the fluorescent particle plume in the forest edge grid to 5% of maximum values (shaded). Line linking points of maximum value is shown (- -). Wind speed and temp profiles at J3 are shown. Release point was C1 at 1240 hours on 3 July 1970.

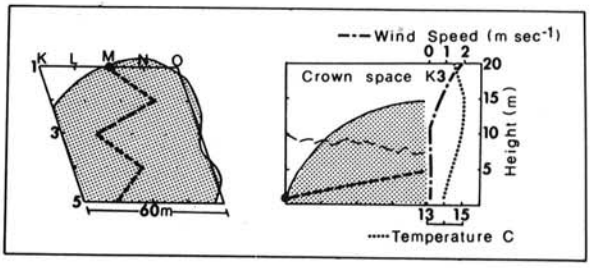

Fig. 8. Horizontal (at 1 m) and vertical extent of the fluorescent particle plume in the forest grid to 5% of maximum values (shaded). Line linking points of maximum value is shown (- -). Wind speed and temp profiles at K3 are shown. Release point was M1 at 1141 hours on 5 Sept. 1969.

TABLE 6. Values of variables used in dispersion model for results appearing in Fig. 9

Date	Release time (h)	Stability constant n	Diffusion coefficients		Deposition velocity V_g (m/s)	Wind speed u (m/s)	Source strength Q (particles/s)
			C_y[a]	C_z[b]			
3 July 1970	0726	0.15	0.59	0.09	0.0025	0.30	45,000,000
4 Sept. 1969	2249	0.015	0.50	0.11	0.00016	0.05	24,791,664
3 July 1970	1240	0.025	0.63	0.50	0.01	2.20	45,000,000
29 Aug. 1969	1517	0.2	0.63	0.16	0.00296	1.54	32,777,777
5 Sept. 1969	1141	0.05	0.80	0.10	0.00175	0.30	41,333,333

[a] C_y = virtual diffusion coefficient in horizontal plane ($m^{1/8}$).
[b] C_z = virtual diffusion coefficient in vertical plane ($m^{1/8}$).

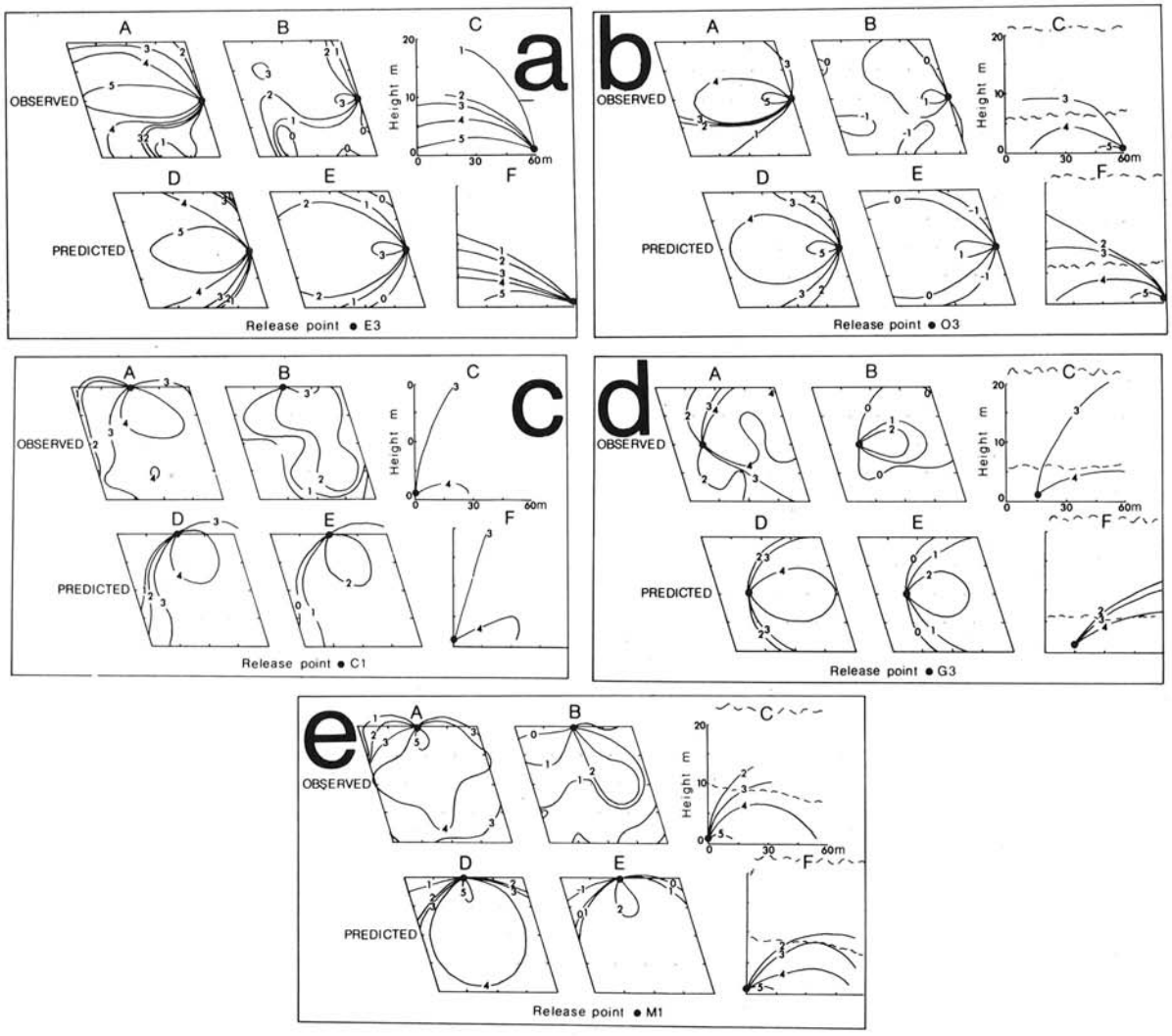

Fig. 9-(a to e). Observed and predicted values of concn (particles per m^3) at 1 m (A, D) and in the vertical plane along the center line (C, F) and deposition (particles per m^2 per second) 30 cm above the ground surface (B, E) for **a)** 3 July 1970 at 0726 hours **b)** 4 Sept. 1969 at 2249 hours, **c)** 3 July 1970 at 1240 hours, **d)** 29 Aug. 1969 at 1517 hours, and **e)** 5 Sept. 1969 at 1141 hours. Isopleths are expressed in powers of 10.

an isothermal vertical temp profile below the canopy. Although there was considerable vertical mixing in the forest, particles did not escape vertically due to the inversion above the canopy. Thus they tend to be channeled beneath the canopy until they come to streams or large bodies of water where up-drafts occur. This indicates that spores of *F. annosus* are capable of traveling long distances since they are released at night (17, 23, 24). Rishbeth (15) found spores of *F. annosus* 320 km from the nearest source.

TABLE 7. Ranges and average values of deposition velocity (V_g)

Date	Release time (h)	Range of V_g (m/s)	Average V_g (m/s)
3 July 1970	0726	7.69 - 0.00023	0.0162
4 Sept. 1969	2249	0.0003 - 0.0000021	0.00016
3 July 1970	1240	0.81 - 0.000046	0.01588
29 Aug. 1969	1517	0.097 - 0.000071	0.00296
5 Sept. 1969	1141	0.86 - 0.000022	0.00145

Spores and particles did not simply settle out in the forest at night because the wind speed was low. High frequency turbulence in the forest caused a large amount of mixing which resulted in less deposition in the forest than in the cleared area. However, deposition at night close to a forest edge may be heavy as a result of local turbulent deposition. Large eddies form at the forest edge. Heaviest deposition occurred in the forest during the day when lower frequency turbulence occurred, which caused fluctuations in vertical dispersion and variable deposition. This may explain some of the low correlation coefficients relating atmospheric concns to deposition during the day. Poor correlations during the day were also found by Melpar (11) in a deciduous forest.

The dispersion model was very sensitive to changes in the values of the deposition velocity (V_g), the wind speed (u), the vertical diffusion coefficient (C_z), and the source strength (Q); but less sensitive to changes in the horizontal diffusion coefficient (C_y). Values of u, C_z, and Q can be determined with some accuracy but determining the value of V_g to be used for prediction is a problem, since it changes with distance from the source. This makes consistent prediction difficult.

Prediction of deposition in the forest was difficult because of the complicated vertical dispersion patterns. Generally, prediction was better for night or early morning releases than day releases. No account was made for deposition on foliage because calculations revealed that less than 1% of particles would be deposited on Douglas-fir needles.

Our findings that maximum natural spore deposition occurred at night or early in the morning agrees with findings of Jorgensen (9) and Stambaugh et al. (19). This is not surprising since maximum basidiospore release occurs at night (17, 23, 24). Sinclair (18), however, indicated that deposition was lowest during the night, increased slowly during the morning hours, and rose sharply to an afternoon peak.

These apparently conflicting natural deposition patterns can be interpreted by examining the patterns of fluorescent particle deposition. Variable deposition patterns of the fluorescent particles occurred, depending on the location of deposition samplers; i.e., cleared area, forest, or forest edge. Sinclair's (18) samplers were located in the forest, so his results agree with the observed fluorescent particle deposition data. Stambaugh et al. (19) failed to report the location of their samplers with respect to the forest edge. However, Jorgensen's (9) study was conducted in a forest nursery and the reported heavier spore deposition at night would be anticipated from fluorescent particle deposition in the cleared area. Fluorescent particle deposition during the day close to the forest edge tended to be light, particularly when the wind was blowing directly into the forest. This may explain why no spores were deposited during the afternoon hours on the Marckworth Forest sampler which was close to the forest edge. There is evidence, however, that deposition near the forest edge at night might be greater than that within the forest because of local turbulence induced at the forest edge in cold air drainage conditions (3). The propeller anemometer at Marckworth Forest indicated that downslope code air drainage conditions were in effect when spores were deposited at night.

Study of the fluorescent particle deposition data has enabled interpretation of the natural deposition of spores of *F. annosus* from a number of studies. However, the spore release and the location of the sampler must be taken into account in the interpretation.

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