Relative Abundance and Deposition Gradients of Clusters of Urediniospores of *Uromyces phaseoli*

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ABSTRACT

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Singlets and clusters of urediniospores of *Uromyces phaseoli* were released naturally from a small area of infected plants within a 0.25-ha bean field. Deposition gradients were assessed by counting the number of singlets and clusters containing 2, 3, 4,...,N urediniospores deposited on sticky, horizontal microscope slides located at various distances downwind of the source and by counting the number of lesions that developed on the leaves of potted trap plants that were exposed in the field concurrently with the slides. Clusters accounted for more than 50% of the dispersal units and about 80% of the total number of spores deposited on the slides. Fully 30% of the clusters contained five or more urediniospores. Both the number of dispersal units deposited on slides and the number of lesions that developed on trap plants decreased approximately with the inverse square of distance from the source.

Additional key words: bean rust, dispersal gradients.

A certain proportion of the spores of many plant pathogens, especially the rusts, become airborne in clusters (11). Clustering of spores reduces the potential number of airborne dispersal units and, therefore, decreases the effective strength of the source of airborne inoculum. Furthermore, clusters settle faster than single spores (5) and may be deposited at a faster rate. Thus, there are two potential ways by which clusters can reduce the number of dispersal units reaching host plants far from the source region. In the first place, there are fewer numbers released. Secondly, a greater number of the available dispersal units are deposited near to the point of origin because of the enhanced deposition (4). Once the turbulent motions of the air carry spores above the plant canopy, however, they are no longer subject to deposition. Thus, in spite of their greater settling speed, clusters that have escaped from the plant canopy have the potential to be carried great distances by the wind (2).

To assess the importance of clusters in the dispersal of spores we determined the relative number of singlets and clusters of urediniospores of *Uromyces phaseoli* (Reben) Wint. (the pathogen of bean rust) deposited at various distances from a small area of diseased snap bean (*Phaseoli vulgaris* L.) plants within a field. These observations are compared with the predictions of a theoretical model (1,8), which accounts both for the effects of turbulent dispersal and differences in settling speeds between singlets and clusters.

MATERIALS AND METHODS

A rectangular (46 × 52 m) 0.25-ha field was planted on 22 May 1984 to snap beans (Bush Bush Blue Lake 47) in east-west oriented rows spaced 76 cm apart. On 14 June 1984, when the first trifoliolates were fully expanded, four source regions were inoculated with urediniospores of *Uromyces phaseoli*. The source regions, located at the centers of the four quadrants of the field, were separated from each other by 30 m and consisted of 1-m lengths of two adjacent rows of bean plants. Numerous spore-bearing pustules developed on these source plants. Three spore dispersal experiments (hereafter called experiments 1, 2, and 3) were performed between 0900 and 1300 hours EST on 26, 27, and

28 June 1984 when the sporulating lesions were 12, 13, and 14 days old (measured from the day of inoculation). In each experiment, we used the source that was upwind of the other three sources to avoid possible interference.

The dispersal of spores away from the sources was assessed by measuring deposition on sticky microscope slides and on potted trap plants. Slides, coated with a thin layer of silicone grease (Dow-Corning high vacuum grease), were placed on the ground within the source region, and on the ground and at a height of 0.25 m along arcs with radii of 1, 2.5, 4, and 5 m downwind from the center of the source. After 4 hr exposure in the field, slides were collected and the number of singlets and clusters containing 2, 3, 4,...,N spores were counted. In addition, 20–25 potted trap plants were placed 3.8 m apart in a square grid downwind of the source. The distance between the center of the source and the trap plants ranged between 1.9 and 16 m. After exposure in the field, the plants were placed overnight in a dew chamber, then moved to a growth chamber (20 C) and incubated for 8–10 days. The lesions that developed on the leaves were then counted.

Data reduction. To facilitate comparisons among experiments, the deposition on slides was expressed in terms of the number of dispersal units deposited per square centimeter of slide per hour of exposure time, which we call the deposition flux. The deposition flux of N-tuplets, D_N (cm^{-2} hr^{-1}), is defined to be the number of clusters containing N urediniospores deposited per square centimeter of slide per hour of exposure time. The total deposition flux of dispersal units of all sizes, D_T, is defined as the sum of the D_N over all N. Because of low counts for dispersal units containing five or more spores, we pooled this data to minimize statistical fluctuations. The deposition flux for clusters containing five or more spores, $D_{N \geqslant 5}$, is defined as the sum of the D_N for $N \geq 5$.

The number of lesions on trap plants was also expressed in terms of a deposition flux. The deposition flux of lesion-producing dispersal units, D (cm^{-2} hr^{-1}), is defined as the number of lesions per square centimeter of leaf area per hour of exposure time. For the trap plants no attempt was made to determine the number of urediniospores causing each lesion.

Close to the source of urediniospores, deposition is high and the resulting lesions formed on the trap plants tend to coalesce. This makes counting lesions difficult. Thus, close to the source, slides give more reliable estimates of deposition. On the other hand, at larger distances from the source, trap plants are preferable because of the large area of trifoliolates (150 cm^{-2}), and the relative ease of counting sparse lesion densities on leaves. To obtain a reliable description of deposition over the entire range of distance, it is

desirable to combine slide and trap plant data. For this reason, slides and trap plants were exposed within 20 cm of each other at two or more distances between 1.5 and 4 m from the source during each experiment. The elevated slides and the leaves of the trap plants were exposed at approximately the same height and thus to approximately the same aerial spore concentrations and ambient wind conditions. Although the efficiency of deposition to each of these trap surfaces may differ, it is reasonable to assume that this difference will not depend strongly on distance from the source of spores. Thus, D for the trap plant leaves is expected to be a relatively constant fraction of D_T for the elevated slides in any one experiment. To compare deposition gradients derived independently from trap plants and sticky elevated slides, the ratio D/D_T was evaluated for the trap surfaces that were exposed in close proximity. This ratio was then used to normalize data at all distances.

Analysis of spatial variation. The decrease in the aerial concentration away from a source of spores is caused by the combined effects of deposition of spores on plants and the ground and by dilution of the spore cloud due to atmospheric turbulence. If the effects of spore deposition dominate turbulent mixing, as when most of the airborne spores are contained within the plant canopy, then the deposit per unit downwind distance should be a constant fraction of the amount still airborne and deposition would be expected to decrease exponentially with increasing downwind distance (7,10). If, on the other hand, deposition is negligible and atmospheric turbulence dominates the dilution of spores, then the decrease in deposit with increasing distance should be described by an inverse power law (14). Thus, we will compare the measured decrease in spore deposition with increasing distance from a source with these two limiting mathematical functions: an exponential law and a power law. In practice both processes can be equally important during the first few meters of travel and neither of these mathematical functions should be expected to completely describe spore deposition (9).

The reduced spore count data gave the deposition fluxes to the slides for any size cluster, D_N, for clusters containing five or more spores, $D_{N \geq 5}$, and for all sizes of clusters combined, D_T, and the lesion density per hour of exposure for the leaves of the trap plants, D, as a function of r and α where r is the horizontal distance from the center of the source and α is the azimuthal angle in a cylindrical coordinate system with a vertical polar axis. Data taken along radii (fixed α) was used to characterize the decrease in deposition with increasing distance from the source. By using least square regression analysis, the data were fitted to exponential and power law functions, which for the trap plant data take the forms:

$$D(r, \text{fixed } \alpha) = D(0) \cdot e^{-ar} \qquad (1a)$$

and

$$D(r, \text{fixed } \alpha) = D(1m) \cdot (r/1m)^{-b} \qquad (1b)$$

where $D(0)$ or $D(1m)\,(\text{cm}^{-2}\,\text{hr}^{-1})$ and $a\,(\text{m}^{-1})$ and b (dimensionless) are parameters obtained by regression.

Meteorological measurements. Wind direction was measured at a height of 2.1 m by using a vane. Wind speed was measured at heights of 0.4, 0.6, 1.0, and 1.8 m by using sensitive cup anemometers. The wind speed data was fitted by regression analysis to a logarithmic law (13) that implies that the eddy diffusivity $[K(z)]$, a measure of vertical mixing, increased linearly with height so that:

$$u(z) = (u_*/k) \cdot \ln[(z-d)/z_0] \qquad (2a)$$

and

$$K(z) = k \cdot u_* \cdot (z-d) \qquad (2b)$$

where k is von Karman's constant equal to 0.4, d is the displacement height taken equal to 0.7 times the crop height. The friction velocity, u_* and the roughness length scale, z_0, are parameters given by the regression analysis. Vane data was used to calculate the mean wind direction, θ, and the standard deviation, σ_θ, about this mean direction. Ambient air temperature and relative humidity (RH) were monitored continuously by a Campbell CR21 datalogger.

Mathematical model of turbulent dispersal. The simultaneous effects of deposition, turbulent mixing, and escape on the aerial concentration of dispersal units downwind of a source can be understood in terms of a previously described model (1,8). The model assumes that spores are released steadily into the air and is modified here by the added assumption that advection is radially outwards from a point (6,9). With these assumptions the airborne concentration C of dispersal units can be described by the following equation (1,8 with rC replacing C):

$$u \cdot \frac{\partial(rC)}{\partial r} = \frac{\partial}{\partial z}\left[K \cdot \frac{\partial(rC)}{\partial z} + v_s rC\right] - rRC + Q, \qquad (3)$$

where K is the turbulent diffusivity, the product RC is the time rate of deposition of dispersal units per unit volume of the plant canopy, $Q(r,z)$ is the number of dispersal units released per unit time, per unit height z and per unit radial distance r and v_s and $u(z)$ were defined previously. Above the crop, both $R(z)$ and $Q(r,z)$ are zero and $u(z)$ and $K(z)$ were assumed to be given by equations 2a and b. Within the relatively short and sparse crop used in these experiments, K was assumed to be a constant and equal to the value at the crop top, and $u(z)$ was assumed to decrease exponentially with distance into the canopy (15). The source term Q was assumed to be uniform and constant in vertical extent between $z = 0.1$ and 0.2 m and in horizontal extent to a distance of 1 m from the center of the source ($r < 1$ m). Outside this region, Q was assumed to be zero. Deposition onto the foliage and ground was assumed to be by sedimentation alone (1,8). The foliage was assumed to be uniformly distributed throughout the canopy. Thus, R in equation 3 was taken as: $R = v_s \cdot \text{LAI}/H$, where H is the height of the crop and LAI is the leaf area index, which is the leaf area per ground area. To calculate concentrations, the derivatives in equation 3 were approximated by finite differences and the resulting difference equation was integrated numerically (1).

RESULTS

Crop and wind measurements. During the experiments there were approximately 17.5 plants per meter of row, H was between 0.2 and 0.3 m, and LAI was between 1.0 and 1.2. For experiment 1, the wind was from the NNW and the NW source region was used. This source had 34 plants with a total of 375 fully expanded leaves and disease incidence (on a per leaf basis) was 73%. For experiments 2 and 3, the wind was from the SSW, so the SW source region was used. This source consisted of 35 plants with 386 leaves and disease incidence was 63%. For both of these sources each infected leaf contained between 100 and 500 pustules that were between 0.5 and 1 mm in diameter. This corresponded to an overall disease severity of approximately 15% diseased tissue within the source regions. The first signs of secondary infection (small chlorotic specks) were observed on 29 June 1984. Therefore, the only source of airborne urediniospores of *Uromyces phaseoli* within the bean field during our experiments was the 0.76×1 m inoculated area immediately upwind of the sampling region.

The wind speed data were fitted well ($r^2 = 0.98$) by equation 2a. These regression fits gave estimates of the appropriate values of u_* for each experiment, which were then used in equation 2a and b to obtain the values of $u(z)$ and $K(z)$ needed for equation 3. The values of u_*, as well as the mean wind speed at a height of 1.8 m ($u_{1.8}$) and σ_θ for each of the three experiments are presented in Table 1.

Abundance of clusters. The fraction of the total number of clusters containing N spores that were deposited on ground slides within the source region (D_N/D_T) is plotted as a function of N in Figure 1. The data have been truncated at $N = 9$, and the cumulative fraction of deposited clusters containing 10 or more

spores ($D_{N\geqslant10}/D_T$) is plotted as a single point. The population distribution for dispersal units deposited within the source region was remarkably constant for the three experiments, perhaps because there was little variation in lesion age (12–14 days), RH (45–55%), or air temperature (18–22 C). These data were fitted well ($r^2 = 0.91$–0.99) by the power law expression $D_N = D_1 \cdot N^{-d}$ where the value of d was 1.0, 1.35, and 1.4 for experiments 1, 2, and 3, respectively.

For the elevated and ground slides outside of the source region the values of D_N/D_T for $N = 2$–9 are indistinguishable from those shown in Figure 1. However, elevated and ground slides outside of the source region did contain a higher fraction of singlets ($D_1/D_T = 40$–50%) and a lower fraction of large clusters ($D_{N\geqslant10}/D_T$ 10%) than the source slides.

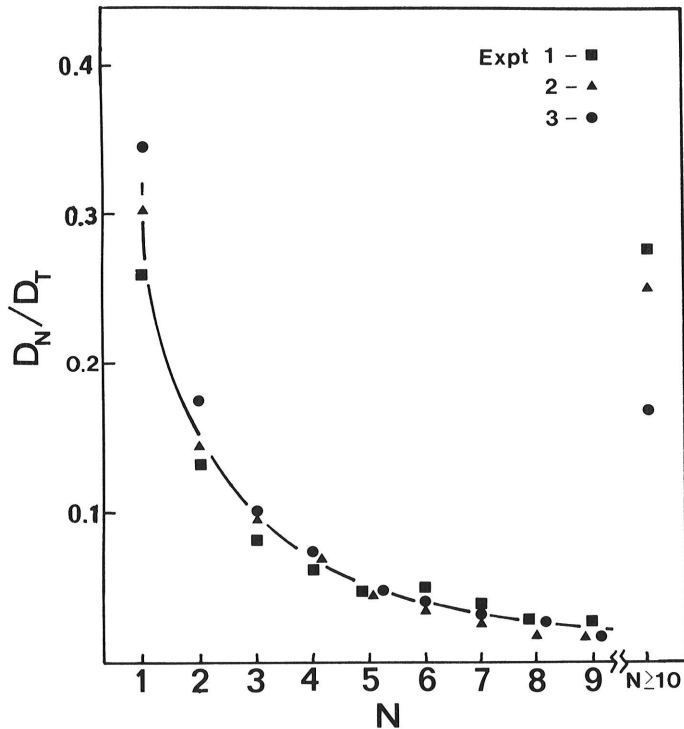The prevalence of clusters in the deposit on the slides can be described in terms of the mean number of urediniospores per cluster, which is defined to be the total number of urediniospores divided by the total number of dispersal units. The mean number of urediniospores per cluster deposited on the ground slides in all experiments was between 5 and 6 within the source region and ranged between 3 and 4.5 everywhere outside the source region.

Inoculum potential. A comparison of D for the trap plants closest to the source and D_T for neighboring elevated slides yielded estimates of the ratio D/D_T of 0.42, 0.21, and 0.16 for experiments 1, 2, and 3, respectively. Thus, if the efficiency of deposition on slides was approximately the same as on trap plant leaves, then the inoculation potential of bean rust dispersal units in our experiments ranged between 16 and 42%. This is somewhat higher than reported elsewhere for single bean rust urediniospores (12,13) and may be explained, in part, by an increased percentage of germination of clusters compared with singlets (3).

Spatial distribution of deposition. Within a central sector bounded by $\alpha = \theta \pm 1.5\sigma_\theta$ the deposits on either slides or plants were relatively independent of angle. Outside of this sector, however, deposits decreased very rapidly with increasing angular distance from θ. Only data from the central sector is included in the following analyses.

The decrease in total deposition with increasing distance from the source, taken singly from either the sticky slides or the trap plants, was described equally well by an exponential law or by a power law (Table 1). However, the fitted value of a (Eq. 1a), for the trap plant data, was significantly smaller than the value obtained from the counts on the sticky slides in each of the experiments, whereas the fitted values of b (Eq. 1b) showed very little variation between the trap plant and sticky slide data. Because of this, the power law seemed better than the exponential law for describing the combined observations for the sticky slides and trap plants, which extended over a distance of 1–15 m.

The comparison of exponential and power law fits for singlets $N = 1$ and large clusters $N \geqslant 5$ is shown in Table 2 where regressions for D_1 and $D_{N\geqslant5}$ are compared for both ground and elevated slides. The mean number of urediniospores in these large clusters was approximately 9. The settling speed and, therefore, the rate of deposition of such clusters is approximately three times the value for a single spore (5). The insignificant differences between the fitted values of b for the singlets and large clusters (Table 2) suggest that deposition played a relatively minor role in determining the deposition gradient at distances between 1 and 5 m from the source.

Model calculations. For given wind and crop data, the solution to equation 3 is determined to within a scale factor that depends only on the strength of the source Q. To compare the model to the field data, the predicted concentrations, the observed deposition fluxes, and the trap plant lesion densities were all normalized to equal unity at a distance of 1 m from the center of the source. For the model predictions and the slide data this normalization was

Fig. 1. The ratio, D_N/D_T, formed by dividing the deposition flux of clusters containing N spores, D_N, by the total deposition flux, D_T, is plotted versus cluster size, N. Data are from the ground slides within the source region. The graph is truncated at $N = 9$ and the fraction of clusters with $N \geqslant 10$ is shown at the far right. The solid line was drawn in free hand through the means of the data points at each value of N.

TABLE 1. Exponential ($D = D(0) \exp(-ar)$) and power law ($D = D(1m)(r/1m)^{-b}$) fits to the deposition flux[a] of urediniospores of *Uromyces phaseoli* vs. distance r from the source (Data are from a sector bounded by $\alpha = \theta \pm 1.5\sigma_\theta$[b])

Expt. no.	$u_{1.8}$[c] (m/s)	u_*[d] (m/s)	σ_θ[b] (degrees)	Collection surface[e]	n[e]	$D(0)$ (cm^{-2}hr^{-1})	$a \pm$ s.e.a. (m^{-1})	c.d.[f]	$D(1m)$ (cm^{-2}hr^{-1})	$b \pm$ s.e.b. (dimension-less)	c.d.[f]
1	2.3	0.24	33	TP	11	0.6	0.3 ± 0.04	0.86	2.6	2.0 ± 0.3	0.84
				ES	8	13	0.9 ± 0.1	0.96	7.6	2.3 ± 0.1	0.98
				GS	11	14	1.0 ± 0.1	0.94	5.8	2.4 ± 0.3	0.93
2	3.1	0.33	22	TP	11	2.6	0.3 ± 0.03	0.94	11	2.3 ± 0.3	0.89
				ES	9	49	0.8 ± 0.2	0.70	35	2.3 ± 0.5	0.73
				GS	15	65	$12. \pm 0.1$	0.89	30	3.0 ± 0.3	0.86
3	2.5	0.24	23	TP	12	0.5	0.3 ± 0.04	0.82	2.8	2.1 ± 0.2	0.90
				ES	8	11	0.7 ± 0.1	0.81	7.4	1.9 ± 0.4	0.80
				GS	12	13	0.9 ± 0.1	0.93	7.2	2.4 ± 0.2	0.93

[a] Deposition flux on trap plants D = number of lesions produced per unit leaf area per hour of exposure. Deposition flux on slides D_T = total number of dispersal units of all sizes deposited per unit area per hour of exposure.

[b] σ_θ = standard deviation about the mean wind direction θ measured at a height of 2.1 m.

[c] $u_{1.8}$ = mean horizontal wind speed at a height of 1.8 m.

[d] u_* = friction velocity determined from the vertical variation of horizontal wind speed (9).

[e] TP = trap plants, ES = elevated slides, GS = ground slides, n = the number of observations.

[f] c.d. = the coefficient of determination of the regression.

accomplished by dividing by the appropriate value at $r = 1$ m. The observed lesion densities on trap plants were first divided by the ratio, D/D_T, to account for inoculation potential and then divided by D_T (1 m) for the elevated slides in order to complete the normalization. The resultant normalized data are compared for ground slides ($z = 0$, Fig. 2) and for elevated slides ($z = H$, Fig. 3) using the crop parameters and wind and deposition data obtained from experiment 2.

On the ground slides within the source region (Fig. 2) $D_{N \geqslant 5}$ (open circles) is larger than D_1 (solid circles). Outside of the source region, however, the deposit of clusters decreases much more rapidly than the deposit of singlets, so that, for distances greater

than 1 m from the center of the source D_1 is larger than $D_{N \geqslant 5}$. The model predictions for singlets (solid line) and for clusters containing nine urediniospores to correspond to the mean size of clusters with $N \geqslant 5$ (dashed line) illustrate this same behavior.

Both the model predictions and the data suggest that the major effect of increased deposition velocity is confined to a relatively small region ($r < 2$ m) near the source. In this region, the number of clusters decreases more rapidly than the number of singlets with increasing r. For $r > 2$ m from the center of the source, the more nearly parallel behavior of the solid and dashed lines (Fig. 2) indicate that the relative numbers of singlets and clusters deposited on the ground remain fairly constant. This result reflects the decreasing importance of deposition as dispersal units escape from the canopy. The model predicts that at 1 m from the center of the source about 90% of the dispersal units, irrespective of size, still airborne are above the canopy and therefore not directly subjected to deposition.

The deposit of dispersal units on elevated slides and the lesions densities on trap plants also are described well by the model predictions (Fig. 3). On the elevated slides, the deposit of singlets
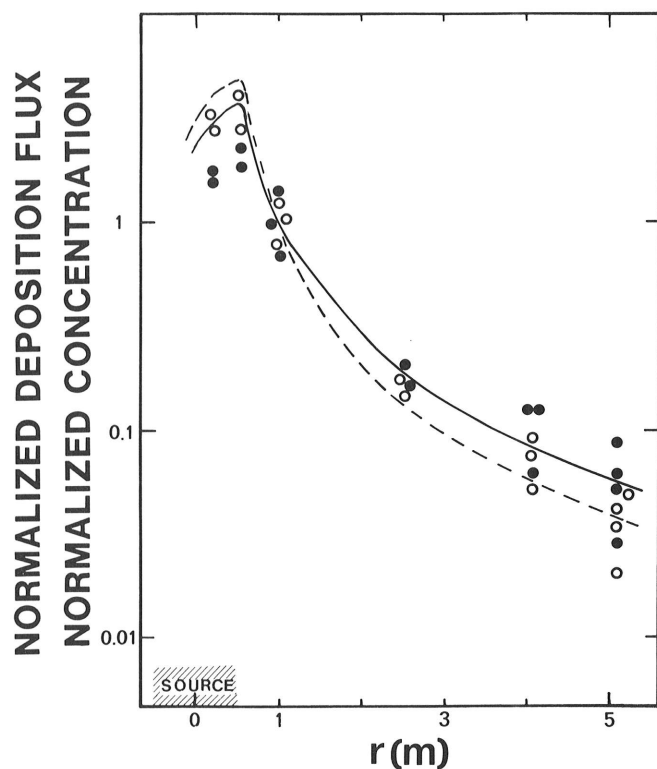

Fig. 2. Log-linear plot of the normalized deposition flux on the ground slides and the normalized ground level concentration versus radial distance from the source, r, for experiment 2. The normalized deposition flux is shown for singlets ($D_1(r)/D_1$ (1 m), solid circles) and for clusters with five or more spores having a mean value equal to nine ($D_{N \geqslant 5}(r)/D_{N \geqslant 5}$ (1 m), open circles). The normalized ground level concentration ($C(r,0)/C(1$ m, 0)) for singlets (solid line) and for clusters of nine urediniospores (dashed line) was calculated from equation 3 with the crop and wind parameters for experiment 2.
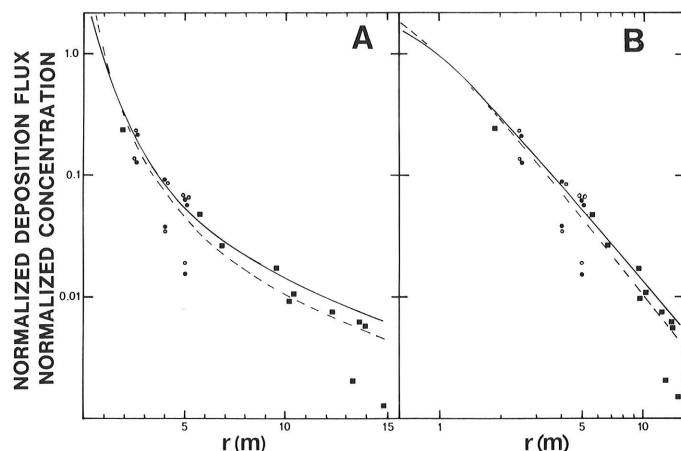

Fig. 3. Log-linear (A) and log-log (B) plots of the normalized deposition flux on the elevated slides, the normalized lesion densities on trap plants, and the normalized concentration at $z = 0.25$ m versus radial distance from the source, r, for experiment 2. The normalized deposition flux on the elevated slides is shown for singlets ($D_1(r)/D_1$ (1m), solid circles) and for clusters with five or more spores having a mean value equal to nine ($D_{N \geqslant 5}(r)/D_{N \geqslant 5}$(1 m), open circles). The lesion densities for the trap plants (solid squares) were first divided by the ratio, D/D_T, to account for inoculation potential (see text) and, then, divided by the value of D_T(1 m) in concert with the normalization for the elevated slides. The normalized concentration at $z = 0.25$ m ($C(r, 0.25$ m)$/C$(1 m, 0.25 m)) for singlets (solid line) and for clusters of nine urediniospores (dashed line) was calculated from equation 3 using the crop and wind parameters for experiment 2.

TABLE 2. Comparison of the exponential ($D = D(0) \exp(-ar)$) and power law ($D = D(1m)(r/1m)^{-b}$) fits to the deposition flux of single urediniospores (singlets) and clusters ($N \geqslant 5$) containing five or more urediniospores of *Uromyces phaseoli* vs radial distance r from the source (Data are from a sector bounded by the two radii $\alpha = \theta \pm 1.5\sigma_\theta$[a]

Expt. no.	Collection surface[b]	n[c]	Particle size	$D(0)$ (cm^{-2} hr^{-1})	$a \pm$ s.e.a. (m^{-1})	c.d.[d]	$d(1m)$ (cm^{-2} hr^{-1})	$b \pm$ s.e.b.	c.d.[d]
1	ES	8	Singlet	4.9	1.0 ± 0.1	0.92	2.8	2.4 ± 0.3	0.93
			$N \geqslant 5$	2.1	0.7 ± 0.1	0.85	1.4	1.8 ± 0.3	0.86
	GS	11	Singlet	4.1	1.1 ± 0.1	0.94	1.7	2.4 ± 0.3	0.93
			$N \geqslant 5$	2.8	1.0 ± 0.2	0.81	1.5	2.5 ± 0.3	0.84
2	ES	9	Singlet	31.7	0.9 ± 0.2	0.74	20.1	2.4 ± 0.5	0.73
			$N \geqslant 5$	9.1	0.8 ± 0.2	0.78	6.3	2.2 ± 0.4	0.79
	GS	15	Singlet	22.0	1.1 ± 0.1	0.87	10.4	2.8 ± 0.3	0.84
			$N \geqslant 5$	14.1	1.1 ± 0.1	0.83	7.0	3.1 ± 0.4	0.84
3	ES	8	Singlet	4.7	0.7 ± 0.1	0.84	3.2	1.9 ± 0.4	0.83
			$N \geqslant 5$	2.0	0.7 ± 0.2	0.75	1.4	1.8 ± 0.5	0.73
	GS	12	Singlet	5.1	0.9 ± 0.05	0.97	2.7	2.3 ± 0.2	0.94
			$N \geqslant 5$	3.6	1.0 ± 0.2	0.82	1.9	2.6 ± 0.4	0.82

[a] σ_θ = standard deviation about the mean wind direction θ measured at 2.1 m.
[b] ES = elevated slides, GS = ground slides.
[c] n = number of data points fitted by regression.
[d] c.d. = the coefficient of determination of the regression.

(solid circles) and the deposit of clusters containing five or more spores (open circles) behave similarly with increasing distance from the source. Thus, the increased settling speed of clusters appears to have very little effect on the relative magnitude of the deposits at this height. When the model predictions for singlets (solid line) and clusters ($N = 9$, dashed line) airborne at the top of the crop are plotted on a log-linear graph (Fig. 3A) they clearly exhibit curvature, which indicates that the parameter a in an exponential law (Eq. 1a) is a decreasing function of r. On the other hand, when plotted on a log-log graph (Fig. 3B) the results are nearly linear, which implies that the power law fit (Eq. 1b) is consistent with both the model predictions and the data over the entire range from $r = 1-15$ m.

DISCUSSION

Once a dispersal unit becomes airborne, it is simultaneously advected more or less horizontally in the direction of the wind, displaced in all directions by the turbulent motions of the air, and deposited on the foliage and ground. The rate of deposition of dispersal units on the foliage and ground depends on their settling speed, v_s, which for a cluster of identical particles increases as the square root of the number of particles in the cluster (5). Thus, as long as the major portion of the dispersal units travels within the canopy where they are subject to deposition, the ratio of clusters to singlets in the air is expected to decline steadily. Away from the source an ever-increasing portion of the dispersal units released are mixed by atmospheric turbulence into the air above the canopy. Particles above the canopy are less subject to deposition and differences in particle settling speed becomes less important in determining aerial concentration. This explains why, although more clusters than single spores were deposited within the source region, this trend did not continue for distances greater than 2 m from the source.

In our experiments, the relative numbers of singlets and clusters deposited at distances greater than 2 m from the source of spores was determined by the relative number that had escaped from the canopy in the first meter of travel. The bean canopy during our experiments was short and sparse, a condition that favors the rapid escape of spores and minimizes the effects of deposition. In this case, we would expect the flux of inoculum above the canopy to be much more important to the spread of disease than it would be for a tall, dense, fully mature bean canopy.

In the absence of deposition, the predicted dilution of substance due to turbulent mixing in a neutrally stable atmosphere (14) yields a power law for the decrease in concentration with increasing distance from the source with a power b equal to about 1.9. We obtained $b = 2.1 \pm 0.3$ for both the elevated slide and trap plant data. When the effects of geometry are taken into account, McCartney and Bainbridge (9) found similar values for b for dispersal of 19 μm diameter droplets from a point source at midcanopy within a barley crop for a wide range of crop height and leaf area index.

A power law, with a negative exponent, predicts concentrations that become indefinitely large as r approaches zero. This unphysical behavior is due to the assumption that the source is conceptually concentrated at a point in space. In reality, sources of inoculum have a finite extent and a power law will always overestimate the actual concentration. For distances from the center of the source that are much larger than the size of the source, however, this presents no difficulty because the error is small. As distance decreases and approaches the size of the source (approximately 1 m for our experiments), we expect the actual concentration to approach a maximum value and not continue to increase indefinitely as the power law predicts. The model

prediction (Eq. 3), when plotted on a log-log graph (Fig. 3B), illustrates this effect by curving slightly downwards for distances approaching the source size.

The model can also be used to estimate the strength of the source for each experiment. We assumed that the deposition to the ground slides was by sedimentation alone so that the observed deposition flux to the ground slides could be set equal to $v_s \cdot C(r,0)$. This allowed us to estimate the rate of release of singlets and clusters from the source region by comparing the model predictions with the observations. Using the estimate of disease severity for each experiment we estimate that approximately 4, 12, and 6 singlets and 6, 6, and 5 clusters with $N \geqslant 5$ were released per lesion per hour for experiments 1, 2, and 3, respectively. Comparable results were obtained elsewhere (1) using a different approach. The bean canopy, in this study, was short and sparse making it relatively easy for spores to escape from the canopy. However, a sizeable number of clusters were also found to escape from a uniformly infected, mature ($H = 0.5$ m, LAI = 3.5) bean field (2).

In our experiments, at least half of the total number of dispersal units deposited were clusters and these contained at least 80% of the total number of deposited spores. In other words, because of clusters, the potential number of dispersal units was only about 20–30% of what it would have been if all urediniospores had become airborne as singlets. This was true at least 5 m from the source, and model calculations predict that many clusters should still be airborne at distances much greater than 5 m. Thus, it is important to account for the effect of clustering of spores and thus the rate of spread of bean rust in a field.

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