Escape of Urediniospores of *Uromyces phaseoli* from a Bean Field Canopy

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ABSTRACT

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Vertical profiles of wind speed and aerial concentration of urediniospores of *Uromyces phaseoli* were measured on several occasions above a 0.25-ha field of bean plants severely diseased with *U. phaseoli*. The aerial concentrations of single (singlets) urediniospores and of clusters of two (doublets) and three (triplets) urediniospores were determined separately, and the upward flux at 0.5 m above the canopy was calculated for each. The upward flux, or escape, of singlets ranged between 6 and 31 spores per square meter per second and was about 2–7 times greater than the escape of doublets and about 5–30 times greater than the escape of triplets. The relative proportions of singlets, doublets, and triplets escaping the canopy agreed with the proportions of each released by the crop, as assessed by the relative numbers of each caught on horizontal, sticky glass slides placed within the crop.

Additional key words: bean rust, spore clusters.

Of the vast amounts of inoculum produced in a diseased crop, only a small proportion may escape the crop canopy (3). Within the canopy, deposition of spores on the plants and on the ground causes their aerial concentration to decrease rapidly with distance from a source (1), and only those spores that escape the canopy into the faster moving air above contribute significantly to spread of disease between neighboring fields. Thus, quantifying the escape of inoculum is a crucial element for calculating the potential for long-distance spread of plant disease (3,4).

Urediniospores of *Uromyces phaseoli* become airborne as clusters as well as single spores and, near a source, clusters can comprise as many as half of the dispersal units deposited in a bean field canopy (F. J. Ferrandino, *unpublished*). Because clusters of urediniospores of *U. phaseoli* are prevalent in the canopy, they are potentially important for long-distance spread of bean rust. They may be especially important as dispersal units under conditions of low spore viability if their survival is enhanced compared to single urediniospores.

Purpose of the research described in this report was to examine the potential for urediniospores, both as singlets or clusters, to escape the canopy and contribute to long distance spread of bean rust.

MATERIALS AND METHODS

Crop and inoculum. On 22 May, a rectangular (46 × 52 m) field in Hamden, CT, was planted to beans (*Phaseolus vulgaris* L. 'Bush Blue Lake 47') in rows spaced 0.75 m apart. Rows were 46 m long and were oriented approximately east-west. Two 1-m lengths of row at the center of each quadrant of the field of susceptible beans were inoculated with urediniospores of *Uromyces phaseoli* (Reben) Wint. on 14 June when the first set of trifoliate leaves were fully expanded. By 10 July, disease had spread to the entire field.

Spatial uniformity of the inoculum was assessed by exposing trap plants in the field on 17 and 23 July. Trap plants in pots were placed on the ground every 3.8 m along both the north-south and east-west transects through the center of the field. Immediately after exposure in the field (for 5 hr on 17 July or for 3.5 hr on 23 July), the trap plants were placed in a dew chamber, kept overnight, and then moved to a growth chamber (20 C and 12 hr light/dark; irradiance of photosynthetically active radiation approximately equal to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$). When lesions developed, the number per leaf were counted. To allow comparison between locations in the field and between the two dates, these numbers were converted to number of lesions per area of leaf per hour of exposure in the field by dividing the number per leaf by the area of that leaf at the time of exposure in the field and by the number of hours exposed.

The average plant height and the leaf area index (LAI) of the crop were measured on 19, 20, and 23 July. An estimate of the vertical distribution of pustules within the bean field canopy was obtained at eight locations in the field on 20 July by counting the number of pustules on leaves in two vertical strata in the canopy between 0–0.25 m and 0.25–0.50 m. We also counted singlets, doublets, and triplets deposited on horizontal, sticky microscope slides placed at the center of the field at midcanopy height. Ratios of these counts are later compared with the derived ratios of escape of singlets, doublets, and triplets.

Aerial concentration of spores. The vertical profile of airborne spore concentration (C) above the field was determined on six occasions (referred to later as experiments 1–6) during 19, 20, and 23 July using eight rotoslide impaction samplers (6) placed at 0.6 (two), 0.8, 1.0 (two), 1.2, 1.5, and 1.8 m above the ground at the center of the field. Spore concentrations were determined from counts on the slides as described previously (3). Singlets, doublets, triplets, quartets, and quintets of urediniospores were tallied separately. Clusters containing six or more urediniospores comprised only about 1% of the total number of dispersal units and were tallied together. The variation of C of singlets, doublets, and triplets with height above the canopy was analyzed by regression analysis and the results were used to calculate their escape from the canopy. The counts for clusters larger than triplets were too small to allow gradients to be calculated reliably.

Escape of spores. The number of spore dispersal units of size N escaping the crop per square meter per second (F_N) was calculated as

$$F_N = -K(dC_N/dz) \mid z_1 - V_{sN}C_N(z_1) \qquad (1)$$

in which K is diffusivity of spores (assumed equal to the diffusivity of momentum [3,7]), C_N is the concentration of clusters containing N spores, z is the vertical distance above the ground, z_1 is a reference height above the canopy, and V_{sN} is the gravitational settling speed for a cluster containing N spores. Above a plant canopy during neutral atmospheric conditions, $K = k\,u_*\,(z - D)$ in which k is

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von Karman's constant equal to 0.4, D is the zero-plane displacement height, and u_* is the friction velocity (8,9) derived from the wind-speed measurements described below. K increases with height above a plant canopy and the second term on the right side of equation 1 is often small compared with the first term. For sporangia of *Peronospora tabacina* escaping from a tobacco field Aylor and Taylor (3) found that gravitational settling reduced the upward flux of spora by only about 10% and neglected it. In the present experiments with *U. phaseoli*, however, we observed relatively smaller concentration gradients, so that the gravitational flux decreased the upward diffusion flux by 20–30% and we have accounted for it.

Aerial concentration C_N and the vertical gradient of concentration dC_N/dz, both evaluated at height z_1, were determined from an exponential fit (obtained using regression analysis) to the measurements of spore concentration at the six sampling heights. The settling speed of a cluster of N urediniospores V_{sN} was calculated as $V_{sN} = 0.98\ V_{s1}N^{0.53}$, in which $V_{s1} = 0.0108\ ms^{-1}$ is the settling speed of a single urediniospore of *U. phaseoli* (5). Thus V_{s2} and V_{s3} were calculated by this formula to be 0.0153, and 0.0189 $m \cdot s^{-1}$, respectively.

We used a previously described mathematical spore transport model (2,3) to calculate the effect of cluster size on the rate of deposition within the canopy and the escape of spores from the crop; from this model we derived estimates of the ratios of the escape of singlets to doublets and singlets to triplets which we compared with measurements. For our calculations, we assumed that urediniospores were released into the air in proportion to the number of pustules. Deposition on the foliage and ground was assumed to be by sedimentation and the density of foliage was assumed to be uniform with height. The model calculations were carried out for wind speeds that increased logarithmically with height above the canopy and decreased exponentially with depth in the canopy, and for diffusivities which increased linearly above the canopy and were set equal to the value at the top of the crop for all heights in the canopy (2,9). This kind of variation for speed and diffusivity above the canopy approximates the wind conditions that occur in a neutrally buoyant atmosphere (8,9). Appropriate wind speed parameters were derived from measurements described below.

Meteorological conditions. Wind speed was measured at 0.6, 0.8, 1.2, and 2.0 m above the ground with Thornthwaite model 104 sensitive-cup anemometers and at 0.3 and 0.6 m above the ground by using Thermal Systems hot-wire anemometers (probe model 1266). All were located 30–40 m downwind of the leading edge of the field of 0.5-m-tall bean plants. In addition, wind direction was measured at a height of 2.1 m with a Weathermeasure model W104 sensitive vane. Measurements made with the vane, and hot wires were recorded about every 4 sec, and the average and variance of these readings were calculated with a model 3/10 Compudas computer-controlled data acquisition system.

The indications of the cup anemometers were recorded every 30 min and used to calculate average wind speeds. The variation of wind speed with height above the canopy was fitted to a logarithmic law (reference 8, equation 7.8) to obtain values for the friction velocity u_* which were used to calculate K, the diffusivity of spores. The measurements made with the hot-wire anemometers inside and just above the canopy were used to estimate the decrease of wind speed with depth in the canopy. Solar irradiance was measured with a LICOR model LI-200S pyranometer and relative humidity and air temperature were measured with either a Bendix forced-ventilation psychrometer or hygrothermograph.

RESULTS

Crop and inoculum. During the experiments, the average height of the crop was about 0.5 m and leaf area index (LAI) was about 3.4 on 19 July, 3.5 on 20 July, and 3.6 on 23 July. An assessment of the horizontal distribution of inoculum in the field, determined by using the trap plants, is shown in Fig. 1 for 17 July (two days before experiment 1) and for 23 July (during experiment 6). At most locations, the number of lesions per square centimeter of trap plant per hour of exposure increased between 17 and 23 July, but the patterns along the transects were similar on the two dates. On 20 July, the number of lesions per plant growing in the field was about 2,000 ± 1,000 with about 48% in the bottom half and 52% in the top half of the 0.5-m-tall canopy.

The number of singlets deposited per square centimeter per hour on the sticky slides at the center of the field at midcanopy height was about 5.1 during experiments 1 and 2, 11.4 during experiments 3 and 4, 12.1 during experiment 5, and 15.4 during experiment 6. The numbers of doublets and triplets deposited per square centimeter per hour on sticky slides was about 1/4 and 1/8 of that for singlets.

Meteorological conditions. The meteorological conditions during the experiments are summarized in Table 1. The vertical variation of average horizontal wind speed measured by the cup anemometers was described well by a logarithmic law and yielded the values of the friction velocity u_*. The average horizontal wind speed at midcanopy height, indicated by a hotwire anemometer was about half as fast as the speed at the top of the canopy. Also shown in Table 1 are the mean and standard deviation of wind direction, the average speed at 2 m above the ground, and the average solar irradiance, air temperature, and relative humidity during each experiment. Wind directions during the experiments were from the south, south-southwest, and west.

Aerial spore concentrations. The aerial concentrations C of spore dispersal units trapped above the bean canopy during experiments 1–6 are shown in Tables 2, 3, and 4 for singlets, doublets, and triplets, respectively. Depending on the experiment, singlets were 76–86%, doublets were 15–10%, triplets were 5–2.5%, quartets were 1.3–1%, and quintets were 0.8–0.6% of the total

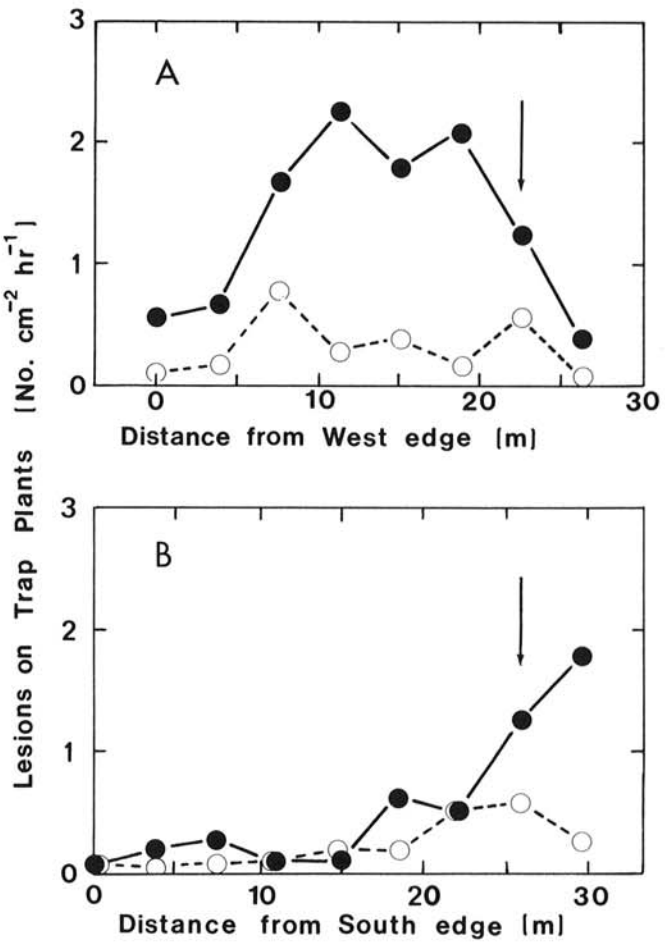

Fig. 1. Number of lesions per square centimeter per hour of exposure in the field which developed on trap plants placed along **A,** east-west and **B,** north-south transects through the center (arrow) of the field on 17 July (O, dashed line) and on 23 July (●, solid line).

TABLE 1. Summary of average meteorological observations over the bush bean field during the spore trapping experiments

Exp. no.	Date (July)	Time[a] (hr)	u_*[b] ($m \cdot s^{-1}$)	u_2[c] ($m \cdot s^{-1}$)	Wind direction[d] (degrees)	Irradiance ($W \cdot m^{-2}$)	T[e] (C)	RH[e] (%)
1	19	0900–1100	0.18	2.1 ± 0.5	267 ± 40	700	24	55
2	19	1100–1300	0.21	2.4 ± 0.3	274 ± 28	840	26	55
3	20	0800–1000	0.14	1.6 ± 0.3	190 ± 28	560	26	56
4	20	1000–1200	0.25	2.5 ± 0.3	207 ± 24	840	28	50
5	20	1200–1400	0.27	2.8 ± 0.3	206 ± 24	840	28	48
6	23	1000–1300	0.26	2.7 ± 0.3	211 ± 25	700	28	68

[a]Time (24-hr clock, Eastern Standard Time) during which spores were trapped.
[b]Friction velocity (u_* derived from vertical variation of horizontal wind speed (10).
[c]Average horizontal wind speed (u_2) at 2 m above the ground.
[d]Wind direction was measured clockwise from 0° at the north edge of the field.
[e]T is temperature and RH is relative humidity of the air 1 m above the crop plants.

TABLE 2. Summary of spore concentration profiles and the verticle flux F_1 of urediniospore singlets obtained over the bush bean field infected with *Uromyces phaseoli*

Height (m)	Spore concentration (singlets per m^3)					
	Exp 1	Exp 2	Exp 3	Exp 4	Exp 5	Exp 6
0.6	359	792	246	1,091	660	719
0.6	358	882	149	1,130	748	628
0.8	292	818	276	854	701	820
1.0	220	704	107	778	536	601
1.0	270	536	191	711	573	676
1.2	223	619	78	675	427	512
1.5	179	392	105	555	448	411
1.8	141	325	42	417	323	330
F_1[a] ($m^{-2} \cdot s^{-1}$)	6.3 ± 0.7[b]	21.3 ± 3.7	···	30.8 ± 2.7	19.0 ± 3.0	19.7 ± 4.4

[a]F_1 is the upward flux (number of singlets per square meter per second) of singlets at 1 m height calculated by using equation 1.
[b]Estimate, ± standard error of the estimate.

TABLE 3. Summary of concentration profiles and vertical flux F_2 of urediniospore doublets obtained over the bush bean field infected with *Uromyces phaseoli*

Height (m)	Spore concentration (doublets per m^3)					
	Exp 1	Exp 2	Exp 3	Exp 4	Exp 5	Exp 6
0.6	48	139	41	261	153	247
0.6	37	150	36	195	170	205
0.8	38	115	56	204	164	234
1.0	25	102	13	133	103	150
1.0	26	73	29	132	122	167
1.2	20	83	8	111	75	125
1.5	20	54	15	84	77	86
1.8	11	39	6	57	55	67
F_2[a] ($m^{-2} \cdot s^{-1}$)	0.9 ± 0.2[b]	4.0 ± 0.6	···	8.5 ± 1.2	5.7 ± 1.1	9.1 ± 1.3

[a]F_2 is the upward flux (number of doublets per square meter per second) of doublets at 1 m height calculated by using equation 1.
[b]Estimate, ± standard error of the estimate.

TABLE 4. Summary of concentration profiles and vertical flux F_3 of urediniospore triplets obtained over the bush bean field infected with *Uromyces phaseoli*

Height (m)	Spore concentration (triplets per m^3)					
	Exp 1	Exp 2	Exp 3	Exp 4	Exp 5	Exp 6
0.6	12	40	12	76	55	113
0.6	9	52	12	69	63	86
0.8	10	31	12	65	65	98
1.0	8	29	2	44	35	53
1.0	8	21	11	46	34	61
1.2	5	16	3	37	22	50
1.5	5	11	5	26	24	34
1.8	3	10	2	23	17	22
F_3[a] ($m^{-2} \cdot s^{-1}$)	0.2 ± 0.04[b]	1.4 ±0.3	···	2.3 ± 0.3	2.3 ± 0.6	4.1 ± 0.7

[a]F_3 is the upward flux (number of triplets per square meter per second) of triplets at 1 m height calculated by using equation 1.
[b]Estimate, ± standard error of the estimate.

number of dispersal units trapped. Although they were present in the air above the canopy, the vertical fluxes of quartets and larger clusters were too small to be quantified by our methods, and these data are not presented. Values of C were lowest early in the day (experiments 1 and 3), greatest around midday (experiments 2 and 4) and declined somewhat in the afternoon (experiment 5). In general, there was a tendency for C to increase with increasing u_* (Table 1).

Escape of spores. Vertical profiles of C generally were fitted well by the equation $C = A \exp(-Bz)$, in which z is vertical distance and A and B are constants determined by regression analysis. The gradient of these fitted lines were used in equation (1) to calculate the Fs shown in the last line of Tables 2–4. The vertical flux of singlets escaping the canopy F_1 ranged between 6.3 and 30.8, F_2 ranged between 0.9 and 9.1, and F_3 ranged between 0.2 and 4.1 dispersal units $m^{-2} \cdot s^{-1}$. The scatter in the data of experiment 3 made the calculation of its gradient unreliable and no Fs were calculated. The ratio of the flux of singlets to doublets F_1/F_2 ranged from 2–7 while the ratio of singlets to triplets F_1/F_3 ranged from 5–30; both ratios decreased with increasing u_*.

Model calculations. The spore transport model (2,3) was used to calculate deposition to the foliage and ground and the upward flux of spores as a function of distance x from the upwind edge of a horizontally uniform diseased field. For an x of about 25 m (at the center of the field) the deposition flux was found to be directly proportional to the source strength and relatively independent of spore cluster size. Thus, the relative number of singlets, doublets, and triplets deposited on the sticky slides should represent the relative source strength of each particle. The model also predicts that, if an equal number of singlets, doublets, and triplets were released from each lesion within a diseased crop, then at the center of the field at a height of 1 m the escape of singlets should be about 1.4 times greater than the escape of doublets and about 1.7 times greater than the escape of triplets. Thus, accounting for the different numbers of each available, as indicated by the sticky slides, it would be reasonable to expect F_1/F_2 to be about 6 and F_1/F_3 to be about 14. The ratios were less than or equal to these limits, except for experiment 1 during which u_* was small and wind speed was highly variable (Table 1); these are conditions for which the assumptions of our model are not expected to hold.

Depending on the direction of the wind, the upwind edge of the field was 23–27 m (46 to 54 crop heights) from the spore sampling location at the center of the field. For these lengths of wind run over diseased crop, the model (2,3) indicates that the cumulative flux leaving the canopy F_{CT} should be about 1.7 times greater than the cumulative flux through the plane $z = 1$ m. The model also predicts that the *average* flux through the plane $z = 1$ m is about 80% of F measured at the center of the field. Combining these results, we estimate that, for a 25-m-long run of wind over our crop, the number of dispersal units escaping per second per meter of crop perpendicular to the direction of the wind would be about $(0.8 \times 1.7 \times 25 \text{ m}) \times F$. Thus, using the Fs from Tables 2–4 we estimate that between 214 and 1,047 singlets, 31 and 309 doublets, and 7 and 140 triplets escaped from the canopy per second and per meter of crop perpendicular to the wind between the edge and center of the field.

DISCUSSION

Greater turbulent mixing of the atmosphere, as indicated by higher values of u_*, is expected to remove greater numbers of spores from the canopy. This is due both to an increase in the number of spores liberated from pustules and to an increase in the upward turbulent transport of airborne spores when the canopy is well ventilated. Our data showed a clear trend for both singlet and cluster concentrations above the canopy to be higher at higher u_*. If the number of spores that become airborne did not depend on wind speed, then higher values of u_* should lead to greater dilution, and thus lower concentrations of spores in the air. When concentrations increase with increasing u_*, however, as they did here, this implies that more spores are released as the ventilation of the canopy increases. In addition, there was a tendency for the relative numbers of doublets and triplets, compared to the numbers of singlets, to increase with u_*. This tendency probably reflects a greater difficulty in freeing clusters than in freeing singlets from the canopy, perhaps because the bulk of the clusters are released from the lower part of the canopy which is ventilated well only when the level of atmospheric turbulence is high.

The calculated upward fluxes of spores were between 50 and 100% of the coincident deposition fluxes on the sticky slides. Assuming that the rate of deposition on the foliage and ground was the same as on the slides, we estimate that between 10 and 18% of the total inoculum escaped from the canopy. This estimate agrees favorably with that of the spore transport model, thus we used the model to make a rough estimate of the strength of the source of spores. Using our estimated mean number of 2,000 lesions per plant, and 17.5 plants per meter of row spaced 0.76 meter apart, we estimate that between 6 and 30 singlets, 1 and 11 doublets, and 0.3 and 6 triplets were released per lesion per hour. Of course, counted lesion densities most likely included nonsporulating lesions and thus these estimates are probably lower than actual. Nevertheless, for the levels of turbulence encountered here ($u_* = 0.25$ m/s), and for a fully closed bean canopy ($H = 0.5$ m, LAI = 3.5) these values might be useful elsewhere for estimating inoculum source strength from bean rust severity.

Because of the way urediniospores are extruded from the pustule, they become airborne as clusters as well as single spores. Once spores enter the turbulent air above the canopy they can travel far (4). The importance of clusters to the spread of disease will depend on their abundance in the air and their viability. A cluster of urediniospores may be more likely to germinate than is a single urediniospore (D. E. Aylor, *unpublished*), especially when spore viability is low which is likely to be true for long distance transport. Thus, clusters may have a higher inoculum potential than singlets and therefore may contribute significantly to the spread of bean rust between fields even if present in relatively small numbers. Finally, it seems important to consider clusters when trying to estimate the potential inoculum produced per lesion, per plant, or per unit area of bean crop infected with *U. phaseoli*.

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