Settling Speed of Clusters of Spores

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ABSTRACT

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The settling speed of single particles and different-sized clusters of *Uromyces phaseoli* urediospores, *Lycopodium* spores, and ragweed (*Ambrosia elatior*) pollen was determined by timing their fall in still air. The settling speed (v_s) of a cluster of N particles, regardless of shape, was described well by the equation $(v_s)_{cluster} = 0.98(v_s)_{single}\ N^{0.53}$.

Gravitational settling, inertial impaction, and interception are the main mechanisms for deposition of fungal spores on plants. The settling speed of a spore falling vertically in still air, or the terminal velocity reached by the spore when the acceleration caused by gravity is exactly balanced by aerodynamic drag on the spore, is fundamental for calculating deposition both by sedimentation and by inertial impaction (1). The settling speed (v_s) (cm/sec) of a single spore follows well-known laws of aerodynamic drag and has been measured for many kinds of spores (4). Some kinds of spores, eg, those of *Cladosporium, Ustilago, rust,* and powdery mildew fungi, are liberated into the air not only as single spores but also as clusters of several spores. It has been suggested that the presence of clusters of *Erysiphe graminis* spores contributes to a more rapid decrease in spore concentration away from a source because of the greater settling speeds of clusters (2). To calculate the transport of clusters of spores in crop canopies, we need to know their settling speed as well as how this speed varies with the number of spores in the cluster. In this paper, we present measured values of v_s for single particles and clusters of *Uromyces phaseoli* (Pers.) Wint. var. *typica* Arth. urediospores, *Lycopodium* spores, and ragweed (*Ambrosia elatior* L.) pollen. These results are then reduced to a standard curve that can be used to estimate v_s for clusters of spores given v_s for a single spore and the number of spores in a cluster.

MATERIALS AND METHODS

Particles were introduced into the top of a small settling chamber and allowed to fall through a pinhole in a membrane sealing the top of a glass settling tube (1.2 m long by 2.5 cm i.d.). The particles in the settling tube were made visible by illuminating the inside of the tube with a collimated "cold" light source in an otherwise darkened room. The actual source of light was kept well away from the settling tube and the light was directed parallel to the length of the tube using a fiber-optics bundle positioned about 20 cm below the bottom of the tube. Illumination was through a microscope slide or petri dish used to seal the bottom of the tube and to catch the falling particles. In some cases, the bottom of the tube was left open and a slide was placed at the bottom in time to intercept a particular particle or cluster of particles. The dimensions of the tube effectively damped air currents so that even with the bottom open, air movement in the tube was negligible. We checked that systematic air currents were not present by timing the fall of particles between successive 10-cm intervals.

The length of the tube was marked off in 10-cm segments by a line extending around the tube; by visually aligning the particle with the line on both sides of the tube, parallax errors were minimized. After entering the settling tube, particles were allowed to settle for about 30 cm, after which their fall was timed through the central 50 cm of the tube. The bottom of the tube was 40 cm below the last timing mark. Relative humidity and temperature in the room were determined using a forced-ventilated psychrometer.

Measurements of v_s were obtained for three kinds of particles: *U. phaseoli* var. *typica* urediospores, *Lycopodium* spores, and ragweed (*A. elatior*) pollen. *U. phaseoli* urediospores were collected from pustules on leaves of diseased plants growing in a greenhouse. In some cases, leaves containing pustules were held directly over the settling tube and rust spores were introduced into the tube by tapping the leaf. Dry, nondefatted *Lycopodium* spores (lot 8H45) and ragweed pollen (lot 18T56-8) were obtained from Greer Laboratories, Lenoir, NC. A small amount of one or the other of these kinds of particles either was placed on a 50-μm mesh screen at the top of the settling chamber or directly on the membrane

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containing a pinhole that sealed the top of the settling tube. Particles were introduced into the settling tube by gently tapping the screen or membrane.

Each cluster of particles timed was caught at the bottom of the tube by introducing a clean microscope slide at the appropriate time. The size and shape of the cluster and the number of particles it contained were determined with a microscope at ×100. For clusters containing many particles, it was necessary to spread them out a little by gently laying a coverslip over them before counting.

To obtain more information on the statistical distribution of v_s for single particles at several values of relative humidity, a sizable number of particles was introduced into the settling tube at one time. The number of particles introduced each time was kept small enough so as not to appreciably increase the density of the air, which could have accelerated the downward movement of the group of particles. This group of particles spreads out in the vertical direction because of differences in v_s for individuals. By replacing a microscope slide at the bottom of the tube with a clean one at set intervals (usually 6 sec), we were able to partition the population of singlets according to settling speed. The number of single particles was counted on each successive slide and the frequency distribution of settling speeds determined. From this distribution, we calculated the mean v_s and standard error of the mean for each kind of particle.

RESULTS

The average settling speed for a single *U. phaseoli* urediospore, *Lycopodium* spore, and ragweed pollen grain is shown in Table 1.

TABLE 1. Mean diameters and settling speeds of single particles

Particle	Diameter ± $SE_{\bar{x}}$ (μm)	v_s ± $SE_{\bar{x}}$ (cm/sec)
Uromyces phaseoli urediospores	21.0 ± 0.3 × 9.1 ± 0.3[a]	0.86 ± 0.01[b]
		1.08 ± 0.05[c]
Ambrosia elatior pollen	21.5 ± 0.4[d]	1.05 ± 0.02
Lycopodium spores	32.8 ± 0.2[e]	1.94 ± 0.02

[a] *U. phaseoli* urediospores are disklike (diameter × thickness).
[b] Air-dried *U. phaseoli* urediospores stored under laboratory conditions.
[c] Fresh *U. phaseoli* urediospores released into settling chamber directly from leaf surface.
[d] Ragweed pollen is nearly spherical and covered with small spines. Diameter given includes the extremities of the spines
[e] *Lycodpodium* spores, though roughly spherical, taper down toward the point of attachment. Diameter given is of distal end.

We found no statistically significant effect of relative humidity on settling speed for these particles over a range of of 30–80% RH. The normalized settling speed for a cluster containing N particles (v_{sN}) (equal to the ratio of the settling speed of a cluster to that of a single particle) is shown in Fig. 1 as a function of the number of particles in the cluster for all tested particles. The settling speeds have been normalized using the data for single particles given in Table 1. All things considered, there is remarkably little scatter and the normalized data are fit well (r^2 = 0.96) by the least-squares regression line ($v_{sN} = 0.98N^{0.53}$). To make sure the regression equation was not dominated by data for any particular kind of particle, or range of N, we determined the regression line for each kind of particle and for various ranges of N. Results given in Table 2 indicate that the overall regression equation fits well over the entire range, although there is a tendency for a slightly lower exponent (about 0.5) for small N and a slightly higher exponent (0.54–0.57) for large N.

Somewhat unexpectedly, we found remarkably little correlation between v_{sN} and the shape of the cluster. Clusters were categorized into five shape classifications: spherical, prolate spheroids with major to minor axis ratios of 1.5:1, 2:1, and greater than 3:1, and

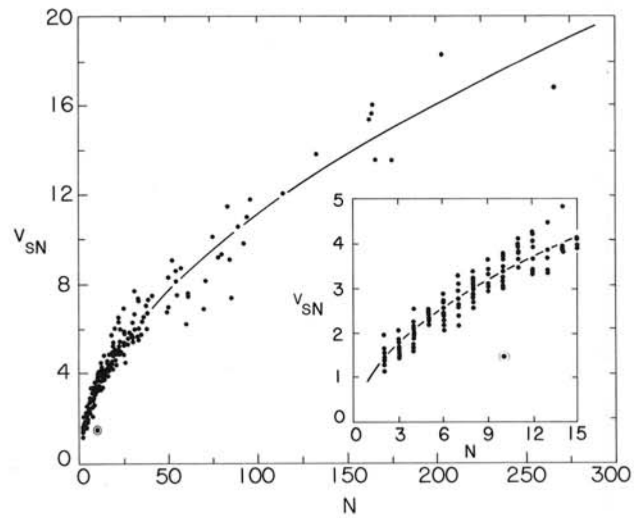

Fig. 1. The normalized settling speed v_{sN} of a cluster of N particles versus N for all particles tested. The line is the best fit regression equation: $v_{sN} = 0.98N^{0.53}$ (r^2 = 0.96). Inset shows data for N ⩽18 plotted on an expanded scale.

TABLE 2. Results of regression analyses for $V_{sN} = AN^B$ over various ranges of N where V_{sN} is the normalized settling speed of a cluster of N particles

Particle	Range of N	A	B	r^2	SEB[a]	n[b]
All	2–10	1.00	0.51	0.87	0.02	121
	11–34	1.03	0.52	0.75	0.03	91
	35–266	0.91	0.54	0.85	0.04	42
	2–266	0.98	0.53	0.96	0.01	254
Dry *Uromyces phaseoli* urediospores	2–10	0.98	0.52	0.85	0.06	17
	11–34	1.33	0.44	0.79	0.06	18
	35–203	0.92	0.55	0.81	0.07	16
	2–203	0.99	0.53	0.97	0.01	51
Fresh *U. phaseoli* urediospores	2–10	0.93	0.57	0.91	0.04	23
	11–34	0.90	0.57	0.71	0.07	27
	2–92	0.99	0.54	0.95	0.02	54
Ragweed pollen	2–10	0.86	0.53	0.92	0.03	27
	11–34	0.75	0.57	0.90	0.05	18
	35–266	0.87	0.53	0.92	0.03	22
	2–266	0.87	0.53	0.98	0.01	67
Lycopodium spores	2–10	1.03	0.50	0.92	0.02	41
	11–34	0.93	0.57	0.80	0.06	26
	2–34	0.97	0.55	0.96	0.02	67

[a] Standard error of B from linear regression of log V_{sN} = A + B log N.
[b] Number of observations in regression.

TABLE 3. Results of regression analysis for $V_{sN} = AN^B$ for each of five shape categories

Shape	A	B	r^2	SEB[a]	n[b]
Spherical	0.94	0.55	0.97	0.01	76
Prolate spheroid (1.5:1)	1.08	0.50	0.96	0.02	37
Prolate spheroid (2:1)	1.03	0.51	0.98	0.01	51
Prolate spheroid (>3:1)	0.91	0.53	0.96	0.02	46
Planar	0.90	0.54	0.87	0.05	17
	0.93	0.55	0.97[c]	0.03	16
All	0.98	0.53	0.96	0.01	254

[a]SEB = standard error of coefficient B.
[b]Number of observations in regression.
[c]r^2 After removing one outlier from the analysis.

TABLE 4. Mean of the relative deviations of the observed normalized settling speed from the regression line calculated as Z = mean of $[(v_{sN\ observed} - v_{sN\ regression})/v_{sN\ regression}]$ for the five shape categories

Shape	n[a]	$Z \pm SE_{\bar{x}}$
Spherical	83	0.008 ± 0.008
Prolate spheroid (1.5:1)	37	0.023 ± 0.012
Prolate spheroid (2:1)	51	0.010 ± 0.013
Prolate spheroid (>3:1)	45	−0.035 ± 0.011*[b]
Planar	17	−0.041 ± 0.040
	16[c]	−0.002 ± 0.028

[a]Number of observations in regression.
[b]* = Values of Z that are significantly different ($P = 0.05$) from spherical clusters.
[c]Results after removing one outlier from the analysis.

planar. The results of the regression analyses for each shape are shown in Table 3. Although there are apparently some differences in the exponent of the power law, the mean of the normalized deviations from the regression line of v_{sN} (Z defined in Table 4) for the five shape categories indicates that only the prolate spheroid greater than 3:1 fell significantly ($P = 0.05$) slower (about 3.5%) than the others. Although the Z for the planar form was the most negative, it was not significant because of the considerable variation in v_{sN} for planar shapes. In fact, most of this variation was due to only one of the 17 planar-shaped clusters (circled dot, Fig. 1) that fell much slower than the rest. This can be easily seen from the regression analysis for this shape (Table 3), where removing the one point increased the r^2 from 0.87 to 0.97.

DISCUSSION

Although differences in shape clearly contributed to the scatter in v_{sN} around the regression line (Fig. 1), we found very little correlation between settling speed and shape of clusters with the same number of particles. Probably, factors we could not measure, ie, the variation in the mass of individual particles and the packing of the cluster, tended to cause clusters of the same shape to fall with a variety of orientations and thus with different speeds. This remarkable result implies that best estimates of v_{sN} are obtained by ignoring shape and simply counting the individuals within a cluster.

Measurements of fall speeds of clusters of particles by others (5–8) are compared with our regression in Fig. 2. Kunkel (5) measured the settling speed in oil of clusters made by gluing together more or less identical 2-mm-diameter glass beads. As expected, the spheres glued in a line fell significantly slower than clusters that were not linear; we rarely found naturally occurring clusters of five or more particles joined in a straight line. Moreover, because the particles used by Kunkel were nearly identical, the linear models preferentially fell in a direction perpendicular to their long axis. For naturally occurring strings composed of particles that vary in mass, many other orientations are possible that have less drag resistance and fall faster. Similarly, it is easy to understand why Kunkel's planar models fell slower than our naturally occurring clusters. For planes, however, the deviation is not as great as for the straight strings of particles simply because, for a given N, the drag on a plane is less than that on string. Kunkel's

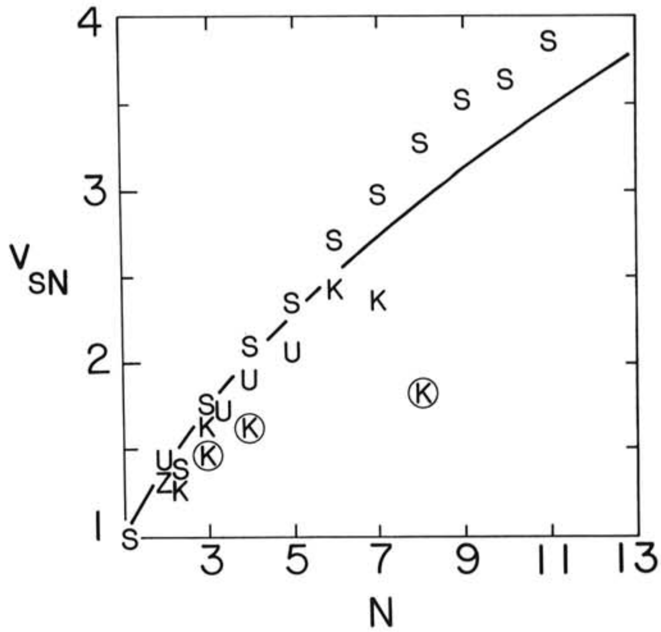

Fig. 2. Comparison of other workers' results with the regression line found in Fig. 1. Data are signified by the initial of the author: S = Stöber et al (6), K = Kunkel (5), and U = Ukkelberg (7). Circled Ks represent Kunkel's data for straight strings of particles.

other two data points, the doublet and a three-dimensional sextuplet, are not significantly different from our results. Zeleny and McKeehan (8) measured the fall speed of singlets and doublets of *Lycopodium* spores. Their determination agrees well with our measurements. Ukkelberg's (7) clusters of four or five fell below our regression line, but considering the uncertainty in his determination of settling time (eg, the error is about ±20% for N = 5), these points are also not significantly different from our results.

Finally, the settling speeds reported by Stöber et al (6) for latex spheres (0.75 μm in diameter) in air and for steel spheres (1,000–2,000 μm diameter) in viscous syrup are fit well by our regression equation up to N = 5 but increase considerably faster for N >6. They proposed that the drag force was proportional to the total surface area of all the particles comprising a cluster. For clusters obeying Stokes' law, this yields that v_{sN} is proportional to $N^{1/2}$ and is quite reasonable for small clusters that have most of their surface area exposed. On the other hand, for larger clusters, many of the particles are shielded from the flow and this simple law should not be expected to work. For perfectly packed spherical clusters obeying Stokes' law, v_{sN} should be proportional to $N^{2/3}$. Note that for N ≥6, the data of Stöber et al does show an increase, with N almost as fast as the 2/3 power. Our regression equation predicts lower values of v_{sN} than found by Stöber et al, probably because the packing of the pollen or spores is less perfect than that of the smooth spheres used by them. This tended to increase the surface area-to-volume ratio and reduce the fall speed. Moreover, unlike the results of Stöber et al, some of our data obtained for large values of N had Reynolds numbers large enough to cause significantly more drag than expected from Stokes' law. For large Reynolds numbers, solid spheres with diameters (D) ranging from 10 to 500 μm have a v_s proportional to D (3). The volume of a "spherical cluster" is about proportional to the number of N particles, thus its diameter (D) is proportional to $N^{1/3}$ so that v_{sN} is proportional to $N^{0.57}$. Considering the less than perfect packing of clusters, this result is in general agreement with our results for large N (Table 2).

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