New Methods Using Simulated Rain to Study the Splash Dispersal of Plant Pathogens

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ABSTRACT

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Methods were developed for studying the effect of simulated rain on splash dispersal of fungal plant pathogens. Spray nozzles were mounted on a horizontal boom that was rotated at 2 rpm by a motorized chain-drive assembly. Water volume distribution was found to be about uniform within a 1-m^2 target area. Low-, medium-, and high-volume spray nozzles produced water-drop volume distributions that closely approximated natural rains with intensities of 15, 30, and 60 mm/hr, respectively. A test of the rain simulator was conducted using spread of leather rot of strawberries as a model disease system. Potted strawberry plants were arranged in concentric circles within a specially constructed wood frame. Ten infected strawberry fruits, placed at the center of the circle of plants, served as the inoculum source. ANOVA results demonstrated that percentage of fruit infection differed significantly in response to rainfall intensity, distance of plants from inoculum, and position of fruit within a plant crown ($P = 0.05$). The only significant interaction was distance by position. Mulch generally reduced infection, but this effect was not significant ($P = 0.05$).

Additional key words: Phytophthora cactorum, Quantitative epidemiology.

Raindrop impaction has been shown to be an important mechanism for liberation and dispersal of propagules of many species of plant-pathogenic fungi and bacteria (6,8–10,12,15,16,18,31). Field studies have demonstrated that increases in disease incidence in aboveground plant parts were highly correlated with occurrence of rainfall (15,17,20,33). Dispersal and infection gradients associated with infection centers of splash-dispersed pathogens have been found to be characteristically very steep (14,23,35,36).

Splash dispersal of plant pathogens was first demonstrated by allowing single drops of water to impact on suspensions of propagules (6,7). Single-drop impacts have also been used to relate the volume of liquid splashed, number of propagules dispersed, and distance of splash droplet travel to incident drop size (6,10,11,18). During rain, inoculum is initially dispersed from an infection source by the impact of single raindrops, but subsequently it is subject to redistribution by repeated resplashing (7). Rain simulation has been used to study inoculum movement to account for the process of resplashing (8,12).

The rain simulator used by Fitt and Bainbridge (8) for studying splash dispersal of *Pseudocercosporella herpotrichoides* (Fron) Deighton from infected wheat straw, which is similar in design to systems used for soil erosion research (27), consists of a bank of small-bore, stainless-steel needles that produce a "rain" consisting of drops that are about uniform in size. This method has proven useful in accounting for the effects of resplashing and in studying the effects of particular drop-size ranges on dispersal within the context of resplashing. However, the results of rain simulation studies using uniform drop sizes cannot be directly related to natural rainfall intensities, since a natural rain is characterized by a spectrum of drop sizes (22,28).

A fuller understanding of the splash-dispersal process requires consideration of a number of factors in addition to drop spectra and resplashing: distance from an inoculum source to a susceptible plant part (8–12,18,23,24), surface characteristics of the inoculum source (34) and the soil surface, presence of barriers within the crop canopy (17,35), alteration in drop size distribution as a result of interception of rain by the plant canopy (29), vertical gradients of inoculum deposition and the position of susceptible plant parts within a plant crown (11,12,15,21), and effect of wind on splash-droplet trajectories (2,3,8). Early studies by Rose (31) clearly indicated that spread of *Phytophthora cactorum* (Lebert & Cohn) Schroet., causal agent of leather rot of strawberry, was highly correlated with rainfall. More recently, Grove et al (18) demonstrated that *P. cactorum* can be splash-dispersed from individual infected fruit in the absence of a strawberry canopy. This paper describes the development of a rain simulation system that is appropriate for studying factors involved in the splash-dispersal process and presents simulation results for spread of *P. cactorum* within a strawberry (*Fragaria* × *ananassa* Duchesne 'Midway') canopy.

MATERIALS AND METHODS

Leather rot of strawberries was used as a model disease system to test the efficacy of our rain simulation approach and to provide an initial quantification of the effects of rainfall intensity and distance from an inoculum source in the presence or absence of plant barriers (distance) on spread of *P. cactorum* in an experimental strawberry canopy. The effects of straw mulch and of vertical position of fruit within the canopy (position) on successful dispersal of *P. cactorum* were also investigated.

Application of simulated rain. Water was supplied to an overhead, horizontal boom through 2.5-cm-diameter pipe (Fig. 1). A wide-angle spray nozzle that produced a conical spray pattern (27W, 35W, or 50W; Spraying Systems Inc., Wheaton, IL) was attached to one end of the boom at a distance of 20 cm from a vertical pipe that was used both to rotate the boom at 2 rpm and to supply water to the nozzle (Fig. 1). Water pressure at the nozzle was maintained at 68.95 kPa with a precision flow valve. The spray was directed upward so that water pressure could be adjusted without affecting incident drop velocities. At 68.95 kPa, spray drops were projected 0.5 m above the nozzle, giving a total height of drop fall of 4.0 m. A sheet-metal trough 2 m long × 5 cm in diameter was suspended from the boom to collect water that either dripped off the boom or ran down the vertical suspension pipe (Fig. 1). Water collected by the trough was thus transported outside the area within which rainfall impact was simulated.

Characteristics of simulated rain. The depth of water received per square meter per hour (intensity) was determined for each nozzle by collecting water in 16 funnels that were placed on a 4×4 grid within an area of 1 m × 1 m. The sample area was placed at a horizontal distance of 30 cm from the position of closest approach of the spray nozzle (Fig. 1, n) on its rotational path (50 cm from pv, which is the axis of boom rotation; Fig. 1) and oriented such that the closest edge of the sample area was parallel to the tangent of the nozzle trajectory at the point of closest approach. Total area sampled by the funnels was 0.1065 m^2. The volume of water collected at each grid position was determined and converted to units of intensity to characterize the spatial variability of intensity. Calibration of intensity for each nozzle was based on two replications of a 20-min simulated rain.

The cumulative frequency (obtained from the manufacturer) of simulated raindrop volume produced by each nozzle was compared with cumulative frequencies of natural raindrop volumes with intensities of 5–100 mm/hr. Raindrop-volume cumulative frequencies were derived from an empirical model for drop concentration in the atmosphere [$N_d(I)$] as a function of intensity (22) and an empirical relation for raindrop terminal velocity, V_d, developed by Reynolds et al (30) from models of Beard (1):

$$F_I(D_\phi \leq d) = 1/\mathrm{T} \int_d N_d(I) \cdot M_d \cdot V_d \cdot dd \qquad (1)$$

in which F_I = the cumulative probability density of drop volume for rainfall intensity I, D_ϕ = drop equivalent diameter (mm) (22), T = total drop volume (mm^3/m^2 per second), $N_d(I)$ = drop concentration as a function of intensity (number of drops of diameter D_ϕ/m^2 per millimeter) (22), M_d = volume of drop of diameter D_ϕ (mm), V_d = terminal velocity of drop of diameter D_ϕ (m/sec), and dd = integration interval (mm).

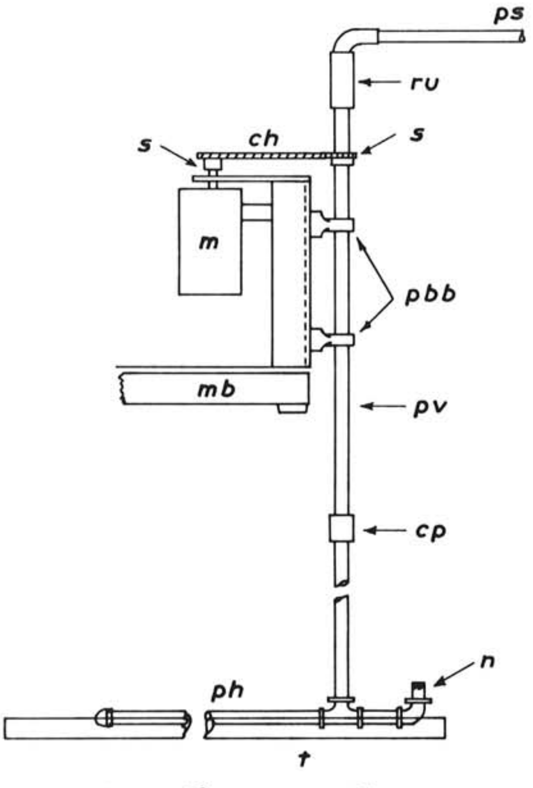

Fig. 1. Schematic of rain simulation system. Water was supplied to spray nozzle (n) through overhead pipe (ps), which was connected to vertical supply pipe (pv) by rotating union (ru). The pv pipe was mounted in pillow-block bearings (pbb) and rotated at 2 rpm by motor (m) and chain-drive mechanism (ch). Spray nozzle was mounted on horizontal boom (ph) that was coupled (cp) to pv pipe. Spray water that hit and ran down pv pipe was collected by trough 2 m long × 5 cm wide and carried outside experimental area. Other components shown are motor mounting block (mb) and chain-drive sprockets (s).

Physical constraints of the simulation system (Fig. 1) only allowed a 4-m height of drop fall, so drops with diameters > 1.75 mm could not attain terminal velocity (30). Consequently, approximate distributions for simulated rainfall kinetic energy also were developed using an expression analogous to equation 1, in which predicted velocity (30) after a 4-m fall was used in place of terminal velocity.

Inoculum production. Ten immature strawberry fruits inoculated by the methods of Grove et al (19) were used as the source of inoculum of *P. cactorum* for each test. Inoculated fruits were incubated for 3 days in chambers maintained at 100% RH. Following incubation, sporulation was induced by placing the infected fruit in a constant-mist chamber maintained at 20 C for 24 hr. Infected fruits were used within 6 hr of removal from the mist chamber.

An assessment of inoculum density was made for each of 10 fruits. Each fruit was placed in a 9-cm-diameter petri dish containing 15 ml of deionized water. Sporangia were removed from the fruit surface by gentle brushing with a wet, fine-tip paintbrush for 3 min and were collected in the deionized water. The sporangial suspension was agitated in a vortex blender for 1 min and returned to the petri dish, and sporangia per fruit were estimated by counting the number of sporangia in 20 randomly selected 1-mm^2 grids under a dissecting scope. Sporangium production per fruit was expressed as the mean number of sporangia per unit of fruit fresh weight (per gram). The inoculum density assessment was repeated three times.

Treatments and assessment of dispersal. Strawberry plants were grown in 15-cm plastic pots in the greenhouse for 5–7 wk (green fruit stage). The potted plants were placed in holes in a wooden form, with each pot supported by its lip (Fig. 2A). Ten holes were arranged on each of two concentric circles with radii of 30 and 60 cm (Fig. 2A). The holes on each circle were placed so that a plant on the outer circle was radially aligned with one on the inner circle. The surface of the form was completely covered to a depth of 4 cm with a layer of either sterilized soil:sand:peat mix (2:1:1, by volume) or straw over soil mix (Figs. 2B and 2C, respectively). Fresh soil and straw were used for each simulated rain application. Immediately before each rain, 10 inoculated fruits that served as an inoculum source were placed in a tight cluster on the soil or straw surface in the center of the wood form. The wood form, measuring 1.5 × 1.5 m, was centered over the sample area that was used to assess water volume distribution. The effect of intensity on splash dispersal was evaluated using 27W, 35W, and 50W wide-angle spray nozzles. Total simulated rainfall volume was held constant for all nozzles by adjusting rain application periods so that total cumulated water depth was 15 mm per nozzle. The effect of distance was assessed as percentage of fruit infection on the inner circle of plants (Fig. 2B) and on the outer circle of plants when no plants were present on the inner circle (Fig. 2C). The effect of canopy barriers on dispersal was assessed as percentage of fruit infection on the outer circle of plants when plants were also present on the inner circle (Fig. 2B). In analyses, this was treated as a third distance effect rather than as a separate treatment since the effect of canopy barriers on success of short-distance dispersal was not evaluated. The effect of a straw mulch on inoculum dispersal was also evaluated (Fig. 2C).

The plants in each circle were arranged so that at least five immature fruits of alternate plants were either touching the ground or held in the air (position effect). For plants with fruit in contact with the ground, fruit-bearing stems were either bent to the ground or, when necessary, removed from the plant and placed on the ground immediately before the rain simulation. Similarly, for plants with fruit suspended above the ground, stems were held up with tape when necessary. Plants were always oriented so that fruits to be sampled were located on the side of the plant crown closest to the inoculum source. The latter procedure was used to minimize within-treatment variation and to minimize edge effects that might otherwise be significant for plants on the outer circle. Within 10 min after each simulated rainfall, at least five fruits per plant were randomly selected from among those nearest the inoculum source, placed in containers, misted lightly with deionized water, and maintained at 100% RH and at ambient laboratory temperatures (20–24 C). Assessment of fruit infection was made by visual examination at 4, 5, and 6 days following application.

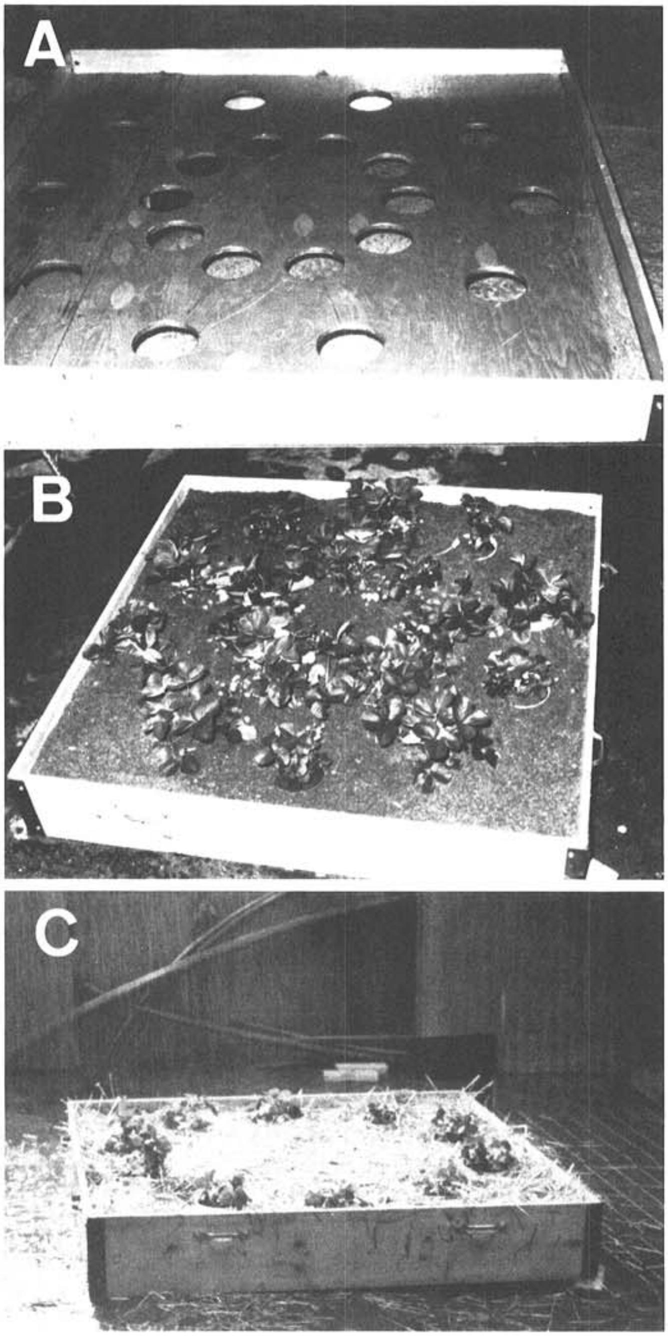

Fig. 2. Wood frame used to hold strawberry plants. **A,** Inner and outer concentric circles showing radial alignment of holes on outer circle with those on inner circle (inner radius = 30 cm, outer radius = 60 cm). **B,** Plants placed in both circles to evaluate effect of distance on dispersal in presence of canopy barriers (shown with soil). **C,** Plants placed only on outer circle to evaluate effect of distance on dispersal in absence of canopy barriers (shown with straw).

Statistical analyses. All possible treatment combinations were used, and each combination was replicated three times. Treatment applications were randomized over intensity (spray-nozzle type) and mulch, whereas distance and position were treated as spatially repeated measures within intensity/mulch combinations. The arcsine square root transformation was applied to incidence data for fruit infection, and the data were analyzed with ANOVA. Means were separated with Duncan's Bayesian least-significant difference (BLSD) ($P \cong 0.05$, $k = 100$) when a main effect or interaction was significant at $P = 0.05$ (37).

RESULTS

Characteristics of simulated rain. The three spray nozzles exhibited only minor departures from uniform water-volume distribution over the 1-m^2 sample area. The mean and standard deviation of intensity for each spray nozzle were consistent between replications (Table 1). The duration of simulated rainfall required to obtain an accumulation of 15-mm depth was determined for each nozzle (Table 1), and these durations were used throughout the study.

The cumulative distribution of simulated raindrop volume produced by the 27W, 35W, and 50W nozzles agreed very well with empirical raindrop volume distributions associated with natural

TABLE 1. Characteristics of spray nozzles used to simulate rainfall

Spray nozzle model[a]	Simulated rainfall intensity (mm/hr) Mean	CV[b]	Time to obtain 15-mm depth (min)	Natural rain match[c] (mm/hr)	Kolmogorov Smirnof statistic[d]
27W	32.6	15.3	28.5	15	0.053 (>0.20)
35W	40.1	10.5	22.5	30	0.045 (>0.20)
50W	48.3	15.4	18.5	60	0.041 (>0.20)

[a] Spraying Systems Inc., Wheaton, IL.

[b] Coefficient of variation.

[c] Matching natural rainfall intensities were determined by comparing water-drop volume distributions produced by nozzle with calculated distributions for natural rainfall intensities that were computed for 5-mm intensity intervals.

[d] Numbers in parentheses indicate significance level of statistic for goodness of fit between spray-nozzle volume distribution and theoretical rainfall distribution (4).

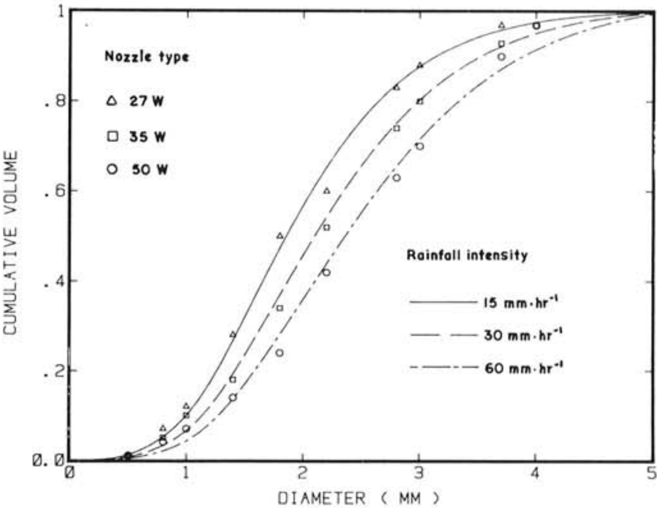

Fig. 3. Comparison of cumulative relative water-drop volume distribution produced by three spray nozzles with three calculated distributions of drop volume for natural rains with intensities of 15, 30, and 60 mm/hr. Data on relative volume distribution for each nozzle were obtained from manufacturer.

rainfall intensities of 15, 30, and 60 mm/hr, respectively, for drop diameters ≤4.0 mm (Eq. 1; Table 1; Fig. 3). For drop diameters >4.0 mm, the cumulative volume distributions of simulated rain are essentially identical to one another (Fig. 3).

The kinetic energy distribution for each nozzle approximated that of rain reasonably well, despite the fact that height of drop fall was only 4 m. The approximate total kinetic energy of the 27W, 35W, and 50W nozzles was 79.6, 77.8, and 76.3% of the total kinetic energy of rains with intensities of 15, 30, and 60 mm/hr, respectively (Fig. 4). For each nozzle, the correspondence of kinetic energy distribution with rain is good up to a drop diameter of 1.75 mm (Fig. 4). The distributions diverged for larger drop diameters, since larger drops attain progressively smaller fractions of their terminal velocities because of the 4-m drop height.

Assessment of dispersal. The number of sporangia that formed per unit fresh fruit weight was variable within a replication, but estimates were consistent among replications. The estimated mean density was 9.3×10^4, and the sample standard deviation was 6.2×10^4 sporangia per gram.

The effects of intensity, distance, and position were all significant at $P = 0.05$, whereas the effect of mulch was not significant ($P > 0.25$; Fig. 5). Plots of residuals against either predicted infection or time of treatment application failed to exhibit any detectable pattern. Percentage of infection at an intensity of 15 mm/hr did not differ significantly from infection levels at intensities of 30 or 60 mm/hr (Fig. 5). However, percentage of infection at an intensity of 30 mm/hr differed significantly from that at 60 mm/hr.

Percentage of infection on the inner circle of plants was significantly greater than that on the outer circle (Fig. 5). When plants were present on the inner circle, providing a possible barrier to inoculum dispersal, percentage of infection on the outer circle appeared to be reduced, but this barrier effect was not significant (Fig. 5).

On either the inner or outer circle of plants, significantly more fruits were infected if they were in contact with the ground than if they were held in the air. Mean percentage of fruit infection in the outer circle of plants was lower when an inner circle of plants was present whether or not fruits were in contact with the ground; however, this barrier effect was also not significant (Fig. 5). Percentage of infection on the ground was 43 and 10% on the inner and outer circles, respectively. The interaction of position and distance was also significant at $P = 0.05$ (Fig. 5). As indicated by this interaction, the reduction in numbers of aerial fruit with infections on the outer circle was not as great as on the inner circle (Fig. 5). Because intensity was a significant main effect, the interaction between distance and position is summarized for each intensity (Table 2).

The interaction of distance and mulch also approached significance ($P = 0.19$). An apparent difference in mean infection can be seen for presence or absence of mulch on the inner circle (Table 2). However, there are clearly no such differences on either the outer circle without or the outer circle with barriers (Table 2).

DISCUSSION

Although the rain simulation system that is described is quite simple in design, drop distributions can be produced that are reasonably good approximations of those found in natural rains (Fig. 3; Table 1). An important criterion for a rain simulation system is the degree to which it reproduces both the drop size

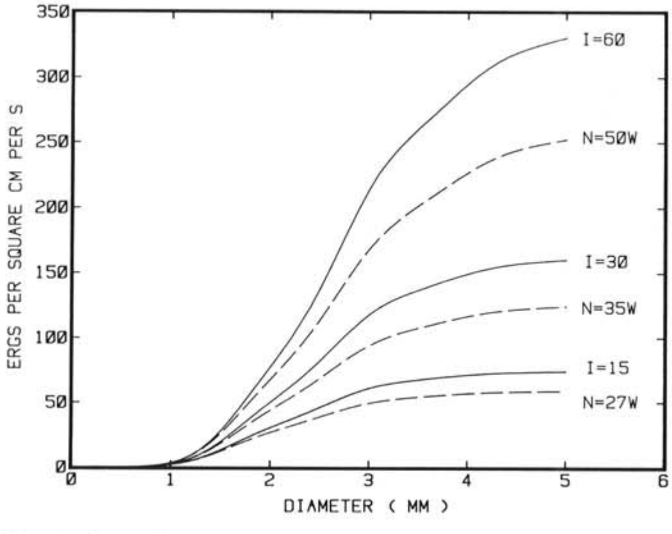

Fig. 4. Comparison of cumulative relative raindrop kinetic energy distribution between three spray nozzles (n, Fig. 1) and natural rainfall intensities of 15, 30, and 60 mm/hr. Curves for 27W, 35W, and 50W spray nozzles (dashed lines) were based on total height of drop fall = 4 m. Curves for natural rain are indicated by solid lines.

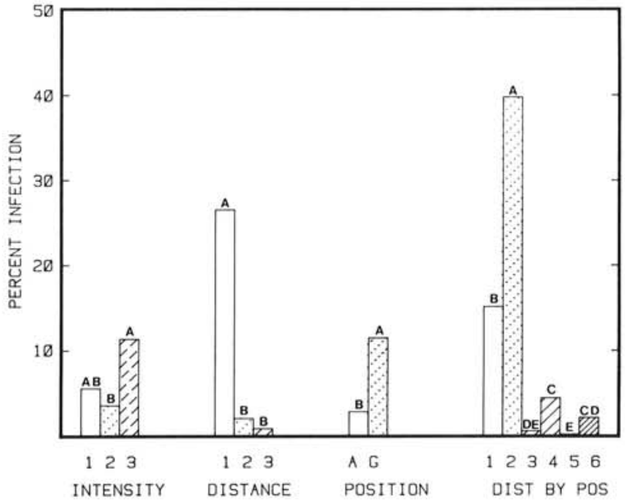

Fig. 5. Percentage of strawberry fruit infection in experimental canopy in response to rainfall intensity, distance, position, and distance × position interaction. Intensity codes: 1 = 15, 2 = 30, and 3 = 60 mm/hr. Distance codes: 1 = inner circle, 2 = outer circle, and 3 = outer circle of plants with inner circle acting as barrier to inoculum dispersal. Position codes: A = fruit held in air, G = fruit in contact with ground. Distance × position codes: 1 = 1×A, 2 = 1×G, 3 = 2×A, 4 = 2×G, 5 = 3×A, and 6 = 3×G, with number indicating distance class and letter indicating fruit position in canopy. Bars topped by same letter within one treatment or interaction indicate that transformed (arcsine square root) means are not significantly different according to Duncan's Bayesian least-significant difference ($k = 100$, $P \cong 0.05$).

TABLE 2. Effects of rainfall intensity, distance of fruit from inoculum source, fruit position within plant canopy, and straw mulch on percentage of strawberry fruit infection by *Phytophthora cactorum* in synthetic strawberry canopy

Rainfall intensity (mm/hr)	Position	Fruit infection (%) at indicated distance from inoculum source		
		30 cm (inner)	60 cm (outer)	60 cm (outer/barrier)
15	Ground	32.2	1.9	3.7
	Air	13.8	1.2	0.0
30	Ground	35.9	2.3	0.4
	Air	7.7	0.0	0.0
60	Ground	51.4	11.4	3.2
	Air	26.1	1.0	1.1
		Mulch treatment		
Present		21.91	1.12	1.00
Absent		31.35	3.09	0.62

distribution of a natural rain and the distribution of kinetic energy over drop size (25). It was noted that the cumulative drop-volume distributions for the three nozzles were essentially identical for drop diameters >4.0 mm (Fig. 3). However, the data presented (Fig. 3) are for relative volume; we have calculated that the 50W nozzle actually produces approximately 1.8 and 1.3 times as many drops >4.0 mm in diameter per minute as the 27W and 35W nozzles, respectively. For an actual rain with an intensity of 60 mm/hr, we have also calculated that drops >4.0 mm in diameter comprise <.4% of the total number received per unit area per unit time, but these drops represent about 8.5% of the total volume received. Thus, results on dispersal using the 50W nozzle will slightly underestimate the effect of a 60-mm/hr rain, since only 3% of the total drop volume produced by this nozzle consists of drops >4.0 mm in diameter. Simulated rainfall intensities ≤30 mm/hr will produce effects on dispersal that are highly representative of real rains.

Because our facilities limited drop height to 4 m, it was possible to achieve only 75–80% of a natural rain's kinetic energy (Fig. 4). However, this limitation is not inherent in the system design; given a drop height of 8 m, virtually all raindrops produced could achieve terminal velocity, in which case the kinetic energy distribution of the simulated rain would closely match that of a natural rain. The highest rainfall intensity used in this study (60 mm/hr) represents an extreme value for average storm intensities (28). However, intensities of this magnitude are not uncommon during short periods in storm episodes (28).

Only distance, intensity, fruit position, and interaction between distance and position were found to be significant at $P = 0.05$ (Fig. 5). However, the interaction term involving distance and mulch approached significance. Within distance and mulch treatment combinations, the presence of mulch appeared to reduce infection on the inner circle of plants, and to a lesser extent on the outer circle when a canopy barrier was not present (Table 2). However, there was clearly no difference in infection between mulch and no-mulch treatments on the outer circle when a canopy barrier was present (Table 2).

The crop canopy is potentially an important factor influencing splash dispersal. Stedman (35) found that a dense field bean (*Vicia faba* L.) canopy restricted the movement of splash droplets. Griffiths and Hann (17) found that splash-dispersal patterns were affected by wind near the top of the canopy but not near its base. In the present study, it could not be demonstrated statistically that dispersal of *P. cactorum* was affected by the presence of a canopy barrier. Although the lack of a barrier effect may have been due to a canopy that was not sufficiently dense, the sharp decline in infected fruit observed in the outer circle made it very difficult to detect a barrier effect. The ability to detect reduced infection levels resulting from a barrier effect should be greater with shorter dispersal distances.

The plant canopy may also influence dispersal by intercepting incident raindrops. Quinn and Laflen (29) observed that raindrop interception by a corn canopy resulted in a larger mean drop diameter and smaller drop diameter variation under the canopy compared with that of incident rain as a result of drip from the foliage. Since drop mass varies with the third power of drop radius, a drop's kinetic energy, and hence its ability to move inoculum, increases rapidly with increasing diameter (5,13,26,32). In addition, rate of drop acceleration when starting from rest increases rapidly with increase in drop diameter. Thus, even though a large drop originates as a drip from plant foliage and falls only a short distance before striking an inoculum-bearing surface, it may still attain a substantial fraction of its terminal velocity (30,32).

Vertical disease gradients have been observed in cocoa black pod disease (15) and rhododendron dieback (21). Vertical inoculum deposition gradients have also been observed (2,3,8,11,12). Our analysis (Table 2) also shows a strong effect of vertical position on the likelihood of fruit infection. The effect of vertical position supports numerous field observations of greater infection when fruits are in contact with the ground rather than in the air (L. V. Madden and M. A. Ellis, *unpublished*). The significant position × distance interaction that was observed (Fig. 5) appears to result from the very low levels of infection that were obtained in the outer circle of plants. The observed differences in infection between fruits on the ground and those held in the air are probably in part the result of differential deposition of inoculum. An additional factor is that a fruit held in the air may be at lower risk of infection even when inoculum deposition occurs. Inoculum may be washed from the surface of a fruit by subsequent rain impacts. However, if a fruit is in contact with the ground, inoculum that is washed from its surface may still be in a position to initiate infection. Under field conditions, additional factors not considered in this study may also affect infection of fruits that are in contact with the soil. For instance, fruits that contact the ground are exposed to prolonged wetting periods that would enhance infection.

Use of the BLSD statistic to separate mean infection levels due to variation in rainfall intensity indicated that percentage of infection was significantly different for intensities of 30 and 60 mm/hr but that percentage of infection for intensity of 15 mm/hr was intermediate. However, the lack of a simple linear relationship between percentage of disease and intensity has been observed previously (9,36). Stedman (36) found that numbers of conidia of *Rhynchosporium secalis* (Oudem.) J. J. Davis collected on spore traps were related to mean intensity for brief rain showers. However, there was no clear relationship between numbers of spores trapped and total rainfall (36). Similarly, Fitt et al (9) recovered significantly more *R. secalis* conidia during the first 5 min of a 12- than a 6.5-mm/hr rain, but total numbers of conidia recovered after 30 min were similar.

A circular arrangement of pots was used in this study because it allowed assessment of the largest number of plants at a given distance from the inoculum source. On the other hand, this pattern may not be optimal for assessing the significance of effects such as plant barriers or mulching. A spatial distribution pattern of plants based on a square or rectangular lattice might be preferable in these instances.

A major advantage in studying the splash-dispersal process with a system such as the one described is the ability to maintain control over several experimental factors simultaneously while maintaining a high degree of realism. Overall, the rain simulation system that has been described appears to offer significant potential to advance our understanding of natural pathogen-dispersal processes, since it allows high levels of both realism and experimental control.

LITERATURE CITED

1. Beard, K. V. 1976. Terminal velocity and shape of cloud and precipitation drops aloft. J. Atmos. Sci. 33:851-864.
2. Brennan, R. M., Fitt, B. D. L., Taylor, G. S., and Colhoun, J. 1985. Dispersal of *Septoria nodorum* pycnidiospores by simulated raindrops in still air. Phytopathol. Z. 112:281-290.
3. Brennan, R. M., Fitt, B. D. L., Taylor, G. S., and Colhoun, J. 1985. Dispersal of *Septoria nodorum* pycnidiospores by simulated rain and wind. Phytopathol. Z. 112:291-297.
4. Brunk, H. D. 1975. An Introduction to Mathematical Statistics. Xerox College Publ., Lexington, MA. 457 pp.
5. Eckern, P. C. 1953. Problems of raindrop impact erosion. Agric. Eng. 34:23-25, 28.
6. Faulwetter, R. F. 1917. Dissemination of angular leafspot of cotton. J. Agric. Res. 8:457-475.
7. Faulwetter, R. F. 1919. Wind-blown rain, a factor in disease dissemination. J. Agric. Res. 10:639-648.
8. Fitt, B. D. L., and Bainbridge, A. 1983. Dispersal of *Pseudocercosporella herpotrichoides* from infected wheat straw. Phytopathol. Z. 106:214-225.
9. Fitt, B. D. L., Creighton, N. F., Lacey, M. E., and McCartney, H. A. 1986. Effects of rainfall intensity and duration on dispersal of *Rhynchosporium secalis* conidia from infected barley leaves. Trans. Br. Mycol. Soc. 86:611-618.
10. Fitt, B. D. L., Lapwood, D. H., and Dance, S. J. 1983. Dispersal of *Erwinia carotovora* subsp. *atroseptica* in splash droplets. Potato Res. 26:123-131.
11. Fitt, B. D. L., and Lysandrou, M. 1984. Studies on mechanisms of splash dispersal of spores, using *Pseudocercosporella herpotrichoides*

spores. Phytopathol. Z. 111:323-331.

12. Fitt, B. D. L., and Nijman, D. J. 1983. Quantitative studies on dispersal of *Pseudocercosporella herpotrichoides* spores from infected wheat straw by simulated rain. Neth. J. Plant Pathol. 89:198-202.
13. Free, G. R. 1960. Erosion characteristics of rainfall. Agric. Eng. 41:447, 455.
14. Gregory, P. H. 1970. Microbiology of the Atmosphere. Leonard Hill Publ. Co., Aylesbury, Burks, England. 377 pp.
15. Gregory, P. H., Griffin, M. J., Maddison, A. C., and Ward, M. R. 1984. Cocoa black pod: A reinterpretation. Cocoa Growers Bull. 35:5-22.
16. Gregory, P. H., Guthrie, E. J., and Bunce, M. 1959. Experiments on splash dispersal of fungus spores. J. Gen. Microbiol. 20:328-354.
17. Griffiths, E., and Hann, C. A. 1976. Dispersal of *Septoria nodorum* spores and spread of glume blotch of wheat in the field. Trans. Br. Mycol. Soc. 67:413-418.
18. Grove, G. G., Madden, L. V., and Ellis, M. A. 1985. Splash dispersal of *Phytophthora cactorum* from infected strawberry fruit. Phytopathology 75:611-615.
19. Grove, G. G., Madden, L. V., and Ellis, M. A. 1985. Influence of temperature and wetness duration on sporulation of *Phytophthora cactorum* on infected strawberry fruit. Phytopathology 75:700-703.
20. Hunter, J. E., and Kunimoto, R. K. 1974. Dispersal of *Phytophthora palmivora* by wind-blown rain. Phytopathology 64:202-206.
21. Kuske, C. R., and Benson, D. M. 1983. Survival and splash dispersal of *Phytophthora parasitica*, causing dieback of rhododendron. Phytopathology 73:1188-1191.
22. Marshall, J. S., and Palmer, W. M. 1948. The distribution of raindrops with size. J. Meteorol. 5:165-166.
23. McCartney, H. A., and Bainbridge, A. 1984. Deposition gradients near to a point source in a barley crop. Phytopathol. Z. 109:219-236.
24. McCartney, H . A., and Fitt, B. D. L. 1987. Spore dispersal gradients and disease development. Pages 104-118 in: Populations of Plant Pathogens: Their Dynamics and Genetics. M. S. Wolfe and C. E. Caten, eds. Blackwell Scientific Pub., Oxford, England.
25. Meyer, L. D. 1965. Simulation of rainfall for soil erosion research. Trans. ASAE 8:63-65.
26. Michara, Y. 1952. Raindrop and soil erosion. Bull. Natl. Inst. Agric. Sci. Ser. A, No. 1. Tokyo.
27. Mutchler, C. K., and Moldenhauer, W. C. 1963. Applicator for laboratory rainfall simulator. Trans. ASAE 6:220-222.
28. Pruppacher, H. R., and Klett, J. D. 1980. Microphysics of clouds and precipitation. Reidel Publ. Co., London. 714 pp.
29. Quinn, N. W., and Laflen, J. M. 1983. Characteristics of raindrop throughfall under corn canopy. Trans. ASAE 26:1445-1450.
30. Reynolds, K. M., Madden, L. V., Reichard, D. L., and Ellis, M. A. 1986. Methods for detailed study of the splash dispersal process. (Abstr.) Phytopathology 76:1141.
31. Rose, D. H. 1924. Leather rot of strawberries. J. Agric. Res. 28:357-376.
32. Saville, D. B. O., and Hayhoe, H. N. 1978. The potential effect of drop size on efficiency of splash-cup and springboard dispersal devices. Can. J. Bot. 56:127-128.
33. Schlub, R. L. 1983. Epidemiology of *Phytophthora capsici* on bell pepper. J. Agric. Sci. 100:7-11.
34. Stedman, O. J. 1979. Patterns of unobstructed splash dispersal. Ann. Appl. Biol. 91:271-285.
35. Stedman, O. J. 1980. Splash droplet and spore dispersal studies in field beans (*Vicia faba* L.). Agric. Meteorol. 21:111-127.
36. Stedman, O. J. 1980. Observations on the production and dispersal of spores, and infection by *Rhynchosporium secalis*. Ann. Appl. Biol. 95:163-175.
37. Waller, R. A., and Duncan, D. B. 1969. A Bayes rule for the symmetric multiple comparisons problem. J. Am. Stat. Assoc. 64:1484-1503.