Splash Dispersal of *Phytophthora cactorum* from Infected Strawberry Fruit

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ABSTRACT

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Strawberry fruits (cultivar Tristar) infected with *Phytophthora cactorum* were used to demonstrate and quantify the effects of splashing water on dispersal and distribution of inoculum. Water drops, averaging 0.026 or 0.41 cm in diameter, were dropped from various heights on infected fruits adjacent to petri plates containing selective media and positioned up to 1.2 m away. Sporangia, zoospores, and mycelia were readily dispersed; as a result of water-splash from the 0.41- and 0.026-cm-diameter drops, colonies formed up to 120 and 50 cm, respectively, from the inoculum source. Numbers of colonies that developed in the plates were negatively correlated with distance from the inoculum source. A multiple regression model was used to describe number of colonies as a function of distance and water drop velocity at impact. Splash dispersal of inoculum from infected fruit to healthy, attached fruit was demonstrated with potted plants.

Additional key words: *Fragaria* × *ananassa*, quantitative epidemiology.

Excessive rainfall in Ohio during the 1980 and 1981 growing seasons was associated with heavy losses in the state's strawberry (*Fragaria* × *ananassa* Duch.) crop due to fruit rots (3). Leather rot, caused by *Phytophthora cactorum* (Leb. & Cohn) Schroet., accounted for up to 40% yield loss. Fruits and blossoms infected with *P. cactorum* were observed 0–20 cm above the soil surface; the frequency decreased with increasing height. Numerous papillate sporangia characteristic of *P. cactorum* were observed microscopically on the surface of infected fruit collected either during or immediately after extended periods of wetness. Rose (14,15) also found that leather rot epidemics occurred either during or immediately after periods of excessive rainfall.

During the 1982 and 1983 growing seasons, in which precipitation was approximately equal to or below, respectively, the long-term average, occurrence of leather rot was sporadic with losses generally ranging 0–5% (3). Diseased fruit observed at those times were generally in contact with soil. However, one grower in an area of localized heavy rainfall had losses due to aerial blossom and fruit infection by *P. cactorum* (M. A. Ellis and G. G. Grove, *unpublished*).

The duration of wetness and temperature conducive to fruit infection by *P. cactorum* have been determined (7). Even when no epidemics occur, temperature and dew durations favoring high infection rates occur nightly in Ohio during the strawberry fruiting season, indicating that other factors contribute significantly to the development of leather rot epidemics. The occurrence of aerial blossom blights and fruit rots after precipitation indicates that splash dispersal of infective propagules of *P. cactorum* may be an important component in the development of leather rot epidemics. Dispersal of some pathogenic fungi via rain splash mechanisms has been well documented (4,5,8,11,18–20).

The purposes of this study were to demonstrate the role of water splash in the dispersal of infective propagules of *P. cactorum* and to quantify the effects of water drop size and velocity at impact on propagule dispersal distance.

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MATERIALS AND METHODS

Splash studies. All studies were performed with detached strawberry fruit (cultivar Tristar) obtained from plants grown to reproductive maturity in a peat:sand:steam-disinfested loam (1:1:1, v:v) mix. All inoculations were performed with cultures of *P. cactorum* freshly isolated from infected strawberry fruit (cultivar Tristar) on pentachloronitrobenzene-benomyl-neomycin sulfate-chloramphenicol medium (PBNC) (17). For sporangial production, mycelial transfers from the edges of of 3-day-old cultures were transferred to lima bean agar (17). Cultures were incubated 7 days at 22 C in continuous light at 2.7 W/m^2. Sporangial germination was induced by flooding each culture with 20 ml of sterile distilled water then refrigerating it at 5 C for 30 min to induce zoospore formation. Zoospore concentrations were adjusted to 10,000/ml with sterile distilled water as measured with a hemacytometer 30 min after removal from refrigeration. Fruits were washed with detergent and sterile distilled water for 5 min, rinsed with five 100-ml aliquots of sterile distilled water, surface sterilized for 30 sec with 9:1 (v:v) sterile distilled water:sodium hypochlorite solution, and then rinsed with five 100-ml aliquots of sterile distilled water. Ten milliliters of inoculum and fruit were then transferred to plastic petri plates and incubated for 4 hr at 22 C in continuous light at 2.7 W/m^2. Inoculated fruit were then placed on metal screens contained in a controlled-environment chamber (Environmental Growth Chambers, Chagrin Falls, OH) and incubated for 48 hr at 20 C in a 14-hr photoperiod at 99 W/m^2. Fruit were then transferred to a 1-m^3 clear plastic chamber (mist chamber) within a second controlled-environment chamber and kept continuously wet with a Herrmidifer mister (Herrmidifer Co., Lancaster, PA) for 24 hr at 20 C and continuously lighted at 39 W/m^2. Sporangial production was then verified by microscopic examination at ×40. One firm fruit with sporulating *P. cactorum* was used for each splash test.

Splash tests were performed by impacting water drops with an average diameter of 0.41 or 0.026 cm on infected fruit surfaces. All tests were performed in a closed stairwell at 18–22 C. The drop sources were a 50-ml glass buret and a 100-ml plastic syringe for the 0.41- and 0.026-cm-diameter drops, respectively.

Drop diameters were determined by releasing a fixed number of drops, calculating average drop volume and then using the equation for the volume of a sphere to estimate average drop

diameter. Terminal velocities for the 0.41- and 0.026-cm-diameter drops were 830 and 217 cm/s, respectively (16). In tests incorporating the 0.41-cm-diameter drops, the glass buret was positioned 8.5, 3.0, or 1.0 m above the infected fruit. Ninety-six 9-cm-diameter plastic petri plates containing 15 ml PBNC medium were used in each test. Plates were arranged level with, 4 cm above, and 4 cm below the infected fruit on 120 × 8.5 × 4 cm (length × width × height) boards. Plates were positioned in straight-line horizontal distances of 29-120 cm, 13-120 cm, and 10-100 cm above, below, and level with the source, respectively. The three plate levels were "staggered", i.e., each line of plates from the source was only at one level to avoid interference with drop flights. Plate tops were removed immediately prior to the beginning of each experiment. Water drops, at a rate of 48 drops/min were allowed to impact on the fruit surface for 14.5 min. Plates were covered immediately after the experiment and incubated 72 hr at 22 C in continuous light at 2.7 W/m^2. Colony numbers in each plate were determined by visual inspection and by microscopic examination (×40).

In tests with 0.026-cm-diameter drops, the 100-ml plastic syringe was placed 2.0 and 0.5 m above sporulating fruit. Ninety-six 5.5-cm-diameter plastic petri plates containing 7.5 ml of PBNC media were positioned on boards level with, 4 cm above, and 4 cm below the infected fruit at horizontal distances of 6-54, 20-68, and 13-76 cm, respectively. Prior to each test, 0.5 ml of sterile distilled water was added to each plate to enhance sporangial germination. The plates were uncovered at the start of the experiment, the drops were released, and the plates were incubated as described for the 0.41-cm-diameter drops. Experiments with the large and small drops were each conducted twice.

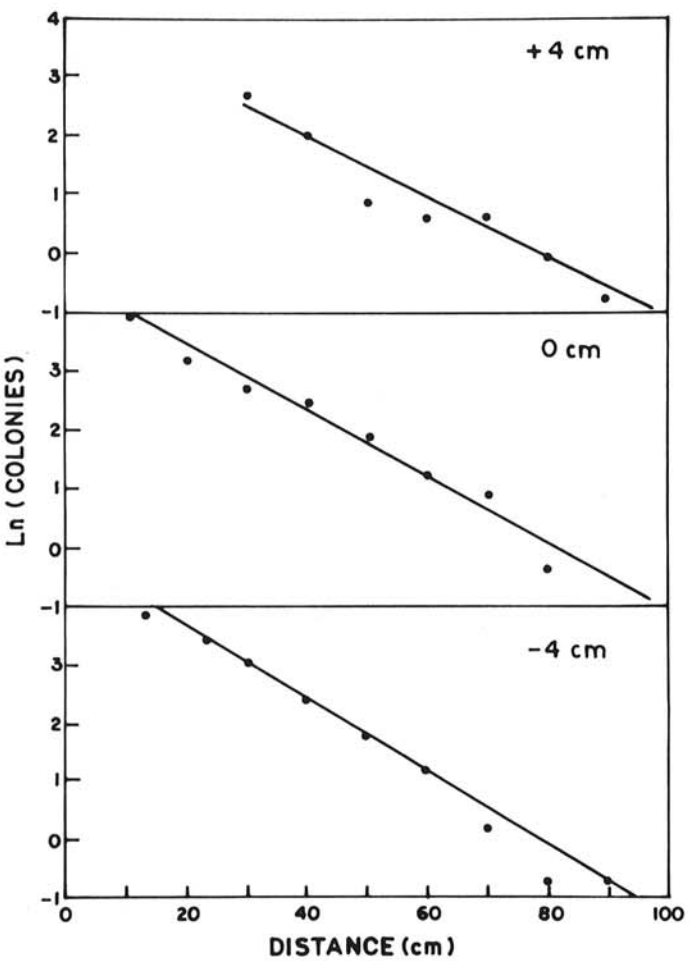

Fig. 1. Observed (•) and predicted (line) numbers of colonies of *Phytophthora cactorum* splash dispersed to different distances from an inoculum source. The prediction lines were derived by fitting equation 1 to the data for 0.41-cm-diameter drops released from a height of 3 m. Based on equation 2, the velocity at impact was 637 cm/s.

Plant-to-plant spread. Attached, immature strawberry fruit were inoculated by applying 1 ml of a 10,000 zoospore per milliliter suspension of *P. cactorum* to each fruit with an atomizer. Plants were incubated in a mist chamber as described above. Inoculations were performed in the mist chamber and the plants were incubated for 6 hr at 22 C in continuous darkness in the same chamber. Plants were removed and incubated an additional 72 hr at 22 C in a 14-hr daily photoperiod (99 W/m^2). To induce sporulation, plants were returned to the mist chamber and incubated in continuous wetness for 24 hr, at 22 C. A 14-hr photoperiod (39 W/m^2) was initiated when the plants were placed in the chamber.

For splash experiments, 6-10 attached, immature fruit (cultivar Tristar) were tagged on each plant. Plants were placed 15 and 30 cm from the sporulating fruit in a closed stairwell and "staggered" to prevent the plants at 15 cm from shielding the plants at 30 cm. Six plants were positioned at each distance; two were covered with clear plastic bags and four were uncovered. Water drops, 0.41 cm in diameter, were dropped from a height of 8.5 m onto the surface of exposed sporulating fruit for 14.5 min at a rate of 48 drops per minute. Following the splash experiment, all plants were transferred to the mist chamber in the controlled-environment chamber and incubated 24 hr at 22 C in a 14-hr photoperiod (39 W/m^2). Plants were then transferred to a second controlled-environment chamber at 20 C in a 14-hr photoperiod (99 W/m^2). Proportions of diseased fruit were determined visually 72 hr after the splash test. Tissue sections from each fruit were placed on PBNC medium to verify the presence of *P. cactorum*.

Data analyses. Regression analysis was used to determine the effects of drop velocity (V, cm/s) at impact, height of plate (L, cm) relative to inoculum source, and horizontal distance from inoculum source (D, cm) on the number of colonies (Y) of *P. cactorum* obtained in petri plates positioned around the inoculum source. Initially, a simple model was chosen of the form:

$$\ln(Y) = b_0 + b_1 D \quad (1)$$

in which $\ln(Y)$ is the natural logarithm of colony number, and b_0 and b_1 are parameters estimated from the data. Kiyosawa & Shiyomi (9) used this model for studying dispersal gradients in the field. The dispersal coefficient (b_1) represents the steepness of the colony gradient away from the source; b_0 is an indication of "source strength", ie, the effective number of propagules at the source. Preliminary analyses made by using eq. 1 were performed on each combination of release height, test, drop size, and plate level. Results from preliminary splash tests indicated that $\ln(Y)$ was linearly related to distance.

Drop velocities (V) for each drop source and release height were determined by using the formula:

$$V = (a/b)^{0.5} (\tanh(\cosh^{-1}(\exp(bZ))) \quad (2)$$

in which $a = g(w - p)$ and $b = 3pc/4Xw$, with V = velocity of the drop (centimeters per second), X = drop diameter (centimeters), p = density of air (0.00129 g/cm^3), w = density of water (1 g/cm^3), c = drag coefficient (0.559), g = acceleration due to gravity (980 cm/sec^2), and Z = vertical distance (centimeters) from the release point to the sporulating fruit (16).

Equation 1 was expanded to evaluate the effect of drop velocity, plate level, and interactions on $\ln(Y)$. Stepwise regression was used to evaluate the significance of: V, D, L, $L*D$, $V*D$, $V*L$, and $D*V*L$, in which the asterisks indicate multiplication. All regression models with combinations of these terms were evaluated for: significance of estimated parameters, coefficient of determination (R^2), R^2 adjusted for degrees of freedom (R_a^2), and pattern of residuals (12,13). The regression analysis was performed on tests one and two, and then on the combined data. A general linear F-test was conducted to determine if the results from the two tests were significantly different (13). Analyses of data from 0.41- and 0.026-cm-diameter drops were at all times kept separate due to the different volumes of water used and the different plate sizes.

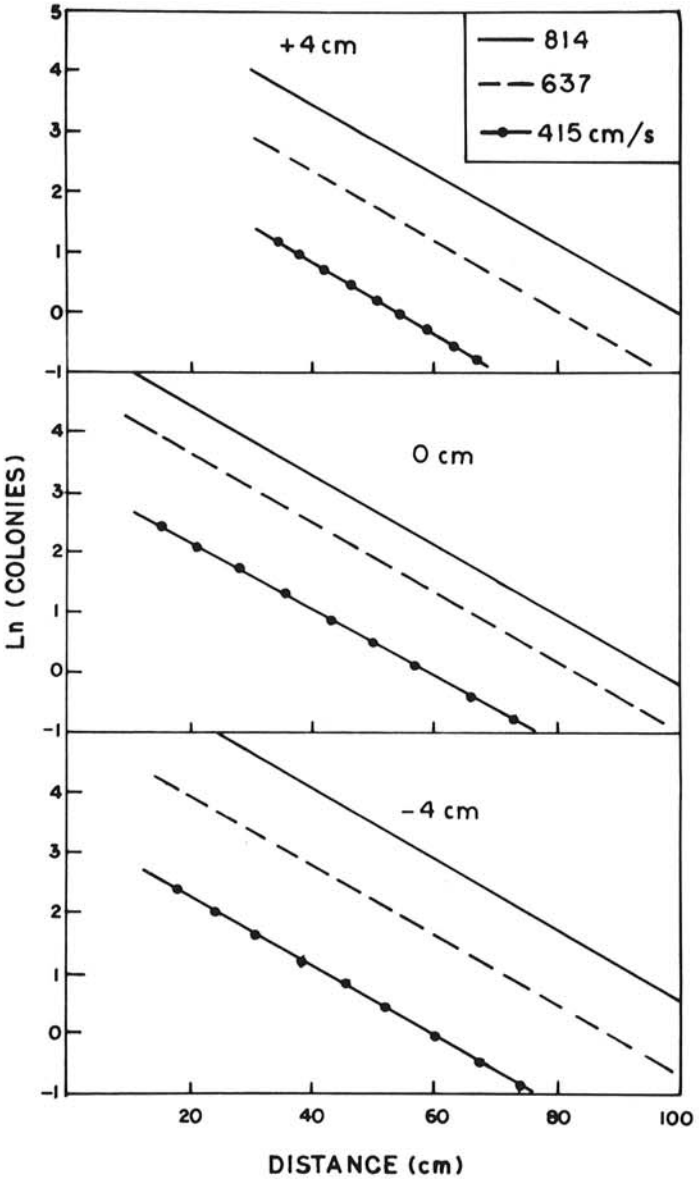

Fig. 2. Effect of impact by 0.41-cm-diameter water drops falling at three velocities on the predicted number of colonies of *Phytophthora cactorum* splash dispersed to locations 4 cm above, level with, 4 cm below, and at various distances from the inoculum source. Curves were generated by using equation 3 with parameters listed in Table 1 for the combined tests. The range of distances used in the prediction equation corresponds to the location of petri plates at the three levels. Velocity of water drops was determined by using equation 2.

RESULTS

Sporangia, zoospores, and mycelial fragments were observed microscopically in petri plates upon completion of each experiment. Colonies of *P. cactorum* developed on plates exposed at distances up to 120 and 50 cm from the inoculum source, as a

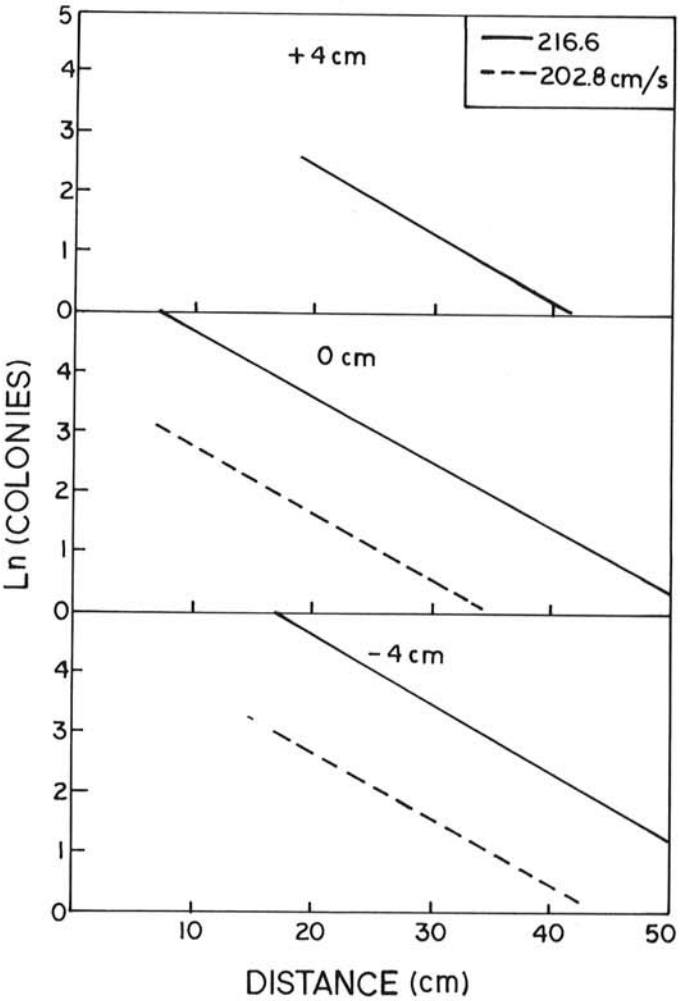

Fig. 3. Effect of impact by 0.026-cm-diameter water drops falling at two velocities on the predicted number of colonies of *Phytophthora cactorum* splash dispersed to locations 4 cm above, level with, 4 cm below, and at various distances from the inoculum source. Curves were generated by using equation 3 with the parameters listed in Table 2 for the combined tests. The range of distances used in the prediction equation corresponds to the location of petri plates at the three levels. Velocity of water drops was determined by using equation 2.

TABLE 1. Estimated parameters of equation 3 for the natural log of colonies of *Phytophthora cactorum* in petri plates as a function of water drop velocity (V) at impact, distance (D) from the source, and level (L) of the petri plates relative to the source, together with the coefficient of determination (R^2), R^2 adjusted for degrees of freedom (R_a^2), and the standard error about the regression curves (S) for 0.41-cm-diameter drops

	Estimated parameters[y]						
	b_0	b_1	b_2	b_3	R^2	R_a^2	S
Test 1	−2.081[z] (0.295)	−0.054 (0.21×10^{-2})	0.010 (0.45×10^{-3})	-0.907×10^{-4} (0.25×10^{-4})	0.936	0.933	0.443
Test 2	1.714 (2.62)	−0.064 (0.002)	0.006 (0.40×10^{-3})	-0.932×10^{-4} (0.27×10^{-4})	0.925	0.922	0.518
Combined	0.361 (0.271)	−0.058 (0.002)	0.007 (0.41×10^{-3})	-0.859×10^{-4} 0.26×10^{-4})	0.860	0.856	0.678

[y] Estimated parameters are the intercept and coefficients for $D(b_1)$, $V(b_2)$, and $L^*V(b_3)$, respectively. Numbers in parentheses under the parameters correspond to their standard deviations.

[z] Intercept (b_0) corresponds to the predicted log of colonies when V, D, and L equal zero.

result of splashing water from the 0.41- and 0.026-cm drops, respectively. Greater drop velocities resulted in more total colonies and in greater horizontal dispersal in all cases. Colony numbers were generally highest in petri plates positioned 4 cm below the inoculum source. No colonies were observed 4 cm above the source when the fruit was impacted by the 0.026-cm drops falling at 202.8 cm/s. Typical colony number data at various distances from the inoculum source are presented in Fig. 1. The data correspond to a single test with the 0.41-cm-diameter drops released from 3 m above the source. The prediction lines were derived by fitting equation 1 to the data.

Based on stepwise regression analysis with the variables described above, the overall best linear model representing the dispersal of propagules of *P. cactorum* by splash mechanisms for both drop sizes was of the form:

$$\ln(Y) = b_0 + b_1 D + b_2 V + b_3 V^* L \qquad (3)$$

in which the *b*s are unknown parameters estimated from the data. Estimated parameters for the large-drop and small-drop tests and other regression statistics are presented in Tables 1 and 2, respectively. All estimated parameters were significant at $P<0.05$. For both drop sizes, the residuals had a random pattern and were normally distributed. Coefficients of determination (R^2) were fairly high (e.g., R^2 equaled 0.860 and 0.805 for 0.41- and 0.026-cm drops, respectively) for the combined data. Coefficients of determination adjusted for degrees of freedom (R_a^2) were almost as large as R^2 in both cases, indicating significant parameter estimates (10,12,13). An *F*-test indicated a significant difference between the two tests with 0.41-cm-diameter drops ($P<0.05$), but no significant difference between the two tests with the 0.026-cm-diameter drops ($P>0.20$). The major difference between the two tests with the large drops was represented by the values of b_0, the predicted $\ln(Y)$ when D, V, and L equal zero. Although b_0 does not have a direct meaning because V in our study never came close to zero, the parameter is proportional to the number of sporangia on the fruit surface. The other parameters for the large-drop tests were of the same magnitude and sign.

Inspection of the model revealed a negative relationship between $\ln(Y)$ and D, substantiating the observed decline in colony numbers as distance from the infected fruit increased. There was a positive relationship between $\ln(Y)$ and V that indicated more colonies were formed (i.e., more sporangia dislodged) as impaction velocity increased. There was also an interaction between V and L, indicating that the number of colonies at each plate level was not consistent at all drop velocities.

Predicted values of $\ln(Y)$ were calculated by using equation 3 with estimated parameters for the combined tests for drop velocities of 814, 673, and 415 cm/s for the 0.41-cm drop, and 202.8 and 216.6 for the 0.026-cm drop (Figs. 2–4). Predicted values of $\ln(Y)$, and therefore Y, increased with increasing drop velocities and decreased with increasing distance from the inoculum source (Figs. 2 and 3). The same relationship was observed at each level. The interaction of V and L is best seen in Fig. 4 in which the assumption is made that there was a linear relation between $\ln(Y)$ and V. Although numbers of colonies decreased from 4 cm below to 4 cm above the inoculum source at all velocities, the differences in colony number between levels increased as velocity increased.

Plant-to-plant-spread. Of the uncovered plants used in splash tests, infection of fruit was 100% at both 15 and 30 cm from the source. Leather rot symptoms failed to develop on any plants covered with plastic bags during the splash test.

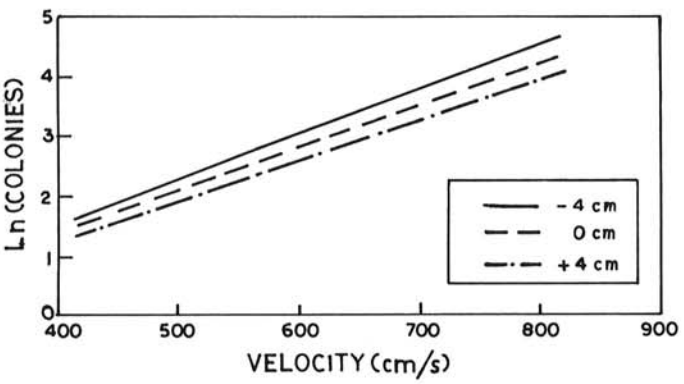

Fig. 4. Effect of impact by 0.41-cm-diameter water drops on the predicted number of colonies of *Phytophthora cactorum* splash dispersed 30 cm from the inoculum source at locations 4 cm above, level with, and 4 cm below. Curves were generated by using equation 3 with parameters listed in Table 1 for combined tests. The range of velocities corresponded to the impact velocities used in the tests as estimated by equation 2.

DISCUSSION

Propagules of *P. cactorum* were readily dispersed from infected strawberry fruit by splashing water; the numbers of colonies were significantly related to drop velocity (V) and the distance (D) of the propagule trap from the source. Negative values of the dispersal coefficent (b_1) were obtained in all cases. Negative gradients (and dispersal coefficients) previously have been shown to indicate dispersal from an inoculum source via wind (6) and water splash (4,5,11). Positive values of b_2, the coefficient of drop velocity, indicated that increasing drop velocities (V) resulted in greater total numbers of colonies being detected at all distances. The effect of velocity at impact was expected since momentum at impact (velocity × drop diameter) powers the splashing of water drops that contain spores (16). Although there was a decline in numbers of colonies as plate level increased from 4 cm below the inoculum source to 4 cm above the source, the steepness of this vertical gradient was not consistent for all drop velocities. The gradient steepness increased as V increased as indicated by the significant V^*L interaction.

Splash dispersal of propagules of *P. cactorum* from infected to healthy fruit was further demonstrated by the high infection levels

TABLE 2. Estimated parameters of equation 3 for the natural log of colonies of *Phytophthora cactorum* in petri plates as a function of water drop velocity (V), distance (D) from the source, and level (L) of the plates relative to the source, together with the coefficient of determination (R^2), R^2 adjusted for degrees of freedom (R_a^2), and the standard error about the regression curves (S) for 0.026-cm-diameter drops

	Estimated parameters[y]						
	b_0	b_1	b_2	b_3	R^2	R_a^2	S
Test 1	−22.14[z] (4.55)	−0.093 (0.011)	0.128 (0.022)	-0.105×10^{-2} (0.218×10^{-3})	0.785	0.757	0.642
Test 2	−25.35 (4.64)	−0.122 (0.11)	0.145 (0.22)	-0.126×10^{-2}) (0.226×10^{-3})	0.839	0.821	0.734
Combined	−24.53 (3.34)	−0.110 (0.008)	0.140 (0.016)	-0.120×10^{-2} (0.162×10^{-3})	0.805	0.794	0.711

[y] Estimated parameters are the intercept and coefficients for $D(b_1)$, $V(b_2)$, and $L^*V(b_3)$, respectively. Numbers in parentheses under the parameters correspond to their standard deviations.

[z] Intercept (b_0) corresponds to the predicted log of colonies when V, D, and L equal zero.

of fruit on test plants, and by the absence of leather rot symptoms on plants that had been covered during the test. However, a negative dispersal gradient was not observed, indicating that either too few fruits were used in the test, or that plants were not placed far enough from the source to detect the negative gradient.

Splash dispersal of infective propagules of species within the genus *Phytophthora* has been documented or suggested (4,8,11,18–20). Hunter and Kunimoto (8) reported that epidemics of blight caused in papaya (*Carica papaya* L.) by *P. palmivora* were favored, in large part, by dispersal of sporangia carried in wind-blown rain. They also speculated on the presence of a similar mechanism contributing to outbreaks of blight caused in taro by *P. colocasiae*. Gerlach et al (4) showed that zoospores of *P. citrophthora* were readily dispersed to potted *Pieris japonica* (Thunb.) D. Don by splashing water; lesion incidence on infected plants in the field was shown to follow a negative vertical gradient. Outbreaks of fruit rot caused in apple (*Malus* sp.) by *P. syringae* in the United Kingdom were, in large part, related to the incidence of heavy rains and it was believed that inoculum was splashed into tree canopies from infested leaf debris on the orchard floor (19,20). Aerial infections of cedar (*Chamaecyparis lawsonia* (Murr.) Parl) were inferred to be dependent upon dispersal of propagules of *P. lateralis* from stem cankers and infected lower branches (18). The incidence of leaf lesions, caused on rhododendron by *P. parasitica*, followed a negative vertical infection gradient with height from container bases; occurrence of lesions was found to be highest on plants in close proximity to areas prone to flooding during irrigation (11). Demonstration of splash dispersal of *P. cactorum*, in addition to the forementioned reports of similar phenomena, emphasizes the importance of the mechanism in development of aerial epidemics caused by various *Phytophthora* spp. Rain splash of *Phytophthora* spp. with caducous sporangia (e.g., *P. cactorum* and *P. palmivora*) likely is more effective than that of species with persistent sporangia (e.g., *P. lateralis*). The latter species probably are disseminated by rain splash of their zoospores. Research is needed to compare the dispersal of sporangia and zoospores of *Phytophthora* spp.

Raindrops reaching the ground usually vary between 0.02 and 0.5 cm in diameter, with small drops being more numerous than large ones (2). However, significant numbers of drops larger than 0.2 cm in diameter can originate from convective clouds, such as cumulus (1). The drop sizes we used were within those ranges. The larger drop also could easily approximate water dripping from within the strawberry canopies. We feel that drop sizes and velocities studied here could easily result in dispersal of propagules of *P. cactorum* from the ground into plant canopies, and dispersal of sporangia, mycelia, or zoospores both within and between rows of strawberry plants. Splash dispersal of *P. cactorum*, in addition to weather that favored infection and sporulation, probably contributed to the severe aerial epidemics of leather rot experienced in recent years. In future investigations, we plan to study droplet trajectories, a range of drop impaction rates, barriers to droplet flight (e.g., strawberry plants), depletion of propagules at the source, and splash dispersal with air movement (wind) to better understand this form of dissemination and eventually use the information in a disease management program for strawberries.

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