Influence of Acidity Level in Simulated Rain on Disease Progress and Sporangial Germination, Infection Efficiency, Lesion Expansion, and Sporulation in the Potato Late Blight System

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ABSTRACT

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The progress of late blight caused by *Phytophthora infestans* race 1,5 on potato (*Solanum tuberosum* 'Kennebec') was monitored in field studies in which ambient rainfall was excluded and simulated rain events at pH 2.8, 3.6, 4.2, 4.8, or 5.6 were applied three times per week in 1984 and twice per week in 1985. There were significant quadratic and cubic effects of acidity of simulated rain on disease progress ($p = 0.024$) in 1985, but no significant effects in 1984. Disease increased most rapidly at pH 4.8 of simulated rain in 1985. Maximum disease severity in each year was approximately 15%. In laboratory studies, direct and indirect germination of sporangia of two isolates (race 1,5 and race 1,3,4,5) were almost completely inhibited in simulated rain solution at pH 2.4. Maximum direct germination occurred at pH 3.0, and maximum indirect germination occurred at pH 5.6 and 3.6 for isolates of race 1,5 and race 1,3,4,5, respectively. Infection efficiencies of sporangia borne in simulated rain solutions of pH 2.4, 3.0, 3.6, 4.2, and 5.6 were similar if misting of plants with deionized water (pH ~ 5.6) commenced immediately or 4 hr after inoculation; however, when misting was delayed until 8 or 16 hr after inoculation, significant numbers of infections occurred only with pH 3.6, 4.2, and 5.6 treatments. Infection occurred only at pH 3.2 and above when sporangia were applied in simulated rain at pH 3.0, 3.1, 3.2, 3.3, 3.4, 3.5, or 3.6, and misting was delayed until 8 hr after inoculation. In the greenhouse, final size of late blight lesions did not differ among simulated rain treatments at pH ~ 3.0, 4.2, or 5.6; however, number of sporangia produced per square centimeter of lesion was lower at pH 3.0 than at pH 4.2 or 5.6. Although laboratory and greenhouse studies indicate that highly acidic rain could potentially reduce severity of late blight of potato, this potential was not realized in the field studies. Duration, frequency, and extent of exposure to highly acidic rain in the field may have been insufficient in our studies and may be insufficient in the ambient environment to produce discernible effects on severity of late blight of potato.

Recent measurements have shown that the pH of rain in the eastern United States varies widely, but values as low as 3.2 are common (4). These levels of acidity are generally considered inadequate to induce significant direct injury to plants (3), but the limited available data suggest that they may influence interactions between plants and their pathogens and alter the epidemiology of plant diseases. Such effects have been shown for both root (8) and shoot diseases (6,9–11).

Presumably, acidic precipitation alters host-parasite relationships by influencing host resistance, pathogen virulence, aggressiveness, or inoculum density. Any of these variables might be altered and interact in such a way as to increase, have no effect on, or decrease the rate of progress of epidemics. Specifically, with late blight of potato (*Solanum tuberosum* L.) our objectives have been to determine the effects of simulated acid rain on disease under field conditions, on sporangial germination, infection efficiency, lesion development, and sporulation capacity of *Phytophthora infestans*. In this paper we report results of these investigations.

MATERIALS AND METHODS

Preparation of simulated rain solutions. Solutions were prepared with deionized water in which background concentrations of ions were added to simulate characteristics of rain in the eastern United States (2). Concentrations of ions in the basal solutions were as follows (μeq/L): Ca^{++}, 21.0; K^+, 2.2; Mg^{++}, 9.8; Na^+, 5.1; NH_4^+, 7.8; Cl^-, 12.0; NO_3^-, 12.0; and SO_4, 22.0. Solutions with this background were used to simulate unpolluted rain (pH 5.6 ± 0.2) or were adjusted with a mixture of $H_2SO_4^{--}$ and HNO_3^- (1N: 60 mol SO_4^{--} : 50 mol NO_3^- to pH 2.8, 3.6, 4.2, or 4.8 for field studies and pH 2.4, 3.0, 3.6, or 4.2 for laboratory and greenhouse studies.

Field studies. A rain simulation and ambient rain exclusion apparatus at a field site located 8 km south of Raleigh, NC, was used in experiments in 1984 and 1985. Motor-driven, corrugated, translucent fiberglass covers permitted exclusion of ambient rain over two 4- × 25-m strips of soil (= two bays). Ten nozzles were mounted 2.3 m above each strip (2.5 m apart) to provide 20 4- × 2.5-m exposure plots. Four plots (two in each bay) were randomly and permanently assigned to each of the simulated rain pH levels. New Fulljet nozzles (316 stainless steel, G 2.8 W, Spraying Systems Co., Wheaton, IL) were installed to ensure median droplet size (by volume) of 1.2 mm and provide a spray diameter of 2 m. Simulated rain solutions were mixed in polypropylene (Nalgene) tanks by recirculation through independent PVC irrigation systems. Plots were treated simultaneously during a simulated rain event.

Soil at the field site consisted of approximately 30 cm of Norfolk loamy sand (fine-loamy siliceous, thermic, Typic Paleudult) placed over approximately 15 cm of Appling sandy loam (clayey, kaolinitic, thermic, Typic Hapludult) in 1980. Soil pH and amendment recommendations were determined for each plot before and after each crop planting based on soil analyses performed by the Agronomic Division of the North Carolina Department of Agriculture.

Tubers of the potato cultivar Kennebec were cut and dusted with the fungicide mancozeb. The prepared seed was allowed to suberize at 13 C in the dark for 5 days before planting. Thirty seed pieces were planted per plot in two rows (51 cm row spacing). Granular fertilizer (10-10-10, 457 kg/ha) was banded at planting in

late March. Plots were sprinkle-irrigated until plant emergence. Subsequently, soaker hoses were used to avoid wetting foliage. Ambient rainfall was excluded after potatoes emerged. Plots were separated by cheesecloth barriers to reduce plot-to-plot inoculum transfer. Insect pests were controlled with two applications of carbaryl and one of methamidophos.

Isolates of *P. infestans* (obtained from Dr. W. E. Fry, Cornell University) were originally obtained from foliage of Russet Burbank potatoes from Langlade County, WI. *P. infestans* was cultured on amended lima bean agar (ALBA) in the dark at 20 C (1). A suspension of 20,000 sporangia per milliliter of isolate 137 of *P. infestans* race 1,5 was prepared by flooding 9-day-old cultures with sterile distilled water. Plants were inoculated by placing a 10-μl droplet of the suspension at vein junctions on the abaxial surface of each leaflet on one leaf/plant. Two inoculated leaves/plot (1984) or one inoculated leaf on each plant in each plot (1985) were sealed in plastic bags overnight. Potato plants were misted several times over a 5–7-day period following inoculation with deionized water until infection was observed.

Rain events were chosen to encourage epidemic develoment. Modifications made in 1985 were chosen to further encourage epidemic development and better detect possible treatment differences. Rain was simulated each Monday, Wednesday, and Friday from 24 May through 16 June 1984 (6 mm in 20 min per event). During 1985, on each Monday and Thursday rain was simulated from 20 May through 20 June; each event lasted a total of 50 min (20 min rain, 10 min pause, 20 min rain) with a total deposition of 10–15 mm. Variation in solution acidity between the mixing tanks and the nozzles never exceeded 0.2 pH units.

For disease assessment, plots were subdivided into six quadrats (25.4 × 40.8 cm). Each quadrat was rated at each disease assessment using the Horsfall-Barrett rating scale. Quadrats were rated two times per week in 1984 and three times per week in 1985. Plant growth stage, canopy height, stand density, and mean number of leaves per stem were monitored throughout the experiments.

Data were analyzed by analysis of variance. Dose-response relationships (pH of simulated rain vs. various dependent variables) were tested by partitioning the pH mean square into single degree-of-freedom orthogonal contrasts for linear, quadratic, and cubic effects.

Greenhouse and laboratory studies. Germination of sporangia. The ability of sporangia of *P. infestans* (isolates 136 race 1,3,4,5 and 137 race 1,5) to germinate in simulated rain solutions was investigated. Sporangia were obtained from ALBA cultures grown in the dark for 10 days at 16 C (1). Sporangia were collected by adding 20 ml of the appropriate simulated rain solution directly to the culture surface and gently rubbing with a rubber policeman to dislodge the sporangia. Concentrations of sporangia were immediately adjusted to 5×10^4 sporangia per milliliter of rain solution. Sporangia suspended in simulated rain solutions (1 ml) were added to small glass vials (9 mm i.d.; 75 mm length) and incubated at 20 C in the dark to favor direct germination. Sporangia were fixed after 1, 3, 8, 24, 32, or 48 hr of incubation by adding two drops of 30% formaldehyde to each vial. Proportions of sporangia that had germinated with a germ tube were determined by counting 200 sporangia per treatment. The experiment was repeated three times for each isolate. Only data for germination after a 24-hr incubation (the time of maximum germination) are reported.

Sporangial suspensions in simulated rain solutions (1 ml) were added to plastic petri dishes and incubated in the dark for 2 hr at 8 C before removal to room temperature (about 22 C) for 30 min to favor indirect germination (zoospore release). Sporangia and zoospores were then transferred to test tubes and agitated vigorously for 3 sec to induce zoospore encystment. Sporangia and zoospores were fixed with formaldehyde as before, and proportions of empty sporangia and ungerminated sporangia were determined. The experiment was repeated three times.

Infection efficiency. Sporangia of *P. infestans* (isolate 137, race 1,5) in simulated acid rain solutions were evaluated for the ability to infect potato leaflets. Kennebec potato plants were obtained by planting tuber pieces with three to five buds per piece into a steamed loam, sand, and perlite mixture (4:2:1, by volume) in 15-cm-diameter clay pots (one seed piece per pot). Pots were incubated in a greenhouse at 23–30 C, and emerging plants were fertilized with 100 ml of a liquid fertilizer. Dry fertilizer formulation was 20-20-20 (N, P, and K) with 5.6% nitrate, 3.96% ammoniacal, and 10.43% urea nitrogen. Plants were used for infection efficiency experiments when sufficient expanded leaf tissue was available (about 3 wk).

Sporangia were obtained as before, and concentrations were adjusted to 5×10^4 sporangia per milliliter of each rain solution at pH 2.4, 3.0, 3.6, 4.2, or 5.6. Sporangia were kept in an ice bath to prevent germination before inoculation. Inoculations were completed generally within 1 hr after sporangia were added to rain solutions. Plants were inoculated by placing 20-μl droplets of sporangial suspensions on the abaxial surface of terminal potato leaflets (one droplet per leaflet). Plants were inoculated with 10–15 inoculation sites per plant. Four plants were inoculated for each pH treatment. Plants were placed randomly in a growth chamber at 21 C immediately after inoculation. In some experiments, relative humidity was raised immediately to 100% by cool-vapor humidifiers with deionized water. In other experiments, the humidification was delayed for 4, 8, or 16 hr following inoculation to account for possible dilution of the simulated rain drops by humidification with deionized water. Proportions of inoculated leaflets that developed lesions were determined 5 days following inoculation.

A separate experiment was performed in the greenhouse to determine possible differences in lesion size and sporulation when infections resulted from inoculum borne in simulated rain solutions of different acidities. Inoculation protocols were as before. Inoculated plants were incubated in a chamber in the greenhouse (temperature 18–22 C) with humidification with deionized water commencing 4 hr after inoculation. Plants were removed from the mist chamber 18 hr after inoculation and arranged randomly on a greenhouse bench. Lesions developed on these plants and were counted 4 days after inoculation. Five leaflets bearing lesions were removed from each plant, and, to induce sporulation, each leaflet was placed (abaxial side up) in a plastic petri dish with 1 ml of deionized water and incubated at 20 C in the dark for 18 hr. A portion of each lesion with the most abundant sporulation was cut from each lesion with a cork borer (12 mm i.d.) and suspended in 2 ml of deionized water in test tubes. Lesion pieces were agitated vigorously for 10 sec by vortexing to dislodge sporangia, and five drops of 30% formaldehyde were added to fix sporangia for counting. Sporangia were counted with the aid of a hemacytometer, and numbers were converted to sporangia per centimeter of leaf tissue.

Lesion expansion and sporulation. An application apparatus for simulated rain was constructed in a greenhouse for use in these experiments. In the apparatus, rain solutions of pH 3.0, 4.2, and 5.6 were mixed and held in 75-L polyethylene tanks. Rain solutions were prepared as before. Solutions in two tanks were adjusted to pH 3.0 or 4.2 with a stock solution of acids as described previously. Solutions from a single tank were delivered to two stainless steel nozzles (Fulljet G 2.8 W, Spraying Systems Co., Wheaton, IL; median volume diameter 1,160 μm). Nozzles were suspended 122 cm above platforms on which plants were placed. Platforms were mounted on casters to allow manual rotation to provide more even coverage of plants with rain solutions. Platforms were rotated clockwise 90° every 5 min during rain applications. Solutions were delivered to nozzles with Jabsco model 12290 selfpriming pumps with neoprene impellers. Excess solutions were constantly circulated as simulated rain solutions were delivered to the nozzles. Solutions were delivered through 2.54-cm PVC pipes with PVC gate valves to allow interruption of solution delivery as desired and, hence, allow critical timing of exposure to plants. Solutions were shunted from PVC pipes into 6.4-mm tubing with nylon connectors. Pressures at nozzle height were measured with glycerin-filled pressure gauges.

Potato plants were inoculated in a greenhouse chamber with humidification using deionized water as before, with at least 10

inoculation sites per plant. After incubation in the mist chamber overnight, plants were placed on the simulator platforms (three plants per platform). Plants were immediately exposed to the first of five simulated rain events. A total of 2 cm of rain per day was applied for 5 days measured with beakers placed among the plants on the platforms. Five leaves bearing lesions per plant were tagged and subsequently measured each day. Lesion areas were calculated as $\pi/4 \times$ length $\times$ width. After the final exposure, wetted leaflets were removed, placed abaxial side up in plastic petri dishes, and incubated at 20 C in the dark to induce sporulation. Sporangia were quantified as before and counts converted to numbers of sporangia per square centimeter of leaf tissue. Lesion area was converted to net increase in lesion area by the following formula: Net increase in lesion area per day (lesion area on day 5 − lesion area on day 3)/2 days. This experiment was performed in two runs in a partially nested randomized block design with three plants per platform, two platforms per pH level (= blocks), and three pH levels. Data were combined over runs.

RESULTS

Field studies. Treatment acidity did not have a significant effect on rate of disease progress in 1984 (Table 1). Disease assessment data were variable (Fig. 1), possibly due in part to error between the two evaluators in 1984. However, the most rapid and greatest amount of disease development was associated with pH 4.2 treatments (Fig. 1). Final treatment ranking in order of decreasing amount of disease was pH 4.2, 3.6, 5.6, 4.8, and 2.8.

Disease assessment data for 1985 were more consistent because

TABLE 1. Analysis of variance for disease severity of potato late blight evaluated two or three times per week on the cultivar Kennebec with five pH levels of simulated rain applied three or two times per week in 1984 and 1985, respectively, at pH 2.8, 3.6, 4.2, 4.8, or 5.6 in an ambient rain exclusion apparatus in the field

Source	Degrees of freedom	Mean square	F-value	Probability of greater F
		1984		
Bay	1	3.24	···	
pH[w]	4	107.29	0.58	0.690
Bay * pH[x]	4	183.53	5.21	0.018
Replicate (Bay * pH)	10	35.22	···	
Time[y]	11	143.58	80.66	0.001
Bay * Time	11	1.78	···	
pH * Time[z]	43	13.85	0.64	0.932
Bay * pH * Time	43	21.95	···	
Corrected total	239			
		1985		
Bay	1	6.55	···	
pH[w]	4	48.09	9.90	0.024
linear[w]	1	8.33	1.71	0.427
quadratic[w]	1	48.43	9.97	0.037
cubic[w]	1	99.94	20.56	0.011
Bay * pH	4	4.86	0.19	0.966
Replicate (Bay * pH)	10	25.21	···	
Time[y]	14	244.26	38.17	0.001
Bay * Time	14	6.40	···	
pH * Time	56	3.04	1.51	0.061
Bay * pH * Time	56	2.01	···	
Corrected total	299			

[w] Test of hypothesis that acidity of simulated rain did not affect disease severity using the ANOVA MS for Bay * pH as an error term; linear, quadratic, and cubic sums of squares were calculated by regression analysis when a significant F-value for pH effect was present.

[x] Test of hypothesis that bay and pH effects did not interact using the ANOVA MS for Replicate (Bay * pH) as an error term.

[y] Test of hypothesis that disease severity did not vary over time using the ANOVA MS for Bay * Time as an error term.

[z] Test of hypothesis that pH and time did not interact using the ANOVA MS for Bay * pH * Time as an error term.

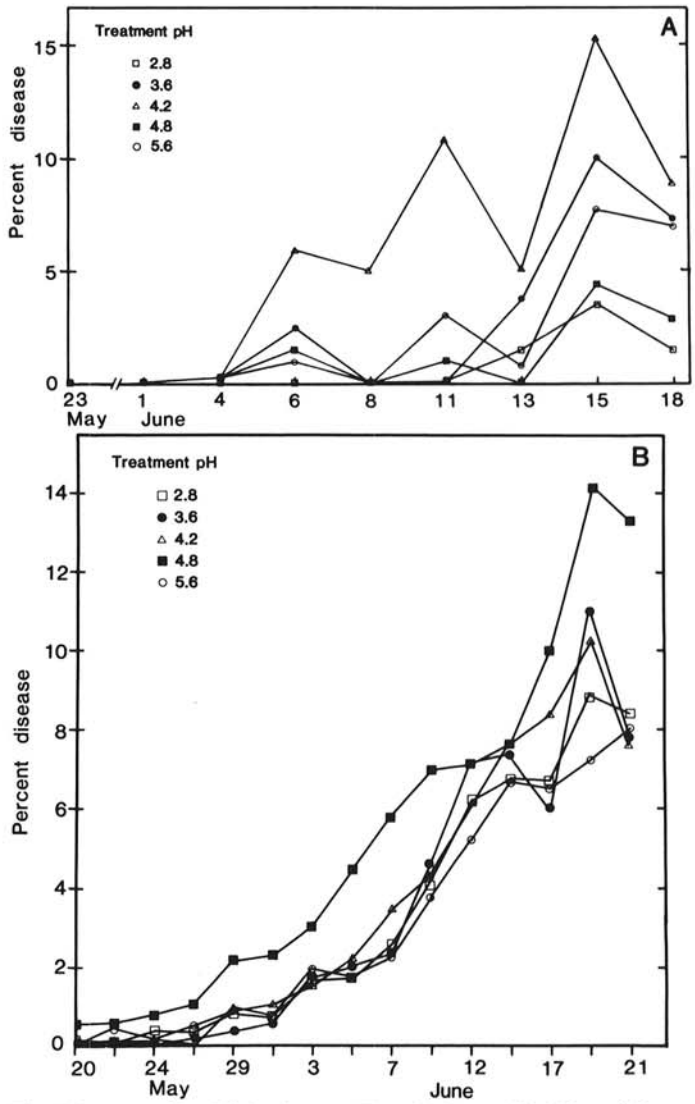

Fig. 1. Progress of late blight of potato 'Kennebec' caused by *Phytophthora infestans* (race 1,5) in field experiments (ambient rain excluded) with simulated rain treatments at pH 2.8, 3.6, 4.2, 4.8, or 5.6. **A,** 1984, three rain events per week. **B,** 1985, two rain events per week.

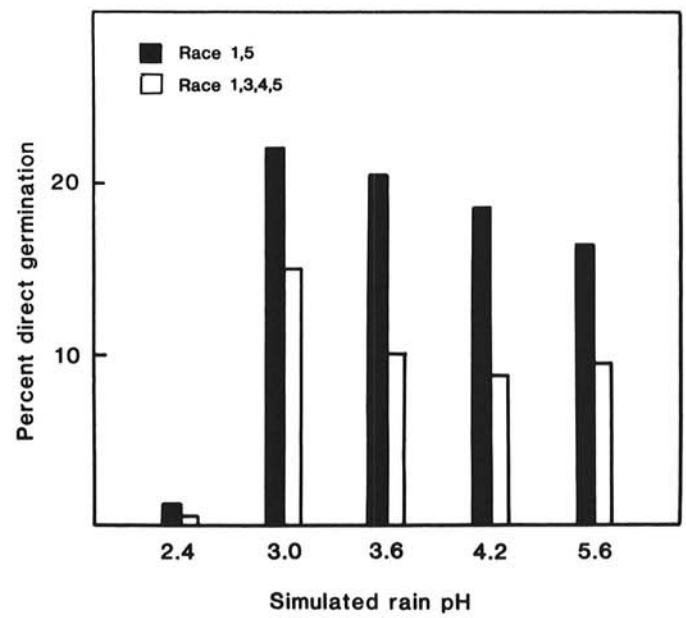

Fig. 2. Influence of acid rain solutions on direct germination of sporangia of *Phytophthora infestans*. Bars represent means of three experiments, with 200 sporangia counted per experiment at each treatment level.

only one evaluator assessed disease severity. Treatment pH significantly affected disease progress (Table 1). Disease severity was consistently greatest when plots were treated with rain of pH 4.8 and was usually least severe when treated with pH 5.6 rain (Fig. 1B). The dose-response relationship was curvilinear, with significant quadratic ($p = 0.04$) and cubic effects of pH ($p = 0.01$). There was also a significant interaction of pH and time, which may have been due to variation in disease severity in the pH 3.6 treatment and the change in ranking of treatments over the last three assessments (Fig. 1B).

Greenhouse and laboratory studies. Sporangial germination. The percentage of sporangia that germinated directly for both isolates of *P. infestans* was relatively low and ranged from 1 to 21% (Fig. 2). Incubation of sporangia in the most acidic simulated rain solutions (pH 2.4) almost completely inhibited direct germination (Fig. 2). Maximum direct germination occurred for both isolates at pH 3.0, with a slight decline at higher (less acid) pH values. The magnitude of direct germination differed between the two isolates, with race 1,5 showing the greater percentage of germination over the range of treatments.

Indirect germination also varied with the initial acidity of rain solutions. Indirect germination was almost completely inhibited at pH 2.4 for both isolates (Fig. 3). Maximum indirect germination was observed at pH 5.6 for the race 1,5 isolate but was observed at pH 3.6 for the race 1,3,4,5 isolate. Effects of acidity on indirect germination were significant for both races and were described by second-order polynomials, indicating a curvilinear effect of pH on germination. Equations describing indirect germination were: Percent indirect germination for race 1,5 $= -141.7 + 82.8\,\text{pH} - 8.4\,\text{pH}^2$; percent indirect germination for race 1,3,4,5 $= -182.8 + 108.3\,\text{pH} - 12.1\,\text{pH}^2$. In all cases, residual plots appeared to have a random scatter of points.

Infection efficiency. Infection efficiency was affected by acidity of the solution containing sporangia of *P. infestans* race 1,5. Effects were significant only when misting with deionized water was delayed for 8 or 16 hr following inoculation (Fig. 4). If misting commenced immediately or 4 hr after inoculation, infection efficiency varied from 25 to 45%, with no significant difference among the treatments. If misting was delayed for 8 or 16 hr after inoculation, infection was not observed at initial pH values of 2.4 or 3.0, but a low level of infection occurred at pH 3.6, 4.2, or 5.6 (Fig. 4).

Because it appeared that there was a possible threshold level of pH on infection efficiency when misting was delayed 8 or 16 hr, an additional experiment was conducted. Simulated rain solutions were prepared at pH 3.0, 3.1, 3.2, 3.3, 3.4, 3.5, and 3.6. Potato plants were inoculated with sporangia (5×10^4) in these solutions as before, with 15 inoculation sites/plant and four plants per pH treatment. Misting with deionized water was delayed for 8 hr following inoculation. Results of this experiment indicated that infection was eliminated if sporangia were borne in solutions of pH 3.0 or 3.1, but at higher pH values (3.2–3.6), there was a low incidence of infection, similar to previous experiments (Fig. 5).

Effects of inoculum in simulated rain solutions on lesion size and sporulation. Infection efficiency varied from 20 to 100% throughout the range of pH treatments, with infection occurring at all pH levels, as expected with the initiation of misting at 4 hr postinoculation. There were no significant effects of initial solution pH on infection efficiency, final lesion size, or sporulation.

Effects of simulated rain on lesion expansion and sporulation. Lesions were noted 3 days following inoculation, with sizes of approximately 0.04 cm^2 each. Lesions increased in size thereafter,

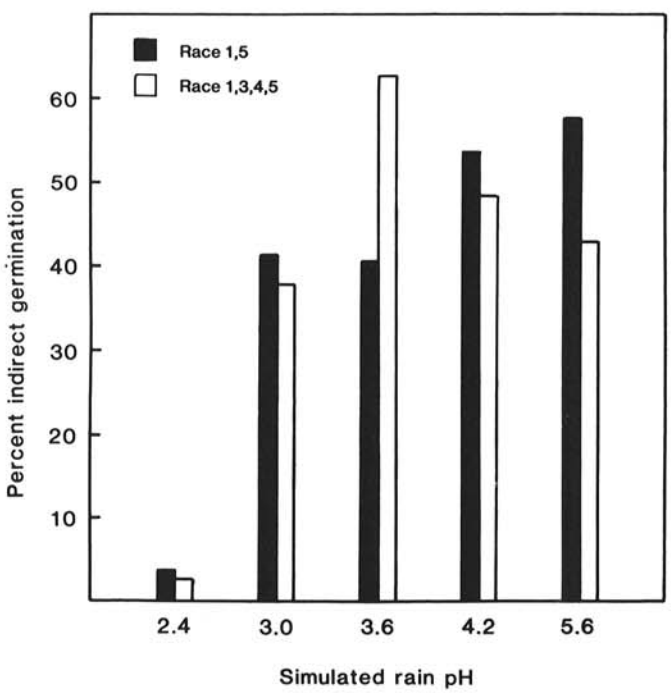

Fig. 3. Influence of acidity of rain solutions on indirect germination of sporangia of *Phytophthora infestans*. Bars represent means of three experiments with 200 sporangia counted per experiment at each treatment level.

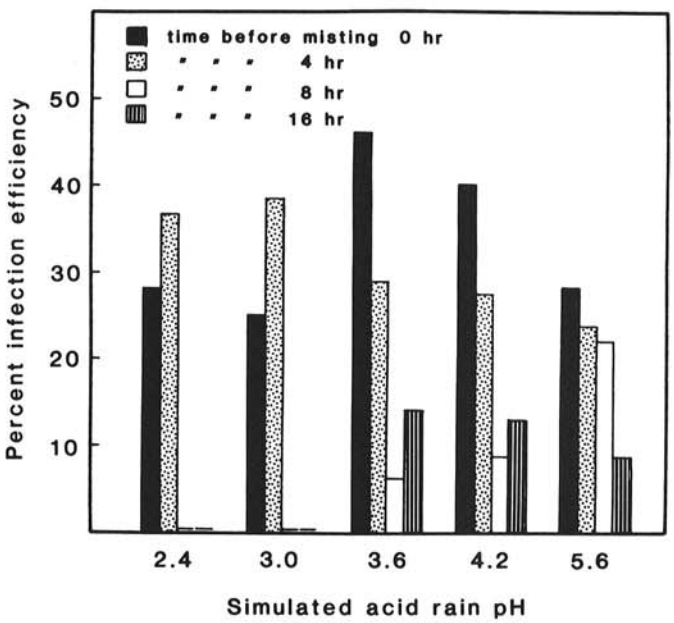

Fig. 4. Influence of acidity of rain solutions bearing inoculum of *Phytophthora infestans* (race 1,5), on infection efficiency in a controlled temperature cabinet (20 C, 70–80% RH). Bars represent mean percent successful inoculations, with 10–15 inoculation sites per plant and four replicate plants per treatment. Experiments were conducted with variable delay (0, 4, 8, or 16 hr) before commencement of incubation at 100% RH.

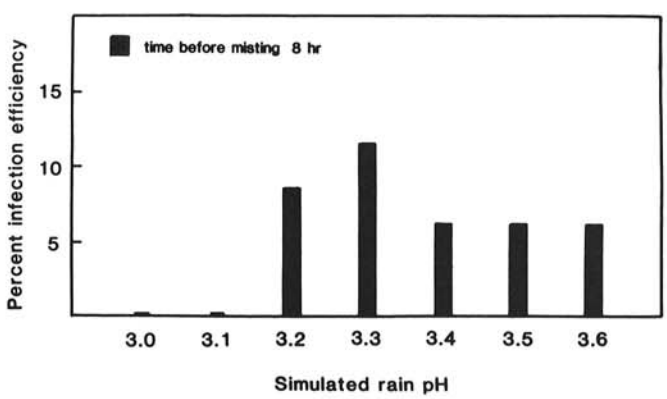

Fig. 5. Infection efficiency indicating the pH threshold for *Phytophthora infestans* (race 1,5) sporangia borne in simulated rain solutions. Bars represent mean percent successful inoculations with 15 inoculation sites per plant and four replicate plants per treatment.

at rates of approximately 140 mm^2 per day. No significant differences occurred among the final sizes of lesions under the influence of simulated rain treatments of different acidities, nor were significant differences in the rate of lesion development associated with the acidity of simulated rain. A significant difference was observed in final sporulation of lesions, where lesions under the influence of simulated rain at pH 3.0 sporulated significantly less than lesions under simulated rain at pH 4.2 or 5.6 (Table 2).

DISCUSSION

Results of our field experiments indicated a possible effect of rainfall acidity on disease progress of late blight of potato. Our results were quite variable in 1984 and were not statistically significant. In 1985, a significant effect of rainfall acidity was detected, with maximum disease severity associated with the pH level of 4.8. There was also a trend in 1984 with maximum disease severity associated with pH 4.2 level.

The results of our field studies were not fully explained by laboratory and greenhouse studies. In attempting to determine direct effects of simulated rain acidity on *P. infestans*, we found that both direct and indirect germination of sporangia were affected. These effects were marked only at the extreme acidity level of pH 2.4. It was noteworthy that neither mode of germination was eliminated at this extreme acidity for either isolate of the fungus. The effect of extremely low pH rainfall might be expected to delay onset or reduce the rate of disease development by adversely affecting germination of sporangia. However, slight acidity (pH 3.5–5.6) would not apparently affect sporangium germination significantly. These results on germination are similar to other studies that have indicated reduced germination of *Phytophthora* spp. at very high levels of acidity (8,10). Implications of this effect for acid deposition were illustrated by Shafer et al (8). They showed a reduction in sporangial formation and zoospore infectivity in soils exposed to simulated acid rain of high acidity.

Our studies on infection efficiency of sporangia in acidic solutions indicated that infection did not occur when sporangia were carried in solutions more acidic than pH 3.2 and humidification was delayed at least 8 hr postinoculation. Direct germination was not inhibited in droplets at pH 3.0, and indirect germination was only slightly inhibited at this acidity level. Therefore, degree of germination per se was probably not the reason for lack of infection by inoculum in solutions of pH 2.4, 3.0, or 3.1. A possible explanation could be an alteration of sporangial death rates by the acid treatments. Normally, sporangial death rate is unaffected by humidity except at high temperatures (5,7). Our experiments were conducted at 21 C, with relative humidity variation between 70 and 80% before deliberate humidification to 100% RH. According to Minogue and Fry (5), the half-life of sporangia exposed to these conditions should be about 6 hr. By extrapolation, in our experiments, sufficient inoculum should survive 8 hr at 70–80% to induce infection. Perhaps inoculum borne in solutions of low pH exhibited accelerated rates of death. Similarly, inoculum potential of sporangial germ tubes on zoospore might have been adversely altered by the low pH solutions.

Failure of simulated acid rain to significantly affect lesion expansion indicated that acid rain would be unlikely to alter disease severity if infection occurred under circumstances that maximize inoculum efficiency. However, sporulation was reduced when lesions were exposed to simulated rain of pH 3.2 in the greenhouse simulator, so the rate of disease progress could be reduced due to suppressed production of secondary inoculum under these conditions. The combination of a lowered sporulation capacity of lesions under extremely acid conditions and possible direct mortality of sporangia or reduced ability of sporangia to withstand brief periods of low relative humidity at moderate low pH would be expected to reduce the rate of disease progress in the field. These effects would probably be discernible only if rain events were consistently of relatively high acidity (pH 3.2 or below) and of sufficient frequency or duration to maintain a nearly continuous exposure of lesions and sporangia to the high level of acidity in moisture on the leaves.

In the field studies, disease severity in plots exposed to simulated rain at pH 2.8 was consistently among the lowest disease levels encountered but was not significantly different for that obtained in other treatments. This inconsistency between significant effects of low pH on germination and sporulation in the laboratory and the lack of a measurable reduction in the field may indicate that the frequency or duration of rainfall events during field studies were insufficient to produce the response observed in the laboratory. The total time diseased plants were exposed to direct application of simulated rain each week was relatively short (20 min per event, three times per week in 1984 and 50 min per event two times per week in 1985). Although frequency and duration of simulated rainfall events were not unrealistic for our area, it is possible that the progress of potato late blight in fields may sometimes be limited by longer periods of leaf wetness due to strongly acidic rain.

Another possible explanation for the absence of a significant effect in the field at low pH levels of simulated rain may be that abaxial leaf surfaces were simply not wetted thoroughly and that lesions coalesced to sporulate uniformly across treatments. We intentionally applied our rain events under calm conditions to prevent the blowing of simulated rain from one plot into the next. Thus, upper leaf surfaces were wetted, whereas lower leaf surfaces may have been left nearly dry. During actual ambient rainfall conditions, wind movement of foliage would result in a more uniform wetting of the entire foliage and highly acidic rain could then affect pathogen sporulation and infection efficiency. Under the conditions of our experiments, normal sporulation could continue to occur at high humidity on lower leaf surfaces. Also, dew deposited on leaf surfaces at night could be at a pH level high enough to allow normal germination and infection, particularly on lower leaf surfaces.

The results of our studies indicate that strongly acid rain could potentially reduce disease due to *P. infestans* on potato when the exposure is of sufficient duration. Rainfall events, however, are not usually of a constant, low pH (4), so the conditions required to reduce severity of late blight probably will be met rarely.

TABLE 2. Influence of simulated acid rain applied through a greenhouse simulator on lesion area, rate of lesion expansion, and sporulation capacity[y] of *Phytophthora infestans* on potato

Simulated rain pH	Lesion area[z] (mm^2)	Lesion rate (mm^2/day)	Sporangia/cm^2
3.0	2.90 a	1.45 a	23,909 a
4.2	2.59 a	1.30 a	34,311 b
5.6	2.59 a	1.30 a	34,406 b

[y] All values are means of five lesions per plant, three plants per pH level, and two runs of the experiment. The experiment was analyzed as a partially nested randomized block design. Means followed by different letters within a column are significantly different ($P = 0.05$).

[z] Final lesion area measured 5 days after inoculation.

LITERATURE CITED

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