# Effect of Soil Temperature on the Field Infection of Potato Tubers by *Phytophthora infestans*

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## ABSTRACT

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Weather data were analyzed to determine conditions that favor field infection of potato tubers by *P. infestans* in soil. Soil temperature during and immediately after rain affected the frequency of tuber rot more than did the amount of rain. Tuber infection was high in wet, cool soil but low in wet, warm soil. Tuber infection was markedly decreased in soils with temperatures above 18 C. Cool water (below 17 C) favored indirect germination of sporangia and prolonged the swimming of zoospores but warm water (above 20 C) did not. Tuber infection depended on the release and motility of zoospores. A soil temperature of 18 C or below appeared to be necessary for tuber infection.

Infection of potato tubers by *Phytophthora infestans* (Mont.) de By. is caused by spores produced in foliage lesions. Sporangia or zoospores come into contact with the tubers in two main ways: at harvest, freshly lifted and wounded tubers come into contact with infected haulms and contaminated soil (11); or in natural infection during crop growth, spores carried into the soil by rain come into contact with the tubers (6,9). Therefore, a simple relationship between rainfall, inoculum concentration, and the amount of tuber rot might be expected. In practice, however, much tuber infection may follow comparatively small amounts of rain when foliage lesions are few (9). Conversely, little or no tuber infection may occur even when there is much rain and abundant foliage lesions. Hirst et al (5) and Lapwood (9) found that at least 5 mm of continuous rain was needed for tubers to become infected, but that infection was particularly prevalent when intense sporulation coincided with at least 12 mm of rain on two or more days. Grainger (4) found a significant relationship between rainfall in September and the number of blighted tubers at harvest. Berkeley (1) recorded the amount of rainfall in London for August and September 1845, as 71 and 45 mm, respectively, when the famous potato "murrain" or famine occurred in Europe. Ready penetration of spores through soil during rain was observed in the field by Lacey (8). In the northern temperate countries a comparatively small amount of rain may result in severe tuber infection. By contrast, in the southern region of Japan, potato crops receive much rain during blight epidemics every year, but tuber blight in soil is uncommon. At Hokkaido in northern Japan, heavy rain sometimes cause severe tuber infection. These apparent contradictions have been observed both seasonally and regionally; this paper reports the results of research designed to investigate these conflicting observations.

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## MATERIALS AND METHODS

**Seasonal differences.** During 10 seasons from 1966 to 1975, plants of the early potato (*Solanum tuberosum* L.) cultivar, Irish Cobbler, were grown on a high-humus clay loam soil at the Hokkaido National Agricultural Experiment Station, which is located in the northern part of Japan (~43° N latitude). Potatoes planted in mid-May flowered in early July, usually were attacked by *P. infestans* in late July or early August, and were dead by late August from late blight and senescence. In 1973 and 1974 the weather was unusually dry, and the haulms were dead by early August. Potatoes in six seasons (1966–1970 and 1975) were exposed to heavy rains that ranged 36–153mm/day when the incidence of disease (3) was >0.80 and the number of active foliage lesions were perhaps 10–20 per plant. In 1971, potatoes were sprayed with mancozeb three times by 8 August, and 1972 eight times by 6 September to delay the blight epidemic until soil temperature decreased and the rains were cooler. The sprayed potatoes were exposed to heavy rains when the incidence of disease was <0.01 and the number of active lesions were few. Twenty to 60 hills were dug weekly and the tubers were checked for blight lesions. Weather data were supplied by the nearest meteorological laboratory.

**Regional differences.** Rothamsted Experiment Station, England (~52° N latitude), was selected to represent regions with climatic conditions that favor tuber blight in soil. For several years Lapwood (9) studied the relationship between rain and tuber infection in soil with the cultivar Up-to-Date. He observed severe tuber infection after comparatively small amounts of rain and in the presence of comparatively few foliage lesions. Oberservations compiled by Lapwood (9) on the progess of epidemics and on the occasions when tuber infection occurred on cultivar Up-to-Date were used (with his permission) along with weather information supplied by J. Lacey (*unpublished*) for analysis of the effect of soil temperature on tuber blight.

A field at the Aino Potato Branch of the Nagasaki Agricultural and Forest Experiment Station in the southern part of Japan (~32° N latitude) was selected to represent regions unfavorable for tuber infection. At that location tuber blight from natural infection in soil is rare despite large amounts of rain and abundant foliage lesions. Eight seasons of observations on the progress of late blight

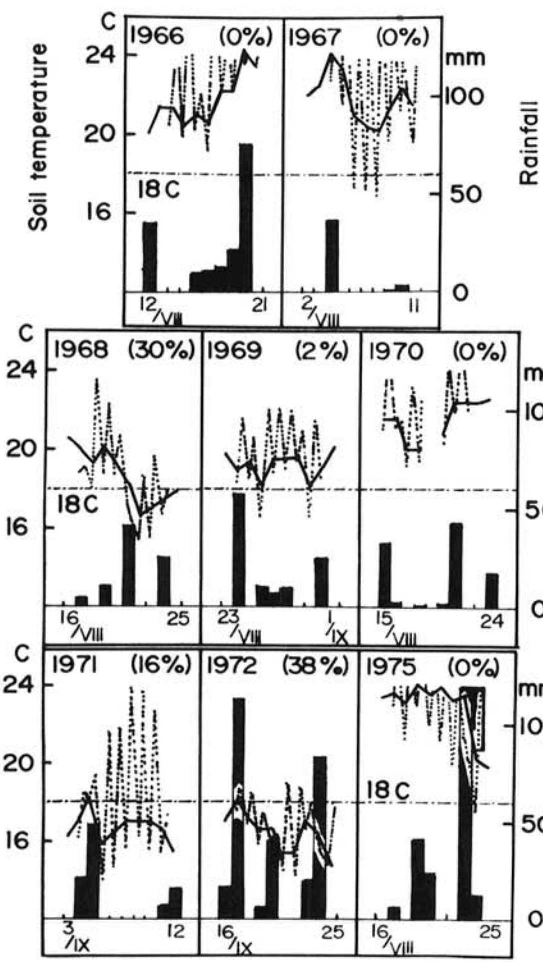


**Fig. 1.** Effect of rainfall and soil temperature on potato tuber infection by *Phytophthora infestans* in the fields at Hokkaido National Agricultural Experiment Station in Japan. Foliage lesions were few (about 10–20 per plant) during the rainy days in all those seasons. The bars indicate rainfall, the solid lines soil temperatures 10 cm below the surface at 0900 hours, and the dotted lines temperatures 5 cm below the surface at 0600 hours and 1500 hours at the meteorological observation station nearest the potato fields. The percentages in parentheses represent the amounts of tuber blight attributable to these 10-day periods.

epidemics on potato cultivar Tachibana and correlated weather information (*unpublished*) supplied by S. Sakaguchi (Nagasaki Agric. and For. Exp. Stn., Isahaya-shi, Nagaski Prefecture, Japan) were used (with his permission) for the analysis.

**Germination of sporangia.** A single-zoospore isolate of *P. infestans*, race 0, was grown routinely at 18–20 C on fresh Irish Cobbler tuber slices. Sporangia were harvested from the surface mycelium in warm tap water (22–24 C), centrifuged (1,000 rpm, 1 min), and resuspended in tap water ($1–4 \times 10^4$ sporangia per milliliter). Aliquots (10 ml) of suspensions in 50-ml Erlenmeyer flasks were incubated at different temperatures without agitation except for a short period of agitation at sampling in controlled temperature (±0.2 C) water baths. About 0.5 ml of suspension was withdrawn from the flasks after 20 min, 1, 2, 4, 6, and 30 hr of incubation and immediately after sampling one drop of 10% formalin was added to stop further germination. The proportion of sporangia (~400 observed with a microscope) that had released their zoospores was estimated.

**Zoospore swimming time.** Suspensions of sporangia were kept at 10 C for 1 hr to stimulate zoospore release. The zoospores were siphoned off and the suspension was centrifuged (1,000 rpm, 2–3 min, three times) to eliminate sporangia. The suspensions (10 ml, containing $1–3 \times 10^4$ zoospores per milliliter) in 50-ml Erlenmeyer flasks were incubated without agitation except for a short period of agitation at sampling in water baths at different temperatures. About 0.5 ml of suspension was withdrawn hourly and one drop of 10% formalin was added. The formalin caused motile zoospores with naked protoplasm to burst and form spheroid, cloudlike structures, but the encysted zoospores remained intact. Thus, the number of zoospores (of ~400 observed with a microscope) that had disrupted was estimated.

## RESULTS AND DISCUSSION

**Seasonal differences.** Field observation data from the eight seasons in which heavy rains occurred during blight epidemics were analyzed. Weather conditions (viz, rainfall and soil temperatures) during a 10-day period around days with heavy rain are correlated with the percent tuber blight (Fig. 1). In 1966–1970 and in 1975, the

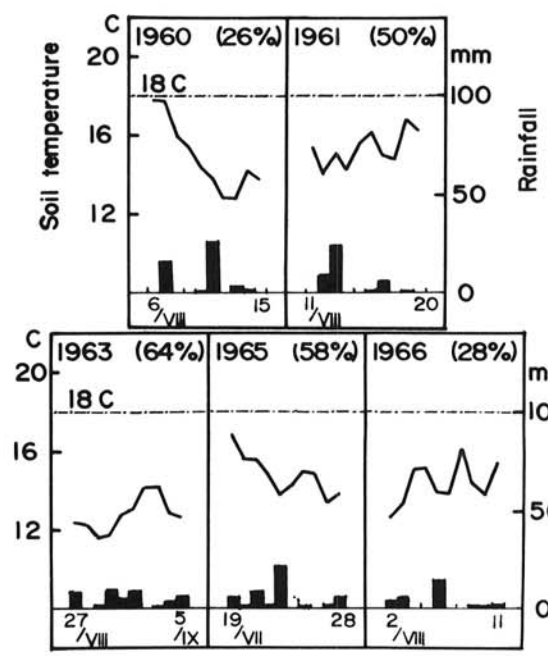


**Fig. 2.** Effect of rainfall and soil temperature on potato tuber infection by *Phytophthora infestans* in the fields at the Rothamsted Experiment Station. Data on periods and amounts of tuber infection on plants of cultivar Up-to-Date compiled by Lapwood (9) were used for the analysis. Foliage lesions were ~20 per plant. The bars indicate rainfall, the lines soil temperature 10 cm below the surface at 0900 hours, and the percentages in the parentheses the amounts of tuber blight.

blight epidemics were near the final stage, with few active foliage lesions. In 1971 and 1972, potatoes that had been sprayed with fungicide were exposed to heavy rains in early and late September, respectively, when the incidence of disease was $<0.01$ and foliage lesions again were comparatively few. Blight lesions began to appear on tubers a few days after heavy rains and increased rapidly for about 10–14 days. Lesions starting at the eyes were seen first as short slender brown branching threads that develop into 1–2 cm diameter rotted spots in about 1 wk. The tuber infections that developed during the 2 wk after heavy rains were attributed to those rains. Tuber blight was severe in 1968, 1971, and 1972 (30, 16, and 38% of tubers infected, respectively); slight in 1969 (~2%); and rare or absent in the other four seasons. As described, comparatively few foliage lesions (~10–20 lesions per plant) developed in all eight seasons. No strong correlation was observed between amount of tuber infection and the numbers of foliage lesions. It was surprising that inoculum from comparatively few foliage lesions per plant could cause so much tuber infection even when the weather conditions were very favorable. As shown in Fig. 1, a comparatively small amount of rain caused severe tuber infection in 1968 and 1971, but in 1966 and 1975, comparatively large amounts of rain resulted in little tuber infection. Thus, even though rainfall is required, another factor must affect tuber infection. Water temperature markedly affects the indirect germination of sporangia and zoospore swimming time (2), which in turn seems to affect tuber infection. Therefore, soil temperature was included in the analysis of the weather conditions. The weather conditions that resulted in much tuber infection were as follows: In 1968, soil temperatures 5 and 10 cm below the surface after 44 mm of rain on August 21–22 fell from around 18 C before the rain to 14.5 and 16.5 C, respectively, after the rain. In 1971, soil temperatures around 18 C were maintained during the 70.5 mm of rain on 4 and 5 September, but by the next morning the soil was still saturated and temperatures at 5 and 10 cm had decreased to 14.0 and 15.8 C, respectively. In 1972, soil temperatures around 18 C during the first half of the 104.5 mm of rain on September 23 and 24 fell sharply and soil temperatures at 5 and 10 cm had dropped to 14.0 and 15.0 C, respectively. Little tuber infection occurred in 1969 when soil temperatures decreased to around 18 C for a short time during a comparatively light rainfall. Little or no tuber infection occurred in 1966, 1967, 1970, and 1975, when the soil temperatures remained above 20 C. Thus, a strong correlation was found

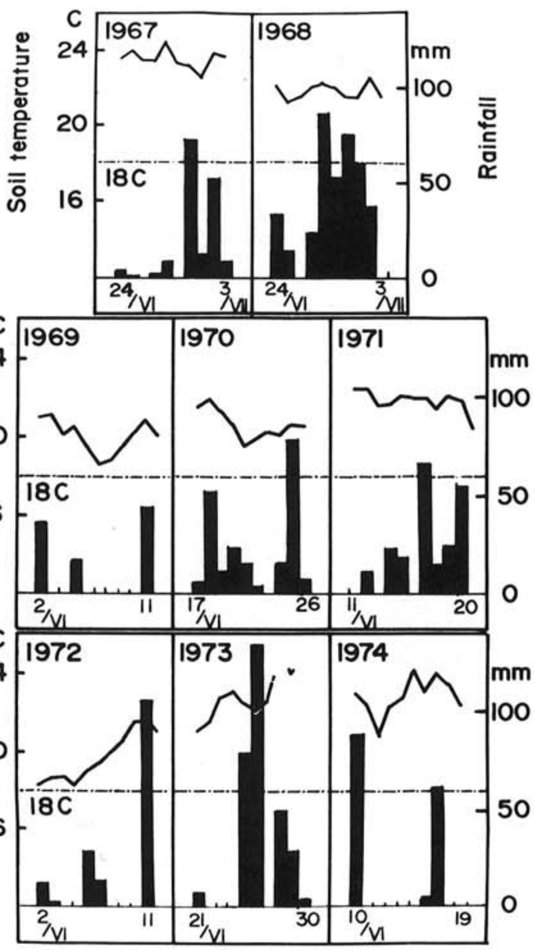


**Fig. 3.** Effect of rainfall and soil temperature on potato tuber infection by *Phytophthora infestans* in the fields at the Aino Potato Branch of the Nagasaki Agricultural and Forest Experiment Station, Nagasaki, Japan. Data on the progress of blight epidemics on plants of cultivar Tachibana compiled by S. Sakaguchi (*unpublished*, Nagasaki Agric. and For. Exp. Stn., Isahaya-shi, Nagasaki Prefecture, Japan) were used for the analysis. Foliage lesions were abundant (approximately 100 or more per plant) during the rainy days. Tuber blight was slight or absent despsite the conditions. The bars indicate rainfall, the lines soil temperature 10 cm below the surface at 0900 hours.

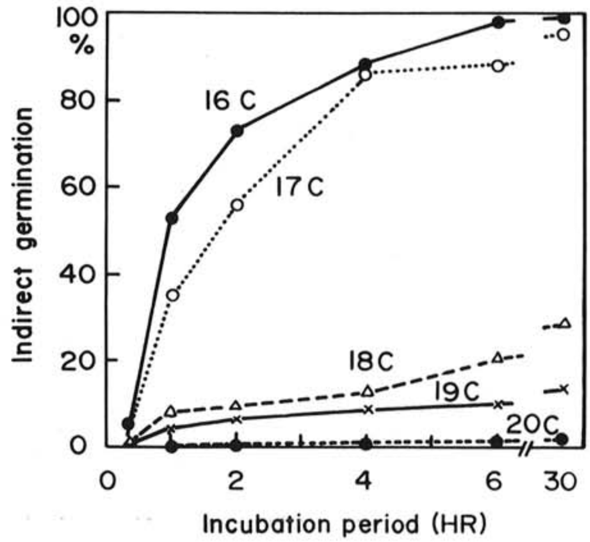


**Fig. 4.** Effect of water temperature on indirect germination of sporangia of *Phytophthora infestans*. Data presented are for one of the time-course experiments.

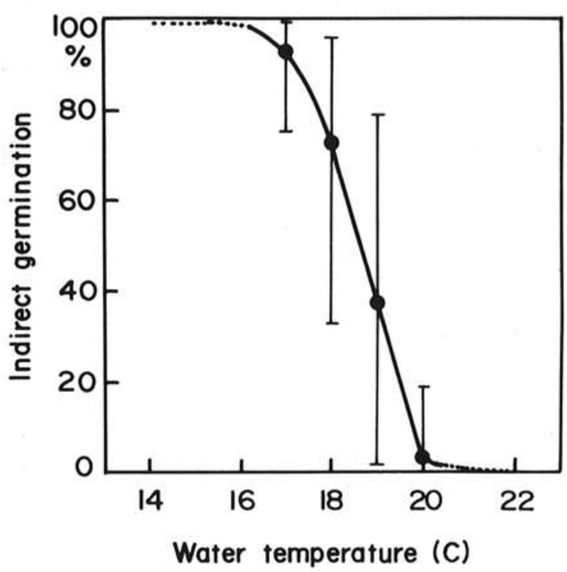


**Fig. 5.** Effect of water temperature on indirect germination of sporangia of *Phytophthora infestans*. Sporangia suspensions were incubated without agitation for 6 hr. Data points represent the mean rate for indirect germination from 24 experiments and the vertical lines the range of the rates.

between the amount of tuber infection and soil temperature during and immediately after rainfall.

**Regional differences.** Data on periods of rain and the amounts of tuber infection of five seasons investigated by Lapwood (9) at the Rothamsted Experiment Station with supplementary weather information supplied by J. Lacey, are presented in Fig. 2. Rains fell when all the epidemics were at an early stage and the foliage lesions were comparatively few. The amount of rain was comparatively small, 26 mm/day at most. Severe tuber infection was initiated during the rainy days even when rainfall was as little as 10 mm/day. Soil temperatures 10 cm below the surface, on the morning after much rain were always cool (~12–14 C). A few foliage lesions and as little as 10 mm of rain per day were enough to promote severe tuber infection even when soil temperatures were as low as 12–14 C. These temperatures are favorable for the indirect germination of sporangia and prolonged zoospore motility.

The progress of blight epidemics on plants of cultivar Tachibana was recorded for several seasons by Sakaguchi (*unpublished*) at Aino, in the southern part of Japan, although little or no tuber rot from natural infection in soil was found. Data on weather conditions for 10 days when the incidence of disease was 0.2–0.8 and foliage lesions were abundant (~100 or more per plant) are presented in Fig. 3. In spite of heavy rains (28–135 mm/day) and abundant foliage lesions, tuber rot was light or absent. Soil temperature 10 cm below the surface on the morning after rain always was warm (~19–24 C). Under these conditions even hundreds of foliage lesions and frequent heavy rains exceeding 50 mm a day did not result in tuber infection if soil temperature was higher than 20 C, which is unfavorable for indirect germination and zoospore motility. Tuber infection occurred when conditions were favorable for indirect sporangial germination and zoospore motility. Therefore, indirect germination of sporangia and zoospore swimming time were investigated in some detail.

**Indirect germination of sporangia.** Many time-course experiments were done to investigate the amount of indirect germination of sporangia at several temperatures; a representative result is shown in Fig. 4. Maximum germination at each temperature was reached after about 6 hr of incubation. Temperatures below 17 C always favored indirect germination, but temperatures above 20 C did not. Erratic results at temperatures of 18 and 19 C required that those temperatures be investigated further. Suspensions of sporangia were incubated at 17, 18, 19, and 20 C for 6 hr, and experiments were repeated 24 times. The results are shown in Fig. 5. Germination at 17 C averaged 92.9 ± 1.0% (range, 75.5–98.5%); at 18 C, 72.9 ± 4.0% (range, 33.1–96.0%); at 19 C, 39.4 ± 4.9% (range, 2.2–79.9%); and at 20 C, 4.1 ± 1.1% (range, 0–19.1%).

The dependence of indirect germination on low temperature was noticed by Jones et al (7). Quantitative records of indirect germination were given by Melhus (10) and confirmed by Crosier (2). My results agree with those of Crosier (2), except that percent germination dropped sharply around 18 C in my experiments. These differences may result from the methods used and may be partly explained by the lack of precise control of incubation temperatures.

**Zoospore swimming time.** The duration of zoospore motility was determined at five temperatures in three seperate experiments. The average percent of motile zoospores at each temperature is shown in Fig. 6. The length of time zoospores remained motile decreased as temperature increased above 10 C. At 10 C, 20% were still motile even after 8 hr of incubation, but at 22 C, all had encysted within 2 hr. Although this tendency was similar to that reported by Crosier (2), swimming times were much longer in my experiments. Again, the differences may have been caused by the methods used. Thus, temperatures below 16 C favored the in vitro release and activity of zoospores; temperatures above 20 C did not.

Potato tubers may be infected through lenticels and especially eyes (9,12). The spores must move through soil to infection sites that represent just a few small areas compared with the total surface area of the tuber. Germ tubes produced by sporangia and encysted zoospores cannot grow far in natural soil (12); Therefore, those that stop growing before reaching an infection court have little chance of infecting tubers. It seems reasonable to assume that tuber infection largely depends on zoospore motility. Thus, the longer zoospores can continue to swim and the greater their number, the greater are the chances of infection. Although we do not yet have experimental records on the swimming time and vigor of zoospores and the times required for the zoospores to reach an infection site in soil, a comparison of the possibility of infection by zoospores at different temperatures would be of value when considering tuber infection in soil. Perhaps it is not easy for the zoospores to move through soil to an infection site during natural rain, and therefore it would not be unreasonable to assume that zoospores that lose motility within 2 hr are unlikely to be involved in the field infection of tubers. Conversely, zoospores that swim longer are more likely to reach an infection site. Based on this assumption and my experimental results on the indirect germination and zoospore swimming time (Fig. 5 and 6), one would expect temperatures below 16 C to be very favorable for tuber infection, but not those above 20 C. This is very similar to the pattern of tuber infection in the field. Factors such as numbers of foliage lesions, susceptibility of cultivars, soil textures, etc. affect the amount of tuber blight (6,9,12). The differences in amounts of tuber blight between fields in the same season or between seasons and regions may be explained by the above factors as well as by the contributions of the critical soil environmental elements examined in this paper.

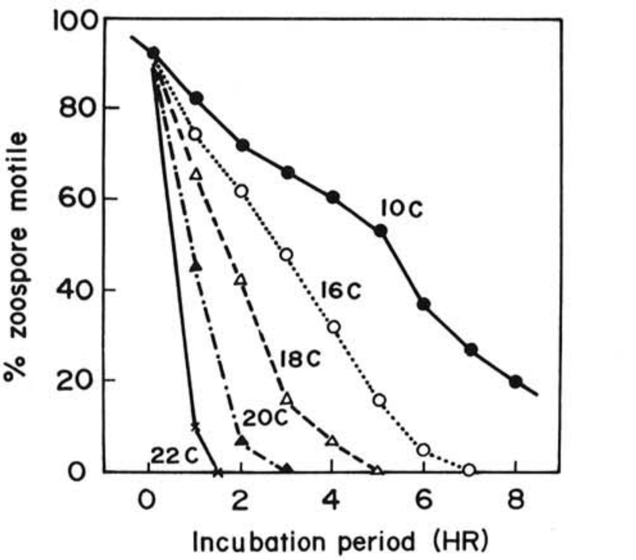


**Fig. 6.** Effect of water temperature on the duration of motility of zoospores of *Phytophthora infestans*. Data points represent the mean rate for swimming zoospores from three experiments.

## LITERATURE CITED


1. BERKELEY, M. J. 1846. Observations, botanical and physiological, on the potato murrain. J. Hortic. Soc. Lond. 1:9-34.
2. CROSIER, W. 1934. Studies in the biology of *Phytophthora infestans* (Mont.) de Bary. N. Y. (Cornell Univ.) Agric. Exp. Stn. Mem. 155. 40 pp.
3. FEDERATION OF BRITISH PLANT PATHOLOGISTS. 1973. A Guide to the Use of Terms in Plant Pathology. p. 11 in: Phytopathol. Pap. 17, Commonw. Mycol. Inst., Kew, Surrey, England. 55 pp.
4. GRAINGER, J. 1957. Blight—the potato versus *Phytophthora infestans*. Agric. Rev. 3(5):10-26.
5. HIRST, J. M., O. J. STEDMAN, J. LACEY, and G. A. HIDE. 1965. The epidemiology of *Phytophthora infestans*. IV. Spraying trials, 1959 to 1963, and the infection of tubers. Ann. Appl. Biol. 55:373-395.
6. JENSEN, J. L. 1887. Moyens de combattre et de detruire le *Peronospora* de la pomme de terre. Mem. Soc. Nat. d'Agric. France 131:31-156.
7. JONES, L. R., N. J. GIDDINGS, and B. F. LUTMAN. 1912. Investigations of the potato fungus *Phytophthora infestans*. U.S. Dep. Agric. Bull. 245. 100 pp.
8. LACEY, J. 1965. The infectivity of soils containing *Phytophthora*

*infestans*. Ann. Appl. Biol. 56:363-380.
9. LAPWOOD, D. H. 1977. Factors affecting the field infection of potato tubers of different cultivars by blight (*Phytophthora infestans*). Ann. Appl. Biol. 85:23-42.
10. MELHUS, I. E. 1915. Germination and infection with the fungus of the late blight of potato (*Phytophthora infestans*). Wis. Agric. Exp. Stn. Res. Bull. 37. 64 pp.
11. MURPHY, P. A., and R. McKAY 1925. Further experiments on the sources and development of blight infection in potato tubers. J. Dep. Lands and Agric. 25:10-24.
12. ZAN, K. 1962. Activity of *Phytophthora infestans* in soil in relation to tuber infection. Trans. Br. Mycol. Soc. 45:205-221.