Epidemiological Patterns of Phytophthora infestans Under Semi-Arid Conditions

J. Rotem and Yigal Cohen

Division of Plant Pathology, The Volcani Center, ARO, Bet Dagan; and the Department of Life Sciences, Bar Ilan University, Ramat Gan, Israel.

Contribution from ARO, 1973 Series, No. 103-E. This work was supported in part by Grant No. FG-15-231 from the U.S. Department of Agriculture.

Accepted for publication 7 December 1973.

ABSTRACT

Epidemic patterns of potato late blight during a period of heavy nocturnal dew followed by hot and dry days, were studied by inducing epidemics in growth chambers and assessing the influence of environmental factors on epidemic development. In all but the hottest regimes of temp, epidemics were enhanced by low daytime relative humidity (RH). The chief factor facilitating epidemic development was abundant sporangial dispersal enhanced by low RH. However, in days with high temp the survivability of dispersed sporangia was reduced; more under low, than under high, conditions of humidity. In such instances, survivability overrides dispersal effect and becomes a major factor in epidemic development. Under extremely unfavorable (but transient) conditions of temp and humidity, the high survivability of mycelium in leaves, and especially in stem lesions, provided the opportunity for subsequent renewal of an epidemic.

Phytopathology 64:711-714.

Additional key word: ecology.

Epidemic development of *Phytophthora infestans* (Mont.) De Bary on potato (*Solanum tuberosum* L.) during the hot and rainless season in Israel contradicts the view that late blight is a temperate climate disease (12). In this season the night conditions (20-22 C and 6-8 h of dew) are favorable for infection and sporulation. However, day temp in excess of 30 C coincident with ca. 50% relative humidity (RH) appear unfavorable for survival of sporangia and of mycelium present in the infected tissues. Overhead irrigation in the morning increases disease by enabling sporangial infection but is not a requisite for disease development (10). During extremely hot and dry spells (maximum temp above 40 C, minimum RH below 30%) disease stops developing but resumes when temp moderate and higher RH conditions return.

Two hypotheses may explain blight development under these conditions: (i) the occurrence of strains with high temp optima, and (ii) the (hitherto overlooked) ability of the common strain to withstand or even to benefit from hot, dry conditions. The first hypothesis was rejected when the temp requirements of 34 isolates collected at various locations in Israel during several hot seasons were found to be similar to those reported for temperate zones (e.g. optimum and maximum for infection and development in the range of 15-20 C and ca. 29 C, respectively; Rotem and Cohen, *unpublished*). Studies to validate the second hypothesis by analyzing the stages of epidemic development in growth chambers are described in this paper.

MATERIALS AND METHODS.—*Plant growth conditions.* —Experiments were carried out on potato plants (*Solanum tuberosum* "Up to Date") grown for 6 wk in a greenhouse, in 0.3-kg pots filled with a sterilized mixture of sandy loam:peat:sand:vermiculite (2:2:1:1, v/v).

"*Epidemics*" *in growth chambers.*—These were induced under four regimes of temp programmed for continuous change between a midnight minimum and a midday maximum, as described for downy mildew of cucumbers (1). Each regime of temp was replicated with two light period regimes of humidity (the moist and dry regimes described below). In all regimes the foliage was covered with drops of water (supplied by humidifiers) during 12-h dark periods. The gradual decrease of the RH levels during the light periods reached a midday minimum of 80 (min 80% RH) and 50% (min 50% RH) in the moist and dry regimes, respectively. Then the RH levels increased until the appearance of "dew" at night. One experiment was done with leaves wetted throughout the light and dark periods.

The variation of conditions in the growth chambers was within 1 C, as determined by thermocouples clipped to the leaves, and ca. 5% RH, as measured by hygrographs; light intensity was 14,500 lx.

The source of inoculum was *P. infestans,* race O, from potatoes. Test plants were first kept for 2 h in a chamber with a few sporangia-bearing plants. Preliminary tests showed that air movement caused by fans dispersed sporangia from diseased to healthy plants. Thirty-five plants per treatment then were transferred to the experimental chambers for periods of up to 20 days. Evaluation of results was made according to the percentage of blighted leaves.

Spore dispersal.—Sporangia dispersal in the field was measured by a Kramer and Collins trap (6). In the laboratory, effects of RH on dispersal were studied in ventilated humidity chambers equipped with a spore trap (9).

Tests for survival.—Survival of dispersed sporangia was tested after a 1:1 mixture of healthy and infected plants bearing sporangia was kept in a growth chamber as described previously. Inoculated plants were exposed to different conditions of temp and RH (15 plants/treatment), sprayed with water, kept for 24 h in a moist chamber, and lastly in a growth chamber at 20 C for 4 days. Disease incidence on all plants was estimated relative to that on control plants (sprayed with water immediately after the dispersal period was over) which was considered 100% (2).

Survival of attached sporangia was tested by exposing sporangia-bearing plants to different conditions of temp and RH (15 plants/treatment) under minimal air

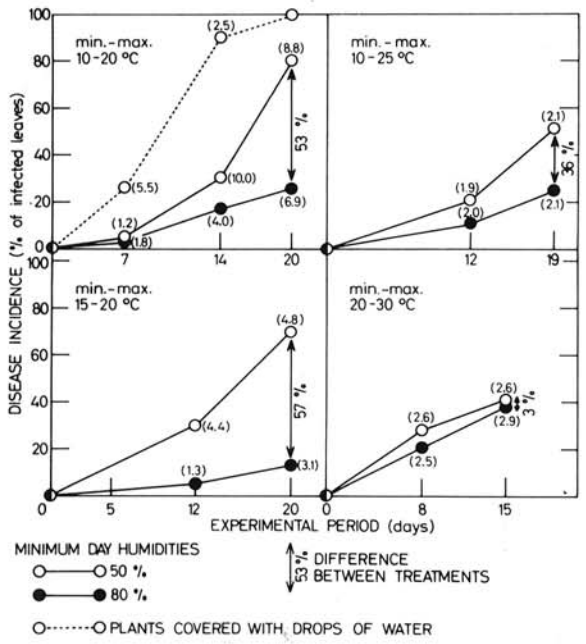

Fig. 1. Epidemic patterns of *Phytophthora infestans* on potatoes under different temp and relative humidity (RH) regimes. Minimum and maximum temp occurred at midnight and midday, respectively. In all treatments, plants were covered with drops of water during the 12-hr dark period. In one treatment, continuous coverage with drops of water was tested. In other treatments RH was decreased to a minimum of either 80 or 50% at midday. (Figures in parentheses are Standard Errors).

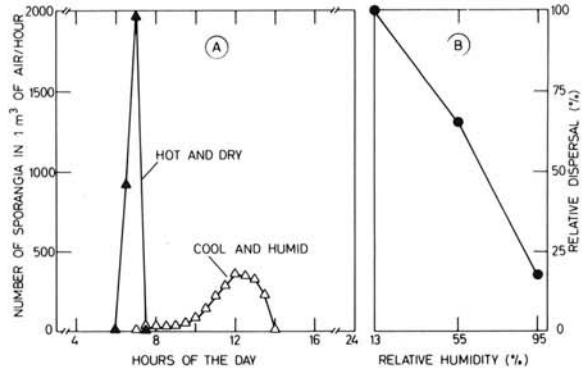

Fig. 2-(A, B). Dispersal of *Phytophthora infestans* under different environmental conditions **A)** Diurnal dispersal in potato fields on a hot and dry day and on a cool, humid day **B)** Effect of relative humidity on dispersal in the laboratory. Values obtained from the most favorable treatment were considered as 100%, and the percentage of dispersal in other treatments was calculated accordingly.

movement. After different periods of exposure, the sporangia were suspended in water and the suspension used for inoculation by Schein's inoculator (11) with 550 ± 55 sporangia applied to a 4-cm² target. Control plants were inoculated with fresh sporangia. The inoculated plants were placed for 24 h in moist chambers at 20 C and

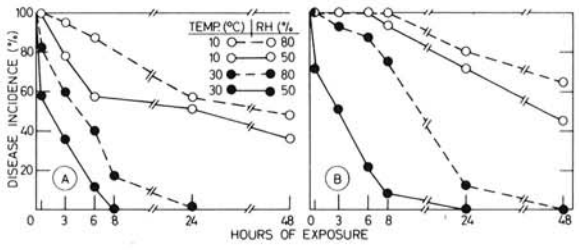

Fig. 3-(A, B). The effect of temperature and relative humidity (RH) on survivability of dispersed **A)** and attached **B)** sporangia of *Phytophthora infestans*. (Evaluated relative to infectivity).

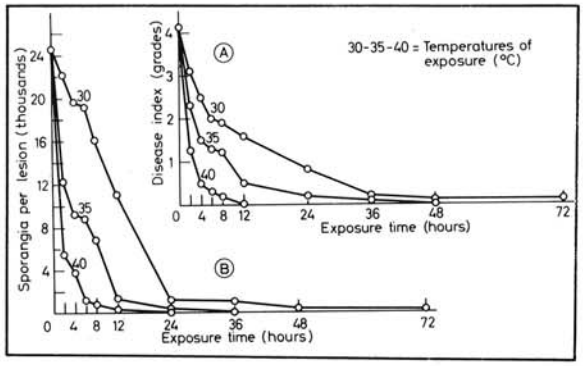

Fig. 4. The effect of high temp on survivability of the pathogens **A)** and on its sporulating potential **B)** in potatoes infected with *Phytophthora infestans*.

for four days in a growth chamber at 20 C. Disease incidence was expressed as the percentage of that which appeared on plants inoculated with fresh sporangia.

Survival of the pathogen inside infected tissue was studied after the test plants were inoculated with Schein's inoculator and kept for 12 h in moist chambers at 20 C. In one test, the infected plants were exposed for up to 72 h to 30, 35, and 40 C and then kept for 4 days in a growth chamber at 20 C. The results were assessed visually and graded according to the extent of the lesions: 0, no infection; 1, traces of infection; 2, 3, and 4, lesions covering up to one-third, two-thirds and the whole of the target area, respectively; and 5, lesions extending beyond the inoculation site. Sporulating potential of the treated plants was assessed by keeping detached leaves for 24 h in moist chambers (20 C), suspending sporangia in water and counting them with the aid of a cytometer. In these and other tests, analysis of variance and calculation of standard errors (SE) were used to detect significant differences at the 95% probability level.

In another test, 162 plants inoculated on leaves and stems were held for 20 days in growth chambers at 20, 25, and 28 C, and 50-60% RH. Infected leaves and stems were detached periodically, placed under conditions promoting sporulation, and examined under a microscope for the presence of sporangia.

RESULTS.—*Epidemic patterns under controlled conditions.*—The highest incidence of disease developed under minimum-maximum temp combinations of 10 and

20 C, and conditions of continuous "dew". In other treatments, disease development under all temp regimes reached a higher degree of incidence under the dry (min 50% RH) than under the wet (min 80% RH) regime. The differences in disease incidence between the dry and the wet regime were not affected by night temp, but decreased with increase in the day temp. Thus, at day temp of 20, 25, and 30 C, the differences between the dry and the wet treatments were 53-57%, 36%, and 3%, respectively (Fig. 1).

To determine whether temp and humidity influence susceptibility of the host, ten plants per treatment were inoculated with *P. infestans* after they exposed to the different treatments of the previous experiment. Such treatment did not influence host susceptibility.

Spore dispersal.—In the field, dispersal on the hot and dry day (max 42 C, min 15% RH) started early, reached a peak rapidly, and stopped abruptly; dispersal on the cool and humid day (max 22 C, min 78% RH) started later, reached its peak gradually, and decreased slowly. The total number or sporangia dispersed during the hot and dry day greatly exceeded the number dispersed under cool and humid conditions (Fig. 2-A).

The effect of 13, 55, and 95% RH on dispersal was studied with eight sporangia-bearing plants kept in humidity chambers for 24 h at 20 C, with air movement at 10 liters/min. Dispersal, evaluated as percentage of maximum released under the experimental conditions, decreased drastically with the increase of RH (Fig. 2-B).

Survivability.—Survival level of dispersed sporangia was evaluated in accordance with their infectivity. In all exposure periods at 10 C, higher infectivity followed exposure to 80% than to 50% RH, but significant differences between the two RH treatments were found only for the 6-h exposure period. At 30 C, the sporangia lost their infectivity after an 8-h exposure to 50% RH, and a 24-h exposure to 80% RH (significant for all treatments) (Fig. 3-A).

In tests with attached sporangia kept at 10 C, higher infectivity occurred after storage at high RH, but without significant differences between the moist and the dry treatments. At 30 C, sporangia survived for 24 h at 80% and 8 h at 50% RH (Fig. 3-B).

In tests on survivability of the pathogen within infected leaves, a comparatively short exposure to 30, 35, or 40 C resulted in a drastic decrease in disease development. However, complete inactivation of the pathogen was achieved only after a comparatively long exposure to these temp (Fig. 4-A). These phenomena were reflected also in the sporulating potential of the treated plants (Fig. 4-B). Differences of about one grade in disease index, and of about 8,000 sporangia per lesion, indicated significant differences between the various treatments.

The trial on longevity of survival in leaves and stems held for 20 days at 20, 25, and 28 C and 50-60% RH was evaluated according to the sporulating potential of lesions. Sporulation on leaf lesions did not occur after plants were in the growth chamber 5-8 days. In contrast, sporulation occurred on 30 of 75 infected stems examined after 20 days. Surprisingly, these results were not correlated with the incubation temp.

In the field during a moderately warm period, better preservation of the pathogen and a longer period of sporulative capacity occurred in stems rather than in leaves. Under these conditions, sporulation on leaf lesions did not occur after nine days, whereas 60% of the stem lesions examined continued to sporulate after ten days.

DISCUSSION.—With nights favorable for infection and sporulation, the ability of late blight epidemics to develop in semi-arid conditions depends on spore dispersal and survivability, which are affected by the hot and dry conditions. Dispersal of the sporangia is favored by low RH, as found in our tests (Fig. 2) and as noted previously by Hirst (4). The epidemiological value of abundant dispersal depends on the ability of sporangia to withstand the adverse daytime conditions. The view that survivability of *P. infestans* is extremely low (3) has been challenged (5, 7, 13, 14). The present studies prove that dispersed and attached sporangia may survive for comparatively long periods of relatively adverse conditions. The sporangia survive better under high rather than under low RH, but the epidemiological significance of this observation is relatively unimportant under low day temp and important with an increase in temp (Fig. 3).

According to the temp- and humidity- dependent interaction between dispersal and survivability, the epidemiological patterns of blight epidemics in the growth chambers and in the field look plausible. In the growth chambers, the most intensive development occurred under conditions of continuous moisture. Such results represent patterns typical of cool and rainy areas where dispersal often occurs via splashing, and survivability is of minor importance. Typical of semi-arid areas are epidemics induced under dry daytime conditions. In such cases, higher disease incidence was associated with the lower level of humidity, especially during low day temp when survival was not the limiting factor. With an increase in day temp the importance of enhanced dispersal was gradually reduced and the factor of survivability became more important. This resulted in no differences in epidemic development between the dry and the wet treatments at a maximum day temp of 30 C (Fig. 1).

These dispersal-survivability interactions seem to occur also in nature, and have been deduced from results of field experiments (8, 10). However, the organism must also withstand transient conditions of extremely hot and dry weather during which the dewless nights do not allow sporulation or infection. The epidemic is then stopped but can later resume if mycelia survive within infected tissue. Sporangia produced on these tissues may provide the inoculum for resumption of the epidemic when hot and dry spells do not last for too long a period. The source of inoculum for renewal of the epidemic after prolonged hot and dry spells is the fungal mycelium in stem lesions which remain sporulative for a few weeks as was found in this study and observed under extremely unfavorable conditions in the field (10).

LITERATURE CITED

1. COHEN, Y., and J. ROTEM. 1971. Field and growth chamber approach to epidemiology of Pseudoperonospora cubensis in cucumbers. Phytopathology 61:736-737.

2. COHEN, Y., and J. ROTEM. 1971. Dispersal and viability of sporangia of Pseudoperonospora cubensis. Trans. Br. Mycol. Soc. 57:67-74.
3. CROSIER, W. 1934. Studies in the biology of Phytophthora infestans (Mont.) De Bary. N.Y. Agric. Exp. Stn. (Ithaca) Mem. 153.
4. HIRST, J. M. 1958. New methods for studying plant epidemics. Outlook Agric. 2:16-26.
5. HOYMAN, W. G., and J. R. WALLIN. 1957. Influence of air-temperature maxima on the survival of Phytophthora infestans in potato leaves. Phytopathology 47:17 (Abstr.).
6. KRAMER, C. L., and S. M. PADY. 1966. A new 24-hour spore sampler. Phytopathology 56:517-520.
7. MARTIN, W. J. 1949. Strains of Phytophthora infestans capable of surviving high temperatures. Phytopathology 39:14 (Abstr.).
8. ROTEM, J., and J. BEN-JOSEPH. 1970. Evaporation rate as an indicator for potato late blight development in plots of different foliage density. Plant Dis. Rep. 54:768-771.
9. ROTEM, J., J. BEN-JOSEPH, and R. REUVENI. 1973. Design and use of an automatic humidity chamber in phytopathological research. Phytoparasitica 1:39-45.
10. ROTEM, J., J. PALTI, and J. LOMAS. 1970. Effects of sprinkler irrigation at various times of the day on development of potato late blight. Phytopathology 60:839-843.
11. SCHEIN, R. D. 1964. Design, performance, and use of a quantitative inoculator. Phytopathology 54:509-513.
12. WALKER, J. C. 1952. Disease of vegetable crops. McGraw-Hill, New York. 529 p.
13. WALLIN, J. R. 1953. The production and survival of sporangia of Phytophthora infestans on tomato and potato plants in the field. Phytopathology 43:505-508.
14. WALLIN, J. R., and W. G. HOYMAN. 1958. Influence of post-inoculum air temperature maxima on survival of Phytophthora infestans in potato leaves. Am. Potato J. 35:769-773.