Inoculum Potential of *Phytophthora infestans* and the Development of Potato Late Blight Epidemics

Esther Bashi, Y. Ben-Joseph, and J. Rotem

Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel.
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ABSTRACT

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The inoculum potential of *Phytophthora infestans* in potato late blight was studied in four spring and three fall epidemics by recording production, dispersal, deposition, and infectivity of sporangia under various conditions. Fall epidemics were more severe than spring epidemics. There were greater amounts of inoculum in the fall, and dew periods were longer. However, no relation was found between the length of the dew period of any given night and the number of sporangia on leaves the following morning. Numbers of sporangia on leaves decreased during the day, but many sporangia formed at night remained attached to leaves until the following evening. Lesions were free of sporangia only after several dewless nights. Most sporangia were caught in mechanical spore traps in the morning to noon hours; few were caught in the evening and night hours. By contrast, infections that developed on trap plants exposed for discrete time periods among diseased field plants indicated that deposition of sporangia also occurred in the evening and night. Sporangia dispersed late in the day were more infectious than those dispersed early. Therefore, the contribution to epidemics of sporangia, relative to their amounts dispersed at different times of the day, was higher for sporangia dispersed late than for those dispersed early in the day. Survival of attached sporangia in the daytime appeared to be of greater importance in spring epidemics, when high temperatures and high light intensity caused greater loss of viability of dispersed inoculum, than under the more favorable fall conditions.

Additional key words: epidemiology, spore dispersal, sporulation, spore survival.

The rates of inoculum production and dispersal as well as the viability and infectivity of the inoculum are the key factors that govern rates of epidemic development. For potato late blight, which is caused by *Phytophthora infestans* (Mont.) de Bary, these factors have so far been described separately. For instance, sporulation has been measured in the laboratory (E. Bashi and J. Rotem, *unpublished*), but not in the field, and without relating the quantities of inoculum produced to infectivity. Dispersal has been measured in the field (7) without measuring infectivity of sporangia trapped at various hours of the day. Crosier (6) concluded from laboratory studies that the sporangia are highly sensitive to adverse weather conditions, but Rotem and Cohen (12) found that sporangia produced in growth chambers retained infectivity after several hours of moderate heat and dryness. Infectivity of sporangia was never studied in the field.

In this study, our approach was to quantify the relationship of inoculum potential to observed patterns of epidemic development by conducting integrated investigations on the production, dispersal, deposition, and infectivity of sporangia in the field.

MATERIALS AND METHODS

Field tests were performed in 0.7-ha potato (*Solanum tuberosum* L., 'Up-to-Date') fields, not treated with fungicides, in the coastal plain of Israel during the peak stages of four spring and three fall epidemics from 1977 to 1980.

The number of leaves with lesions was counted periodically in samples of 20 plants in a 200-m^2 plot in which most of the tests were carried out. The number of sporangia per leaflet with lesions (most lesions covered 30–70% of the affected leaflet) was counted in samples of 50 leaflets collected at random at various hours of the day. The collected leaflets were shaken for 30 min in a solution of formalin, acetic acid, and alcohol, and the suspension was filtered on membrane filters on which the sporangia were then counted as described elsewhere (4). Numbers of sporangia in the experimental plot were estimated by multiplying the number of sporangia per lesion by the number of lesions per plant and by the number of plants (about 1,300) per plot.

Spore trapping was done in three seasons with Burkard traps (Burkard Mfg. Co., Rickmansworth, England) and in two seasons with Rotorod traps (Ted Brown Associates, Los Altos Hills, CA 94022). The results were expressed as the number of sporangia per unit time per cubic meter of air. Deposition of dispersed sporangia on plants was estimated by exposing healthy, potted, 4-wk-old potato trap plants in the field and transferring them into dew chambers (20 ± 1 C) immediately after termination of a given exposure period (eg, after 2 hr). The immediate transfer of trap plants to moist chambers minimized loss in infectivity of the deposited sporangia. After 24 hr in the dew chamber, the trap plants were incubated for 6 days in growth chambers at 20 ± 1 C, 50–60% relative humidity (RH) and a 12-hr photoperiod. Results were expressed as the percentage of infected leaflets.

The combined effects of deposition and survival of sporangia during the dry day periods and their infectivity during the following dew period at night were estimated by exposing trapping plants in the field from various hours of the day until the next morning and then incubating them in the growth chambers without wetting after removal from the field.

Infectivity of sporangia removed from plants in the field at various hours of the day was measured as follows: Sporangia on detached leaflets were removed by shaking in water, the suspension was diluted to 14,000 sporangia per milliliter and sprayed with a modified Schein inoculator (14) onto 4-cm^2 targets on the underside of leaflets of potted potatoes. These were incubated in dew- and growth chambers and evaluated as described previously.

Dew-period was measured in the field with a Taylor dew recorder (16). Other meteorological data used for interpretation of some experiments were measured by thermohydrographs protected by small screens placed within the foliage in the experimental fields. Not all parameters were measured in every season.

The rates of production and dispersal of sporangia and the levels of their viability and infectivity varied in seasons according to the

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influence of weather factors on disease development. In order to compare the effects of these components on inoculum potential in various seasons, we converted some of the data from absolute measurements to percentages. Either the value of the earliest measurement on a given day, or the total of all measurements for a given period, were equated to 100%. Data from subsequent measurements were then expressed in terms of the 100% base value. Seasonal averages were calculated from the daily values.

RESULTS

Seasonal differences in inoculum potential. Inoculum potentials at the peak period of the spring and fall epidemics were estimated by measuring the mean values of the following four parameters: number of lesions per plant and the percentage of leaflets infected; the number of sporangia collected from lesioned leaflets at 0800 hours; the number of sporangia trapped by mechanical traps; and the percentage of blighted leaflets following incubation of trapping plants. Trapping plants were exposed in the center of the 200-m^2 plots during the day (0800–1750 hours) and night (1800–0750 hours), and were immediately transferred to a dew chamber after being removed from the field. In only four seasons were all these parameters tested simultaneously.

Most of the lowest and highest levels of all four components of inoculum potential occurred in spring (S) 1980 and fall (F) 1978, respectively (Table 1). Because the plants were unusually small in F-1980, there were fewer lesions per plants in this season than in S-1978. Even though the number of sporangia per lesion was about twice as high in F-1980, the resultant numbers of sporangia in the experimental plot was about the same in both seasons. The number of sporangia caught by mechanical traps and the percentage of infected leaflets on trapping plants, which indicate deposition of sporangia, seemed to be influenced by canopy density in the field as well as by the number of sporangia produced in the plot. Reduction of wind speed by dense plant canopy is known to result in decreased spore dispersal (3,17). We found that the number of sporangia trapped by mechanical traps and the percentage of infected leaflets on trapping plants was five and two times higher, respectively, within the sparse canopy in F-1980 than within the dense canopy in S-1978, even though similar numbers of sporangia were produced in the plots in both seasons (Table 1).

Relation of dissemination of sporangia to dew periods and failures of sporangia detachment. The average number of sporangia per lesion collected at 0800 hours was 12.5×10^3 for spring seasons and 62.6×10^3 for three fall seasons (not all data are listed in Table 1). We found no association between temperature and RH conditions in these seasons and the numbers of sporangia produced. Closer association was found between sporulation and mean length of dew periods; dew periods averaged 9 hr per night in the spring and 13 hr per night in the fall. However, no association was found between dew duration in any given night and the number of sporangia collected the next morning. For instance, in November 1979, 14,600 and 16,700 sporangia per lesion were collected after nights with 14 and 6 hr of dew, respectively.

In some instances, sporangia were found on leaves after dewless nights. For instance, 21,500 sporangia per lesion were collected on 6 November 1979, after a 14-hr dew period. This night was followed by a dry spell with RH below 40%. Despite these conditions, 5,500 and 2,600 sporangia per leaflet were collected after the first and second dewless night, respectively. In most cases, three to four consecutive dewless nights were necessary for complete disappearance of sporangia from lesions. The reason for the slow disappearance of sporangia was the strong attachment of sporangia to sporangiophores on the leaf surface, as demonstrated in laboratory and field trials. In the laboratory, infected plants produced sporangia after a 16-hr exposure in dew chambers (15 C). Leaves of these plants were submerged in water and brushed with a camel's hair brush to remove sporangia. The plants were then placed in growth chambers (20 C, 40–50% RH, and light), where the moisture present on leaves disappeared within 20 min). The same leaves were repeatedly submerged and brushed to remove sporangia after various periods of time. The mean number of sporangia per leaflet (five plants with 10 leaflets each) removed after termination of the dew period was 34,600. Repeated removals from the same leaflets resulted in the following numbers of sporangia: first hour, 7,600; second hour, 2,400; third hour, 1,600; fourth hour, 600; fifth hour, 600; and 24th hour, 100. (Standard errors between replicates ranged from 10 to 50% of the average values.) In the field, sporangia from the same, previously tagged leaflets were removed in the morning and afternoon hours during five days of lesion development (four replicate plants with 10 test leaflets on each). Dew periods preceding each day of removal were 9, 8, 12, 7, and 9 hr, respectively. The number of sporangia collected per leaflet at 0800 hours and 1600 hours, respectively, during this period was: first day, 500 and 700; second day, 4,900 and 600; third day, 1,600 and 700; fourth day, 300 and 200; and fifth day, 300 and 100 (standard errors ranged from 13 to 40%).

Ratio of day:night dispersal and deposition of sporangia. To

TABLE 1. Seasonal differences in production, dispersal, and deposition of sporangia of *Phytophthora infestans* in potato fields in Israel

Season[a] (no. days)	Leaflets per plant[b]	Infected leaflets (%)	Sporangia (1,000s) per lesion[c]	Sporangia (1,000s) per plot[d]	Sporangia per m^3 air (daily mean)	Infected leaflets in trapping plants (%)	Percent day/night sporangia catch: traps[e]	Percent day/night sporangia catch: plants[f]
S-1977 (20)	560	15.0	10	1,100	49	10	85/15	60/40
S-1978 (20)	610	7.5	29	1,740	92	16	88/12	64/36
S-1980 (30)	488	1.4	6	54	11	8		
F-1978 (16)	690	26.4	141	33,417	836	33	90/10	66/34
F-1979 (12)	554	27.8	137	27,429		40		68/32
F-1980 (7)	123	19.5	56	1,736	467	33	99/1	71/29

[a] S = spring, F = fall; the number in parentheses represents the number of days during the peak of the epidemic during which data were collected.
[b] Data are means from samples of 20 plants per plot.
[c] Data are means from 50 lesion-bearing leaflets per plot.
[d] Each plot contained 1,300 plants.
[e] Sporangia were caught in Burkard traps (three seasons) or on Rotorods (two seasons); numerators represent mean percentages of spores trapped during the day, and denominators of those trapped during the night.
[f] Trapping plants were explosed in the field and then incubated in a dew chamber; numerators represent percentages of total infected leaflets on plants exposed during the day; denominators on those exposed during the night.

evaluate data from mechanical traps the 24-hr periods were divided into 12-hr day (0600–1759 hours) and 12-hr night (1800–0559 hours) periods. Because trapping plants had to be manually introduced into the field, the day and night periods were 10 hr (0800–1750 hours) and 14 hr (1800–0750 hours), respectively. In both cases the number of sporangia trapped during a 24-hr period was equated to 100% and the day/night trapping was calculated accordingly. Ten trapping plants were exposed in the field for each day and night period.

With mechanical traps, 85 to 99% of sporangia caught during a 24-hr period were caught from 0600 to 1759 hours; with trapping plants, 60 to 71% of leaflets infected during a 24-hr period caught sporangia in the period from 0800 to 1750 hours, and 29 to 40% became inoculated during the night (Table 1). It is likely that some of these infections were caused by sporangia dispersed in the early morning hours (see Table 3).

Presence, dispersal, and deposition of sporangia at various hours of the day. Retention of sporangia on leaflets in the field was estimated from their numbers, as collected from infected leaflets at progressively later hours in the day. The numbers at the earliest count were equated to 100% for comparison with the numbers collected at other hours. Dispersal was measured by counting sporangia caught with mechanical traps at various hours. Deposition of sporangia was indicated by the percentage of infected leaflets in trapping plants exposed in the field for "fractions" of the day (10 plants per fraction), then incubated in dew- and growth chambers. The number of sporangia trapped over the whole day, and the sum of infected leaflets in trapping plants exposed for all fractions of the day period, were equated to 100%, and the amounts for different hours were calculated accordingly.

The number of sporangia collected from infected leaflets decreased as the day advanced, but remained relatively high in the afternoon (Table 2). From 26 to 50% of the sporangia present in the morning were dispersed during the period from 0800 to 1600 hours. Between 88 and 93% of the sporangia caught by mechanical traps in the period from 0600 to 1759 hours were trapped between 0600 and 1300 hours (Table 3). These are seasonal averages. On some days the peak of dispersal passed before or after these hours. Figure 1A shows that although the main deposition of sporangia occurred in the morning, the number of sporangia deposited at later hours of the day on trapping plants exceeded that recorded by mechanical traps (compare with Table 3). The data in Fig. 1A also indicate that the confinement of peak deposition to morning hours is more characteristic of the spring than of the fall season, during which relatively more sporangia were deposited in the afternoon.

Integrated effects of deposition, survival, and infectivity. Trap plants (10 replicates per treatment) were exposed in the field at progressively later hours of the day and left until the next morning. Thus, in comparison with plants introduced into the field at early

TABLE 2. Retention of sporangia of *Phytophthora infestans* on infected potato leaflets at various hours of the day during the peak period of potato late blight epidemics in Israel

Season[b]	Sporangia (%) present on leaflets at the following hours[a]					
	0600	0800	1200	1600	1700	1800
S-1977	···	100	73	50	···	···
S-1978	100	75	56	49	···	39
S-1979	···	100	88	68	···	···
F-1978	···	100	90	69	···	···
F-1980	···	100	···	···	66	···

[a] Seasonal averages of daily counts of sporangia collected from 50 lesion-bearing leaflets at various hours of the day. The number of sporangia collected at the earliest hour was equated to 100% and the numbers collected at other hours were calculated accordingly.
[b] F = fall; S = spring.

TABLE 3. Seasonal averages of sporangia in percentages caught by mechanical spore traps at various hours of the day during the peak period of potato late blight epidemics in Israel

Season[b]	Sporangia (%) trapped at the following hours[a]											
	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700
S-1977	1	2	2	13	25	19	11	15	4	4	2	2
S-1978	21	19	11	11	4	5	13	6	5	1	1	3
F-1978	12	17	6	10	8	16	15	7	4	3	2	2

[a] The total number of sporangia trapped per day was equated to 100%, and percentage of sporangia trapped each hour and seasonal averages were calculated accordingly.
[b] F = fall; S = spring. In an additional fall trial (F-1980) counts were made for periods of several hours; 93% of the sporangia were caught between 0800 and 1259 hours, and 7% were caught between 1300 and 1759 hours.

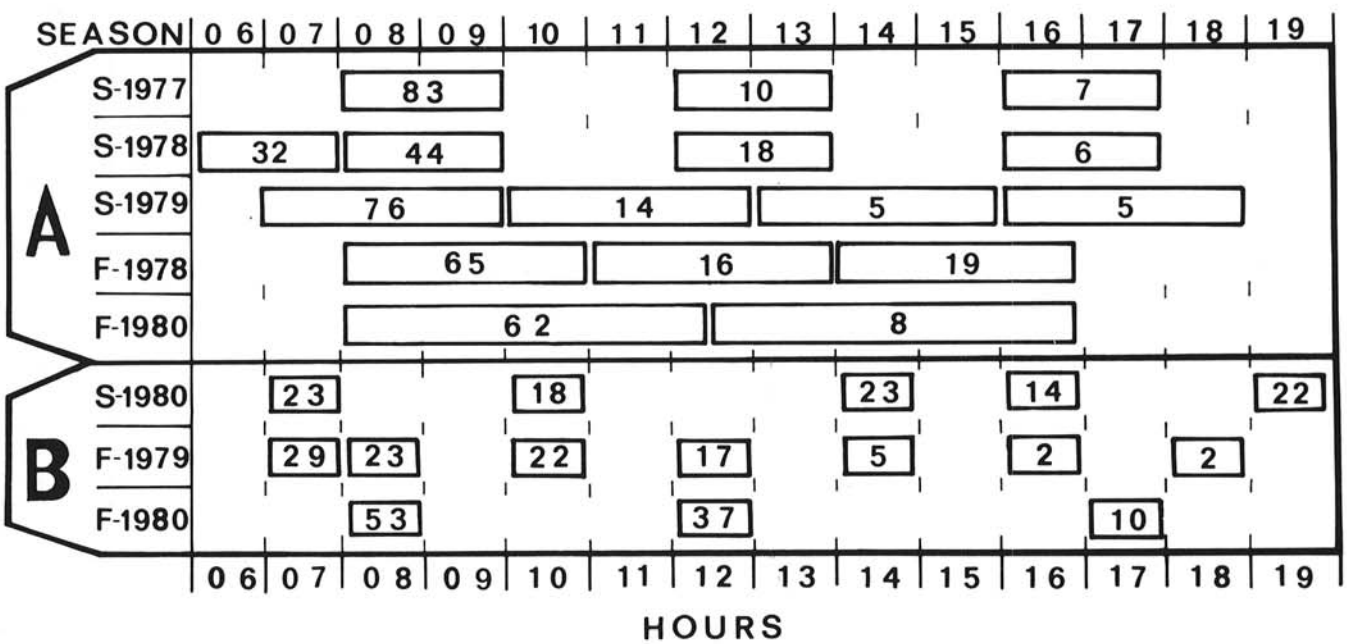

Fig. 1. A, Deposition of sporangia of *Phytophthora infestans* on potatoes at various hours of the day during the peak period of late blight epidemics, assessed by the percentage of infected leaflets on trapping plants exposed in the field for fractions of the day, then placed in moist chambers. **B,** The infection potential of sporangia dispersed and deposited at progressively later hours of the day, then subjected to field conditions affecting their survival and infectivity, assessed by infection on trapping plants left in the field overnight to allow infection to take place. In both trials daily total of leaflets infected = 100%.

hours of the day, those introduced later were subjected to a lesser impact of inoculum and shorter duration of dryness, but to the same duration of dew periods facilitating infection during the night. Results of these trials (Fig. 1B) are compared with those indicating deposition (but not survival or infectivity of sporangia) at different hours of the day as presented in Fig. 1A. The plants wetted after short periods of exposure indicated the highest amount of deposition of sporangia in the morning hours (Fig. 1A). However, plants introduced into the field at progressively later hours and left until the next morning showed relatively high percentages of infection (Fig. 1B). In the integrated effects of deposition, survival and infectivity, the contribution to disease of sporangia deposited in the afternoon seems to be relatively greater in spring (59%) than in the fall (9–10%).

Survival of attached sporangia. Infectivity of sporangia removed from infected leaflets at various hours of the daytime increased at later hours of removal. However, unless extremely adverse weather conditions prevailed, it remained fairly high even in the late afternoon. Table 4 shows that with temperature maxima of 25 C, and RH decreasing to as low as 25%, a considerable amount of infection was induced by sporangia removed at 16 and 18 hr. Some sporangia removed at noon caused infection although temperature had risen to 35 C and RH had dropped to 2–8%. Only in the afternoon of such a hot and dry spell did sporangia collected from lesions fail to induce infection (Table 4).

Survival of dispersed and deposited sporangia. In May 1978, four groups of 10 trapping plants each were exposed in a heavily infected field from 0800 to 1000 hours; ie, during the peak of dispersal. The first group was transferred to a dew chamber at 1000 hours. The other three groups were transferred to a distant, healthy field not exposed to inoculum from the blighted plot, and transferred to dew chambers at progressively later hours. The percentages of infected leaflets in trapping plants transferred to dew chambers at 1000, 1200, 1400, and 1600 hours, and incubated in growth chambers for 6 days, were 38, 8, 13, and 1%, respectively; ie, lower than the infection caused by sporangia detached at similar hours under similar weather conditions (see Table 4).

Survival of sporangia produced in dew chambers. Differences in survival of sporangia produced in the field and in the laboratory were determined in several trials. In one typical trial infected plants were left in a dew chamber from 1700 to 0800 hours. At the time of removal (0800 hours), sporangia collected from these plants induced infection in 98% of inoculated leaflets. Sporangia collected in the field at the same time induced infection in only 47% of the inoculated leaflets (average of 10 inoculated plants per source of sporangia). Sporangia-bearing plants from the laboratory were exposed in the field from 0800 hours until noon (21–25 C and 38–52% RH). Sporangia collected from these plants at noon induced infection in only 6% of the inoculated test plants, while those collected from infected plants in the field induced infection in 40% of inoculated leaflets. Similar results were obtained in other trials of this sort.

TABLE 4. Infectivity[a] of sporangia of *Phytophthora infestans* collected from lesions on potato plants in the field at various hours of the day

Season[b] and year	Days (no.)	Field conditions: Temperature (C)	Field conditions: RH (%)	Infectivity[c] of sporangia detached at the following hours: 0800	1100	1200	1400	1600	1800
S-1979	6	18–25	25–52	64	···	59	···	75	48
S-1979	1	31–35	2–8	17	···	12	···	0	0
S-1980	8	20–25	48–69	81	65	···	47	18	···
F-1979	5	20–25	40–70	74	···	45	···	···	···
F-1979	5	20–25	10–30	89	···	10	···	···	···
F-1980	5	20–25	68–78	100	···	94	···	32	···

[a] Infectivity was evaluated according to the percentages of infected leaflets on test plants inoculated with detached sporangia in the laboratory (10 replicate test plants per treatment).

[b] F = fall; S = spring. Sporangia were collected during the peak of each epidemic.

[c] Standard errors ranged from 9 to 14% of the average values.

DISCUSSION

In the context of our study, the meaning of inoculum potential is restricted to effectiveness of inoculum in contributing to epidemic development as determined by events between sporulation and infection.

The greater numbers of sporangia per lesion produced in the fall compared with the spring season, may in part explain the severity of fall epidemics. The total amount of inoculum in the field is determined by the number of lesions, which is to some extent influenced by plant size. More numerous lesions with fewer sporangia in the larger plants in the S-1978 trial produced numbers of sporangia similar to those produced by fewer lesions with more sporangia on each, in the smaller plants in the F-1980 trial. However, dispersal of sporangia from the plot with low canopy density in F-1980 greatly exceeded that in S-1978 (Table 1). Enhanced dispersal at low canopy density may compensate for the reduction in number and survival of spores, and for reduced infection under conditions marginal for the pathogen in the microclimate of the low density canopy (11). Such marginal conditions are more typical in the spring when potato fields with low canopy density are not endangered by late blight, than in the fall when the weather is more favorable to blight (13).

The number of sporangia per lesion produced in spring and fall was associated with the average length of dew periods in these seasons. However, no relation was found between the length of a dew period in any given night and the number of sporangia present the following morning. This, and the presence of sporangia after dewless nights, suggests that, as in some other pathogens (10,17), only some of the sporangia produced during a given night disperse during the following day. Stepanov (15) found that a wind speed of 12 km/hr is not sufficient to remove sporangia of *P. infestans*. Wind speed inside the plant canopy may be lower than this (3). Sporangia of *P. infestans* appear to resist easy detachment, not only by wind but also by brushing. This may explain the relatively large number of sporangia present on lesions late in the day (Table 2). The persistence of sporangia on leaves for several days promotes continuity of pathogen development after periods which temporarily inhibit sporulation. Retention of spores on sporophores, or in pycnidia is known for several pathogens (5,9,10); such retention helps species survive periods of adverse weather. Although *P. infestans* is not considered to be a resistant organism, it was found less vulnerable to environmental hazards (8,12,18, and Table 4) than described by Crosier (6). It is possible that different determinations of sporangial sensitivity derive from use of sporangia produced under different conditions. We found sporangia produced in the laboratory to be more sensitive than those produced in the field. Sporangia still attached to lesions are more resistant to adverse environmental conditions than the previously dispersed ones (12) and are more infectious in the late hours of the day (Table 4). This means that the later sporangia are dispersed during hot and dry days, the better are their chances to induce infection during the following wet night. The majority of sporangia caught in mechanical traps are caught in the morning hours (7 and Table 3). However, it appears likely that the mechanical traps are not sensitive enough to record the small numbers of sporangia dispersed in the evening and night. Obviously, they do not indicate the number of sporangia deposited on plants or the infectivity of these sporangia. Information provided by trap plants indicated a relatively higher deposition rate in the late hours of the day and at night (Table 1 and Fig. 1A), than may be deduced from spore trap records during the same periods. It is possible that some sporangia deposited during these periods were not airborne and thus not available to be caught by mechanical traps, but were transferred by rubbing of leaves, as shown, for example, for *Rhynchosporium secalis* on barley (2).

Sporangia deposited late in the day were more infectious during the following night than those deposited earlier in the same day, but the magnitude of this reduction in infectivity depends on weather conditions. In the fall, when relatively short days and mild radiation do not greatly depress sporangial viability, the larger amounts of sporangia dispersed early in the day contribute

relatively more to the epidemic development than they do in spring, when sporangia dispersed early may have difficulty in surviving the long, dry days and strong radiation (13). This is when the importance of inoculum dispersed late in the day increases (Fig. 1B).

The greater infectivity, but smaller numbers, of sporangia dispersed late in the day exemplifies the phenomenon of compensation (1,11), which enables epidemics to develop in less favorable habitats. Comparison of the weather regimes in spring and fall in Israel with those prevailing in summer in Europe and the United States suggests that the processes described in this paper may also be important in these areas.

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