

Weather Variables in Relation to an Epidemic of Onion Downy Mildew

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ABSTRACT

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Development and spread of downy mildew (*Peronospora destructor* (Berk.) Casp.) from a point source of inoculum was observed in relation to weather factors in a field plot. Disease developed in a succession of two minor steps and two major steps of spread and intensification. Production of spores (sporangia) in the predawn hours required temperatures below 23–24 C on the previous day and continuous high relative humidity ($\geq 95\%$) at favorable temperatures from 0200 hours until dawn. No sporulation was observed on portions of leaves with moisture films of rain or dew. Initial dispersal of spores at 0700 hours occurred 1.5 hr after sunrise but generally did not coincide with initial decline in relative humidity, with

initial rise in temperature, with initial wind, or with the end of wet periods. Peak dispersal of spores at 0800–0900 hours coincided with declining relative humidity, drying of the leaves, and increasing wind speeds. Spores were trapped mainly when wind speeds in the onion canopy were 0.3–1.0 m/sec. Spores apparently survived and infected the leaves on days with persistent moisture and cloud cover but not on dry and sunny days. The steplike pattern of the epidemic appeared related to a sequence of short periods (<1–2 days) required for sporulation and infection alternating with long latent periods (10–16 days).

Additional key words: *Allium cepa* L., sporulation-infection periods.

Downy mildew of onions (*Allium cepa* L.) caused by *Peronospora destructor* (Berk.) Casp., was prevalent in areas of intensive onion production on organic soils near Bradford, Ontario, during 1977–80. Destructive epidemics occurred in one muckland area, the Cookstown Marsh, even though the onions were sprayed regularly with recommended fungicides. Development of improved and more reliable strategies for controlling downy mildew requires more detailed information on epidemics in relation to weather and crop factors.

Some relationships between environmental factors and stages of the infection cycle of *P. destructor* have been examined in the greenhouse or laboratory. Yarwood (20) observed emergence of

sporophores from stomata around midnight and maturation of spores (sporangia) at 0600 hours. Sporulation requires high humidity or dew (5,14,17,20), temperatures of 4–7 to 22–25 C (20) and darkness (19,20), but also a light period before the darkness (19). Spores are released during the day (20), but relationships of environmental variables and spore release have not been determined. Spores may survive 1 day after release (5,17,20) or 3–5 days while attached to sporophores (1,20). Infection occurs in free moisture at 1–25 C (optimum near 13 C) and requires 2–6 hr at 3–14 C but longer at higher temperatures (5,16,20). Latent periods for abundant sporulation are about 10–16 days (16,20).

Information on relationships between weather and polycyclic development of downy mildew in the field is sparse. The disease spreads in the direction of prevailing winds, and outbreaks are related to frequency and duration of humid weather (14,16,18). Rainy weather is unfavorable (7,12). The time of infection is not known but may occur in the same humid period as sporulation or during the following night (18,20). In the present study, we

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examined quantitative relationships of weather variables, crop factors, infection cycles, and disease development during an epidemic in a field plot.

MATERIALS AND METHODS

A field plot (18.5 × 10 m) of onion cv. Autumn Spice was established on sandy loam soil amended with mushroom compost at the research station in Arken, Ontario, in 1979. Seeds were sown on 9 May at a rate of 4.5 kg/ha in 24 rows each 18.5 m long and spaced 0.41 m apart. A trickle irrigation system (Twin-wall® hose, Chapin Watermatics Inc., Watertown, NY 13601) was used to maintain soil moisture during dry periods. Weeds were controlled with Dacthal 75 WP (chlorthal dimethyl, Diamond Shamrock Canada Ltd., Willowdale, Ontario M3J 4R3) applied at a dose of 15.7 kg in 164 L of water per hectare on 10 May. Onion maggots (*Hylemya antiqua* (Meig.)) were controlled with a band spray of Birlane 25 WP (chlorfenvinfos, Shell Canada Ltd., Don Mills, Ontario, Canada M3C 2Z4) applied at a dose of 5.0 kg in 80 L of water per hectare on 22 May and foliar sprays of Diazinon 12.5 EC (Ciba-Geigy Canada Ltd., Mississauga, Ontario, Canada L59 2H5) applied at a dose of 2 L in 200 L of water per hectare on 20 June and 7 July. Plant height and number of emerged leaves in 20 random onions were recorded weekly beginning 20 June.

P. destructor was isolated from overwintered onions in the Cookstown Marsh, Ontario, in May 1979 and maintained on onions in controlled environment. For initial inoculum, eight pot-grown onions were inoculated by the method of Abd-Elrazik and Lorbeer (1), kept in a growth cabinet at 15 C and 70–80% relative humidity (RH) for 10 days, then placed in the center of the field plot. This point source of inoculum was maintained for the period of 20 June to 8 August by replacing source plants after sporulation with freshly inoculated plants.

Incidence and spread of downy mildew in the field plot was monitored after 20 June. The plants were observed each morning for presence or absence of fresh spores of *P. destructor*. Sporulation and subsequent leaf necrosis on individual plants was used to indicate disease incidence. Spread of disease was monitored daily according to frequency of diseased plants in each of 44 quadrats in the plot. Quadrats were established in every third row and arranged diagonally across the rows. Quadrats were each 0.8 m long and spaced 1.6 m apart within the row.

Incidence of airborne spores of *P. destructor* was measured with a 7-day Kramer-Collins drum sampler (G.R. Manufacturing, Manhattan, KS 66506), positioned near the center of the plot. The

trap sampled air at 10 L/min at 0.4 m above the ground. Tapes coated with petroleum jelly and exposed in the trap were mounted on microscope slides in a solution of water-soluble plastic (Gelvatol, Carleton Instruments Ltd., Ottawa, Ontario), and the spores were counted. No corrections were made for variations in trapping efficiency associated with wind speed.

Weather variables were monitored in the onion plot from 20 June to 31 August. Temperatures and RH were measured with a hygrothermograph (Lambrech, model 252, Göttingen, Federal Republic of Germany) located in a Stevenson screen (instrument shelter) at ground level. Rainfall was measured with a tipping bucket gauge (model 6010, Weathertronics Inc., Sacramento, CA 95841). Leaf surface wetness was monitored at 0.2 m above ground level with a DeWit recorder (DeWit, Hengelo, The Netherlands). Wind speed was measured with a cup anemometer (model T16100-16112 Casella, London, England) initially mounted 15 cm above the ground and adjusted at intervals to remain about 5 cm below the top of the crop canopy. Bright sunshine was recorded with a Campbell-Stokes recorder (Casella, London, England). Data, manually transcribed or digitized by computer, were analyzed as frequency data.

RESULTS

Onion growth and development. The onions emerged on 23–25 May and increased in height until 1–7 August, after which many older leaves bent over in various directions to partially close the canopy (Fig. 1). Abundant leaf growth was observed between 15 July and 10 August, and a marked increase in erosion of surface waxes through mutual abrasion of leaves was observed when long leaves developed. Bulbs enlarged rapidly after 25 July. Leaf tips did not die back before development of downy mildew. Leaf emergence continued until 21 August, but the last two or three leaves remained small.

Spore production and dispersal. *P. destructor* sporulated in inoculum source plants at intervals of 1–6 days beginning 25 June (Fig. 1). Within the plot, the pathogen sporulated in two plants on 11 July, in two other plants on 27 July, but in many plants on 8 August and at 1–3 day intervals thereafter. Leaves usually withered about 1–4 days after sporulation.

Estimated numbers of *P. destructor* spores in the air over the onion plot are expressed as daily spore counts, which equal the hourly numbers of spores per 0.6 m³ of air summed for each day (Fig. 1). Numerous spores were trapped on 8 August and on subsequent days favorable for sporulation. A few spores were recovered also on 14, 23, 24, and 25 August when no sporulation was observed. No spores were trapped before 8 August, even though *P. destructor* often sporulated abundantly in the source plants, or on 10, 15, and 18 August when no sporulation occurred.

Disease development and spread. Downy mildew developed as a progression of two minor "steps" on 11 and 27 July (Fig. 1), and two major "steps" on 8–17 and 18–22 August, respectively (Fig. 2).

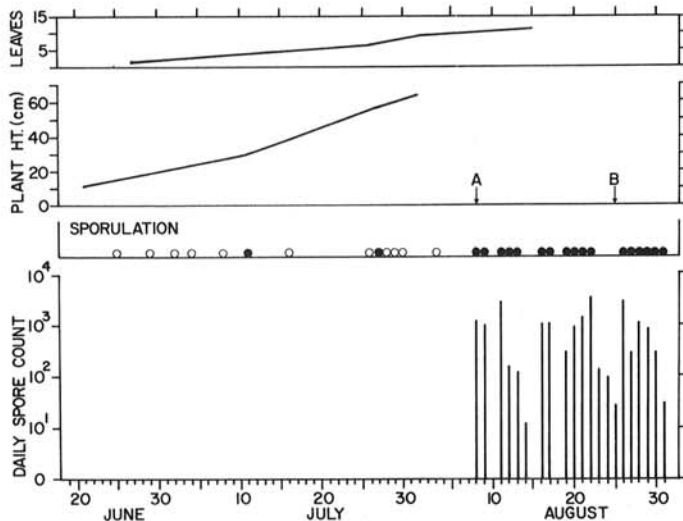


Fig. 1. Number of leaves per plant, height (HT) of plants, occurrence of sporulation in inoculum source plants (○) or in plot plants (●), and number of airborne spores of *Peronospora destructor* trapped in an onion field plot during June, July, and August 1979. Leaves bent over to partially close the canopy on 8 August (A), and most were destroyed by 25 August (B).

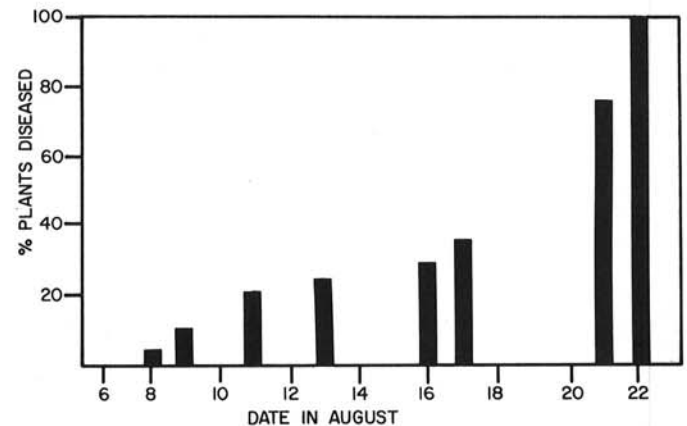


Fig. 2. Steplike increases in incidence of downy mildew in onions during August 1979.

In each minor step, only two plants sporulated in the plots, none within quadrats. The first major step led to symptoms on 35% of the plants. It probably was initiated by spores produced during 26–28 July. The second major step led to symptoms on all plants by 22 August and probably was initiated by spores produced by the first major step.

The disease spread as a diffuse focus around the inoculum source plants (Fig. 3). Disease intensity within the focus initially was nonuniform, and incidence of diseased plants within quadrats generally declined with distance from the source plants. Later, however, disease intensity increased and the focus extended rapidly to encompass the entire plot. Disease progressed more rapidly in the path of prevailing winds.

Relation of weather variables and sporulation. *Temperatures at night.* Mean temperatures at night (2000–0600 hours) throughout the season ranged from 4.7 to 20.6 C and thus were favorable for sporulation of *P. destructor*. However, sporulation occurred on only 30 nights, and temperatures on those nights were in the range of 4.7–20.4 C.

RH. High humidity was defined as RH \geq 95%. *P. destructor* sporulated on nights when periods of high RH began before sunset or up to 6 hr after sunset and persisted until dawn or later. The pathogen failed to sporulate when mean hourly values for RH at 0200–0600 hours were $<$ 95% (Table 1). When RH was \geq 95%, the pathogen sporulated on 30 (58%) of 51 nights. *P. destructor* failed to sporulate on 21 nights even though RH and temperature at 0200–0600 hours were favorable. We observed, however, that humid nights with no sporulation followed days with high temperatures.

Temperatures of previous day. Sporulation on humid nights was examined in relation to mean hourly temperatures at 0800–2000 hours of each preceding day. These ranged from 10 to 27 C. Sporulation was observed on 26 (84%) of 31 nights, on 3 (33%) of 9 nights, and on only 1 (9%) of 11 nights when daytime temperatures were $<$ 23 C, 23–24 C, and $>$ 24 C, respectively (Table 1). Light sporulation on one night after daytime temperatures were $>$ 24 C (screen temperature 25.4 C) possibly was associated with cooling of air near ground level by trickle irrigation water applied throughout that day. Failure of the pathogen to sporulate on five nights when RH was \geq 95% and temperatures of the previous day were $<$ 23 C is not accounted for.

RH $<$ 95% at 0200–0600 hours occurred on only two of 13 nights

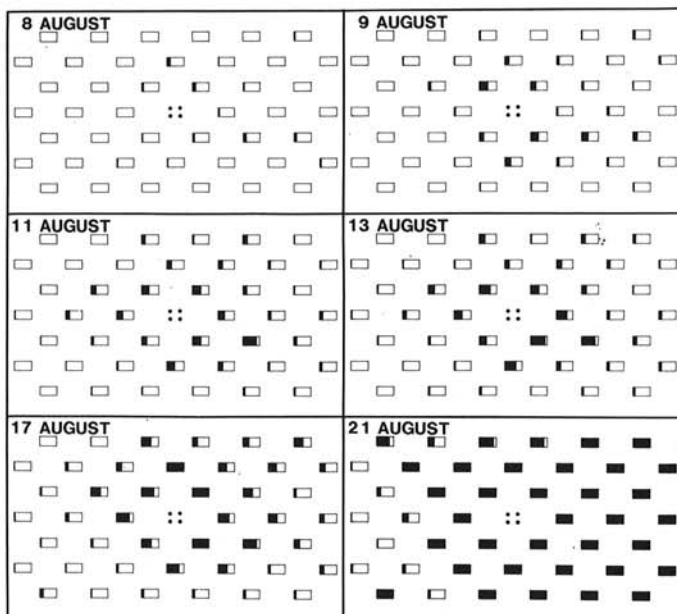


Fig. 3. Focal development of downy mildew in an onion field plot from a point source of inoculum (represented by four central dots) during August 1979. Rectangles represent quadrats, and shading is proportional to disease incidence within respective quadrats. Prevailing winds were from the left.

that followed days when average hourly temperatures were $>$ 24 C. Hence the effects of high daytime temperatures on sporulation generally were not mediated through reduced RH at night.

Leaf wetness. During dew periods, moisture was absent from areas of leaves with sporulation or was deposited as fine droplets on or among the sporophores. No sporophores or spores were observed on portions of leaves with moisture films from dew or rain.

Rain. *P. destructor* failed to sporulate on eight of 10 nights when RH and temperature were favorable but rain occurred. No sporulation occurred on nights when the following amounts of rain fell at the times indicated: 45.5 mm at 2000–0200 hours, 3.3 mm at 2000–0100 hours, 2.0 mm at 2100 hours plus 0.3 mm at 0500 hours, 27 mm at 2200–0300 hours, 7.5 mm at 2400–0200 hours, 1.5 mm or 0.3 mm at 0300 hours, and 4.0 mm at 0300–0600 hours. Sporulation did occur, however, on two nights when light rain (about 2.0 mm) fell during the early part of the night (2300–0100 hours and 2400–0100 hours).

Relation of weather variables and spore release and dispersal. *Daily release and dispersal.* Spore counts increased initially (\geq 20/hr) at 0700 hours, peaked at 0800–0900 hours, then declined (Figs. 4 and 5). Few spores ($<$ 10/hr) were trapped between 1800 and 0600 hours. The diurnal pattern of spore release occurred on days that were rain-free, generally sunny, and showed a marked rise in temperature and decline in RH.

Initial spore release. The initial dispersal of airborne spores occurred consistently at 0700 hours, or about 1.5 hr after sunrise, in the period of 9–27 August (Fig. 6). Initial release did not coincide with initial decline in RH on 11 of 13 days, with initial rise in temperature on eight of 13 days, or with initial wind (\geq 0.18 m/sec) on nine of 13 days. Wind speeds at the time of initial release were \geq 0.3–0.4 m/sec on 11 of 13 mornings (Fig. 6). Wet periods ended 1.0–2.5 hr after the initial increase of spores on 11 of 13 days.

Spore peaks. On sunny days, peak numbers of spores normally were trapped during the mornings as temperatures increased and RH decreased from near saturation. Low peaks of spores sometimes were encountered when RH increased late in the day (Fig. 5).

Spore peaks were delayed when heavy cloud cover persisted through most of the day. A spore peak on 17 August coincided with a short sunny interval at 1100 hours (Fig. 4). On 28 August, also a cloudy day, one peak occurred at 1000 hours and a second coincided with 6 min of sun at 1300 hours. On 23 August, when heavy cloud cover persisted all day and no fresh spores were observed, a peak of old spores occurred at 1400 hours.

Rain and spore release. Spores sometimes were released at night during brief rain showers (2–3 mm rain). On 9, 17, and 23 August, spores (20, 41, and 99/hr) were trapped during rain at 2100, 1900, and 0300 hours, respectively (Figs. 4 and 5). The spores were formed the previous night or earlier.

Wind and spore release. Mean hourly wind speeds recorded in the onion canopy ranged up to 2.1 m/sec during turbulent weather but on most days did not exceed 1.0–1.5 m/sec. Spores of *P. destructor* were trapped mainly when wind speeds were 0.3–1.0 m/sec. Few spores were trapped when wind speeds were below the inertial threshold of the anemometer (0.18 m/sec). Incidence of

TABLE 1. Number of nights^a when *P. destructor* sporulated or failed to sporulate in relation to relative humidity (RH) at night and temperatures of the previous day

	Temperature (C) ^b					
	$<$ 23		23–24		$>$ 24	
	RH \geq 95%	RH $<$ 95%	RH \geq 95%	RH $<$ 95%	RH \geq 95%	RH $<$ 95%
Sporulation	26	0	3	0	1	0
No sporulation	5	11	6	1	10	2

^a Based on 65 nights in the period of 20 June to 31 August when rain did not prevent sporulation.

^b Mean temperature during 0800–2000 hours of the previous day.

^c Mean RH during 0200–0600 hours.

spores at various hours of the day generally did not correlate with wind speed.

Relation of weather factors and infection. *P. destructor* probably infected the onions after sporulation on 29 June, on 11 July, on 26, 27, and 28 July and 3 August, and on 8 August because steps of sporulation incidence in plot plants occurred 10–16 days later. On days of apparent infection, RH was near saturation, leaf wetness persisted until 0900–1000 hours, and temperatures remained moderate (<20 C) all day (29 June, 26 July) or until 1–3 hr after the wet period ended (11, 27, and 28 July and 3 and 8 August). Heavy cloud cover persisted until 0900 hours on 11 July and 3 August, 1000 hours on 27 July, 1400 hours on 8 August, through most of the day and with fog on 29 June, and all day on 26 and 28 July. The leaves became wet again at 1900–2100 hours on 11, 26, and 27 July, on 3 and 8 August, and in association with rain at 1200 and 1400 hours on 29 June and 28 July, respectively.

P. destructor sporulated on source plants but evidently failed to infect the plot plants on 25 June and 16 July. On these days, the

humid period ended early (about 0600 hours), and the leaves dried at 0700 hours but were not rewetted until 2100–2200 hours. Temperatures were moderate (<23 C) and little cloud cover occurred. Dry and sunny weather thus appeared to block events leading to infection.

DISCUSSION

Simultaneous monitoring of several weather factors, crop development, and incidence of sporulation and airborne spores revealed quantitative and temporal relationships among these variables. Earlier field studies considered only RH and temperature in relation to disease (14,16,18).

RH $\geq 95\%$ at night was required for sporulation, but only after 0200 hours. Sporulation was prevented when RH was <95% at 0200–0600 hours. A lower humidity threshold for sporulation (RH $\geq 90\%$) was reported by Yarwood (20). Virányi (18) claimed that the threshold of RH was $\geq 95\%$ and the minimum humid period was ≥ 6 hr. The present study defines the temporal relationship of the humid period and sporulation.

The observation that *P. destructor* failed to sporulate on areas of leaves with moisture films of rain or heavy dew indicated that free moisture inhibited sporulation. Light dew in the form of fine and scattered droplets, however, was not inhibitory. These observations are contrary to an earlier report that free water on leaves was required for sporulation (5). Moisture films may have mediated the observed antispore effect of rain, although rain before dawn may have injured sporophores. The present study revealed a specific effect of rain on sporulation and corroborated earlier reports that rainy weather was unfavorable for disease progress (7,12,20).

The inhibition of sporulation at night in association with high

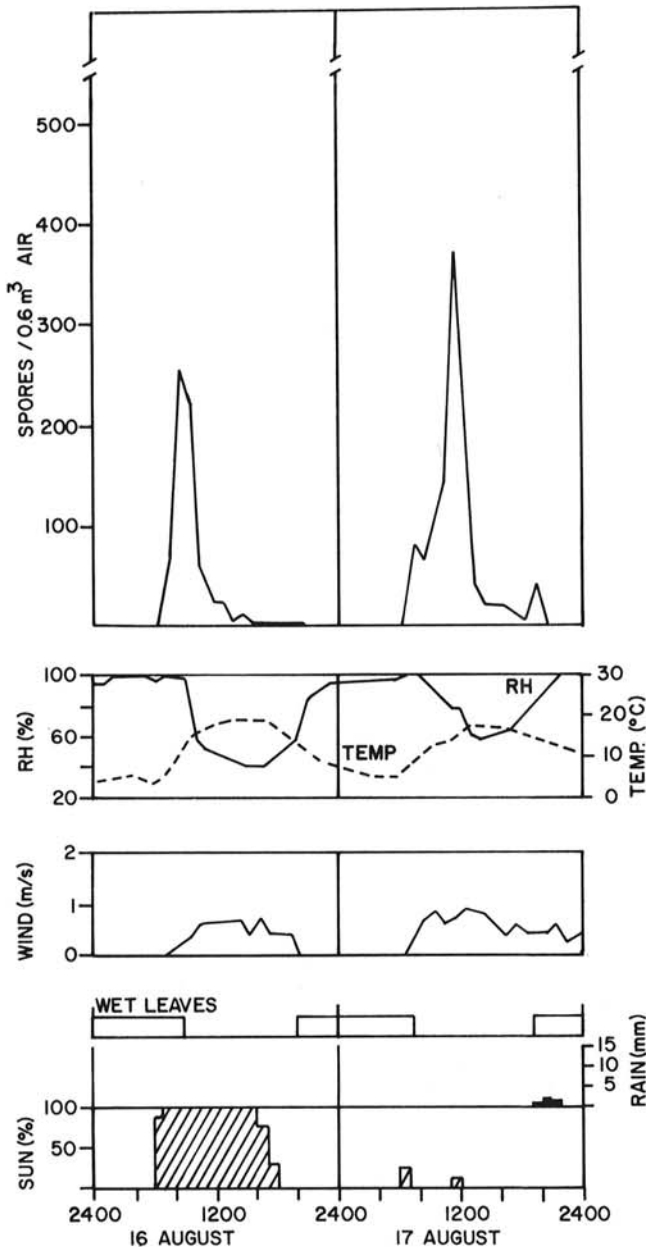


Fig. 4. Incidence of airborne spores of *Peronospora destructor* in relation to relative humidity (RH), temperature, wind speed, leaf wetness duration, rainfall, and bright sunshine on 16 and 17 August 1979.

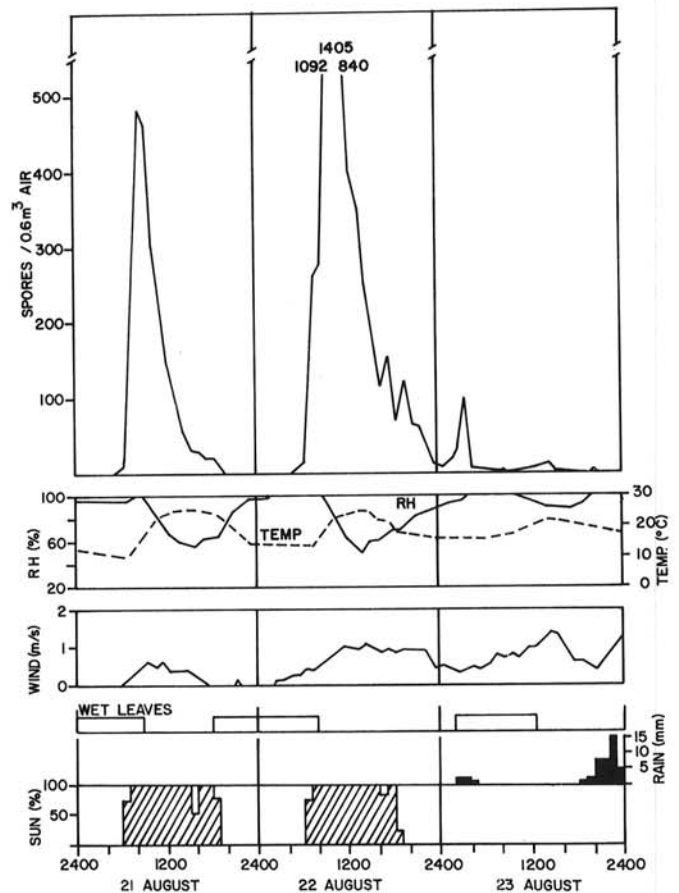


Fig. 5. Incidence of airborne spores of *Peronospora destructor* in relation to relative humidity (RH), temperature, wind speed, leaf wetness duration, rainfall, and bright sunshine on 21, 22, and 23 August 1979.

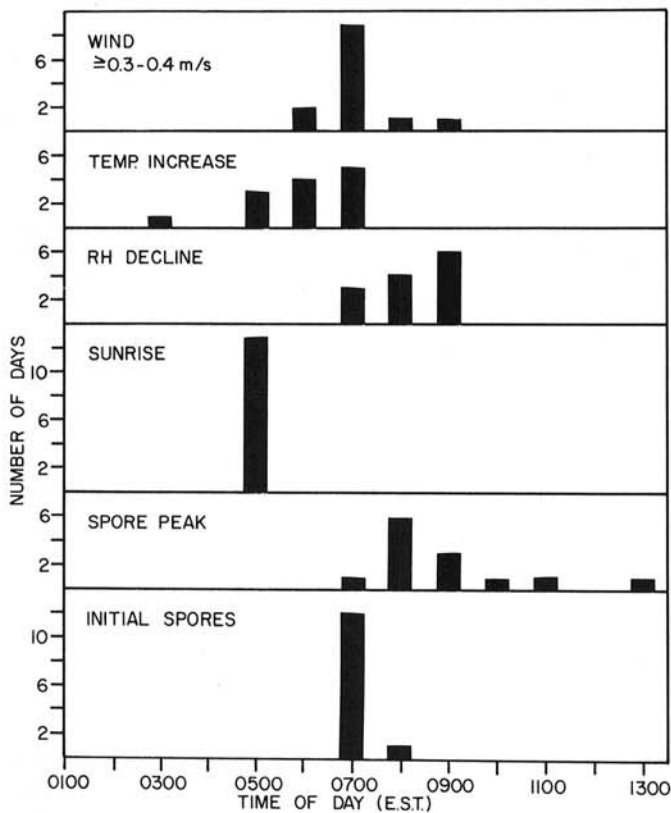


Fig. 6. Frequency distributions of times of initial spore release and daily spore peaks of *Peronospora destructor* in relation to time of sunrise and times of initial decline of relative humidity (RH) from saturation, initial temperature increase, and wind at $\geq 0.3-0.4$ m/sec on 13 days in August 1979.

temperatures (>24 C) the previous day (0800–2000 hours) confirms and refines a general observation made in the greenhouse by Yarwood (20). Daytime temperatures <23 C were not inhibitory. These observations appear compatible with the antispore hypothesis of Cohen (3) and Cohen and Eyal (4). They postulated that observed inhibition of sporulation in *Peronospora tabacina* and *Pseudoperonospora cubensis* by light and enhancement of the inhibition when temperatures were warm was associated with a light-activated and temperature-dependent accumulation of a sporulation inhibitor that decayed in the dark. In infected onions, a similar inhibitor produced in large amounts on warm days may fail to “decay” sufficiently during the night to allow sporulation of *P. destructor*.

According to available data, sporulation of *P. destructor* may be predicted according to the following variables, provided that the required period of latency has been satisfied: mean hourly temperatures $<23-24$ C on the previous day (0800–2000 hours), favorable temperatures at night (about 4–24 C), RH $\geq 95\%$ beginning at 0200 hours or earlier and persisting at least until 0600 hours, and absence of rain at night (except light rain of ≤ 2.0 mm before 0100 hours).

The initial release of spores at dawn was observed consistently at 0700 hours during August but often preceded initial humidity decline and drying of the leaves. Fine droplets of dew among sporophores at the time of initial dispersal indicated that moisture conditions were at or near saturation. Evidently, spore release was not prevented during periods of leaf wetness and high RH. The correlation of initial release with 1.5 hr after sunrise may be associated with red-infrared radiation, which is known to promote spore release in several dry-spored fungi (8,10). Radiation produces a surge of electrostatic charges in the atmosphere after dawn that may impel spore release through an electrostatic discharge mechanism such that as proposed by Leach (9). A similar phenomenon may trigger the initial release of *P. destructor* spores at dawn. Correlative evidence indicated, however, that winds of

0.3–0.4 m/sec also may have a role in initial dispersal (Fig. 6).

Peak numbers of airborne spores usually occurred 1–2 hr after initial spore release and coincided with decline in atmospheric humidity, drying of the leaves, and increasing wind speeds. Spore release in many dry-spored fungi coincides with lowering of humidity (6,8,11,13,15), and Leach (10) demonstrated the role of humidity in spore release independently of temperature. Spores of *P. destructor* were trapped when wind speeds in the onion crop were as low as 0.18 m/sec; thus dispersal usually was not limited by low wind speeds.

Infection of onions by *P. destructor* required at least 2–3 hr of leaf wetness (5,20), but the time of infection in relation to daily spore production and dispersal remains undetermined. The association of infection with persistence of wet periods until 0900–1000 hours indicated that spores dispersed at dawn may infect new leaves during 0700–1000 hours. Frequent lack of disease spread following sporulation indicated that spores do not always remain infective until subsequent wet periods.

The steplike pattern of the epidemic appeared related to sequences of short periods ($<1-2$ days) required for sporulation and infection alternating with long latent periods (10–16 days). Because disease was evident only when the pathogen sporulated, disease appeared to progress in steps coincident with sporulation. Plot plants that sporulated on 11 and 27 July evidently were infected during a sporulation-infection period on 29 June and 11 July, respectively. Thereafter, sporulation-infection periods on 26–28 July and 3 August and on 8 August produced two massive steps of disease spread and intensification in which all plants became infected. Thus the epidemic was completed essentially in four infection cycles.

The major steps of disease increase, and hence the explosiveness of the epidemic, undoubtedly were related to prolific sporulation of *P. destructor* and frequent infection of the onions. At the times of the major disease steps, sporulation frequency was high, and infection may have been enhanced by the erosion of surface waxes, as found in previous studies in the laboratory (1,2). Because released spores remain infective for ≤ 1 day (5,17,20), failure of infection shortly after dispersal may arrest disease progress. Weather unfavorable for infection on several days when sporulation occurred appeared to delay the epidemic, especially in June and July. Occurrence of the sequence of weather factors that condition sporulation-infection periods, and thus maintain the continuity of infection cycles, is critical for downy mildew epidemics and a key to strategies for controlling the disease.

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