Interactive Effects of the Dark Period, Humid Period, Temperature, and Light on Sporulation of *Peronospora destructor*

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This research was supported by the Natural Sciences and Engineering Research Council of Canada (Grant A6119) and the Ontario Ministry of Agriculture and Food.
Accepted for publication 6 July 1984.

ABSTRACT

Hildebrand, P. D., and Sutton, J. C. 1984. Interactive effects of the dark period, humid period, temperature, and light on sporulation of *Peronospora destructor*. Phytopathology 74:1444-1449.

Onion plants infected wtih *Peronospora destructor* were exposed in growth cabinets to light for 14 hr then to various conditions of darkness, high relative humidity (RH), and temperature. The end of the light period was designated as 2000 hours. The pathogen sporulated in the range of 6–22 C when the humid period began at 2200 hours, but not at 6, 10, 14, and 22 C when humid periods at these respective temperatures began at 2400, 0100, 0300, or 0300 hours or later. When conditions favored sporulation, numbers of spores produced increased as the humid period was extended from 0400 to 0700 hours. Deferred onset of high humidity during the dark period delayed development of sporophores and spores, and usually reduced the numbers of spores produced. The optimum temperature for sporulation increased from 10 to 18 C when onset of high humidity was changed from 2200 hours to 0300 hours. Spores matured 2 hr earlier at 14 C when the dark period was started at 1800 hours instead of 2000 hours. Interruption of the humid period by RH 80–90% for 0.5 hr at 0100–0400 hours stopped sporulation. Exposure of young sporophores to light at 0100–0400 hours resulted in production of deformed spores.

Additional key words: *Allium cepa*, downy mildew, weather factors.

Peronospora destructor (Berk.) Casp., the cause of downy mildew of onion (*Allium cepa* L.), sporulates prolifically on host leaves when environmental conditions are favorable. The spores are produced at night and are subsequently dispersed during the day (8). Knowledge of relationships of weather factors and sporulation is important for developing a predictive model of downy mildew.

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Yarwood, in 1937 (14), discovered the dependency of sporulation by *P. destructor* on daily cycles of light and darkness. The pathogen sporulates when infected onions are exposed to a light period then a dark period, but not when kept in continuous light or darkness (14). High relative humidity (RH) is required during the dark period (14,15). In a recent field study (8), we observed that the pathogen requires RH $\geqslant$95% for sporulation, but only after 0200 hours. Reduced humidity between 0200 and 0600 hours is inhibitory. Sporulation at night requires temperatures of 4–7 to 22–25 C (10,15) but is inhibited when mean temperatures of the preceding day exceed 23–24 C (8).

Quantitative and temporal relationships of temperature, humid

periods, photoperiods, and dark periods to sporulation remain to be clarified. In the present study, we examined temperature, time of onset of high humidity during the dark period, light, and reduced humidity as interactive variables affecting the incidence and process of sporulation and numbers of spores produced.

MATERIALS AND METHODS

Onion plants for sporulation studies were grown from sets (cultivar Yellow Ebenezer) and inoculated with a spore suspension (3×10^4 spores per milliliter) of *P. destructor* as described previously (7,9). The inoculated plants were placed in a dark moist chamber at 10 C for 24 hr to promote infection, then kept in a growth cabinet operating with a 14-hr photoperiod, a photon flux density of 350 $\mu E/m^2/sec$, and at 20 C for 9 days to provide a latent period.

In sporulation studies, the daily dark period was initiated at the end of a 14-hr photoperiod. The time of initial darkness was designated as 2000 hours to aid interpretation of biological observations in terms of daily cycles of light and darkness encountered in the field. To verify the ability of the pathogen to sporulate, four of the inoculated plants in each experiment were placed in a dark humidity chamber at 14 C at 2000 hours.

Morphologic development of sporophores (conidiophores) and spores (conidia) was studied on plants placed at 14 C in dry darkness (RH 80–90%) at 2000 hours then in humid darkness (RH $\geqslant$95%) at 2200 hours. Pairs of plants were removed from the humid darkness at 30-min intervals until 0800 hours. Sporophores were immediately excised from the leaves with a scalpel, then mounted in lactophenol-acid fuchsin, examined microscopically and photographed. A series of morphologic phases of sporulation was identified and recorded photographically to provide a standard key for subsequent studies.

Small humidity chambers (22 × 22 × 45 cm) were constructed for studies of humid periods in relation to sporulation. Each chamber was made of a wood frame covered with clear polyethylene film and fitted with a flap door. A cover of black plastic was placed over each chamber when darkness was required. Eight of the chambers were installed in a single growth cabinet. High humidity was provided in the chambers as a fine fog produced by water nebulizers (model 841; DeVilbiss Ltd., Barrie, Ontario, Canada). Temperature and RH were monitored in the growth cabinet with a hygrothermograph (model 252; Lambrecht, Göttingen, Federal Republic of Germany).

Chambers of the same dimensions and materials were used for quantifying spore release. Small perforations were made in the sides of these chambers to allow circulation of air but little loss of spores. The chambers were positioned in a growth room operating at 23 C and RH 55–60%, and illuminated with cool-white fluorescent tubes and incandescent bulbs. Photon flux density within the chambers was about 65 $\mu E/m^2/sec$. Airborne spores in each chamber were monitored with a Kramer-Collins drum sampler (G. R. Manufacturing, Manhattan, KS) modified to sample for 24 hr instead of 7 days. Air was sampled at 10 L/min. Tapes coated with petroleum jelly and exposed in the traps were mounted on microscope slides in a solution of water-soluble plastic (Gelvatol, Carleton Instruments Ltd., Ottawa, Ontario, Canada) and the spores were counted.

Effects of constant temperatures and time of onset of high RH during the dark period on the phase of sporulation and numbers of spores produced were studied using the humidity chambers and spore-relase chambers (Fig. 1A). Temperatures used were 4, 6, 10, 14, 18, 22, and 26 ± 0.5 C. Infected onion plants were placed in a growth cabinet in dry darkness (RH 80–90%) at 2000 hours, then removed at intervals to dark humidity chambers in the same growth cabinet. One humidity chamber with four replicate plants was taken from the growth cabinet at 0400, 0500, 0600, and 0700 hours and the plants were quickly transferred to the spore release chambers in the growth room. Airborne spores sampled in the chambers during 1 hr provided estimates of relative numbers of mature spores produced. One random leaf was excised from one plant in each chamber and observed microscopically to determine the most advanced phase of morphologic development of sporophores and spores in accordance with the standard photographs. Each temperature and dry period treatment was repeated once.

Time of onset of high humidity during the dark period also was examined in relation to spore production while the duration of the humid period was kept constant. In this experiment, a mark was made near the basal end of each leaf with a nontoxic marker at the time of inoculation to distinguish inoculated areas of leaves from subsequent growth. Infected onions were placed in dry darkness (RH 80–90%) at 18 C at 2000 hours, and four of the plants were transferred to the dark humidity chambers at 2200, 2400, 0200, 0300, or 0400 hours for 9 hr (Fig. 1B). Spores on the inoculated areas of two leaves per plant (eight leaves per treatment) were immediately aspirated into water (spore recovery 85–90%) and counted on a hemacytometer. Surface areas of the leaves were measured with a digitizer (model MOP-3; Carl Zeiss Inc., Oberkochen, Federal Republic of Germany), and the number of spores per square centimeter was calculated for each leaf.

Possible effects on sporulation of early initiation of dry darkness were explored by exposing plants at 14 C to dry darkness beginning at 1800 hours instead of 2000 hours, then to humid darkness after 2200 hours (Fig. 1C). Plants were transferred to the spore release chambers at 0200, 0300, 0400, and 0500 hours and morphologic development of sporophores and spores was assessed as before.

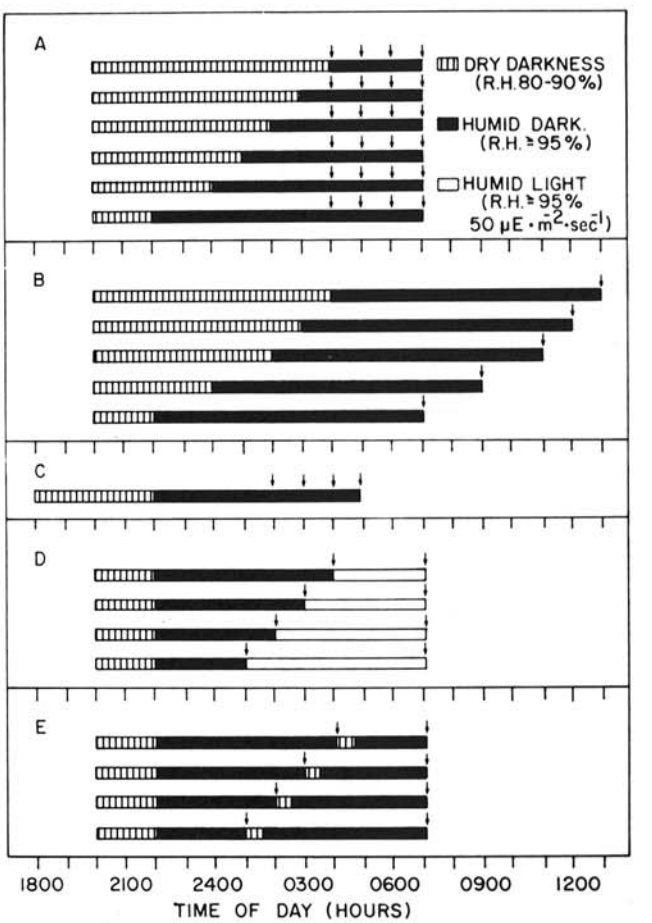

Fig. 1. Sequences of dry dark periods, humid dark periods, and humid light periods used in studies on the interactive effects of darkness, high humidity, temperature, and light on sporulation of *Peronospora destructor* on onion leaves. Arrows indicate times when the phase of sporulation was determined or when spores were sampled and quantified. **A,** Study on effects of the time of onset of high RH during the dark period at various constant temperatures (4–26 C). **B,** Study on effects of time of onset of high RH during the dark period, while duration of high humidity was constant (9 hr). **C,** Study of effects of early initiation of dry darkness. **D,** Study on effects of light during the humid period. **E,** Study on effects of discontinuities in the humid period (RH 80–90% for 0.5 hr).

To examine the influence of light on developing sporophores and spores, infected plants were exposed to light during the humid period. The plants were kept in dry darkness in the growth cabinet from 2000 to 2200 hours and then transferred to the dark humidity chambers. The cabinet lights were turned on at 0100 hours, and the black plastic covers on the humidity chambers were removed at 0100, 0200, 0300, or 0400 hours to initiate the light period while high humidity was maintained (Fig. 1D). At each of these times, and at 0700 hours, the phase of sporophore and spore development was determined for one leaf detached from each plant. The growth cabinet was maintained at 18 C and was illuminated with cool-white fluorescent tubes and incandescent bulbs which provided a photon flux density of 50 $\mu E/m^2/sec$ in the humidity chambers.

Effects of discontinuities in the humid period on sporulation were investigated using infected plants which were exposed in darkness in the humidity chambers at 14 C beginning at 2200 hours. The plants were moved outside the humidity chambers, but within the same growth cabinet (RH 80–90%) for 0.5 hr at 0100, 0200, 0300, and 0400 hours, then returned to high humidity (Fig. 1E). At each time of exposure to the lower humidity, and also at 0700 hours, one leaf was removed to determine the phase of sporophore and spore development.

RESULTS

Morphologic development of sporophores and spores. Four phases of sporophore development and four phases of spore formation were recognized for a total of eight successive phases of sporulation (Fig. 2A to H). Phases of sporophore development were: emergence and elongation, primary branching, secondary branching, and formation of sterigmata. A single sporophore, or (less frequently) two or three sporophores, emerged from each stoma. Spores developed acropetally on the sporophores (Fig. 2E and F) and normally were pyriform and papillate at the distal end when completely developed (Fig. 2H). Recognized phases of spore formation were: development of spore initials, enlargement of spores on lower branches to about one-half full size, enlargement of spores to about full size but without papillae, and finally, the development of papillae on the distal ends of the spores (papillate spores were readily detachable from the sporophores).

Temperature and time of onset of high humidity. *P. destructor* sporulated at 6, 10, 14, 18, and 22 C, but not at 4 and 26 C, when infected plants were exposed to high humidity beginning at 2200 hours, 2 hr after the dark period began (Table 1, Fig. 1A). The pathogen did not sporulate at 6, 10, 14, and 22 C when humid periods at these temperatures began at 2400, 0100, 0300, and 0300 hours or later, respectively. A few sporophores and immature spores developed at 18 C when the humid period began as late as 0400 hours.

Temperature and time of onset of the humid period affected the time of initiation and rates of development of sporophores and spores (Table 1). Development according to the eight morphological phases was delayed at each temperature when initiation of the humid period was deferred. Sporophores and spores developed faster at 10 and 14 C than at other temperatures when the humid period began at 2200 hours. However, when onset

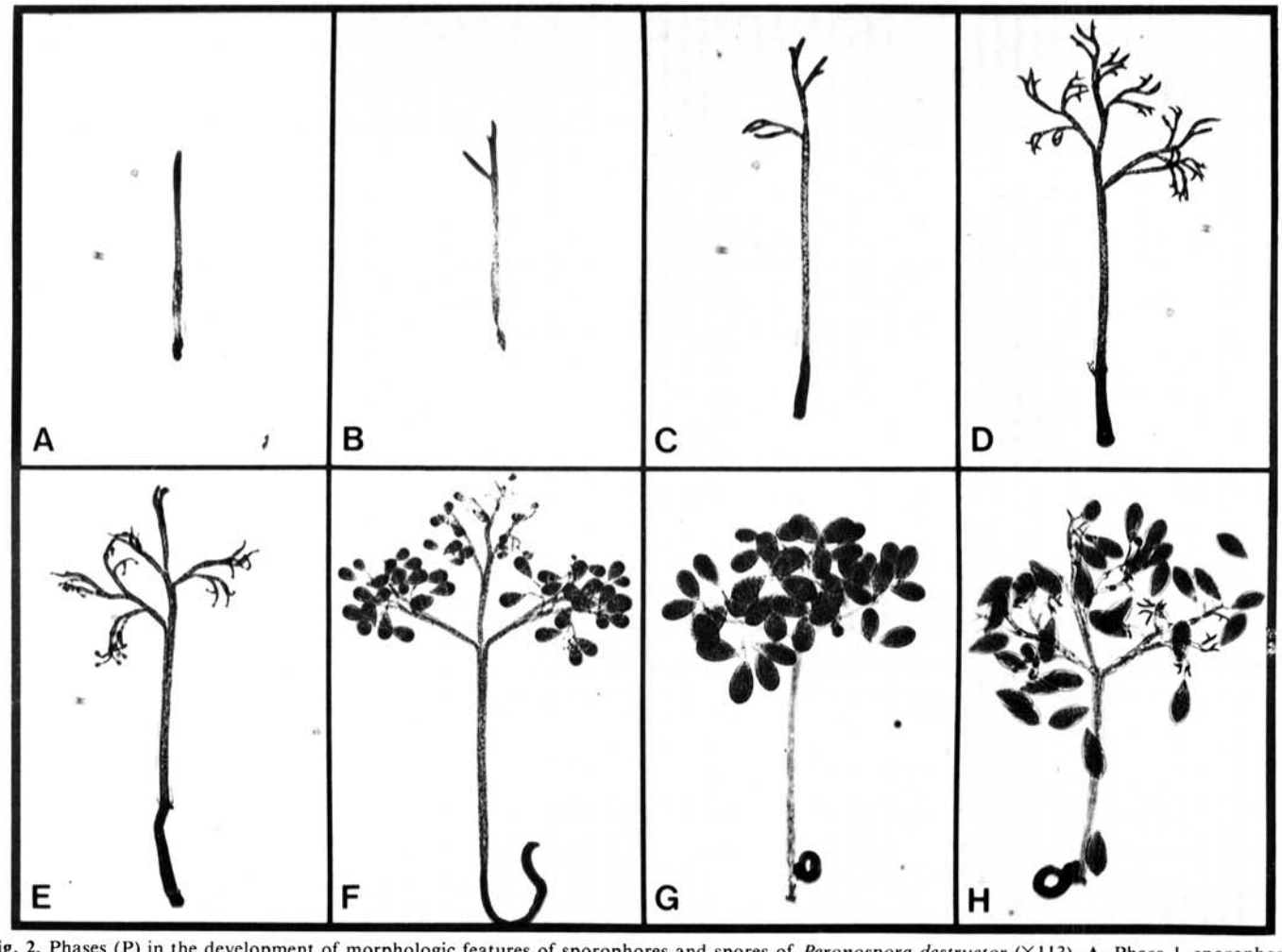

Fig. 2. Phases (P) in the development of morphologic features of sporophores and spores of *Peronospora destructor* (×113). **A,** Phase 1, sporophore emerging from host stomate and elongating. **B,** Phase 2, sporophore developing primary branches. **C,** Phase 3, sporophore developing secondary branches. **D,** Phase 4, sterigmata developed. **E,** Phase 5, spore initials developing on sterigmata. **F,** Phase 6, spores enlarging to approximately half their maximum size. Note the acropetal sequence of development. **G,** Phase 7, spores almost completely developed but not papillate. **H,** Phase 8, spores completely developed, papillate, and readily detachable.

of high humidity was progressively delayed the higher rates of development shifted at first to 14 and 18 C, and finally to 18 C only. For example, when high humidity began at 2200 hours, some spores dispersed at 0400 hours at 10 or 14 C and were in phase 6 at 18 C. However, after the humid period began at 0200 hours observations at 0400 hours revealed sporulation in phases 1 and 5 at 14 and 18 C, respectively.

Numbers of spores trapped per hour in the spore release chambers increased as the period of exposure of the infected plants to high humidity was extended to 0700 hours from 0400 hours (Table 1). Greatest numbers of spores were trapped from plants exposed at 14 C to high humidity between 2200 and 0700 hours. Total numbers of trapped spores generally decreased as the onset of the humid period was delayed at each temperature. This was related not only to the delay in development of the sporophores and spores, but to reduced densities of sporophores and spores on the leaves. Reduced spore production in response to delayed onset of the humid period was observed also when duration of high RH was kept constant at 9 hr (Figs. 1B and 3). These observations at 18 C indicated that the decreased sporulation was a function of time of high humidity during the dark period.

However, numbers of spores trapped after a humid period of 6 or 7 hr often increased when the humid period was delayed. At 18 C, for example, 16 and 1,209 spores were trapped after 7 hr of high humidity from 2200 to 0500 hours and from 2400 to 0700 hours, respectively, and 1,011 and 6,387 spores were trapped after 6-hr humid periods from 2400 to 0600 hours and from 0100 to 0700 hours, respectively (Table 1). Similar increases were found also at 14 C.

Early initiation of the dark period. Spores matured 2 hr earlier at 14 C when the dark period was started at 1800 hours instead of 2000 hours, even though the humid period was initiated at 2200 hours in both treatments (Fig. 1A and C). When darkness began at 1800 hours, numbers of spores trapped per hour at 0200, 0300, 0400, and 0500 hours were 2, 16, 1,558, and 6,826, respectively.

Light and sporulation. Light affected spore development when initiated at early stages of sporulation. When the dark and humid periods began at 2000 and 2200 hours, respectively, and the light period began at 0100, 0200, 0300, and 0400 hours (Fig. 1D), the most advanced phases of sporulation at the onset of light were, respectively, phases 1, 3, 5, and 8. Sporophores exposed to light in phase 1 or 3 produced spores that appeared to be deformed when examined at 0700 hours (Fig. 4). These spores were variable in size, usually unpigmented, and occasionally constricted near the midpoint. Basal portions of spores often were of greater diameter than the distal portions. Most spores produced on sporophores that were in phase five or eight at the onset of light appeared to be normal and were of various shades of violet. These spores were readily detached at 0700 hours.

Interrupted high humidity. Sporulation was in phases 3, 4, 6, and 8 when the humid period was interrupted for 0.5 hr at 0100, 0200, 0300, and 0400 hours, respectively (Fig. 1E). Branches and sterigmata on sporophores in phases 3 and 4 collapsed in response to the lowered humidity and no spores were produced on these sporophores during subsequent high humidity. Exposure of sporophores and spores to lowered humidity when in phase 6 prevented further development of spores, but no deformities were observed. A few spores were completely developed (phase 8) when exposed to drier air at 0400 hours, but less mature spores and sporophores did not develop further when high humidity was resumed.

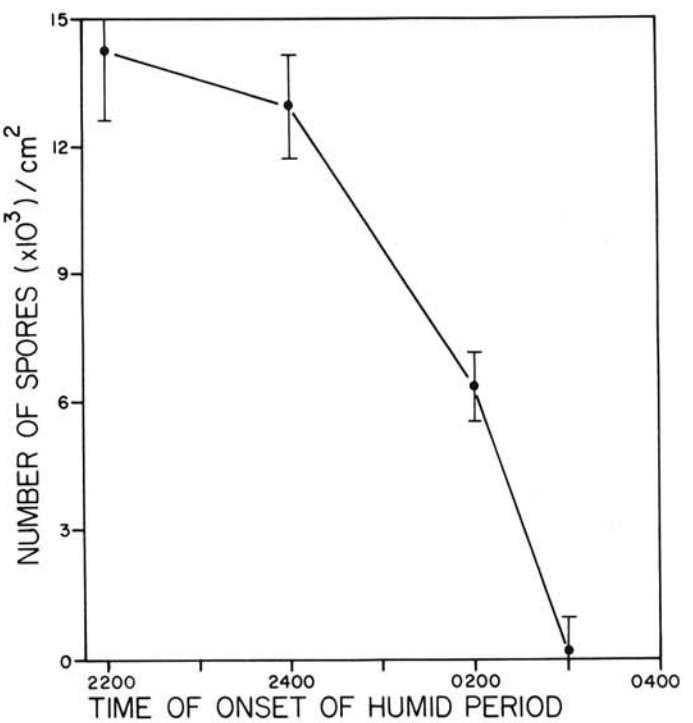

Fig. 3. Spore production of *Peronospora destructor* on onion leaves in relation to the onset of high humidity during the dark period at 18 C. Plants were exposed to darkness beginning at 2000 hours and RH 80–90% before being transferred to humid chambers for 9 hr. Each point is the average number of spores from eight leaves and the bars represent standard errors.

DISCUSSION

Relationships of temperature, humid periods, and dark periods to sporulation of *P. destructor* are more complex than was reported earlier. The results of the present study confirm the observations of

TABLE 1. Interactive effects of temperature and time of onset of high humidity on the development of sporophores and spores of *Peronospora destructor*

Time[a] of onset of high humidity (hours)	Time[a] of observations on sporulation (hours)	Phase of sporulation[b] or number of trapped spores[c] at the following temperatures (C):						
		4	6	10	14	18	22	26
2200	0400	–[d]	P6	18	3	P6	P5	–
	0500	–	1	55	106	16	P6	–
	0600	–	36	940	4,137	1,868	39	–
	0700	–	34	2,366	15,430	5,283	1,721	–
2400	0400		–	P6	4	P5	P3	
	0500		–	P7	170	9	P5	
	0600		–	P8	605	1,011	P7	
	0700		–	P8	3,433	1,209	200	
0100	0400			–	P5	P5	P3	
	0500			–	P7	P7	P5	
	0600			–	42	31	P6	
	0700			–	1,651	6,387	4	
0200	0400				P1	P5	P1	
	0500				P3	P7	P3	
	0600				P4	12	P5	
	0700				P6	105	P8	
0300	0400				–	P1	–	
	0500				–	P3	–	
	0600				–	P5	–	
	0700				–	8	–	
0400	0400				–	–		
	0500					P1		
	0600					P4		
	0700					P6		

[a] Dark period began at 2000 hours.
[b] Eight phases of sporulation were designated phases 1 to 8 (Fig. 2). The most advanced phase of sporulation observed is indicated when no spores were trapped.
[c] Numbers of spores trapped from four onion plants during 1 hr in a spore release chamber (average of two replications).
[d] Minuses (–) indicate no sporophores were observed.

Hiura (10) and Yarwood (15) that the pathogen sporulates at 6–22 C, and optimally at about 14 C when high humidity begins early in the dark period. However, it further demonstrates that temperature and time of onset of high humidity during the dark period interactively affect the sporulation process and numbers of spores produced. Delay in the onset of high humidity during the dark period produced temperature-dependent decreases in the rate of development of sporophores and spores and in total spores produced. Yarwood (14) noted that *P. destructor* did not sporulate in greenhouse-grown onions at 13 C when the humid period began at 0400 hours, but he did not examine effects of other temperatures and humid periods. Progressively reduced spore production in response to increasing delays in onset of high humidity during the dark period has been observed also in *Peronospora tabacina* (13).

Though delay in onset of the humid period reduced numbers of spores trapped from 0400 to 0700 hours (Table 1) and reduced spore production when the humid period was kept constant at 9 hr (Fig. 3), delays in 6- or 7-hr humid periods increased spore production (Table 1). This paradox probably was associated with the initial phase (about 4–5 hr) of the dark period when high RH is inconsequential to sporulation (7). Overlap of the humid period with the initial or "conditioning" phase (3) shortened the period of postconditioning high RH which is required for the sporulation process and spore maturation. Substantial overlap of brief humid periods (6 or 7 hr) with the conditioning phase shortened postconditioning high RH sufficiently to limit maturation of spores; however, spores matured normally when the overlap was short.

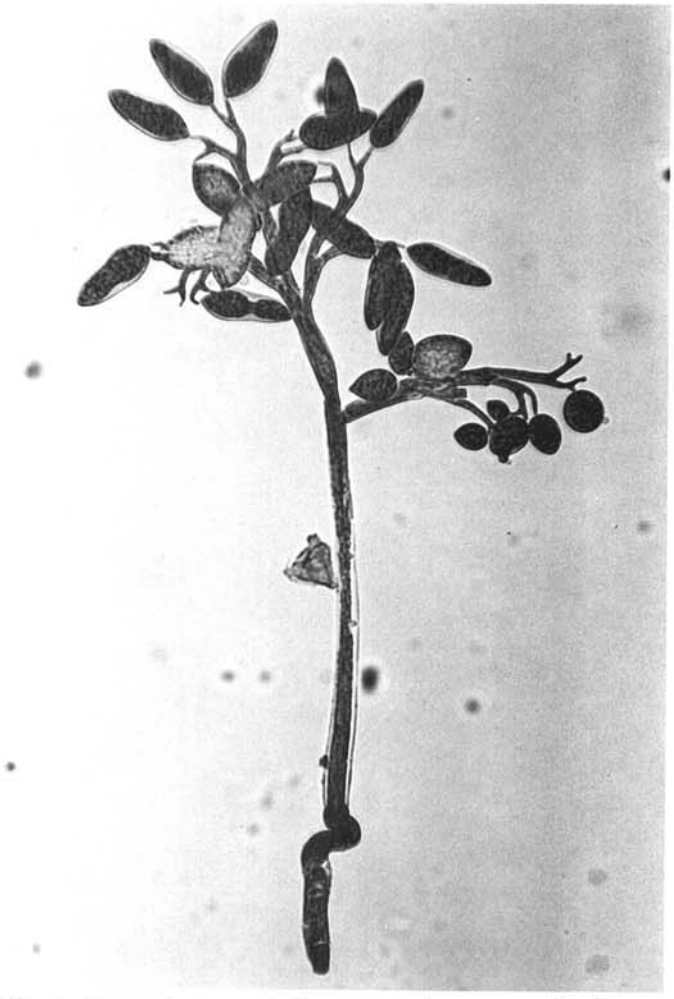

Fig. 4. Abnormal spores of *Peronospora destructor* produced on a sporophore on an onion leaf exposed to light (50 $\mu E/m^2/sec$) at 18 C beginning at 0100 hours (×180). Sporophores were in developmental phase 1 when exposed to light. See Fig. 2 for phases of development.

Decreased spore production by downy mildew fungi associated with late onset of high humidity during the dark period has been attributed to depletion during darkness of host photosynthates formed during the preceding light period (1,15). Relationships of photosynthesis and sporulation, and utilization of a large proportion of photosynthates for sporangial production in the dark period have been demonstrated for *Pseudoperonospora cubensis* (4,11). While photosynthate depletion probably influenced spore production by *P. destructor*, the observed effects of dark-period temperatures on spore production implicate a role of additional metabolic processes. At low temperatures (6 or 10 C), the pathogen sporulated only when high humidity was initiated shortly (2–4 hr) after darkness began, but at higher temperatures (14 or 18 C) the pathogen was able to sporulate normally when the humid period began as late as 5 or 7 hr after the onset of darkness. Because photosynthates probably became depleted more slowly at the lower than at the higher temperatures, a temperature-dependent enzyme system is postulated as an additional regulator of sporulation.

Possible regulation of sporulation by an enzyme system is supported by the sporulation response after various delays in onset of high humidity during the dark period at various temperatures. For each temperature increment of 4 C from 6 to 18 C, *P. destructor* was able to sporulate when the onset of the humid period was delayed a further 1–2 hr (Table 1). The longest delay that still allowed sporulation was at 18 C. At 22 C the pathogen sporulated only after delays shorter than at 18 C. Maximum delays in the humid period for sporulation at each temperature resembled a typical temperature-dependent enzyme response. The postulated enzyme may originate from the pathogen, the host, or both.

The observations that spores of *P. destructor* matured 2 hr earlier when darkness was initiated 2 hr earlier, and the continuation of the sporulation process in the light after 5 hr of darkness, indicated that sporulation was a dark-induction phenomenon which otherwise proceeded in continuous light. Similar observations and conclusions have been made for the related pathogens, *P. tabacina* (5,13) and *Bremia lactucae* (12). The results for *P. destructor* also were compatible with a hypothesis propounded for *P. tabacina* and *P. cubensis* that inhibition of sporulation by light is associated with a light-activated accumulation of a sporulation inhibitor that subsequently decays in the dark (1,2).

Although sporulation of *P. destructor* proceeded in the light after plants had been exposed to darkness, the spores frequently were deformed. Bottle- or dumbbell-shaped spores (Fig. 4) have been observed previously in *P. destructor* (15), *P. tabacina* (1), and *P. cubensis* (2) after developing sporophores were exposed to light. Cohen (1) demonstrated that the red portion of the visible spectrum (0.6–0.7 μm) caused this effect. Our study has revealed that the phase of development during which sporophores were exposed to light determined whether morphologically normal or abnormal spores would be formed. Deformed and unpigmented spores were produced when sporophores were exposed to light during the early phases (P1–3, Fig. 2 A to C) but not the later phases of development (P5–7, Fig. 2 E to G). Under field conditions in Ontario, sporulation probably does not progress to completion when the humid period begins at 0300 hours and temperature during the dark period is 18 C or when the humid period begins at 0200 hours and temperatures are 14 or 22 C. Developing sporophores would be vulnerable to the effects of light at sunrise which occurs at about 0500 hours during the growing season.

Blockage of the sporulation process by a brief (0.5 hr) exposure of developing sporophores and spores to air below saturation (RH 80–85%) indicated that sporulation probably requires an atmosphere that is continuously saturated or nearly saturated. Yarwood (14) also observed that incompletely developed spores failed to mature when exposed to reduced RH. Hartmann et al (6) demonstrated that *Peronospora parasitica* sporulated on cabbage seedlings only when the atmospheric water potential was about −30 bars or lower (≥97% RH at 15 C).

Results of our study demonstrate that sporulation of *P. destructor* is regulated by complex temporal interactions of

humidity, temperature, light, and darkness. The results generally confirmed field observations that the pathogen sporulated only when the humid period began at 0200 hours or earlier (8). Continuous monitoring of the interacting variables within the onion crop and the quantitative data of their interactive effects are critical for accurate prediction of the sporulation of *P. destructor* in disease management schemes.

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