Survival of Detached Sporangia of *Peronospora destructor* and *Peronospora tabacina*

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ABSTRACT

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Detached sporangia of *Peronospora destructor* were exposed for various lengths of time to different laboratory combinations of temperature and relative humidity (RH); temperatures of 10, 25, and 35 C were used in combination with 33, 53, 76, and 95% RH. Germination indicated survival. For all RH tested, *P. destructor* sporangia survived best at 10 C and poorest at 35 C. For all temperatures tested, sporangia survived poorest at 33% RH, and differences in survival between 53 and 76% RH generally were not significant. Sporangia of *P. destructor* and *P. tabacina* were also exposed outdoors on cloudy or sunny days before being put into standard conditions to germinate. Of temperature, RH, and sunlight, sunlight was the most important factor in determining sporangia survival. On cloudy days, the average germination of detached sporangia of *P. destructor* was reduced from 83 to 68% in 6 hr, whereas on clear, sunny days germination was reduced from 46 to 0% in 6 hr. The effect of solar irradiation on the germination of sporangia of *P. tabacina* was similar to that for sporangia of *P. destructor*.

Additional key words: downy mildew, epidemiology, germination, relative humidity, solar irradiation, temperature.

The spread of plant diseases by airborne spores depends on the ability of spores to withstand environmental stresses while detached from the host. Sporangia of downy mildew fungi disperse mainly during the morning and early afternoon (6,8,15). To cause infection, they often must survive in the field for several hours until conditions are more suitable, such as those at night. Detached sporangia must survive for an even longer time for long-distance transport to succeed. Sporangia that cause blue mold on tobacco may be transported by wind over several hundred kilometers; to remain viable during such a long journey they must survive in the atmosphere for 12–48 hr (4).

The effect of temperature and relative humidity (RH) in a controlled environment on the survival of detached spores has been examined (2,9,13,17); exposure of spores to solar irradiation, however, was not investigated. Studies of effects of solar irradiation on spores have not been quantitative (3,7,9,11,14,18,21). We examined the survival of detached sporangia of *Peronospora destructor* (Berk) Casp. and of *Peronospora tabacina* Adam when exposed to various temperatures, RHs and intensities of solar irradiation.

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MATERIALS AND METHODS

We measured the ability of sporangia of *P. destructor* and *P. tabacina* to germinate after they were detached from their sporangiophores and exposed for different lengths of time to various air temperatures, RHs, and intensities of solar irradiation. We used germination as an indication of the ability of sporangia to survive and withstand environmental stress. Material from plants grown in a greenhouse and in fields were used in the experiments.

Plant material. Onion plants (*Allium cepa* L.) were grown in a greenhouse from bulbs (cv. Sentinel) and from seeds (cv. Early Yellow Globe D56 and White Spanish Bunching; Harris Seed Co., Rochester, NY 14624) from October 1981 to April 1982. The plants grown from bulbs were inoculated 7–8 wk after planting, and plants grown from seeds were inoculated 17–18 wk after planting. We compared the germination of sporangia of *P. destructor* produced on Sentinel to that on Early Yellow Globe and White Spanish Bunching and found that germination among them was similar when conditions of temperature and RH were the same. The procedure of inoculation and incubation described by Abd-Elrazik and Lorbeer (1) was used to inoculate onion plants with *P. destructor*. Two weeks after inoculation, infected plants were sealed in moistened plastic bags overnight (14 hr darkness). The next morning the bags were opened, but the plants and sporangia were not removed, allowing them to dry slowly during the next

1.5–2 hr. This procedure was intended to simulate the drying of plants in the field.

Onion sets (cv. Ebenezer) were planted on 20 April 1982 in a fine sandy loam soil at Lockwood Farm, Hamden, CT. Four blocks, each containing 10 rows 6 m long, were planted with 1 m of separation between the blocks. Rows were 10 cm apart, and sets were spaced at 7 cm within rows. On 10 June 1982, onion seeds (cv. White Spanish Bunching) were planted densely in two blocks of four rows 6 m long and 20 cm apart. The plants were later thinned so that they were about 1–2 cm apart in the row. The soil had been previously amended with 670 kg/ha of 10-10-10 fertilizer, 22 kg/ha of Diazinon (TM Ciba-Geigy Corp., Greensboro, NC 27419) (14%) and 13 kg/ha of Dacthal (TM Diamond Shamrock Corp., Cleveland, OH 44144) (75 WP).

On 15 June, the plants in the field were inoculated when several pots containing sporulating onion plants were placed among the healthy plants grown from sets. The first sporulation on field plants occurred between 25 and 28 June. Sporulation was widespread from 29 June to 16 July following nights with free leaf moisture.

Tobacco (*Nicotiana tabacum* L. 'Connecticut Broadleaf') seedlings were transplanted to the field on 22 July 1982. About 700 seedlings were planted in rows 1 m apart in a 0.04-ha field. Several plants were inoculated with *P. tabacina* on 23 August when the leaves were sprayed with a suspension of sporangia obtained from diseased plants maintained in a greenhouse. By the end of August the inoculated plants showed symptoms of blue mold, and sporulation was heavy. By mid-September, nearby plants were infected by natural spread.

Sporangia of *P. destructor* were deposited on thoroughly washed and dried glass coverslips (22 × 22 mm). So that a representative sample could be obtained, each coverslip received sporangia from four or five different leaves. In the laboratory, we collected sporangia by gently touching the sporangia-laden leaves with the coverslips. In the field, we collected sporangia by tapping a leaf held just above the coverslip and letting the sporangia settle onto its surface.

Experiments with *P. tabacina* differed from those with *P. destructor* only in that *P. tabacina* sporangia were deposited on strips of cellophane. Preliminary tests had indicated that *P. tabacina* did not germinate well on glass slides.

We assumed that, like sporangia of *Phytophthora infestans* (13), germination of detached sporangia of *P. destructor* and *P. tabacina* is enhanced by gradual rehydration. Sporangia were allowed to rehydrate, therefore, in a petri dish containing wet filter paper at room temperature. After about 10 min in this small rehydration chamber, a fine mist formed on the coverslips or cellophane. In experiments with *P. destructor*, the coverslips were removed and placed on a droplet of water on 2% agar in a petri dish, with the sporangia between the coverslip and the agar. In experiments with *P. tabacina*, the sporangia-laden cellophane was placed on the water droplet on the agar, with the sporangia on top. Inside the germination chamber, wet filter paper placed inside the top of the dish maintained a moist atmosphere. To assess germination after 24 hr incubation in the dark at 10 C, spores were examined in 10 microscope fields at ×100 for each sample. About 300–1,000 sporangia were counted for each treatment.

Constant temperature and RH experiments. Sporangia of *P. destructor* were exposed to various constant RHs and temperatures by being placed in sealed 11 × 11 × 3-cm plastic boxes containing saturated solutions of various salts. These boxes were placed in incubators that maintained temperature to within 1 C. The salt solutions used and the nominal RHs maintained were: KNO_3, 95%; NaCl, 76%; $Mg(NO_3)_2 \cdot 6H_2O$, 53%; $MgCl_2 \cdot 6H_2O$, 33% (12). To check the RHs, the boxes containing the various saturated salt solutions at 20 C were sealed and placed in a water bath in which the temperature was gradually decreased until the dew point was reached. The saturated salt solutions covered the bottom of the plastic box. The coverslips or cellophane with the sporangia were placed in the bottom half of a petri dish (9 cm diameter) that was floated on the salt solution. The boxes were closed, sealed with Parafilm, and put in an incubator at 10, 25, or 35 C.

After various lengths of exposure, samples of sporangia were removed from constant temperature and RH, and placed first in the rehydration chamber and then in the germination chamber. For each set of tests, some sporangia were immediately put into the rehydration and then into the germination chamber without any exposure to the temperature-RH conditions being tested; these sporangia were used to assess initial (zero time) germination. Replicated tests were done at 10 C and 33, 53, 76, or 95% RH, and at 25 and 35 C and 33, 53, or 76% RH, each for various lengths of exposure. We present the data as the average and standard error of the mean (SEM) of percent germination for each combination of temperature, RH, and exposure time. We also analyzed each constant temperature test separately with a two-way analysis of variance, using RH and exposure time as the two factors, excluding germination percentages at zero time. Duncan's multiple range test was used to test for significant differences in sporangial survival at different RH values averaged over all exposure times, and to test for significant differences in survival at different exposure times averaged over all RH values.

Aluminum plate experiments. We compared the survival of sporangia of *P. destructor* collected from plants grown in a greenhouse and exposed to the same level of solar irradiance (SR) but to different temperatures. This was accomplished by attaching sporangia-laden coverslips to aluminum plates 20 × 20 × 0.5 mm thick with a small spot of petroleum jelly. The plates had been painted either black or white on both sides with flat-finish paint. In the sun, the black or white plates achieved different temperatures. To measure the temperature at the center of each plate, a small thermocouple probe (#SCPSS-04OU-6, Omega Engineering, Stamford, CT 06907) was placed along and held in good thermal contact with the underside of the plate. Two black and two white plates were used. Nine coverslips containing about 100–1,000 sporangia each were stuck to the 15 × 15-cm center area of each plate. The plates were supported horizontally about 0.5 m above the top of an unpainted wooden table and were 1.5 m above the ground. One black and one white plate were placed so that the sporangia were facing upward, exposed to direct sunlight. The other black and the other white plate were placed with the sporangia facing downward, shaded from direct sunlight by the plate itself. The irradiance reflected from the table top onto the latter sporangia was about 30% of that received by sporangia facing the sun. Sporangia on two black and two white plates were exposed to four different conditions: direct sun and temperatures about 20 C above ambient air temperature (upward-facing black plate); shade and temperatures about 20 C above ambient (downward-facing black plate); direct sun and temperatures about 8 C above ambient (upward-facing white plate); and shade and temperatures about 8 C above ambient (downward-facing white plate).

Samples of sporangia were removed from the plates and put into conditions that allowed them to germinate after different lengths of exposure. This experiment was repeated three times, each on a different clear day in early June.

Shade tent experiments. Sporangia of *P. destructor* or of *P. tabacina* were collected from plants grown in the field. The sporangia were either exposed to full sun or were partially shaded by cloth screens for different lengths of time. The coverslips or the strips of cellophane containing the sporangia were attached with double-stick tape to plastic screening supported on 20 × 20-cm wooden frames. These frames were supported horizontally on coarse-mesh wire held about 0.5 m above the ground by wooden stakes. Some samples were exposed to full sunlight, and others were shaded by a 1.2-m square tent consisting of two, four, or eight layers of loosely woven orlon cloth stretched over a wooden frame. The cloth had about three threads per centimeter and was reinforced with more closely woven threads at intervals of 23 cm in one direction and 30 cm in the other direction. The tent roof was about 1 m above the ground and the sides extended below the level of the wire mesh that supported the plastic screens holding the samples of detached sporangia.

SR ($W \cdot m^{-2}$) was reduced 25% by two layers, 50% by four layers, and 70% by eight layers of cloth; thus samples of sporangia could be exposed simultaneously to 100, 75, 50, or 30% of full sun. SR inside and outside the tents was measured with a pyranometer (LI 200SB,

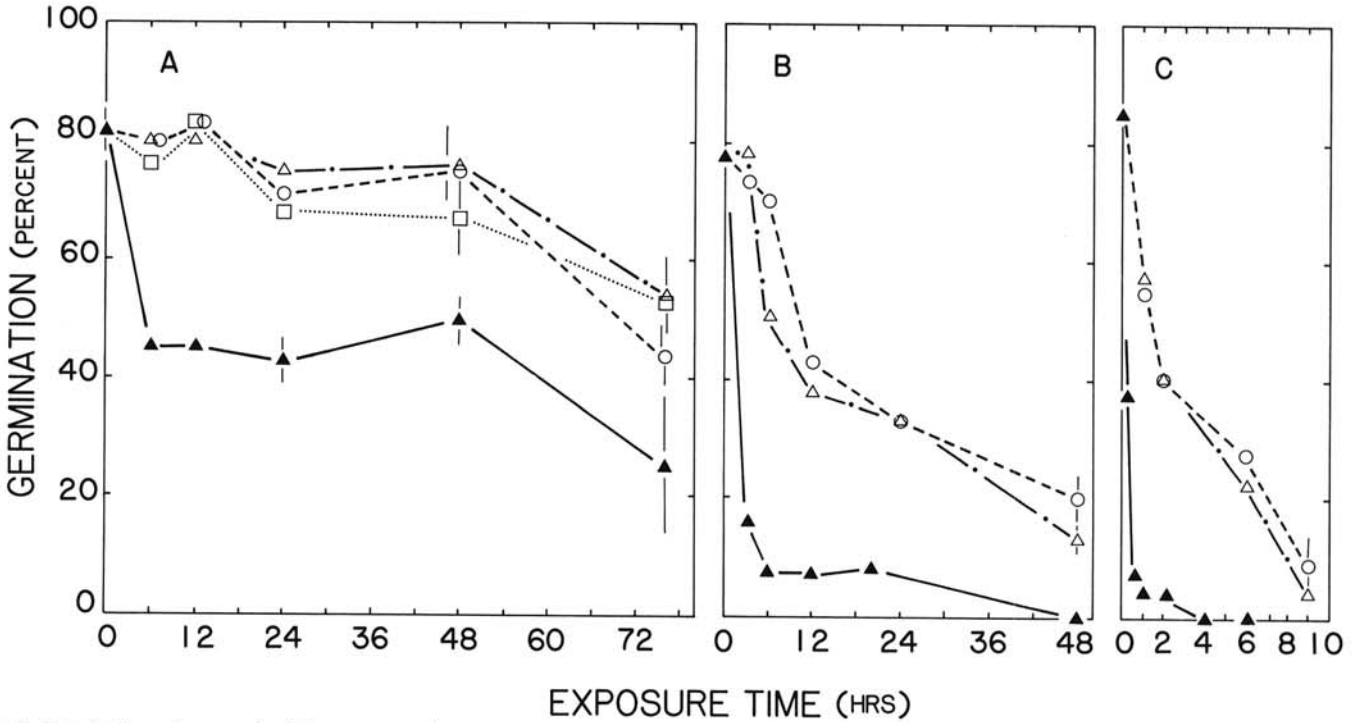

Fig. 1. Germination of sporangia of *Peronospora destructor* exposed to constant temperature and relative humidity in the laboratory for various lengths of time. Temperature was maintained at **(A)** 10 C, **(B)** 25 C, or **(C)** 35 C. Relative humidity was maintained at 33% (—▲—), 53% (--O--), 76% (·—Δ—·), or 95% (···□···). Typical SEM values are shown by vertical bars.

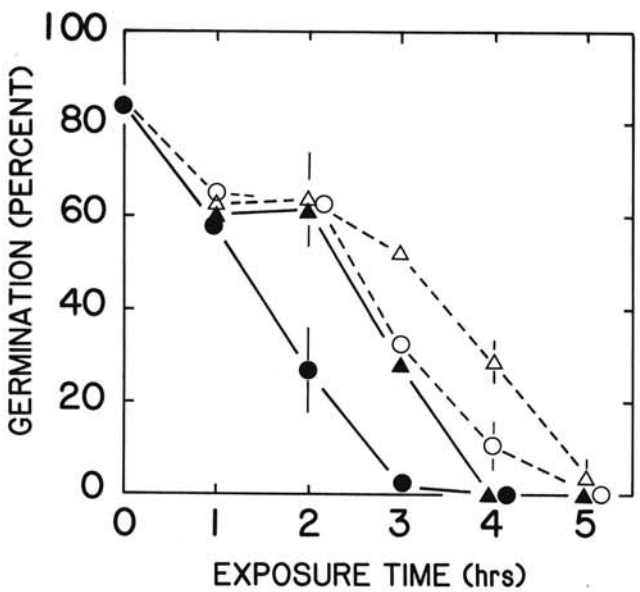

Fig. 2. Germination of sporangia of *Peronospora destructor* exposed to different levels of solar irradiation and to different temperatures achieved on white and on black plates. Sporangia received direct solar irradiance of about 700–900 $W \cdot m^{-2}$ (•,▲) or a reflected irradiance of about 210–280 $W \cdot m^{-2}$ (o,Δ). The temperature of the black plates (•,O) averaged 45–51 C, and the temperature of the white plates (▲,Δ) averaged 29–33 C. Typical SEM values are shown by vertical bars.

LI-COR, Inc., Lincoln, NE 68504). Temperature and RH inside and outside the tents was measured with a force-ventilated psychrometer. The permeability of the cloth top and sides and the wire mesh support at the bottom of the shade enclosures allowed free air exchange with the outside. Air temperature inside the enclosures was about 1 C lower, and the RH was about 2% higher than the temperature and RH outside. The temperature of the coverslips on the screens was measured with a fine (0.15-mm diameter) thermocouple. In full sun, the coverslips were 3–5 C warmer than ambient air, whereas in shade they were within 1 C of air temperature. These experiments allowed us to compare the effect of different levels of SR at approximately the same temperature and RH. SR also was measured with a recording pyrheliograph, and RH and air temperature were measured with a recording hygrothermograph in a nearby standard weather shelter. Wind speed at height of 1.5 m was measured by a Thronthwaite sensitive cup anemometer.

RESULTS

Constant temperature and RH. In general, germination decreased as exposure time increased, and decreased fastest at the highest temperature and at the lowest RH (Fig. 1). Sporangia survived best at 10 C (Fig. 1A), less well at 25 C (Fig. 1B), and poorest at 35 C (Fig. 1C). Comparison of the means and SEMS of percent germination indicates that, for most exposure times, there were no significant differences between RH values of 53, 76, and 95% at 10 C, or between 53 and 76% RH at either 25 or 35 C. For all temperatures tested, however, germination at 33% RH was clearly lower than that at the higher RH values. A two-way analysis of variance indicated no significant differences between germination at 53, 76, and 95% RH at 10 C, but significant differences between 53 and 76% RH at 25 and 35 C, with germination at 76% RH being significantly lower than at 53% RH. This analysis also showed a significant effect of exposure time at all three temperatures tested and a significant interaction between RH and exposure time at 25 and 35 C but not at 10 C. The interaction was mainly due to the more rapid decrease in germination at 33% RH than at the higher RH values.

Exposure to 33% RH at any temperature resulted in the fastest and greatest reduction in germination. Under moderate temperatures and RHs, detached sporangia maintained their ability to germinate for several days.

Aluminum plate experiments. A measure of the relative importance of SR and high temperatures on the germination of *P. destructor* sporangia exposed to the sun on either a white or a black aluminum plate is shown in Fig. 2. The germinability of sporangia exposed to direct sun decreased faster than for those shaded from direct sun. For the same solar irradiance, germination decreased

faster on the black plates than on the relatively cooler white plates, but shaded sporangia on the black plate survived better than those in direct sun on the cooler white plate.

Germination of sporangia exposed to direct sun on either the black or the white plate was zero after 4 hr. In contrast, a few sporangia still germinated after 4 hr when shaded from direct sun. The data in Fig. 2 are the averages of three experiments on days with similar average SRs (730, 950, and 820 $W \cdot m^{-2}$) and air temperatures (24, 25, and 24 C). The relative humidities on the three days were 43, 35, and 55%, respectively. Because the temperature of the black plates were higher, the RH for sporangia on black plates would be lower than for sporangia on white plates; this also may have contributed to the differences in germination. For the conditions tested, solar irradiation seemed more lethal to sporangia than did relatively high temperature.

Shade tent experiments with *P. destructor*. The effect of SR on survival was tested further by exposing sporangia of *P. destructor* in the field to levels of SR determined by cloth shades on selected days from 30 June to 15 July 1982, and from 27 to 31 August 1982. Sporangia were collected and exposed to the weather on clear, partly cloudy, and overcast days. Weather conditions in the field for the dates of experiments are summarized in Table 1.

The germination of sporangia of *P. destructor* detached either at 0830 hours or at 1130 hours and exposed to field conditions for various lengths of time is shown in Fig. 3. The data were grouped according to the average SR during the 6-hr exposure. SR was 70–280 $W \cdot m^{-2}$ for the weak-irradiation group, 280–630 $W \cdot m^{-2}$ for the moderate-irradiation group, and 630–900 $W \cdot m^{-2}$ for the strong-irradiation group. In all but two cases, use of the shade tent shifted the classification of SR from the strong to the moderate group. With one exception, weak SR occurred on overcast days.

We began assessing germination after the sporangia were detached from their sporangiophores. Before being detached, the sporangia were exposed to SR between sunrise and either 0830 or 1130 hours. The effect of this predetachment exposure was very different on clear than on cloudy days. The initial germination for sporangia detached at 0830 hours and exposed on overcast days was 83%, while it was 57% for those exposed to moderate SR, and 46% for those exposed to strong irradiation. During 6 hr of exposure following detachment, germination decreased to 68, 5, and 0% for sporangia exposed to weak, moderate, and strong SR, respectively.

Survival of sporangia exposed to weak SR was much higher than for those exposed to moderate or strong SR. Comparisons of the means and SEMS of the percent germination at the various exposure times indicated no significant difference between moderate or strong SR, but percent germination of spores exposed to weak SR was significantly higher.

The initial germination of sporangia detached at 1130 hours on cloudy days was essentially the same as for those detached at 0830 hours and exposed for 3 hr. After a 5-hr exposure, germination of the sporangia detached at 1130 hours had decreased to about 55%. Under moderate or strong SR, germination of sporangia detached at 1130 hours was higher than for those detached at 0830 hours and exposed for 3 hr. After a 5-hr exposure to moderate or strong SR, germination of the sporangia detached at 1130 hours decreased to 13 and 0%, respectively. The rate of decrease in germination for these sporangia was very similar to that for those detached at 0830 hours and exposed to moderate or strong SR.

Some samples of detached sporangia, after being exposed in the field for 5 or 6 hr, starting at either 0830 or 1130 hours, were kept indoors until the next morning before being put in conditions to germinate. Germination percentage of sporangia exposed to weak SR and kept overnight remained at about 50%. For sporangia exposed to moderate or strong SR, however, germination was 0% for those collected at 0830 hours and 5% for those collected at 1130 hours.

Shade tent experiments with *P. tabacina*. The germination of *P. tabacina* exposed with or without cloth shades on an overcast day (2 September) and on a sunny day (17 September) (Table 1) is shown in Fig. 4. The effect of SR on the germination of *P. tabacina* sporangia was very similar to that shown for *P. destructor* (Fig. 3). On 2 September, sporangia were collected at 1000 hours after the dew had evaporated from the plants. There was no difference in germination between sporangia exposed without shade and those shaded by four layers of cloth (50% reduction in irradiance). These sporangia maintained nearly full germinability, even after 5 hr of exposure. For sporangia collected at 1200 hours on 2 September

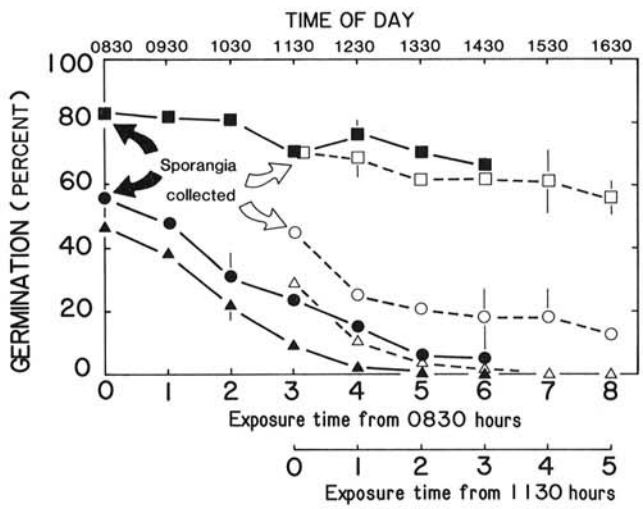

Fig. 3. Germination of sporangia of *Peronospora destructor* collected from onion plants in the field at 0830 hours EST (■,●,▲) and at 1130 hours EST (o,□,Δ). The sporangia were exposed for different lengths of time to solar irradiance ($W \cdot m^{-2}$) of 70–280 (■,□), 280–630 (●,o) and 630–930 (▲,Δ). Typical SEM values are shown by vertical bars.

TABLE 1. Summary of meteorological conditions in the field during the shade tent experiments

Date	Time of exposure[a]	SR[b] ($W \cdot m^{-2}$)	T[b] (°C)	RH[b] (%)	Wind speed[c] ($m \cdot s^{-1}$)	Sky conditions
30 June	0815–1215	790	23	72	···	Intermittent clouds
1 July	0900–1400	930	22	42	2.8	Clear
6 July	0900–1400	890	26	45	2.7	Clear
7 July	0830–1430	640	22	66	3.0	Mostly sunny
15 July	0800–1500	720	29	59	1.3	Clear
27 August	0815–1330	150	21	79	1.6	Overcast
28 August	0900–1500	590	21	52	1.0	Intermittent clouds
31 August	0840–1600	410	23	63	1.3	Mostly cloudy
2 September	0830–1500	250	23	83	1.5	Overcast
16 September	0845–1445	180	18	94	···	Mostly cloudy
17 September	0830–1530	650	17	55	1.6	Clear

[a]Time (Eastern Standard Time) during which detached sporangia were exposed in the field.
[b]SR = solar irradiance; T = air temperature; RH = relative humidity.
[c]Average wind speed measured at 1.5 m above the ground. Three dots represent a missing observation.

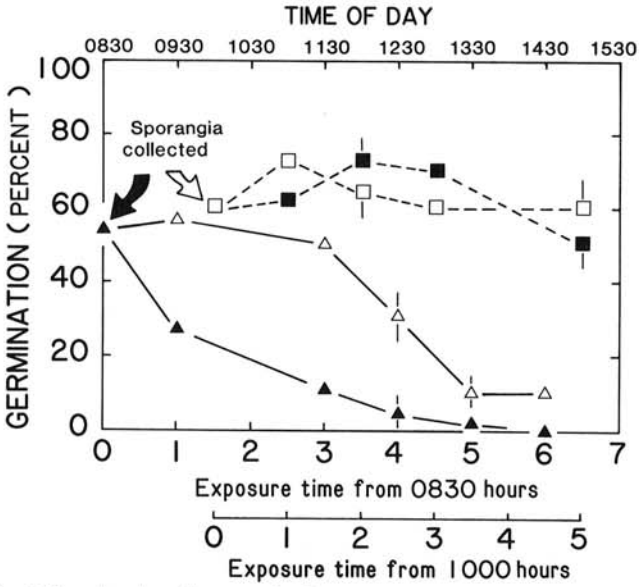

Fig. 4. Germination of sporangia of *Peronospora tabacina* collected from tobacco plants in the field at 0830 hours EST on a sunny day (——) and at 1000 hours EST on a cloudy day (----). The sporangia were exposed for different lengths of time to solar irradiances ($W \cdot m^{-2}$) of 650 (▲), 200 (△), 250 (■), and 125 (□). Typical SEM values are shown by vertical lines.

(data not shown), there was no decrease in germination after 3 hr of exposure. For sporangia exposed outdoors for 5 hr and then kept indoors until the next morning before being put in conditions to germinate, germination was still about 16%.

On 17 September, the germination of sporangia collected at 0830 hours and exposed to full sun decreased faster than for those shaded by four layers of cloth. After 4 hr of exposure, sporangia kept in the sun did not germinate, whereas about 10% of those that were shaded still germinated.

DISCUSSION

Survival of *P. destructor* was decreased most markedly by exposure to the extreme temperature of 35 C and extreme RH of 33%, which are both rare conditions in Connecticut. We found no significant differences in germination for RH values of 53, 76, and 95% at 10 C, but found significant differences for RH values of 76 and 53% at either 25 or 35 C, where germination was higher at 53 than at 76% RH. This was in disagreement with data of Newhall (14), who found that germination decreased regularly with decreasing RH. Survival was better at high than at low RH, in qualitative agreement with results for *Phytophthora infestans* (13,16).

SR rather than temperature or RH was the dominant factor affecting survival of *P. destructor* and *P. tabacina* sporangia in the field. Because of the differences among the techniques used and lack of details in earlier studies, it is difficult to compare our results to those of other researchers. For instance, in some studies the SR was not measured (3,11,18,21) and in some the sporangia were immersed in water (14,20). In our experiments, strong (630–900 $W \cdot m^{-2}$) and moderate (280–630 $W \cdot m^{-2}$) SR resulted in a rapid decrease in germination of the detached sporangia of *P. destructor* and *P. tabacina*. In contrast, both kinds of sporangia survived for many hours in conditions of weak (70–280 $W \cdot m^{-2}$) SR (Figs. 3 and 4). The relatively small differences between the effect of strong and moderate levels of SR suggest that the effect of sunlight may not be gradual but acts only after the sporangia receive a critical dose of irradiation. A critical-dose hypothesis is also suggested by data of Visser et al (19), who found that germination of *Exobasidium vexans* spores is little affected by exposure to sun up to 3 hr, but declines rapidly with an additional hour of exposure.

In comparison to sporangia detached early, those of *P. destructor* and *P. tabacina* retained a higher germinability when detached from their hosts in later hours of the day. Our data are in qualitative agreement with those of Yarwood (21), who found that sporangia of *P. destructor* survived longer when they remained attached to their sporangiophores on the original sporulating leaves than when they were detached. The relatively higher viability of sporangia detached later in the day, and the epidemiological significance of this, has been described for some *Phytophthora* species (5,10). Sporangia produced on different nights might differ physiologically and thus may respond differently in subsequent treatments. We did not study the effects of such preconditioning.

Our results support observations by Hildebrand and Sutton (8) that dry and sunny weather block events leading to infection by *P. destructor*. But our data also indicate that successful transfer of inoculum could occur on sunny days over relatively short distances, eg, within the same field, especially when sporangia land inside the crop canopy and are shaded by it. Long-range transport of viable inoculum over several hundred kilometers could occur probably on cloudy days but is not likely on sunny days.

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