Effect of Radiation, Temperature, and Moisture on Conidial Germination of *Alternaria solani*

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ABSTRACT

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Conidia of *Alternaria solani* germinated only when the measured relative humidity (RH) was ≥92% and free moisture encompassed the conidia. When maintained under controlled temperature and moisture conditions, conidia germinated most rapidily in darkness when ambient temperature was near 25 C and RH ≥96%. For conidia irradiated with simulated sunlight (>300 nm), inhibition of germination increased as light intensity increased. Light between 300–500 nm appeared to be responsible for the inhibition in germination. Wavelengths >750 nm did not inhibit germination, indicating that inhibition was a true light phenomenon, not a response to increased temperature.

Additional keyword: light radiation.

In nature, many fungi are exposed to solar radiation in the visible and nonvisible region (approximately 290–2,200 nm) of the electromagnetic spectrum. This radiation influences many aspects of the behavior, growth, development, and reproduction of fungi. Information on the precise measurement of the qualitative and quantitative relationship of light to germination is limited (13).

Light stimulates spore germination in some fungi and inhibits it in others. Depending on the *Tilletia* sp. irradiated, light (daylight and artificial) stimulates, partially inhibits, or has no noticeable effect on spore germination (21). Irradiating sporangia of *Physoderma maydis* with blue light results in high germination, low germination when irradiated with green light, and no germination when irradiated with yellow or red light (8). Stimulation of oospore germination of three *Phytophthora* sp. is observed when irradiated by monochromatic light with peaks at 450 nm or 750 nm at 0.02 W/m^2, an intensity over the range of 400–750 nm that is encountered under dense vegetation (23).

Uredospore germination of several *Puccinia* sp. is inhibited when the spores are irradiated with white light. This inhibition, however, appears partial, temporary, and often temperature sensitive (5). Other workers found that blue light (419–425 nm) and far red light (720 nm) at intensities of 8 W/m^2 for 2 hr inhibits uredospore germination and that light in the spectral region from 450–600 nm does not affect germination (3). Irradiating uredospores with light at 720 nm inhibits their germination. However, irradiating uredospores with light of both 653 and 720 nm partially nullifies the inhibitory response, although light at 653 nm alone appears to have no effect on germination (15). Irradiating spores with ultraviolet light (300–380 nm) generally reduces spore germination and far-ultraviolet light (< 300 nm) is commonly lethal or has mutagenic effects on spores (2,20).

Previous work dealing with effects of radiation on various growth stages of the fungus *Alternaria solani* (Ell. & G. Martin) Sor. and other *Alternaria* sp. has resulted in a generalized scheme for conidiophore and conidial development (12,16,28). Release and dissemination of conidia occur primarily during daylight periods (7), and, thus, radiation received by spores during dissemination could affect their germinability (19).

The purpose of this investigation was to examine the effects of moisture, temperature, and radiation on germination of conidia of *A. solani*.

MATERIALS AND METHODS

Conidia production. An isolate of *A. solani* was obtained from one early blight lesion on a ripe tomato fruit (*Lycopersicon esculentum* Mill. 'Merit') grown at The Pennsylvania State University's Agricultural Research Center at Rock Springs, Centre County, PA. Cultures derived from this isolate were maintained on an autoclaved medium of 20% (v/v) V-8 juice, 0.3% $CaCO_3$ (w/v), 2% agar (w/v), contained in plastic petri plates, grown at 27 ± 1 C under cool-white fluorescent light (17 W/m^2) for 5–7 days, and stored in darkness at 3 ± 1 C until needed.

Mycelial plugs from these stock cultures were transferred to 24 plastic petri plates containing V-8 juice agar and grown at 27 ± 1 C under cool-white fluorescent light (17 W/m^2) for 4–8 days to initiate conidiophore formation. Four plates were removed each day for five consecutive days then placed in darkness for two days at 20 ± 1 C to promote conidial formation.

Two-day-old conidia were harvested by gently rolling a cotton swab over the periphery of the sporulating mycelial mat. Conidia were then deposited on 18-mm-square glass coverslips by gently rolling the cotton swab over one surface of the coverslip. Forty coverslips were prepared in this manner for each treatment. Conidia usually were deposited uniformily over the coverslip surface; however, when clumping of conidia did occur, those conidia within the clumps were excluded from germination assessments.

Exposure methods. Conidia were irradiated at various intensities of broadband electromagnetic radiation with a solar simulator (Kratos Inc., Schoeffel Instruments Division, Westwood, NJ) consisting of: a universal power supply (Model LPS-255HR), universal lamp housing (Model LH-151n), xenon compact-arc lamp (1,000 watt) with suprasil envelope for transmission of ultraviolet light, f1.0 condensing lens system (Model LHC-151/3ss), sunlens diffuser (Model LHA-150/3s-1), multiple filter holder with cooling blower (Model LHA-161/3s), liquid filter with path length of 10 cm (Model LHA 162/3), 90° light tube (LHA-154/3), and an exhaust system for ozone removal.

Twenty conidia-laden glass coverslips were placed on window glass (20 × 13 × 0.3 cm) located within the output beam of the solar simulator. The solar simulator was operated in a temperature-controlled chamber (Model M-2, Environmental Growth Chambers, Chagrin Falls, OH). Desired intensities of simulated sunlight were obtained by varying the distance between the coverslips and the radiation source. Temperature of conidia was estimated by a thermocouple positioned beneath one of the coverslips located at the center of the output beam projected by the

solar simulator. This temperature was recorded at 10-min intervals on a multichannel recorder (Model Electronik 16, Honeywell, Inc., Philadelphia, PA). All exposure periods were of 11-hr duration at a constant radiation intensity, conidia temperature controlled at 20 ± 0.3 C, and with RH fluctuating between 30 and 70%. To study the effect of broadband radiation on germination, conidia were irradiated with simulated sunlight (>300 nm) at intensities of 62, 243, 545, 1,060, and 1,459 W/m^2 (Fig. 1).

In a second experiment, conidia were exposed to specific wavebands of simulated sunlight by using various filters separately or in combination to achieve the desired spectral radiation treatment. The filters used and their respective cutoff values included: a 3-mm-thick Schott RG780 (>750 nm), Schott GG420 (>400 nm) (F. S. Gray Co., Jamaica, NY), an ultraviolet transmitting filter (300–400 nm) (Barr Associates, Inc., Concord, MA), window glass (>300 nm), and the previously described liquid filter. The liquid filter containing distilled water removed all infared radiation beyond 950 nm and transmitted 40% at 900 nm. Transmission characteristics of filters (Fig. 2) were determined with an Hitachi Model 100-80 Spectrophotometer (Nissei Sangyo America, Mountain View, CA). Spectral quality of light from the solar simulator and light transmitted through the filters were measured with an EG&G Model 580/585 Spectroradiometer (EG&G Inc., Salem, MA) from 300 to 800 nm. Intensities used for specific exposures were calculated from radiation tables (14) for the specific wavebands transmitted by a given filter. The distance from conidia to light source was varied to approach the calculated intensities. Radiation intensity was measured with an Eppley Precision Pyranometer (Model PSP, The Eppley Laboratory Inc., Newport, RI), sensitive from 280 to 2,800 nm. All exposure periods were of 11-hr duration at a constant radiation intensity, conidia temperature controlled at 20 ± 0.3 C, and with RH fluctuating between 30 and 70%. Conidia were irradiated with light at intensity/quality levels of 30 W/m^2 (300–500 nm), 422 W/m^2 (300–900 nm), 486 W/m^2 (400–900 nm), 778 W/m^2 (>750 nm), and 1,206 W/m^2 (>400 nm) (Fig. 3).

In addition to those conidia exposed to either simulated sunlight or specific wavebands of simulated sunlight, an equal complement of 20 conidia-laden glass coverslips was placed in open glass petri plates and placed in a dark, temperature-controlled chamber (Model I23, Puffer Hubbard, Grand Haven, MI) for 11 hr at 20 ± 1 C with RH fluctuating between 30 and 70%. These conidia held in darkness served as a control for making comparisons between irradiated and nonirradiated conidia.

Germination apparatus. At the end of each exposure period, the irradiated conidia were placed in an open-ended airflow apparatus to test germination response to light, temperature, and atmospheric moisture content.

Components of the open-ended airflow apparatus (Fig. 4) included an air pump, humidifying chamber, eight germination chambers, optical dewpoint hygrometer, and an air flow controller connected in series by nonhygroscopic tubing. The entire airflow apparatus was within a temperature-controlled chamber (Model M2, Environmental Growth Chambers, Chagrin Falls, OH).

Air flowing through the apparatus was drawn by an air pump (Neptune Dyna-Pump, Model 2, Neptune Products Co., Dover, NJ) from within the temperature-controlled chamber and regulated at 0.24–0.47 L/hr with a flowmeter (Dwyer Visi-Float, Series VFA, Dwyer Instruments Inc., Michigan City, IN). Temperature of air flowing through the apparatus was maintained by controlling the air temperature in the chamber housing the

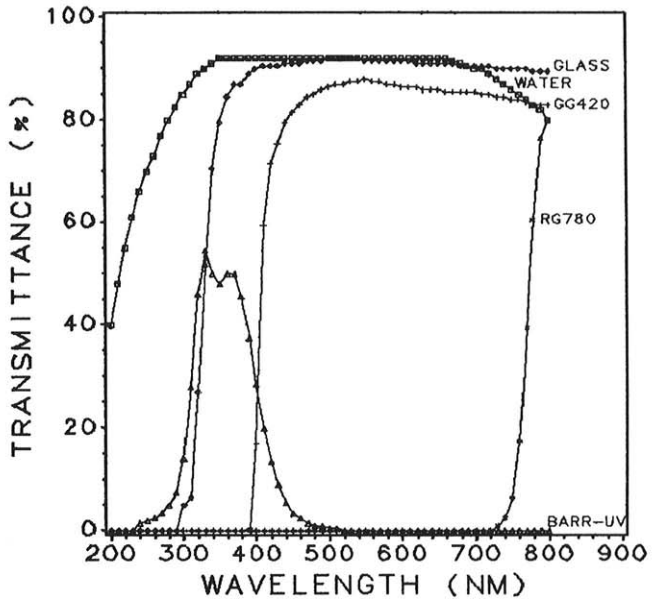

Fig. 2. Spectral transmission of Schott GG420, RG780, distilled water, window glass, and Barr UV filters.

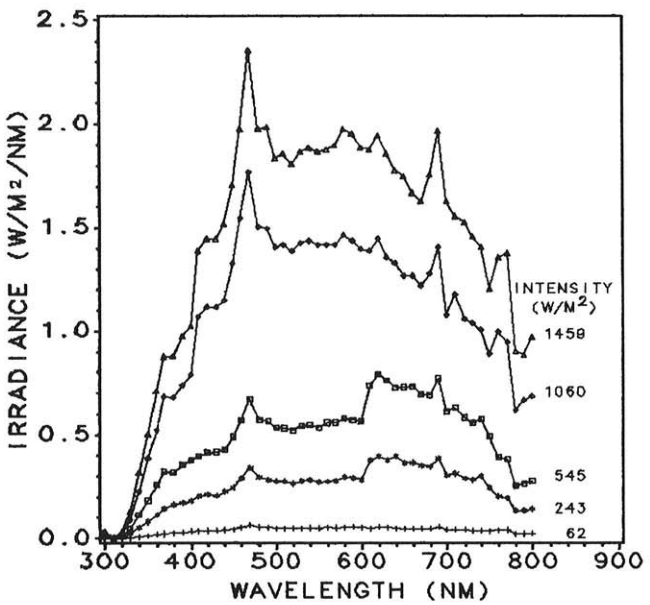

Fig. 1. Spectral distribution and intensity of the five treatments of simulated sunlight used for irradiating conidia of *Alternaria solani* for 11 hr. Treatment intensities (W/m^2) were measured over the range of 280–2,800 nm.

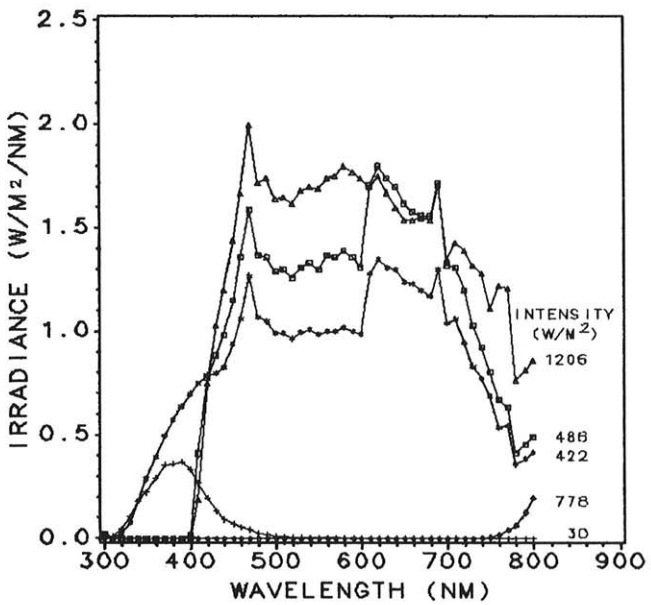

Fig. 3. Spectral distribution and intensity of the five treatments of selected wavebands of simulated sunlight used for irradiating conidia of *Alternaria solani* for 11 hr. Treatment intensities (W/m^2) were measured over the range of 280–2,800 nm.

germination apparatus.

Precise humidity control of air passing through the apparatus was obtained by bubbling air, supplied by the air pump, through distilled water or a mixture of glycerol (99.9% anhydrous glycerol, J. T. Baker Chemical Co., Phillipsburg, NJ) and distilled water (6) contained in the humidifying chamber. The humidifying chamber was a water bath (Thelco, Model 82, Precision Scientific, Chicago, IL) modified to make it an airtight vessel by attaching a Plexiglas cover with fittings attached for air lines, adding liquid, and with a port for inserting a thermocouple. Temperature of liquid in the humidifier was maintained at or above treatment temperature. Upon leaving the humidifier, the temperature and humidity controlled air was supplied to eight germination chambers.

The germination chambers were constructed from 450-ml petri dishes with two holes in opposing sides, through which nonhygroscopic tubing was inserted and affixed with a silicone caulking compound. The outer surface of each germination chamber and lid was painted with a layer of high-gloss-white enamel paint, a layer of flat-black paint, then with a final layer of high-gloss-white enamel paint to exclude light during germination studies. After samples were inserted, chambers were made air tight by covering the top opening with clear polyethylene film, secured by elastic bands, and lids replaced to prevent entrance of light. Each chamber had a three-valve bypass setup attached to allow for sample removal without disturbing conditions in adjacent germination chambers.

Temperature of air within each germination chamber and exiting the last chamber was measured (±0.25 C) with thermocouples (Type T, 0.003″, Omega Engineering Inc., Stamford, CT) positioned 5 mm above the conidia-laden coverslips and recorded at 15-min intervals on the previously described multichannel recorder.

Dewpoint temperature of air exiting the open-ended airflow apparatus was measured (±0.2 C) with an optical dewpoint hygrometer (1200APS, Model 1211P, General Eastern Instruments Corp., Watertown, MA) and monitored continuously.

Germination procedures. Six conidia-laden glass coverslips (three irradiated/three nonirradiated) were placed in germination chambers one, two, five, and six, and four conidia-laden coverslips (two irradiated/two nonirradiated) were placed in chambers three and seven (Fig. 4). Chambers eight and four were not used during the germination studies but remained in the airflow apparatus. Conidia were incubated at temperatures of 10, 15, 20, 25, 30, and 32 ±0.3 C for initial RH levels of 85, 90, 95, and near 100%. Germination was assessed immediately on removal of samples at 3-, 6-, 9-, and 12-hr intervals. Samples were examined at incubation time zero to determine if any conidia had germinated before their placement in the germination chambers. This arrangement resulted in four replications per light intensity and light quality treatment. Before spores were counted, each conidia-laden coverslip received a drop of lactophenol cotton blue and was covered with a glass microscope slide. Germination was determined for the first 100 conidia encountered in parallel paths across the microscope slide when examined at ×125 then standardized by dividing the number of irradiated and nonirradiated conidia germinated by the maximum number of nonirradiated conidia germinated within each incubation temperature treatment and multiplying by 100. Conidia were considered germinated if germ tube length was equal to or greater than spore length.

Data analysis. Response surfaces representing the percent of conidia germinating as a function of the independent variables, incubation time and incubation temperature, were determined for conidia irradiated at each light intensity and light quality treatment and for the nonirradiated conidia. The volume under each response surface was estimated by using a bicubic spline quadrature computer subprogram DBCQDU (9), an algorithim for calculating the volume under an irregular surface. These volumes have units of percent centigrade hour and represent the integrated effect of the two independent variables on the germination of conidia.

Percent inhibition of conidial germination due to each irradiation treatment was calculated from the formula:

$$\% \text{ inhibition} = [(1 - \text{IVURS}/\text{NVURS}) \times 100]$$

where IVURS = volume under response surface representing germination of irradiated conidia, and NVURS = volume under response surface representing germination of nonirradiated conidia.

The relationship between percent inhibition of germination of conidia and simulated sunlight intensity was investigated with regression techniques. Data from light quality treatments were subjected to analysis of variance and Duncan's multiple range test

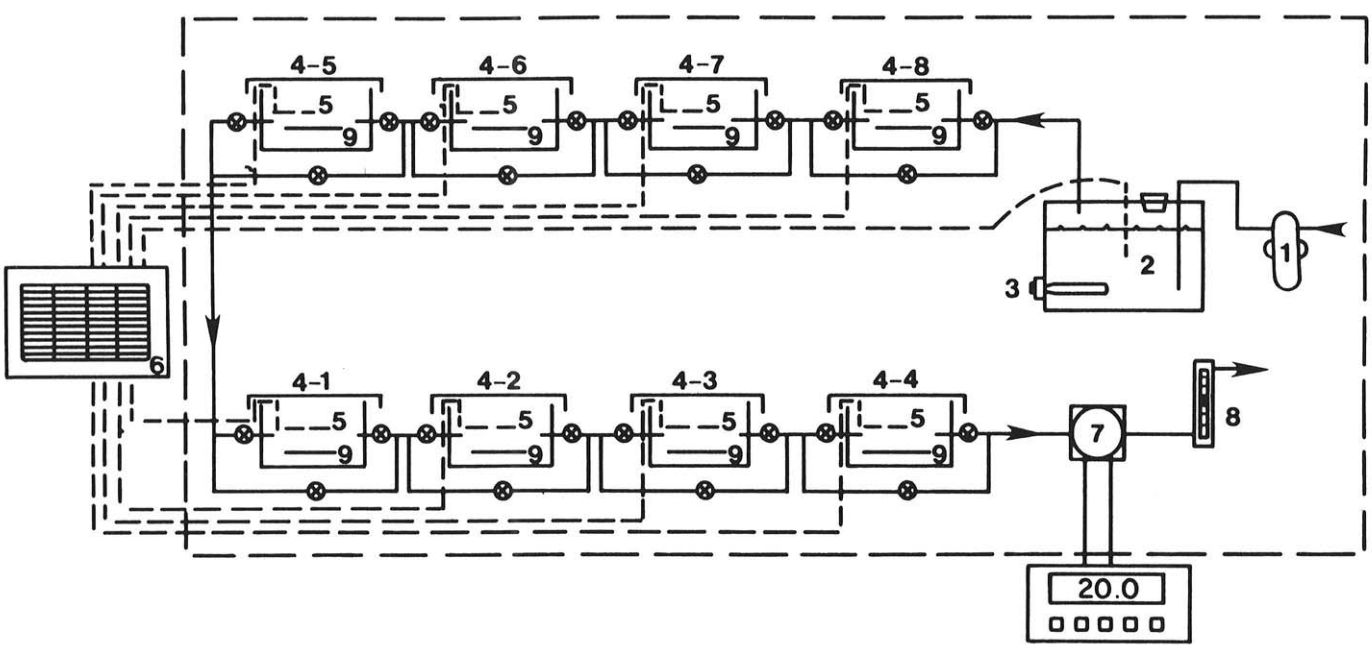

Fig. 4. A schematic diagram of the conidia germination apparatus: 1, air pump; 2, humidifier; 3, temperature control; 4, germination chambers (numbers 1–8); 5, thermocouples; 6, temperature recorder; 7, optical dewpoint hygrometer; 8, air flow control; 9, support for conidia-laden coverslips. Items within dashed rectangle were housed in a temperature-controlled chamber.

($P = 0.05$) to detect differences among treatments with respect to percent inhibition in germination of conidia. The response in germination due to relative humidity also was explored using the volume under the response surface criterion.

RESULTS

Temperature and moisture effects on germination. A preliminary experiment conducted to determine the response in germination of conidia to RH, incubation temperature, and irradiation resulted in the observation that no germination occurred at any of the six incubation temperatures whether irradiated or nonirradiated when RH was <92%. Differences between volume under the response surface for irradiated conidia at 96 and 92% RH were significant, as were differences between nonirradiated conidia at 96 and 92% RH (Table 1). At 96% RH, a continuous minute layer of condensation was observed on the conidia-laden coverslips during incubation. Condensation was not observed at relative humidities ≤92%. At this lower moisture condition, only four conidia germinated within 12 hr. At 20 C, one germinated conidium was observed at 6 hr for the irradiated treatment, and one at 3 hr and two at 9 hr for the nonirradiated treatment. Average maximum germination occurred at 12 hr/25 C incubation for irradiated conidia and at 12 hr/30 C incubation for nonirradiated conidia with RH at 96%. Based on this response in germination to the presence of free moisture on the glass coverslips, all remaining studies were conducted with RH ≥96%.

Effects of simulated sunlight on germination. A steplike increase in inhibition (32.6%) was observed when light intensity increased between 62 and 243 W/m^2 (Table 2). Further increases in light intensity from 243 to 1,060 W/m^2 resulted in only a 13.2% increase in inhibition. A second steplike increase in inhibition (34.2%) occurred when light intensity was raised to 1,459 W/m^2.

Calculated treatment doses and the percentages that these treatment doses are of the naturally occurring average daily solar radiation for the northeastern United States during the months of June and July are shown in Table 2. Doses for the 62, 243, and 545 W/m^2 treatments were within the range of natural sunlight. However, doses at the 1,060 and 1,459 W/m^2 treatment levels would be obtained in a 24-hr period only in an artificial environment using supplemental lighting.

In general, increasing the radiation dosage (intensity × time) significantly increased inhibition in germination. Inhibition due to dosages between 682 and 16,049 W-hr/m^2 may be estimated by the linear ($R^2 = 86\%$) equation:

$$\% \text{ inhibition} = -130 + 48.3 \log_{10} \text{dose}.$$

Average maximum germination occurred when conidia were incubated in darkness for 9–12 hr at temperatures of 25–30 C. RH was held at 98 ± 1% during incubation.

Effects of selected wavebands of simulated sunlight on germination. An inhibitory response in germination was observed when conidia were irradiated with light containing wavelengths in the ultraviolet and visible region of the spectrum (Table 3). Germination was reduced 29.9% for the 422 W/m^2 (300–900 nm), 16.2% for 486 W/m^2 (400–900 nm), and 10.2% for the 30 W/m^2 (300–500 nm) light treatments. Germination at the 1,206 W/m^2 (>400 nm) light treatment was reduced 3.9% and increased 5.9% at the 778 W/m^2 (>750 nm) light treatment. RH was held at 97 ± 1% during incubation.

DISCUSSION

The open-ended airflow apparatus used for germination studies in this investigation performed satisfactorily. Desired levels of atmospheric moisture were achieved and maintained within ±1% RH. Temperature within and among individual germination chambers oscillated ±0.3 C. The optical dewpoint hygrometer provided a means to maintain accurate measurements (±0.2 C) of atmospheric moisture over extended periods of time (4).

The effects that temperature and incubation period have on conidia germination observed in this study correspond closely with previous work (24). For conidia germinating in darkness, maximum germination occurred at approximately 25 C with moisture levels ≥96% RH. However, evidence was obtained supporting the hypothesis that free moisture must be present to germinate conidia of *A. solani* (24,25). In our studies, germination proceeded at all incubation temperatures when relative humidity was ≥96%, but only when visible condensation was present. Because the transparent film covering the germination chambers allowed us to observe the coverslips supporting the conidia, condensation was seen at these high humidities.

The effects of light on germinating propagules of several fungi have been previously reported (8,21,23); however, light quality and quantity were not always specifically defined. It was within the scope of this study to report the quality of radiation used for each exposure treatment and to adjust the intensity of radiation to approximate levels occurring in nature during July in the northeastern United States (10). The 1,000-watt solar simulator used in our studies was an excellent system for irradiating biological specimens at various intensities of broadband radiation.

TABLE 1. Volume[a] under the response surface for conidia of *Alternaria solani* germinated in darkness following an 11-hr radiation treatment

RH (%)	Treatment intensity	
	0 W/m^2	1,459 W/m^2
92	12 a[b]	2 a
96	6,678 b	3,687 b

[a] Volume equals germination (%) × incubation time (hr) × temperature (C).
[b] Each value represents the average of four replications. Means followed by the same letter within a column are not significantly different according to Duncan's multiple range test ($P = 0.05$).

TABLE 2. Effect of simulated sunlight (>300 nm) on inhibition of *Alternaria solani* conidial germination

Treatment		Percent of average daily dose[b]	Percent inhibition in germination[c]
Intensity (W/m^2)	Dose[a] (W-hr/m^2)		
62	682	11	7.6
243	2,673	43	40.2
545	5,995	98	44.8
1,060	11,660	191	53.4
1,459	16,049	263	87.6

[a] Dose (intensity × time) based on 11-hr irradiation period.
[b] Daily total radiation received during the months of June and July in the northeast U.S. averages 525 cal/cm^2 (22) or 6,103 W-hr/m^2.
[c] Percent inhibition calculated as [(1 − IVURS/NVURS) × 100]. For calculation of IVURS and NVURS see Materials and Methods. Each value represents the average of four replications.

TABLE 3. Effect of specific wavebands of simulated sunlight on inhibition of *Alternaria solani* conidial germination

Intensity (W/m^2)/ Waveband (nm)	Dose (W-hr/m^2)		Percent of average daily dose	Percent inhibition in germination[c]
	Treatment[a]	Daily[b]		
30 (300–500 nm)	330	1,291	25	10.2 ab[d]
422 (300–900 nm)	4,642	3,384	137	29.9 a
486 (400–900 nm)	5,346	3,118	171	16.2 ab
778 (750–2,800 nm)	8,558	2,904	294	−5.9 b
1,206 (400–2,800 nm)	13,266	5,438	243	3.9 b

[a] Treatment dose (intensity × time) based on 11-hr irradiation period.
[b] Average daily radiation dose within noted wavebands received at earth surface during the month of July from 1970 to 1973 at Rockville, MD (10).
[c] Percent inhibition calculated as [(1 − IVURS/NVURS) × 100]. For calculation of IVURS and NVURS see Materials and Methods.
[d] Each value represents the average of four replications. Values followed by a common letter do not differ significantly at $P = 0.05$ according to Duncan's multiple range test.

When some combinations of narrowband absorbing filters were used, it was not possible to obtain average daily doses expected from natural sunlight (Table 3). However, when used without filters, the lamp system was capable of creating 1.06 suns at Air Mass 1 with a uniform intensity over a 27.94-cm-diameter output beam (11).

The condition created by this solar simulator resulted in decreasing germinability of conidia of *A. solani* with increasing intensity of simulated sunlight when conidia were irradiated continuously for 11 hr. A similar relationship was reported for uredospores of several species of *Puccinia* (19).

Data from this study indicate significant decreases in germinability of conidia would be expected to occur in nature more often on days with no cloud cover or when incoming solar radiation approaches 40% of the average daily radiation dose received during June and July in the northeast United States (Table 2). Spore release by *A. solani* exhibits a diurnal periodicity (27) coincident with the diurnal solar radiation curve. Conidia aerially disseminated during this time would be most susceptible to damage from solar radiation during transport. In the field, spores deposited on upper leaf surfaces at the top of the plant canopy may be exposed to doses of solar radiation that could damage spores before conditions occur that favor germination.

High-intensity supplemental lighting used in greenhouse environments may also result in radiation dose levels sufficient to inhibit germination of conidia.

Inhibited germination resulting from irradiating conidia of *A. solani* appears to be a true light phenomenon and not caused by high temperature effects from exposure to infared radiation. If the effects on germination were a result of high temperature one would have expected inhibition of germination during the 778 W/m^2 treatment where only those wavelengths >750 nm were present and at a level 294% of the average daily radiation dose (Table 3).

All radiation treatments containing wavelengths <750 nm reduced the number of *A. solani* conidia that germinated below that of nonirradiated conidia. Inhibition was most pronounced when some near-ultraviolet (300–380 nm) and/or violet-blue (380–490 nm) light was present even though the dose at the 30 W/m^2 (300–500 nm) treatment level was only 25% of the average daily radiation dose (Table 3). The 400–500-nm waveband region affects germination of propagules of other fungi (3,21,23) and the sporulation processes of *A. solani* (1,17).

The degree of pigmentation of the *A. solani* conidia used in this study varied considerably. Pigmented spores in general often survive longer exposures to ultraviolet radiation than nonpigmented spores (13). This variability in spore pigmentation may explain in part why inhibition in germination was not strongly associated with a specific region of the 300–500-nm waveband. Pigmented spores may be more resistant than nonpigmented spores to wavebands of light that inhibit germination.

A direct relation exists between the relative humidity of the atmosphere surrounding uredospores of *Puccinia* species and the lethal effects of X-ray and ultraviolet radiation (26). Sharp increases in the sensitivity of uredospores to radiation occurred at relative humidities greater than 79%. Relative humidities were less than 70% during light exposure treatments of *A. solani* when germination of conidia was inhibited. Higher levels of inhibition might possibly be obtained if the microenvironment of the *A. solani* conidia had a higher relative humidity during exposure to solar radiation. Hydration of conidia may further increase the sensitivity to radiation.

Conidia from other isolates of *A. solani* need to be tested to determine if the radiation effects on germination indicated in this study are universal on *A. solani* or specific to the isolate tested in this study. If the relationship holds for other isolates, it might be possible to include a solar radiation effects model in disease forecasters such as FAST (18) to make more sensitive predictive systems with respect to available, viable inoculum levels.

LITERATURE CITED

1. Aragaki, M. 1962. Quality of radiation inhibitory to the sporulation of *Alternaria solani*. Phytopathology 52:1227-1228.
2. Buxton, E. W., Last, F. T., and Nour, M. A. 1959. Some effects of ultraviolet radiation on the pathogenicity of *Botrytis fabae*, *Uromyces fabae*, and *Erysiphe graminis*. J. Gen. Microbiol. 16:764-773.
3. Calpouzos, L., and Chang, H. S. 1971. Fungus spore germination inhibited by blue and far red radiation. Plant Physiol. 47:729-730.
4. Funk, S. D. 1980. Assessment of test cell humidity measurement control. Tech. Rep. EPA-AA-EOD-80-13. 19 pp.
5. Givan, C. V., and Bromfield, K. R. 1964. Light inhibition of uredospore germination in *Puccinia graminis* var. *tritici*. Phytopathology 54:382-384.
6. Grover, D. W., and Nicol, J. M. 1940. The vapour pressure of glycerin solutions at 20 C. J. Soc. Chem. Ind. 59:175-177.
7. Harrison, M. D., Livingston, C. H., and Oshima, N. 1965. Epidemiology of potato early blight in Colorado; I. Initial infection, disease development and the influence of environmental factors. Am. Potato J. 42:279-291.
8. Hebert, T. T., and Kelman, A. 1958. Factors influencing the germination of resting sporangia of *Physoderma maydis*. Phytopathology 48:102-106.
9. International Mathematical Statistical Libraries, Library LIB-0009. IMSL Inc. Houston, TX. December 1985. 4 vols.
10. Klein, W. H., and Goldberg, B. 1975. Solar Radiation Measurements 1968–1973. Smithsonian Radiation Biology Laboratory, Rockville, MD.
11. Kratos, Inc. 1979. Technical data on solar simulator power application. Kratos Inc., Schoeffel Instruments Div., Westwood, NJ. 7 pp.
12. Leach, C. M. 1967. Interaction of near-ultraviolet light and temperature on sporulation of the fungi *Alternaria*, *Cercosporella*, *Fusarium*, *Helminthosporium*, and *Stemphylium*. Can. J. Bot. 45:1999-2016.
13. Leach, C. M. 1971. A practical guide to the effects of visible and ultraviolet light on fungi. Pages 609-664 in: Methods in Microbiology. Vol. IV. C. Booth, ed. Academic Press, New York. 795 pp.
14. List, R. J. 1968. Smithsonian Meteorological Tables. 6th rev. ed., Smithsonian Institution Press, Washington, DC. 527 pp.
15. Lucas, J. A., Kendrick, R. E., and Givan, C. V. 1975. Photocontrol of fungal spore germination. Plant Physiol. 56:847-849.
16. Lukens, R. J. 1963. Photo-inhibition of sporulation in *Alternaria solani*. Am. J. Bot. 50:720-724.
17. Lukens, R. J. 1966. Interference of low temperature with the control of tomato early blight through use of nocturnal illumination. Phytopathology 56:1430-1431.
18. Madden, L., Pennypacker, S. P. and MacNab, A. A. 1978. FAST, a forecast system for *Alternaria solani* on tomato. Phytopathology 68:1354-1358.
19. Maddison, A. C., and Manners, J. G. 1972. Sunlight and viability of cereal rust uredospores. Trans. Br. Mycol. Soc. 59:429-443.
20. Maddison, A. C., and Manners, J. G. 1973. Lethal effects of artificial ultraviolet radiation on cereal rust uredospores. Trans. Br. Mycol. Soc. 60:471-494.
21. Meiners, J. P., and Waldher, J. T. 1959. Factors affecting spore germination of twelve species of *Tilletia* from cereals and grasses. Phytopathology 49:724-728.
22. Reifsnyder, W. E., and Hull, H. W. 1965. Radiant Energy in Relation to Forest. U.S. Dep. Agric. For. Serv. Tech. Bull. 1344. 111 pp.
23. Ribeiro, O. K., Zentmyer, G. A., and Erwin, D. C. 1975. Comparative effects of monochromatic radiation on the germination of oospores of three *Phytophthora* spp. Phytopathology 65:904-907.
24. Rotem, J. 1962. Studies on the early blight disease of tomato and potato caused by *Alternaria porri* (Ell.) Neerg. f. sp. *solani* E. & M. (English Abstr.) PhD thesis. Hebrew University, Jerusalem. 173 pp.
25. Schein, R. D. 1964. Comments on the moisture requirements of fungus germination. Phytopathology 54:1427.
26. Schwinghamer, E. A. 1958. The relation of survival to radiation dose in rust fungi. Rad. Res. 8:329-343.
27. Sreeramulu, T. 1959. The diurnal and seasonal periodicity of spores of certain plant pathogens in the air. Trans. Br. Mycol. Soc. 42:177-184.
28. Zimmer, R. C., and McKeen, W. E. 1969. Interaction of light and temperature on sporulation of the carrot foliage pathogen *Alternaria dauci*. Phytopathology 59:743-749.