Influence of Relative Humidity and Red-Infrared Radiation on Violent Spore Release by Drechslera turcica and Other Fungi

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Approved for publication as Technical Paper No. 3993 of the Oregon Agricultural Experiment Station.

Research was conducted within the Plant Diseases Division, Dept. of Scientific and Industrial Research, Auckland, New Zealand, and was supported by a Senior Science Research Fellowship awarded by the N. Z. National Research Advisory Council.

Acknowledgment: K. Young (D.S.I.R., Auckland, N. Z.) contributed significantly to this investigation by loaning the author equipment and advising him on instrumentation.

Accepted for publication 17 June 1975.

ABSTRACT

The relationship of relative humidity and light to spore release by *Drechslera turcica* was studied under precisely controlled and monitored conditions of temperature, light, air velocity, and relative humidity. Spore release was triggered (i) by lowering relative humidity from near saturation; (ii) by increasing the relative humidity from a lower to a higher level; and (iii) by exposing sporulating specimens to light. Both infrared and shorter red wavelengths stimulated spore release. Direct observation of spore discharge by utilization of the Tyndall effect, demonstrated that spores are violently propelled into the air.

The relationship of relative humidity and light to spore release was studied for miscellaneous other fungi having exposed, nonmucilaginous spores borne singly or in chains on simple sporophores (*Phytophthora infestans, Cercospora* sp., *Stemphylium botryosum, Alternaria tenuis, Cladosporium fulvum, Sphaerotheca fuligena*). Spore release in all those tested was similar to that in *D. turcica;* spores were discharged as the relative humidity was lowered from saturation in the presence of light (infrared lamp); and, all violently discharged their spores when exposed to light from an incandescent lamp. Uredospores of a rust associated with *Hordeum vulgare,* aeciospores of a rust associated with *Senecio vulgaris* and basidiospores of *Agaricus bisporus* also violently released their spores when exposed to light.

Phytopathology 65:1303-1312

Additional key words: Spore discharge, *Helminthosporium,* northern leaf blight, corn diseases, rusts.

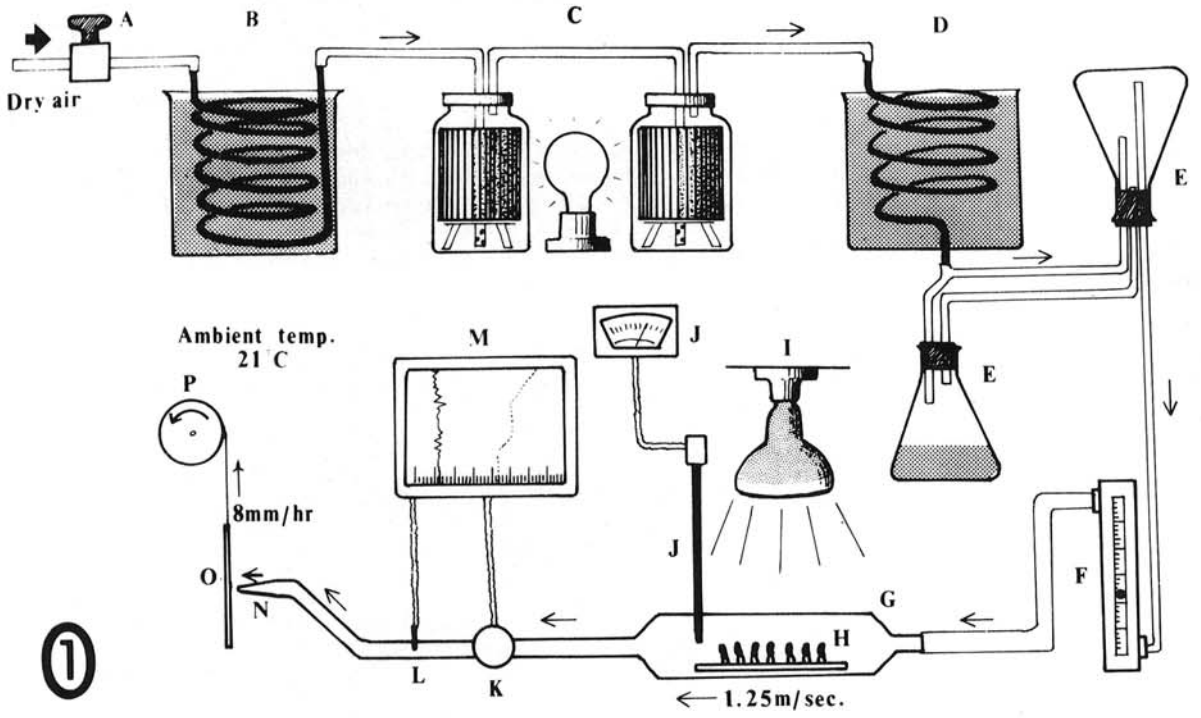
Airborne conidia of *Drechslera turcica* (Pass.) Subram. and Jain (= *Helminthosporium turcicum* Pass.), the cause of northern leaf blight of maize, commonly show a diurnal pattern of release. Spores first appear at sunrise, increase to a maximum around noon and then diminish to zero with the approach of sunset (9). Normally, spores are not released at night except when caused by wind and rain (Leach, *unpublished*). This diurnal pattern of release is typical of many fungi (14). Meredith (8) has reported that spores of *D. turcica* are released into the air when the humidity is lowered and that conidia are violently propelled into the air; however, Kenneth (5) was unable to demonstrate violent release. Meredith, on the basis of microscopic observations, postulated that violent release by *D. turcica* (8) and several other fungi (6, 7, 10) is caused by a water stress mechanism which causes a violent twisting movement of conidiophores during drying that flings the spores into the air.

The results of 6 months of continuous spore trapping over diseased maize plots near Pukekohe, New Zealand revealed that spores of *D. turcica* formed mainly at night when relative humidities were above 90% for approximately 10 hours (Leach, *unpublished*). When these conditions were satisfied, subsequent spore release occurred during the day and correlated with decreasing relative humidity as reported by Meredith; but, there was also some evidence that exposure to light might also be involved.

The purposes of this investigation were to further clarify the relationships of relative humidity and light to spore release by *D. turcica,* and other fungi, under precisely controlled laboratory conditions; and to test the validity of Meredith's observation that spore release is a violent process.

MATERIALS AND METHODS.—*Source of spores.*—Large numbers of young northern leaf blight lesions (10-15 cm long) were collected from diseased maize, dried in a plant press, and stored in sealed containers at −20 C until needed. To induce heavy spore production, lesions were first cut into 20 × 150 mm (approx.) pieces and stapled to strips of filter paper. The specimen was soaked for approximately 10 minutes in distilled water, removed and shaken, and then incubated at 22 C for 48 hours under a 12-hour light/12-hour dark regime (two 40W daylight fluorescent lamps and two 40W near-ultraviolet 'black light' fluorescent lamps) in a loosely sealed 30 × 300 mm Pyrex glass test tube. After incubation for 48 hours, the specimen was transferred to the specimen chamber of the spore release apparatus (Fig. 1) and the experiment was begun. Light was used during incubation period to reduce growth of surface mycelium and to synchronize spore development.

Spore release apparatus and humidity control.—The influence of relative humidity (RH) and light on spore release were studied by placing sporulating lesions in the specially constructed spore release apparatus shown in Fig. 1. Dry air (< 30% RH) at constant pressure, was fed into the apparatus from the laboratory air supply. A valve (Fig. 1-A) was used to adjust the air velocity to a standardized 1.25 m/second at the plane of the specimen. A low air velocity was used to lessen the possibility of "wind" removal of spores. Air flow rates in the 34 mm diameter Pyrex glass specimen chamber (Fig. 1-G) were periodically monitored with a hot-wire anemometer (Alnor Type 8500 "Thermo-anemometer"). A flow meter (Fig. 1-F) was used for approximate adjustments of air velocity and as a warning device to signal developing air leaks. The key part of the apparatus was the humidification system (Fig. 1-C and 2). RH was adjusted



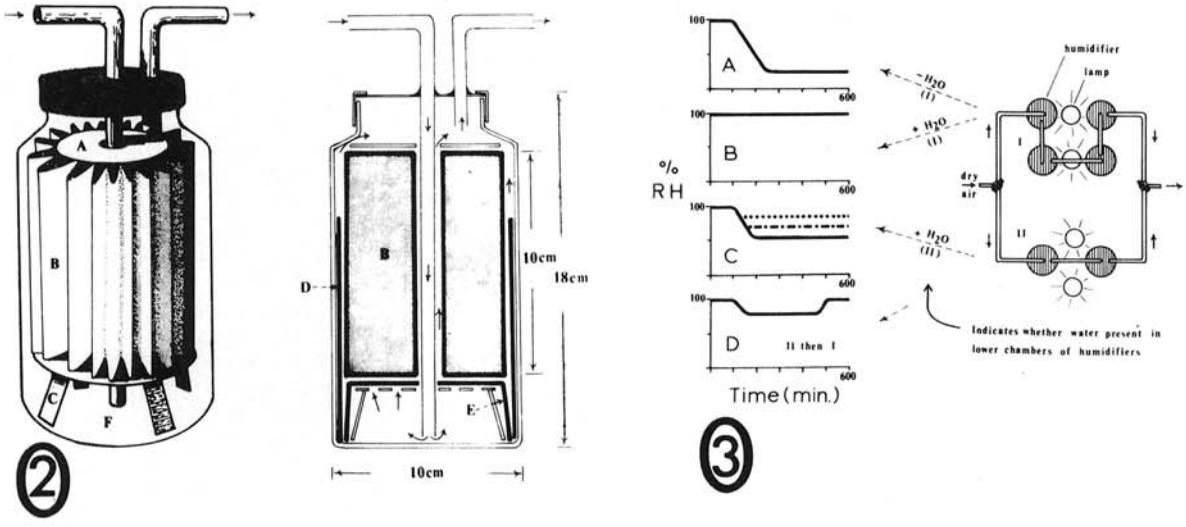


Fig. 1-3. Arrangement and structural details of apparatus for studying the effects of relative humidity and red-infrared radiation on violent spore release by *Drechslera turcica* and other fungi. **1**)-(A to P) Spore release apparatus (diagrammatic): A) dry air supply valve; B) ambient temperature regulator; C) humidifiers; D and E) condenser and temperature regulator; F) flow meter; G) specimen chamber (Pyrex glass); H) sporulating specimen; I) infrared lamp; J) hot-wire anemometer; K) thermocouple psychrometer; L) air temperature thermocouple; M) recorder for air temperature and humidity; N) orifice (2 × 15 mm); O and P) spore trap (greased glass microscope slide and a motor driven pulley). **2**)-(A to F) Humidifier (right drawing is sectional). A) air baffle; B) cylinder of folded filter paper; C) stainless steel platform; D) filter paper collar (not shown in left drawing; E) filter paper wick (not shown in left drawing); and F) chamber (empty or filled with water depending on humidity regime). **3**)-(A to D) Different humidity regimes used in spore release apparatus, and the arrangement of humidifiers used to obtain those regimes: A) air first saturated and then relative humidity (RH) decreased to that of the air supply; B) air maintained at saturation; C) air saturated and the RH decreased to a selected level and kept constant; D) air saturated, then RH lowered to a selected level and later returned to saturation (combination of B and C).

by using a series of simple humidifiers constructed from screw-capped household preserving bottles containing cylinders of moistened, folded filter paper (112 × 10 cm before folding). The humidifiers were initially designed to simulate the characteristic lowering of relative humidity that occurs at dawn in nature (Fig. 3-A). When used in this manner, the rate of RH decrease was dependent on the rate of drying of the filter paper cylinders (Fig. 2-B) and this could be modified by either altering the distance of the humidifiers from two incandescent lamps (used as heaters), or by changing the wattage of lamps, or by altering the number of humidifiers in series. Several arrangements of humidifiers (Fig. 3) were used to obtain different regimes ranging from saturation (Fig. 1-B), saturation followed by lowering the RH to a specified level (Fig. 3-C), and, saturation followed by lowering the RH and then later restoring it to saturation (Fig. 1-D).

After passing through the humidifiers the air flowed through a temperature control-condenser system (Fig. 1-D and E) and then through a flow meter (Fig. 1-F) to the specimen chamber (Fig. 1-G). The condenser was needed to prevent flooding of the apparatus with condensed water when saturated air was used. From the specimen chamber, the air flowed through grounded copper tubing (to eliminate electrostatic charges) to a greatly modified Hirst spore trap (Fig. 1-O and P). Released spores were collected on a greased microscope slide (25 × 75 mm) moving at 8 mm per hour past a 2×15-mm orifice (Fig. 1-

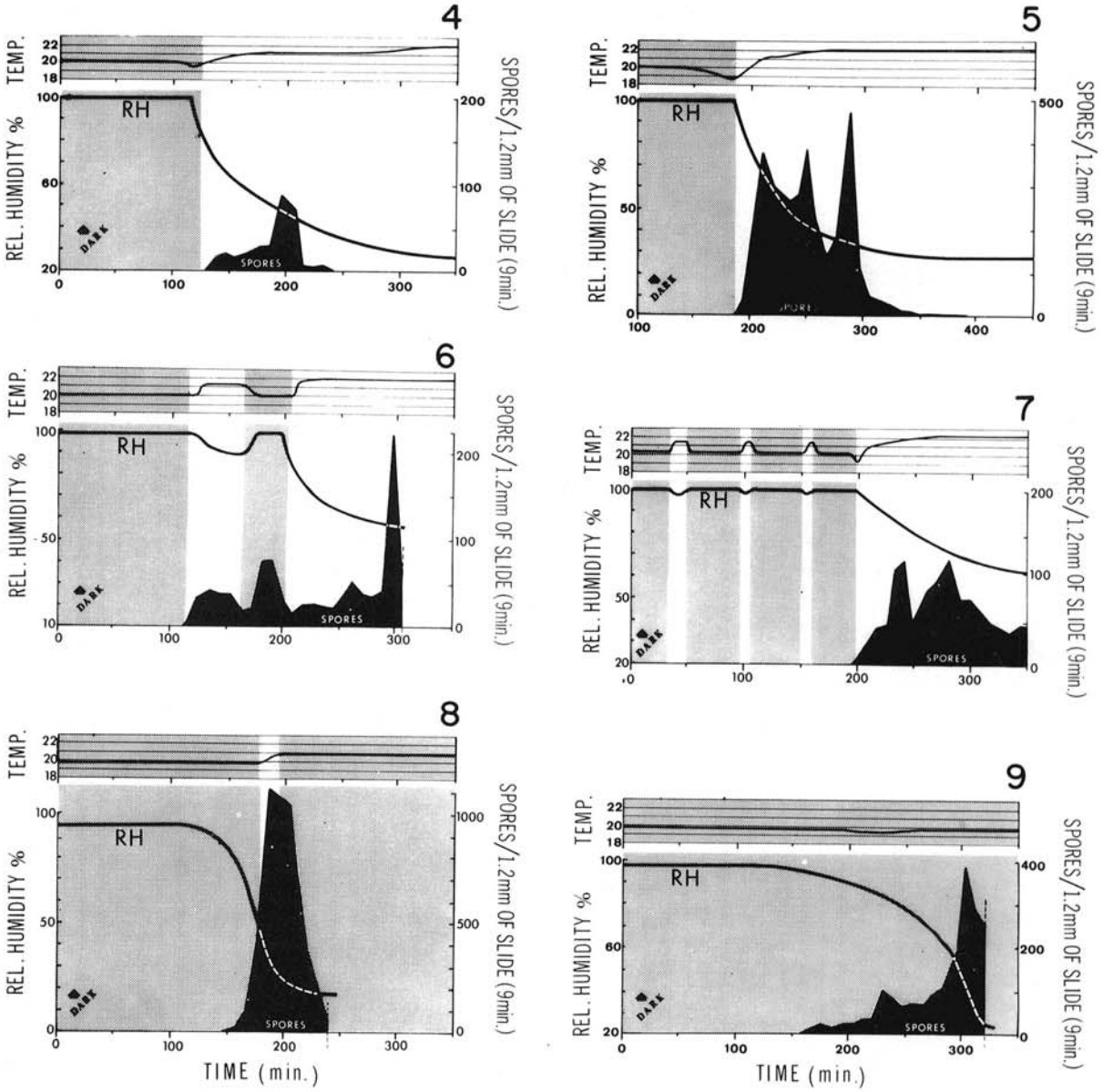


Fig. 4-9. 4-8) Influence of unfiltered light and decreasing relative humidity (RH) on spore release by *Drechslera turcica* (Combination of lamps used in the experiment shown in Fig. 4; others used only an infrared lamp). **9)** Spore release by *D. turcica* in darkness triggered by decreasing RH.

N). Spores deposited on the whole slide were systematically counted at a magnification of ×80. Counts were made across the slide at 1.2 mm intervals (diameter of the ×80 microscope field) along the slide, and this was aided by an eyepiece reticule and a mechanical stage. Spore counts shown in the results (Fig. 4-17) are plotted at 9-minute (approximate) intervals along the abscissae. As the air emerged from the orifice and impinged on the slide (gap approximately 1 mm), divergence of the air stream caused spores to be scattered over an area slightly wider than the width of the orifice.

The apparatus (Fig. 1) was located in a constant-temperature room at 21 C. The air stream temperature within the apparatus was controlled by two coiled copper tube regulators (Fig. 1-B and D). Temperature was recorded continuously using a thermocouple accurate to 0.25 C (Fig. 1-L) located just beyond the specimen chamber. Atmospheric humidity was monitored continuously by means of a small wet-wick thermocouple psychrometer (Fig. 1-K) sensitive to 0.25 C (designed by K. Young, Plant Diseases Division, D.S.I.R., Auckland, New Zealand).

Influence of light and decreasing relative humidity on spore release by Drechslera turcica.—Using the spore release apparatus (Fig. 1), a series of experiments was conducted in which sporulating lesions of *D. turcica* were first placed in a saturated air stream and then exposed to light as the RH was being lowered (Fig. 4, 5, 6, 8). These results were compared to spore release occurring in darkness (Fig. 9). Initially a combination of three spectrally different lamps were used to obtain a broad spectrum of radiation. Included were one 40W cool-white daylight fluorescent lamp, one 40W near-ultraviolet 'black light' fluorescent lamp (peak emission at 360 nm), and one 250W infrared lamp (Phillips IRR 250W B22 13352B/44). The fluorescent lamps were suspended 33 cm above the specimen chamber and the infrared (IR) lamp at 49.5 cm. After the first few experiments (Fig. 4 is an example) the combination of lamps was discontinued and only the IR lamp (49.5 cm from specimen chamber) was used in subsequent experiments (Fig. 5-18). The IR lamp emitted both visible and infrared radiation.

In the first series of experiments (Fig. 4-8) it was not possible to separate spore release caused by lowering the RH from that possibly triggered by light. In addition, heating of the air stream by the IR lamp (Fig. 4-8) made it

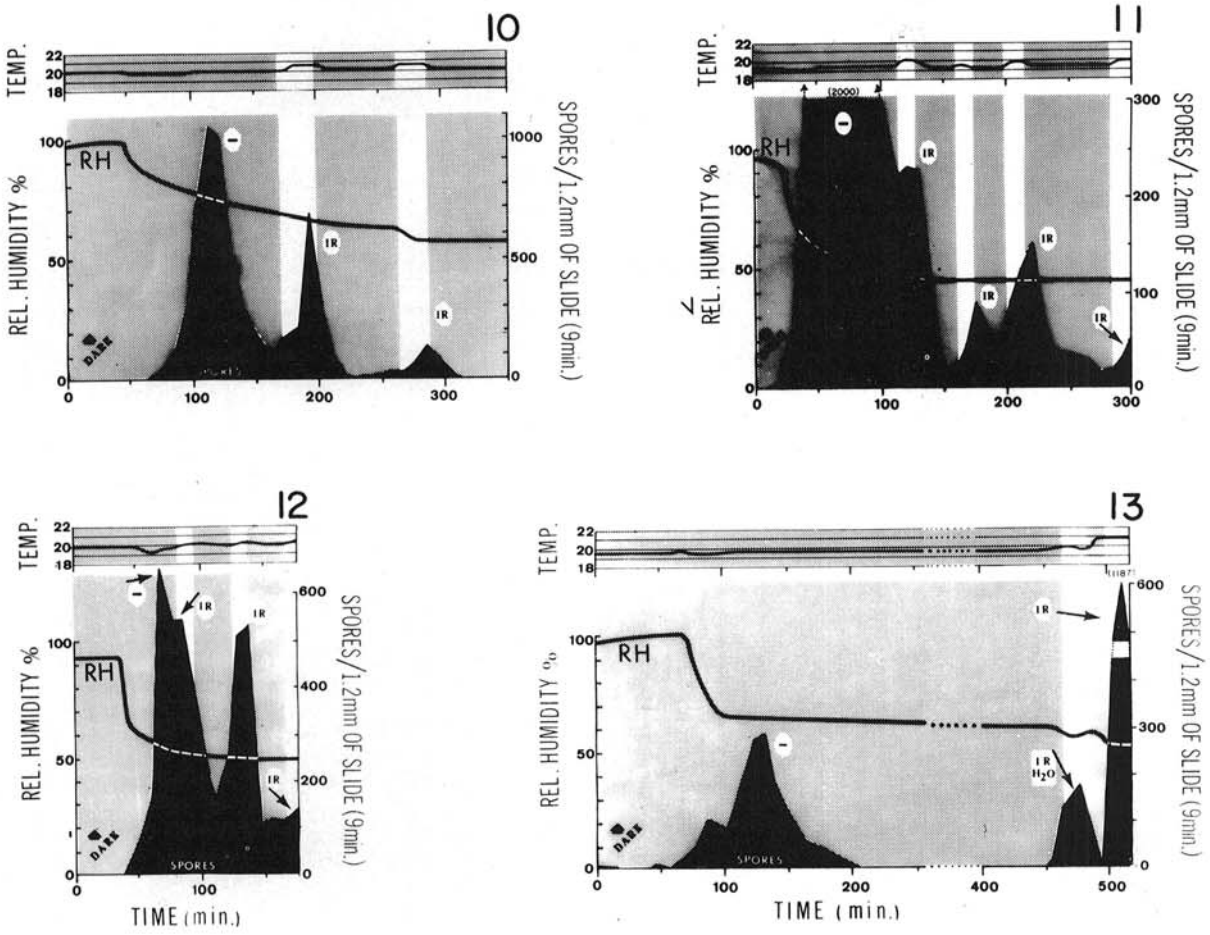


Fig. 10-13. 10-12) Spore release by *Drechslera turcica* caused by multiple exposures to filtered infrared light (IR) at constant or near-constant relative humidity (RH); also shows release caused by decreasing the RH (−). A 9-cm water filter was used in all three experiments. **13)** Spore release by *D. turcica* triggered by infrared filtered (IR H_2O) and unfiltered (IR) light at near-constant RH; also shows release caused by lowering the RH (−).

TABLE 1. Exploratory experiments on the relationship of light quality to spore release by *Drechslera turcica*

Expt.[a] no.	Filters	Wavelengths[b] transmitted (nm)	Light intensity[c] ($\mu w/cm^2$)	RH %[d]	Spore release
1	H_2O (9-cm deep)	< 1,190	11	55	Yes
	No filter	280-4,500	6,534	50	Yes
2	$CuSO_4$ 100 gm/liter (9 cm)	310-590	14	63	Yes
	Kodak Wratten 88A	> 725	3,419	60	Yes
3	Kodak Wratten 88A + H_2O (25 cm)	725-960	...	74	Yes
	Wratten 88A	> 725	3,419	71.5	Yes
4	Cinemoid Red + Mylar W	> 570	4,501	65	Yes
5	Wratten 87C	> 800	5,190	65	Yes
1,2,3,4,5	DARK	0	0	50-74	No

[a]Design of all experiments essentially the same as that shown in Fig. 13.
[b]Wavelengths transmitted are approximate and do not take into account the transmission of the pyrex glass specimen container. Wratten 88A was mounted between two sheets of glass.
[c]Same IR lamp used in all experiments at standardized distance of 49.5 cm from specimen container. No attempt made to standardize intensities, which were measured with a thermopile radiometer.
[d]Constant RH at time of irradiation.

difficult to ascertain whether the light effect was bonafide or merely an RH effect caused by an increase in air temperature. To circumvent these difficulties, a new series of experiments were conducted using a different arrangement of humidifiers as shown in Fig. 3-C. Sporulating specimens were placed in the spore release apparatus under saturated conditions and the RH lowered at a controlled rate to a selected level and there kept constant or fairly constant (Fig. 10-13). At this lower constant level, specimens were subjected to several exposures of IR radiation as shown in Fig. 10-13. In these experiments, the RH was reduced only to the 50-70% level on the assumption that spore release triggered by decreasing the RH (Fig. 9) would be incomplete, thus leaving some spores to be released by exposure to the IR radiation. To reduce the heating effect of the IR lamp, a water filter (distilled H_2O 9 cm deep in a Pyrex glass container) was placed between the IR lamp and specimen and this kept increases of air stream temperatures to less than 0.75 C. Water filters were used in experiments shown in Fig. 10-16, but not in experiments shown in Fig. 4-8, 16, and 17.

Light quality and spore release by Drechslera turcica.—To determine approximately what wavelengths of light triggered spore release, sporulating specimens were again studied in the spore release apparatus using various filters (Table 1). Specimens were first subjected to a saturated air stream, the RH was then lowered to a constant level (50-60% range) and while at this level the specimen was exposed to radiation from the IR lamp through filters. A typical light quality experiment is shown in Fig. 13; others are summarized in Table 1. No attempt was made to standardize intensities because of a number of technical difficulties. Intensities were measured with a thermopile radiometer.

Effect of raising the relative humidity on spore release by Drechslera turcica.—The results of several early experiments (Fig. 6) suggested that increasing the RH from a lower level to saturation might also be triggering spore release. To confirm this observation several experiments were conducted in which the RH was lowered from saturation to a constant level, maintained at this level for varying periods of time, and then returned to saturation (Fig. 14-16). These experiments again utilized the spore release apparatus and were conducted in darkness, except for one (Fig. 17). In two experiments (Fig. 16, 17) the regimes of decreasing and increasing the RH were repeated through several cycles.

Response of miscellaneous fungi to decreasing relative humidity and light.—Many fungi discharge their spores into the air in a diurnal pattern and it seems unlikely that the response of *D. turcica* to RH changes and red-infrared radiation is unique. To determine the behavior of other fungi, miscellaneous species were collected near Auckland (New Zealand) and subjected to varying conditions of RH and IR (Fig. 18) in the spore release apparatus. All the selected fungi had exposed, nonmucilaginous spores borne singly or in chains on simple sporophores. The species tested and the procedures used for obtaining abundant sporulation were as follows: leaves of *Lycopersicon esculentum* infected with *Cladosporium fulvum* Cooke were incubated in a moist chamber for 48 hours at 22 C under a regime of 12 hours light (two 40W daylight fluorescent lamps and one 40W near-ultraviolet fluorescent lamp at a distance of 56 cm) and 12 hours of darkness; leaves of *Solanum nigrum* infected with a *Cercospora* sp. were incubated the same as for *Cladosporium;* leaves of *Solanum tuberosum* infected with *Phytophthora infestans* (Mont.) de By. were placed at 15 C in darkness for 48 hours; leaves of *Cucumis sativus* covered with the conidial stage of *Sphaerotheca fuligena* (Schl.) Pollacei, were collected at dawn from greenhouse-grown plants and taken to the spore release apparatus in a light-proof humidity chamber; *Stemphylium botryosum* Wallr., isolated from *Asparagus officinalis,* was grown in pure culture on 2% malt extract agar for 7 days under the same conditions described for *Cladosporium* (small pieces of colony used); and maize leaves contaminated

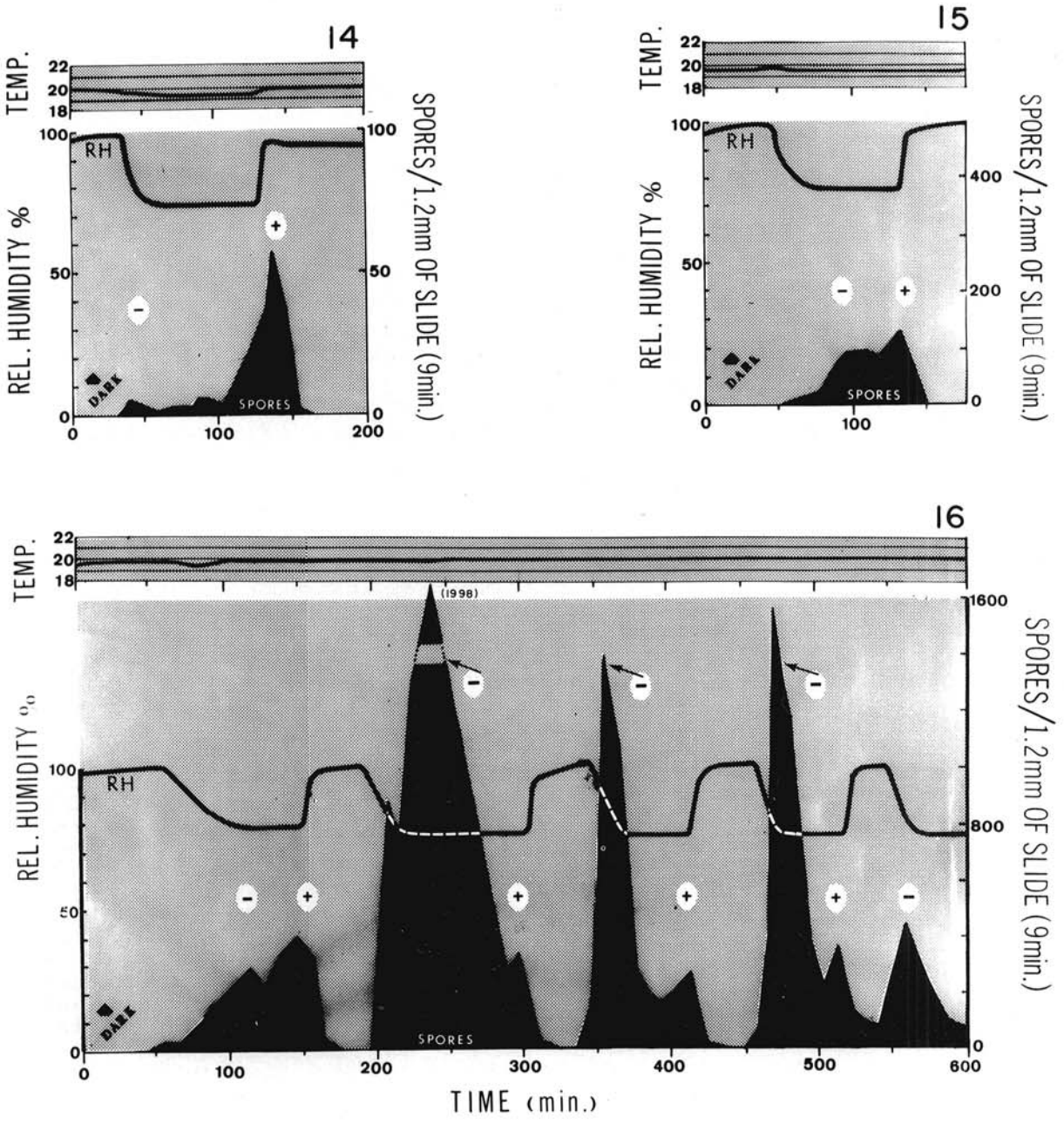


Fig. 14-16. Influence of decreasing relative humidity (−) and increasing RH (+) on spore release by *Drechslera turcica* in darkness (Fig. 16 shows the effect of repeated cycles of increasing and decreasing the relative humidity.).

with *Alternaria tenuis* were incubated the same as *Cladosporium*. Leaf lesions were stapled to strips of moist filter paper before being placed in the specimen chamber of the spore release apparatus.

Demonstration of violent spore release by Drechslera turcica.—Meredith (8) has reported violent release of conidia of *D. turcica* but Kenneth (5) was unable to demonstrate this phenomenon. To resolve this question, a modification of a technique used by W. Hartill (Plant Diseases Division, D.S.I.R., Auckland, N.Z.), but first described by Buller (3), was utilized. Hartill demonstrated "puffing" of apothecia of *Sclerotinia* spp. by directing a narrow light beam across the apothecium in a darkened room. As the ascospores pass through the beam they scatter light (Tyndall effect) and become clearly visible to the naked eye.

A "dark-box" (Fig. 19) was constructed from a cardboard shoebox (33 cm long). A partition (light baffle) was glued across the center of the box and a hole (approximately 20 mm in diameter) was cut at its center. Another hole was cut at the top end of the box. The inside of the box was painted with nonreflectant black paint to reduce light reflection and provide a black background against which the discharged spores could be seen. A 12-

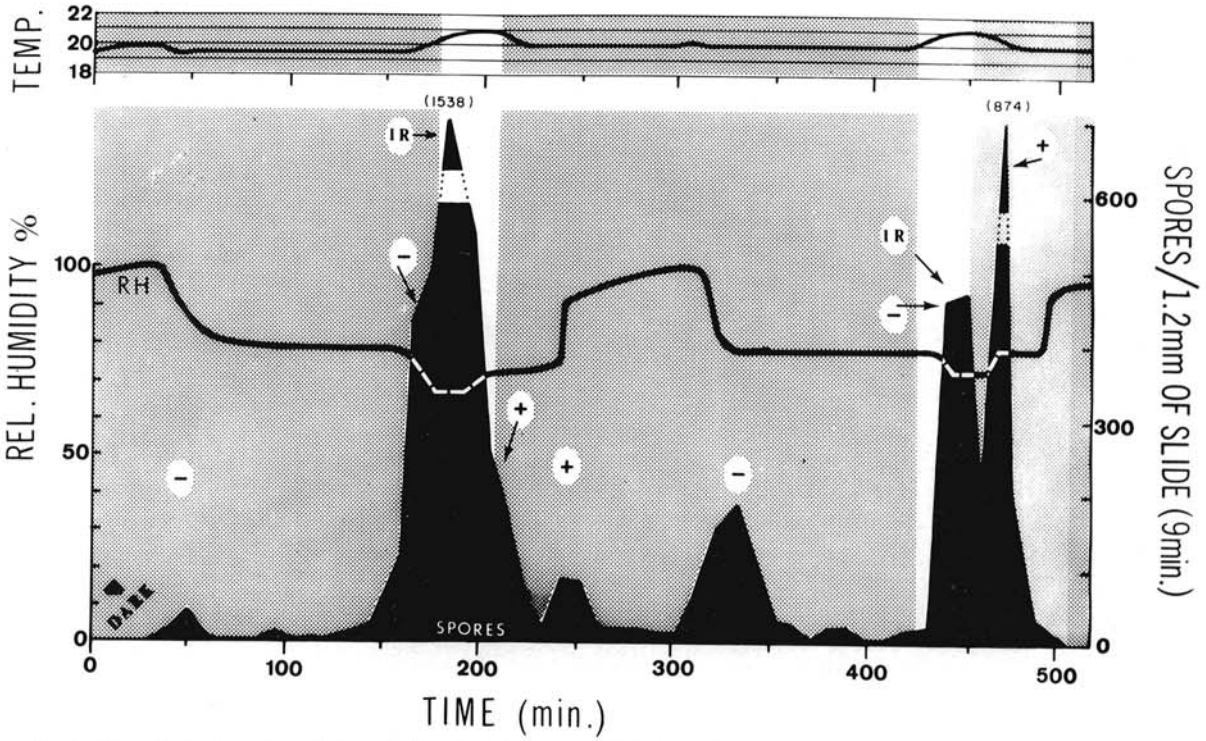


Fig. 17. The effect of unfiltered infrared light (IR), decreasing RH (−), and increasing RH (+) on spore liberation by *Drechslera turcica*.

volt incandescent microscope lamp, operated at 6.5 amps (emits some infrared radiation), was placed above the "dark-box" with light directed through the two holes onto the specimen resting on the bottom. Visual observations of spore release at room temperature (20 C approx.) were made in a darkened room at right angles to the beam of light (Fig. 19).

Demonstration of violent spore release by miscellaneous fungi.—On the basis of a hypothesis that violent spore release is a common phenomenon possibly involving the same mechanism, miscellaneous fungi were tested for violent liberation of spores. Sporulating specimens of *Sphaerotheca fuligena* (conidia), *Stemphylium botryosum, Cercospora* sp., *Phytophthora infestans, Agaricus bisporus* and two unidentified rusts infecting *Hordeum vulgare* (uredospores) and *Senecio vulgaris* (aeciospores), were transferred from a humidity chamber and exposed to light in the "dark-box" (Fig. 9) in a similar manner to *D. turcica*. The pileus of the *A. bisporus* specimen was inverted and the gills carefully pushed apart.

RESULTS.—*Spore release caused by decreasing relative humidity.*—Conidia were liberated by *D. turcica* when the RH was lowered from saturation to the 25-70% range (Fig. 4-9); they were never released when the air was saturated. Liberation occurred in darkness (Fig. 9) though the abundance varied greatly from experiment to experiment ranging from many (Fig. 9) to few (Fig. 14). There was evidence that light, particularly radiation from an infrared lamp, might also stimulate spore liberation (Fig. 4-6, 8), but not when the air was saturated (Fig. 7).

Spore release triggered by light.—In a second series of experiments in which *D. turcica* was exposed to radiation from an IR lamp at a constant or fairly constant RH (50-65% range), it was possible to distinguish spore release triggered by decreasing RH from that stimulated by IR radiation. It was evident from these experiments (Fig. 10-13, 17) that IR radiation alone was sufficient to trigger release of spores.

Quality of light influencing spore release.—It was soon discovered that a single IR lamp was as effective in triggering spore release by *D. turcica* as a combination of lamps emitting a much broader spectrum. It was also evident that the stimulatory wavelengths were transmitted by a water filter (Fig. 10-12) although release was always greater without a filter (Fig. 13). A series of light quality experiments (Fig. 13 and Table 1) indicated that a broad band of red-infrared wavelengths were stimulatory. Infrared radiation alone triggered spore release, but so did shorter wavelengths minus infrared. The exact limits of the stimulatory wavelengths were not determined.

Spore release triggered by increasing the relative humidity.—An early observation suggested that increasing the relative humidity from a lower level to near saturation might be triggering spore liberation by *D. turcica* (Fig. 6). When this possibility was tested experimentally, the results of a number of experiments consistently showed release of spores when the RH was raised from a lower level to near saturation (Fig. 14-17) and that this could occur in darkness (Fig. 14-16). In those experiments involving repeated cycles of decreasing and increasing RH (Fig. 15, 17), the numbers of spores liberated by increasing RH were usually far less than

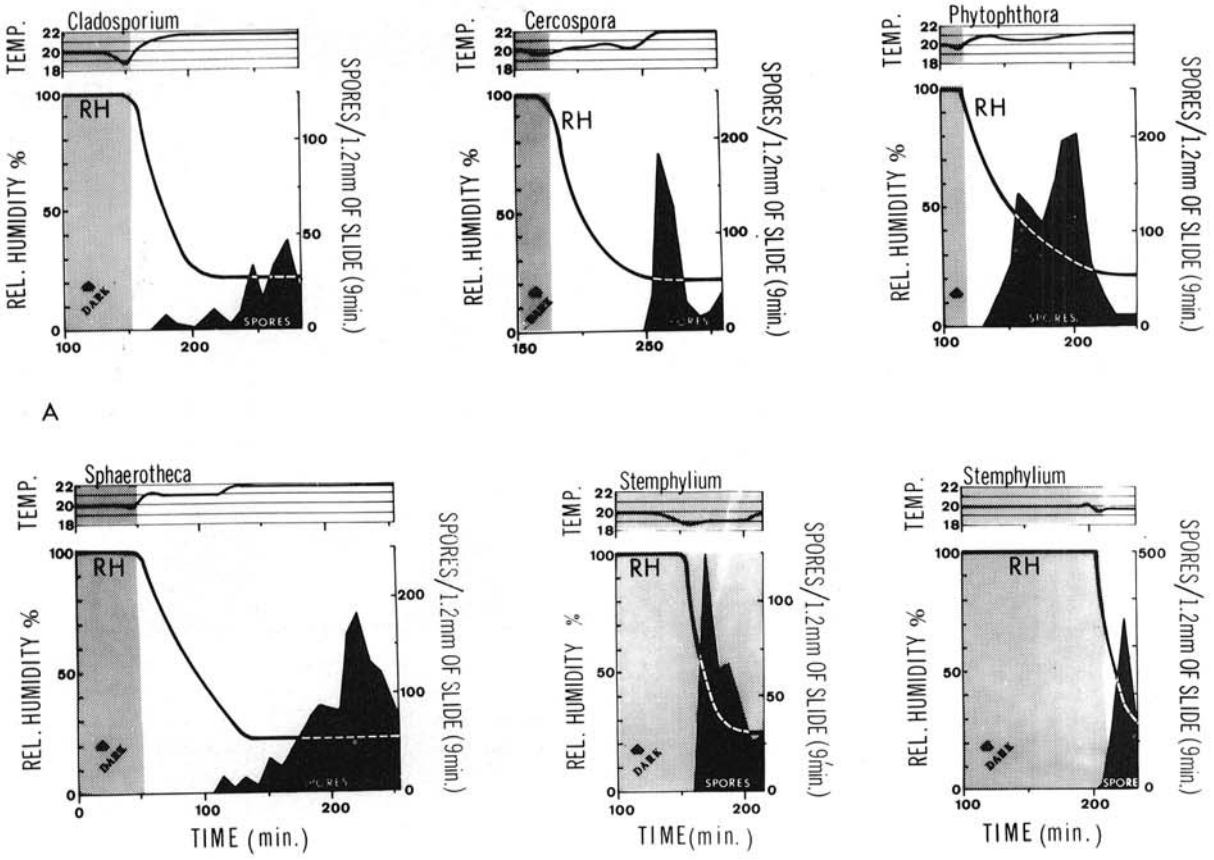


Fig. 18. Spore release by miscellaneous fungi exposed to infrared light during regimes of decreasing relative humidity. (*Stemphylium botryosum* also was subjected to decreasing RH in darkness.).

those released by lowering the RH.

Response of miscellaneous fungi to relative humidity and light.—When *Cladosporium fulvum, Cercospora* sp., *Phytophthora infestans, Sphaerotheca fuligena* (conidia), *Stemphylium botryosum,* and *Alternaria tenuis* were exposed to radiation from an IR lamp as the RH was being lowered from saturation (Fig. 18), all those fungi liberated their spores in a manner similar to that reported to *D. turcica* (Fig. 4-9). *Alternaria tenuis* (not shown), *P. infestans,* and *S. botryosum* were most like *D. turcica; S. fuligena,* the *Cercospora* sp., and *C. fulvum* needed longer periods at low relative humidities before spores were liberated. *S. botryosum* released spores in darkness though liberation was more massive when specimens were exposed to light.

Violent spore release.—Within minutes of exposing specimens of *D. turcica* to radiation from an incandescent lamp in the "dark-box" (Fig. 19), conidia could be seen glistening in the light beam as they were violently propelled into the air. The spores travelled in a straight line for the first few millimeters, then lost momentum and thereafter floated hapazardly in the air. The precise distance of projection was not determined, but it was estimated to be approximately 10 mm.

When *C. fulvum, Cercospora* sp., *Phytophthora infestans, Sphaerotheca fuligena, S. botryosum, Agaricus bisporus,* a rust fungus (uredospores) on barley, and a rust fungu (aeciospores) on *Senecio vulgaris* were exposed to light in the "dark-box" (Fig. 19), all violently discharged their spores several millimeters into the air.

DISCUSSION.—In New Zealand under field conditions, three distinct patterns of spore release by *D. turcica* were observed. Most common was a diurnal pattern of release, the subject of this article, but also encountered was liberation caused by wind and rain. Meredith (9) first reported a diurnal pattern of release for *D. turcica* in which spores were liberated in the early morning with a maximum reached around noon. He concluded that spore release is triggered by decreasing relative humidity and that liberation is a violent process (8, 9). Meredith's conclusions were derived mainly from observational data and he ignored the possible involvement of light. My studies on *D. turcica* have confirmed Meredith's conclusions, but they also reveal that the diurnal type of spore release by *D. turcica* is a more complex phenomenon than he realized. In addition to spore release being triggered by decreasing RH (Fig. 4-16), it can also be triggered by an increase in RH (Fig. 14-16) as well as by exposure to red-infrared radiation (Fig. 10-13, 16). The complex nature of spore release may account for the multiple peaks of trapped spores shown in Fig. 4-7.

The discovery that infrared radiation (Table 1) alone will cause massive release of spores is possibly the first

record of an infrared effect among the fungi. Brook (1, 2) reported a red, far-red effect on ascospore discharge by *Venturia inaequalis,* but he did not extend this study into the infrared spectrum; furthermore, it is unlikely that violent release of conidia involves the same process as ascospore discharge, though the triggering stimulus might be the same. Infrared radiation alone (i.e., transmitted by a Kodak 87C filter) is effective in stimulating spore release by *D. turcica;* however, when IR wavelengths were removed by filters (Table 1) stimulatory wavelengths were still present indicating that the effective wavelengths extend at least into the red spectrum. The exact limits of effective wavelengths has still to be determined.

Under field conditions, clear days accompanied by a marked lowering of relative humidity beginning at dawn should be most favorable to diurnal type spore release. On these days solar radiation at sunrise is strong in red-infrared radiation (4). When skies are overcast spore release should be reduced because of the strong absorption of infrared radiation by atmospheric water vapor. If overcast skies are accompanied by high relative humidity, my results suggest that few if any spores are likely to be released.

The nature of the red-infrared effect on spore release is not understood. The following are suggested as possibilities: (i) radiation causes an increase in air temperature in the microclimate of the conidium and conidiophore which in turn causes a decrease in RH and this triggers release; (ii) radiation causes an increase in evaporation rate of surface moisture (dew) and thereby influencing the RH; (iii) radiation directly effects the rate of dehydration of conidium and conidiophore thereby influencing the release mechanism; (iv) radiation affects cell wall substances, causing a weakening of the juncture between conidium and conidiophore; (v) radiation influences an endogenous cellular mechanism associated with spore release.

The discovery that both decreasing and increasing RH will trigger spore release in *D. turcica* suggests that under natural conditions this fungus might show a bimodal pattern of release. One maximum could be expected to occur during the morning as the RH decreased, and the other maximum in early evening as the RH increased. However, my own unpublished spore trapping data do not show bimodal patterns for *D. turcica.* I believe the explanation for this is the fact that this fungus normally produces spores only at night (Leach, *unpublished*). At dawn, northern leaf blight lesions should be covered with an abundance of spores and these will be violently released into the air during the morning as the RH decreases and as the lesions are exposed to solar radiation. Thus by late afternoon, when the RH characteristically begins to rise, very few spores would be left for liberation. For a bimodal pattern of release to occur in nature it would be essential that a supply of spores be available on lesions throughout the daylight hours. Do other fungi exhibit bimodal patterns of release? If it is assumed that violent release of spores is a common phenomenon among those fungi with exposed spores borne on simple sporophores, and that the same mechanism is involved, then any fungus having a supply of spores available during the day should show bimodal release under the right conditions of humidity (i.e., decrease during the morning, increase late afternoon). Bimodal release (often referred to as "double maxima") have been reported for a number of fungi (12, 13, 16). Pady et al. (11) in their study of spore release by *Gymnosporangium* noted that "in late afternoon or evening a smaller, secondary peak in spore release often occurs, for unknown reasons". Rich and Waggoner (15) have postulated a mechanism for bimodal release in *Cladosporium.* They suggest that spores liberated during the morning are carried into the atmosphere by turbulent air currents and that these later settle back to the ground to provide a second maximum. My own experiments on *Cladosporium fulvum* reveal that spores are violently released in response to decreasing relative humidity and light (Fig. 18) in a similar manner to *D. turcica.* On this basis, I would suggest that the double maxima reported by Rich and Waggoner is more likely to be caused by violent release triggered by decreasing RH during the morning followed by a second release in late afternoon caused by increasing RH. I offer this as an explanation for bimodal release in many fungi.

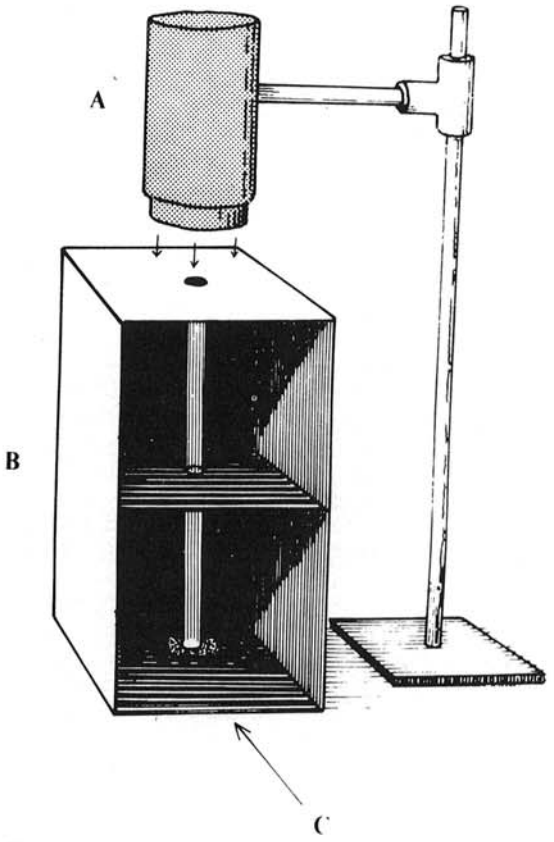


Fig. 19-(A to C). A simple Tyndall-effect apparatus for observing violent release of fungal spores: **A)** lamp; **B)** "dark-box" having a light baffle at center (sporulating specimen is placed on the bottom of the box); and **C)** direction for viewing spore release.

Meredith reported that conidia of *D. turcica* (8) and other fungi (6, 7) are forcibly propelled into the air. Kenneth (5) was unable to observe violent release in a number of *Drechslera* spp. including *D. turcica.* My own

attempts to repeat Meredith's studies on violent release of *D. turcica* were also unsuccessful. When conidia and conidiophores were exposed to an incandescent light source and observed microscopically, the conidiophores and conidia could be seen to gyrate, then collapse and become dehydrated. In some instances spores became detached, but it was impossible to know whether they had been merely knocked off by brushing against other conidiophores in close proximity, or whether they had been violently discharged. Later by observing spore discharge in an apparatus which utilized the Tyndall phenomenon it was possible to confirm visually Meredith's observation that release of *D. turcica* conidia is a violent process. It was similarly possible to demonstrate violent release of spores in a number of unrelated fungi, all of which form exposed, nonmucilaginous spores borne singly or in chains on simple sporophores. Is this merely coincidence or does it indicate the presence of a common mechanism? The fact that spore release by these same fungi followed a similar pattern to *D. turcica* when they were exposed to light (IR) while the RH was being lowered (Fig. 18), supports the possibility of a common mechanism.

On a number of occasions I have observed on days having a fairly low relative humidity, that a brief rain shower will cause an unusually large release of spores by *D. turcica* (Leach, *unpublished*). The accepted concept of splash dispersal of spores is that it is mainly a mechanical process in which rain drops impacting on a sporulating surface physically break loose spores and carry them into the air associated with the many resulting droplets. If increase in relative humidity will trigger violent release of spores as has been demonstrated in this investigation, then it is possible that rain dispersal of spores may also involve violent release of spores triggered by a rapid increase in RH in the microclimate of the conidium and conidiophore. The concept of splash dispersal needs to be reexamined.

LITERATURE CITED

1. BROOK, P. J. 1968. Stimulation of ascospore release in Venturia inaequalis by far red light. Nature 222:390-392.
2. BROOK, P. J. 1969. Effects of light, temperature and moisture on release of ascospores by Venturia inaequalis (Cke.) Wint. N.Z.J. Agric. Res. 12:214-227.
3. BULLER, A. H. R. 1909. Researches on fungi. Vol. I. Longmans, Green, London. 287 p.
4. HENDERSON, S. T. 1970. Daylight and its spectrum. American Elsevier, New York. 270 p.
5. KENNETH, R. 1964. Conidial release in some Helminthosporia. Nature 202:1025-1026.
6. MEREDITH, D. S. 1963. Further observations on the zonate eyespot fungus, Drechslera gigantea, in Jamaica. Trans. Br. Mycol. Soc. 46:201-207.
7. MEREDITH, D. S. 1963. Violent spore release in some fungi imperfecti. Ann. Bot. 27:39-47.
8. MEREDITH, D. S. 1965. Violent spore release in Helminthosporium turcicum. Phytopathology 55:1099-1102.
9. MEREDITH, D. S. 1966. Airborne conidia of Helminthosporium turcicum in Nebraska. Phytopathology 56:949-952.
10. MEREDITH, D. S. 1973. Significance of spore release and dispersal mechanisms in plant disease epidemiology. Annu. Rev. Phytopathol. 11:313-341.
11. PADY, S. M., C. L. KRAMER, and R. CLARY. 1968. Periodicity in aeciospore release in Gymnosporangium juniperi-virginianae. Phytopathology 58:329-331.
12. PADY, S. M., C. L. KRAMER, and R. CLARY. 1969. Sporulation in some species of Erysiphe. Phytopathology 59:844-848.
13. KRAMER, C. L., and S. M. PADY. 1966. A new 24-hour spore sampler. Phytopathology 56:417-420.
14. INGOLD, C. T. 1970. Fungal spores their liberation and dispersal. Clarendon Press, Oxford. 302 p.
15. RICH, S., and P. E. WAGGONER. 1962. Atmospheric concentration of Cladosporium spores. Science 137:962-965.
16. SREERAMULU, T., and A. RAMALINGAM. 1966. A two-year study of the airspore of a paddy field near Visakhapatanam. Indian J. Agric. Sci. 36:111-132.