Environmental Factors Initiating Liberation of Conidia of Powdery Mildews

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ABSTRACT

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Patterns of spore release were examined for *Sphaerotheca pannosa* on rose, *Erysiphe pisi* on pea, and *E. graminis* on brome-grass to determine the importance of environmental factors in removal of conidia from conidiophores of powdery mildews. No conidia of *S. pannosa* or *E. pisi* were released in the dark or light (80 μE m^{-2} sec^{-1}) in still air (ambient air velocity <0.1 m sec^{-1}) at 100% relative humidity (RH) but when the relative humidity was lowered rapidly, conidia of *S. pannosa* were liberated in light and darkness. *E. pisi* released conidia in still air when decreasing relative humidity was accompanied by increasing temperature. Liberation of conidia of *E. graminis* from infected detached leaves was examined in a specially designed spore release apparatus using a linear air velocity of 0.5 m sec^{-1}. Conidia were liberated in darkness whenever the relative humidity was abruptly reduced or raised. Exposure to unfiltered infrared light also triggered discharge. The evidence for liberation of powdery mildew conidia by an active discharge mechanism is discussed.

Additional key words: light, relative humidity, temperature, wind.

The mechanism of liberation of conidia by powdery mildews is controversial. Three brief accounts (12,17,35) have noted an apparent active discharge of conidia. Others have proposed that powdery mildew conidia are released passively by wind velocities of high magnitude, ranging from 0.6 to 2.0 m sec^{-1} (7,8,14,15). Ambient wind speeds within plant canopies seldom reach 0.5 m sec^{-1} (2,4,33), or greater than 0.25 m sec^{-1} within a glasshouse (8). However, brief gusts of high velocity apparently occur in canopies (28,33) and it has been demonstrated that winds of 0.6 m sec^{-1} can shake leaves with forces sufficient to dislodge powdery mildew conidia (4). In addition to wind, periods of high spore release in powdery mildews under field conditions have been correlated with rainfall (13), high temperature (5,13,34), low relative humidity (or high saturation deficit) (5,13,30,34), high solar radiation (34), and leaf surface dryness (13).

Light effects on the diurnal periodicity of spore discharge have been studied thoroughly for several species of mildews; however, the interrelationship between light, temperature, and relative humidity (RH), has received little attention experimentally. Several researchers (16,30,32) have concluded that greatest liberation occurs at lower humidities, though few laboratory experiments provided convincing evidence that relative humidity directly influences spore discharge by powdery mildews. Evidence of temperature eliciting spore discharge is sparse.

The objective of our study was to determine the relationship of air temperature, relative humidity, and light to liberation of conidia when air movement was minimal. We hypothesized that if an active mechanism existed, discharge should occur in still air in response to environmental factors that trigger spore release in other dry-spored fungi for which an active mechanism has been proposed (18,23,24). We purposely selected species of mildew that were monoconidial (*Erysiphe pisi*) and bore their conidia in chains (*Erysiphe graminis* and *Sphaerotheca pannosa*).

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MATERIALS AND METHODS

Three species of the Erysiphaceae were studied: *Sphaerotheca pannosa* (Wallr.:Fr.) Lev on rose (*Rosa domestica* L. 'Mary Devor' and 'Tropicana'), *Erysiphe pisi* (DC.) St.-Am. on pea (*Pisum sativum* L. 'Corvallis') and *E. graminis* DC. on brome-grass (*Bromus catharticus* Vahl.).

Glasshouse studies. A 24-hr Kramer-Collins spore sampler with a 12-mm-diameter orifice was situated within 0.5 m of four 5-yr-old roses growing in containers in a glasshouse. The youngest leaves of these roses were heavily infected with actively growing and sporulating colonies of *S. pannosa*. Spore release was monitored for 7 days under natural light entering the glasshouse to determine diurnal periodicity. Canopy humidity and air temperature were monitored and recorded with a humidity probe and a thermocouple connected to a chart recorder.

Still air studies in chambers. Vigorously growing 5-yr-old potted rose plants were used to obtain actively expanding colonies of *S. pannosa* with abundant young conidia. These were first pruned to fit the test chamber ($100 \times 56 \times 56$ cm). All leaves were initially removed from a plant, followed by cultivation in a glasshouse until new leaves began to unfold. At this time the plant was placed in a growth chamber and incubated under a 16-hr light (21 C, approximately 50% RH) and 8-hr dark (21 C, approximately 100% RH) cycle. The light was broad spectrum (combination of daylight-fluorescents and incandescents; 80 μE m^{-2} sec^{-1}). Viable conidia obtained from infected source plants were brushed daily onto new leaves as they unfolded. Actively growing powdery mildew colonies were abundant on leaf surfaces after 1 wk of incubation. Each infected plant could be used daily over a period of 2–3 wk for different experiments.

In studies on the powdery mildew of pea (*E. pisi*), seeds were planted in cylindrical pots and seeded pots were incubated in a growth chamber using a cycle of 14 hr light (24 C, approximately 30% RH) and 10 hr dark (18 C; approximately 60% RH). An infected pea plant was placed in the growth chamber with the seeded pots and infection occurred naturally. Infected seedlings were considered ready for experimental use when approximately one fourth of the stem was visibly colonized with mildew. At this stage, when the plants were approximately 40 cm in length, they were moved into the test chamber. Six pots (120 plants) were laid

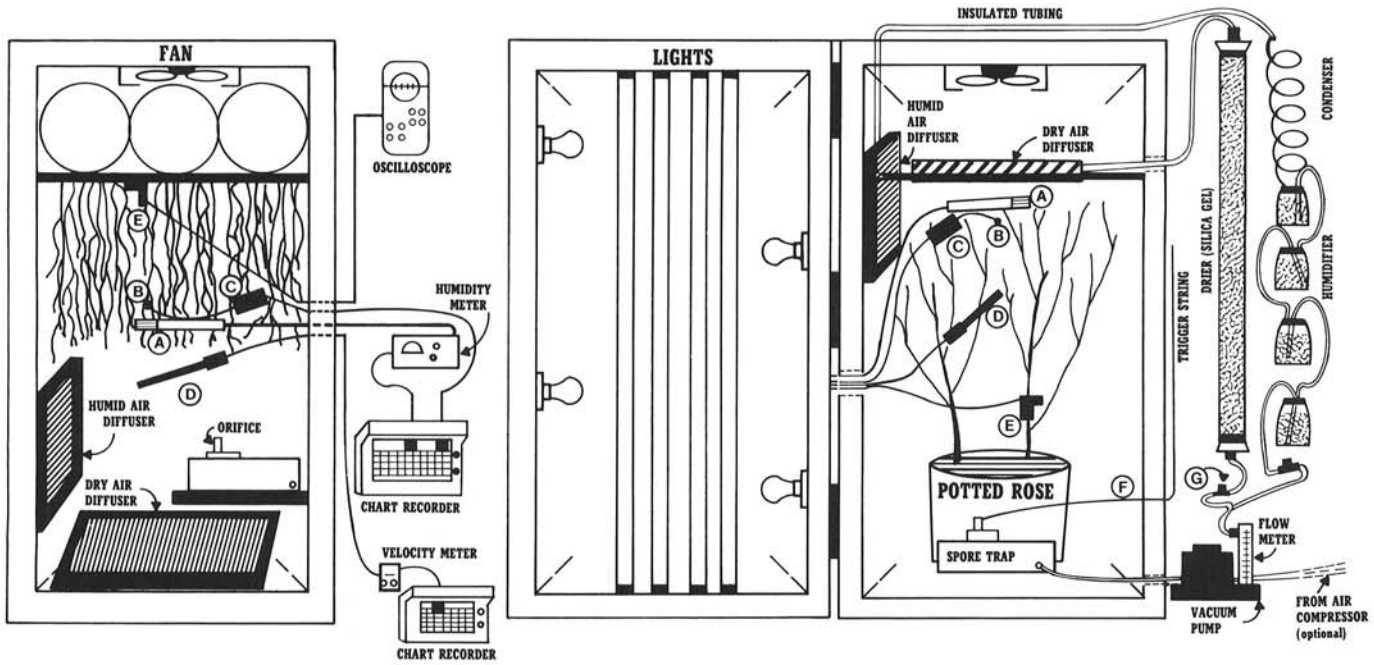

Fig. 1. A schematic diagram of a growth chamber modified for still air studies of spore release: **A,** Humidity probe; **B,** Thermocouple; **C,** Solid state ice-point reference junction; **D,** Anemometer; **E,** Quartz accelerometer; **F,** Trigger string; and **G,** Diversion valves. The external drier was often replaced by an internal drier, Figure 2.

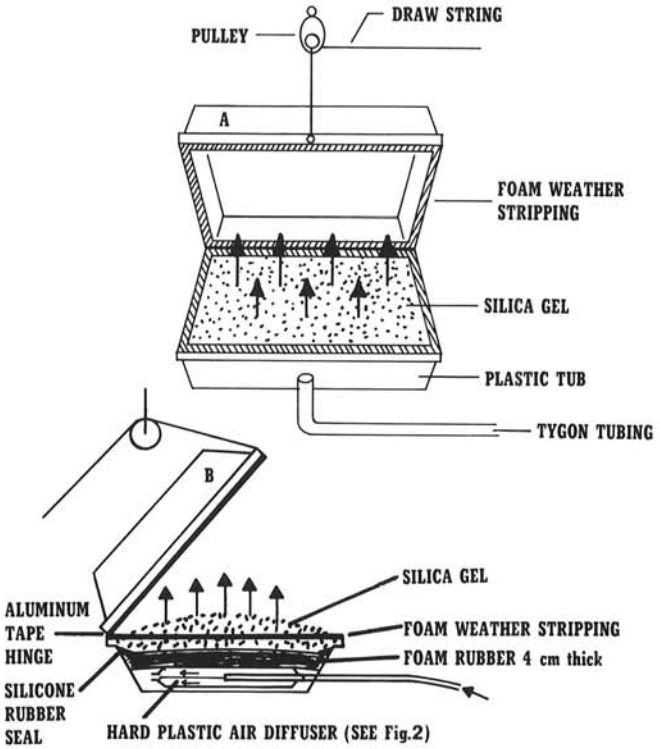

Fig. 2. A representational drawing of the internal air drier system. **A,** Front view of open drier as during operation. **B,** Transparent side view showing internal design. Arrows represent direction of air movement.

horizontally on shelves in the upper part of the chamber with the foliage hanging down into the chamber. Pea plants could be used experimentally for approximately 10 days before being discarded.

Design of the test chamber. A standard vertical growth chamber (internal measurement 125 × 56 × 56 cm) equipped with light banks, refrigeration and heating, and controlled by time clocks, was modified to permit external control of relative humidity (Fig. 1). A 6-hr Kramer-Collins spore sampler was stationed inside the chamber. The spore sampler was modified to permit triggering of the hand-wound motor from outside the chamber. The vacuum pump of the spore sampler was placed outside the chamber and air moving through the spore sampler at a rate of 20 L/min was circulated by plastic tubing.

Manipulation of relative humidity was dependent on operation of a spore sampler. Relative humidity was controlled by alternatively circulating the air flow of the spore sampler through a humidifier or a dehumidifier (air drier) outside of the chamber. The humidifier and external dehumidifier were of a design described previously (19), consisting of a series of water baths or a column of dry silica gel through which air passed. An internal air drier (Fig. 2) was used in certain experiments to reduce humidity gradually. The external drier was used for more rapid change as the volume of air flow through the latter could be supplemented with an air compressor (Fig. 1). Air flow was directed by two manually controlled electrical solenoids [diversion valves, Fig. 1(G)] at a fork along the path of the tubing. External tubing was insulated with foam wrapping to dampen temperature fluctuations and prevent condensation. Humidified or dehumidified air reentered the chamber through an air velocity diffuser (Fig. 3). The diffuser consisted of the exit tube fitted into a sandwich formed of two sheets of foam rubber (each 45 × 35 × 2.5 cm) sealed together (100% silicone rubber sealant) along their perimeters (Fig. 3). The velocity of the air exiting the diffuser was measured as described below and reached 0.02 m sec^{-1}. The velocity of air pulled into the spore sampler was 0.4 m sec^{-1} directly at the orifice and 0.1 m sec^{-1} 5 cm above the orifice. The nearest leaves in plant canopies were at least 40 cm above the orifice.

The chamber was outfitted with a wide spectrum light source. Six lamps were in the chamber on the back wall [five 40W cool-white fluorescent lamps and one 40W black-light fluorescent lamp (model F40/BLB, General Electric Co., Cleveland, OH)]. Four 40W warm-white fluorescent lamps and four 15W incandescent lamps were external, separated by the glass pane (100 × 50 × 0.5 cm) of the chamber door (Fig. 1). Total illuminance and photon energy was measured at six locations in the chamber with a Li-Cor light meter (model Li-85, Lambda Inst. Corp., Lincoln, NE) and averaged 4,550 lx (Lambda Type SR-PH 319 Photometric Sensor) and 80 μE m^{-2} sec^{-1} (Lambda Type SR-Q650 Quantum Sensor).

Monitoring of humidity, temperature, air velocity, and vibration. Relative humidity and air temperature were monitored continuously during experiments. Relative humidity was monitored with a thin-film-capacitor humidity sensor (models HMP-144 and HM-111, WeatherMeasure Corp., Sacramento,

CA) located in the plant canopy (Fig. 1). The sensor was connected to a dual-channel chart recorder (model 8373, Cole-Parmer Inst. Comp., Chicago, IL). A copper-constantan thermocouple with electronic ice-point reference junction (model MCJ, Omega Engineering, Inc., Stanford, CT) recorded canopy air temperature fluctuations on the chart recorder (Fig. 1). Air velocity was measured by a hot-wire anemometer and velocity meter (model W241M, Weather Measure Corp.). The anemometer was located at various positions in the chamber during different experiments and was connected to a chart recorder (Fig. 1). Vibration was measured using a low-impedance high-sensitivity quartz accelerometer with built-in amplifier (model 308 A, PEB Peizotronics, Inc., Buffalo, NY). The accelerometer had a dynamic range of 0.01–50.0 G and a frequency range of 1–3,000 Hz. Vibrations were periodically monitored on an oscilloscope.

Moving air studies. Brome-grass plants grown in pots were infected by brushing conidia onto leaves from an infected source plant. Inoculated plants were incubated in a sealed polyethylene chamber at 25–30 C. Leaves having severe infection and luxuriant sporulation were excised and placed in a specially designed spore release apparatus (19) the evening preceding an experiment. Light was supplied by a 250W red-infrared (IR) incandescent bulb (General Electric). Spectral output of this bulb was 60% in the red-IR range and 40% throughout the remaining visible range. Excised leaves were placed in the chamber in still air and darkness about 10 hr preceding an experiment. Leaves were situated so that mildew colonies were inverted and discharged spores fell into a moving air stream. The air velocity (0.5 m sec^{-1}) impacted spores onto a moving slide (11.5 mm hr^{-1}) of a spore sampler (9,19). The number of conidia deposited per 1.3 min were counted with a microscope at 500 × magnification.

Monitoring spore release. The test chamber containing powdery mildew infected rose or pea was preset to completely switch off all lights, refrigeration, and spore sampling 4–6 hr before an experiment on spore release. During this time, the chamber remained undisturbed to safeguard any possibility of modifying the environment or mechanically dislodging spores. The temperature of the chamber reached equilibrium with the room temperature, the air within the chamber became essentially still and the relative humidity rose to 98–100%.

An experiment began by starting the spore sampler using a nonintrusive remote control mechanism and switching on the vacuum pump to the spore sampler. Spore release in still air and darkness was sampled for 1 hr before any changes in humidity or exposure to light. This permitted the measurement of any background release that might occur in still air and darkness. Numbers of conidia that impacted onto the petrolatum-coated microscope slide were determined by counting across intervals of 1 mm length × 25 mm width with an eyepiece reticle.

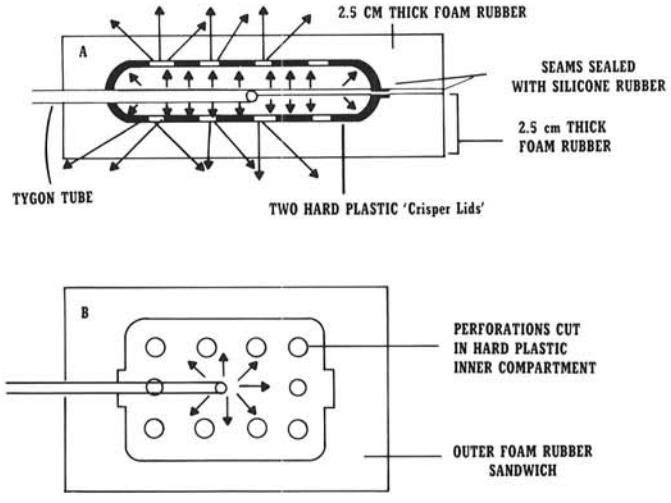

Fig. 3. A schematic diagram of the air diffuser. **A,** Side view showing sandwich design. **B,** Top or bottom view. Arrows represent direction of air movement.

Each experiment was performed four to six times; data reported are representative of the results obtained.

RESULTS

Spore liberation in *S. pannosa* in the glasshouse. Spore liberation from glasshouse-grown roses occurred in a distinctive diurnal pattern with peak catches near noon and sparse catches during night. Spore release patterns were positively associated with rising temperatures, increasing intensity of solar radiation, and decreasing relative humidity. Furthermore, chart recordings marked patterns of fluctuating temperature and relative humidity within the plant canopy. The fluctuations increased in frequency and magnitude as solar radiation increased. Fluctuations decreased as solar radiation decreased regardless of the ambient temperature. The cause of the fluctuations appeared to be partially due to drifting clouds, which briefly obscured the solar influx, decreasing leaf surface temperature. As canopy temperature dropped, a corresponding increase in canopy relative humidity occurred. Conversely, when cloud cover receded, leaf surface temperature increased rapidly and relative humidity dropped precipitously in the microclimate.

Spore liberation by *S. pannosa* in still air. The chamber's normal cyclical heating and cooling caused a consistent fluctuation of both

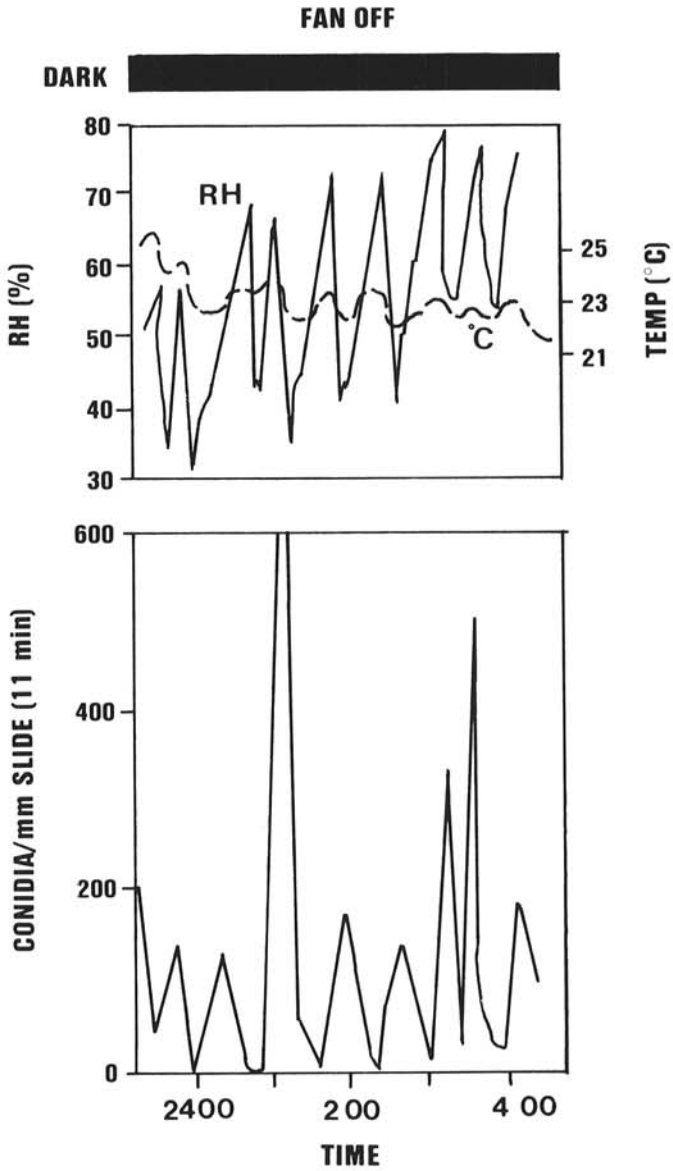

Fig. 4. Liberation of conidia by *Sphaerotheca pannosa* on rose in a standard growth chamber set for constant temperature operation but with the air circulation fan off.

temperature and humidity in the plant canopy when the chamber was set at a constant temperature and the air circulating fan was switched off (Fig. 4). Fluctuations of relative humidity were of greatest magnitude at high relative humidity (about 100%) and much less at low relative humidity (about 50%); temperature fluctuations remained the same at both relative humidities. These fluctuations of temperature and relative humidity were closely associated with the cycling peaks and troughs of spore liberation (Fig. 4). Measurable air turbulence in the growth chamber was negligible with the fan off and did not exceed 0.1 m sec^{-1}. An accelerometer was positioned at several locations on the plant pot during the tests. No vibrations greater than 0.005 G were detected during engagement of the cooling compressor.

To separate the influence of relative humidity and temperature on spore liberation, temperature was held constant by switching off the test chamber fan, compressor, and lights before experiments. This also eliminated any possible vibration introduced by the compressor. The test chamber temperature reached equilibrium with the room's ambient temperature within 4 hr and experiments were conducted after this equilibration. Under these conditions, discharge of conidia of *S. pannosa* occurred with abrupt decreases in relative humidity (Fig. 5) at constant temperature in still air and darkness. Discharge of conidia did not increase when light or increasing temperature accompanied the change in relative humidity (Fig. 6). The recorded air movement never exceeded 0.04 m sec^{-1} regardless of the orientation of the anemometer sensor during these constant temperature experiments.

Spore liberation by *E. pisi* in still air. *E. pisi* did not discharge spores in response to relative humidity changes alone when there was a 50% drop of relative humidity from near saturation in darkness (Fig. 7A). However, a precipitous decrease in relative humidity accompanied by exposure to light with increasing temperature, initiated a major liberation of conidia, which was 40-fold greater than background spore counts (Fig. 7A). Liberation of conidia continued in darkness as temperature subsequently decreased (Fig. 7B). A significant increase in relative humidity (greater than 10%) always halted the liberation.

Marked increases of temperature in the chamber caused measurable increases in air turbulence. This was evident, particularly, when lights were switched on. Greatest air movement was near to the fluorescent lamps at the back of the chamber (anemometer positioned between adjacent lamps). Air velocity reached a maximum of 0.13 m sec^{-1} during the abrupt temperature changes initiated by switching on lamps. The most extreme manipulations of the test chamber environment did not create air turbulence approaching the minimum velocities (0.4–1.0 m sec^{-1}) reported to be required for dislodgment of conidia in wind tunnel experiments (7,8,14,15). No movement of leaves within the test chamber (as viewed through the glass pane of the door) was detectable in any experiment.

Spore liberation by *E. graminis* in moving air. Experiments on detached leaves revealed a pronounced effect of reduced relative humidity on spore liberation of *E. graminis* (Fig. 8). Abrupt decreases and increases in relative humidity triggered discharge of conidia, but the response to sudden rising relative humidity levels was not uniformly evident. Conidia continued to discharge under constant reduced relative humidity and liberation tended to increase during prolonged (10 min) exposure to IR at low relative humidity (Fig. 8). Discharge was initiated by sudden decreases in relative humidity from saturation and terminated by continuously high relative humidity levels. The influence of unfiltered red-IR light (60 μE m^{-2} sec^{-1}) did not enhance discharge over the influence of abrupt reduction of relative humidity (Fig. 8).

DISCUSSION

These experiments provided the first clear evidence that conidia were liberated in still air (less than 0.1 m sec^{-1}) in response to

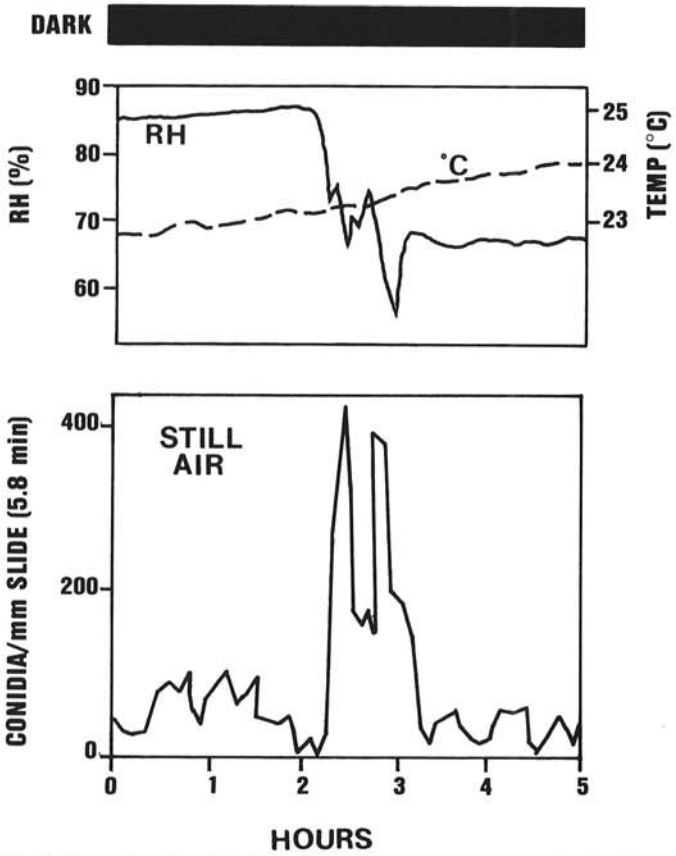

Fig. 5. Liberation of conidia by *Sphaerotheca pannosa* on rose in still air in darkness in response only to decreasing relative humidity. Air movement was less than 0.04 m sec^{-1}.

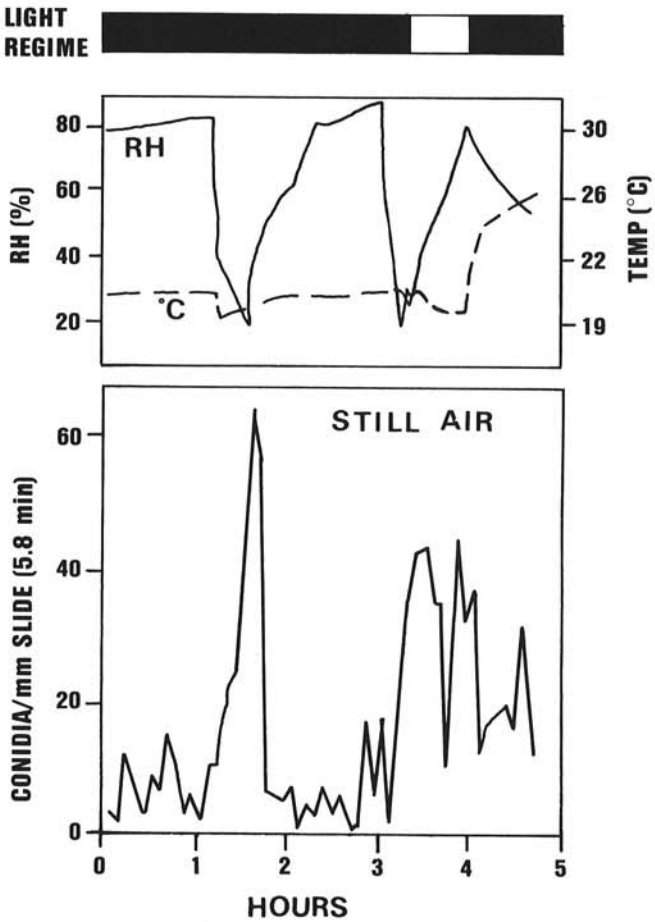

Fig. 6. Release of conidia by *Sphaerotheca pannosa* on rose in darkness and in light in response to decreasing relative humidity at a relatively constant temperature. Air movement was less than 0.04 m sec^{-1}.

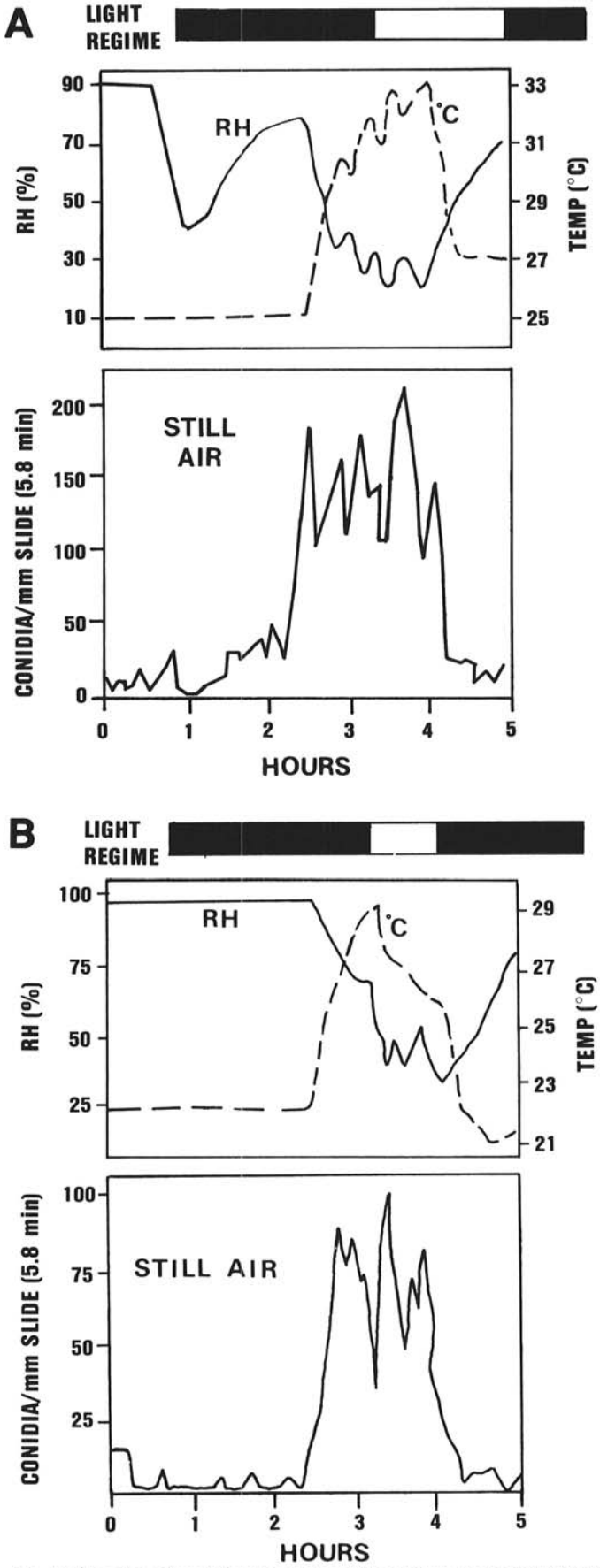

Fig. 7. Liberation of conidia by *Erysiphe pisi* in darkness and in light (80 μE m^{-2} sec^{-1}) in response to relative humidity and temperature. **A,** Comparing relative humidity change alone to combined affects of relative humidity, temperature, and light. **B,** Liberation initiated by light and increasing temperature with decreasing relative humidity and continuing in darkness with decreasing temperature and relative humidity.

fluctuating relative humidity and temperature. Previous studies on liberation of conidia in powdery mildews have emphasized the role of wind shearing as a mechanism of spore dislodgment. Wind velocities exceeding 1.0 m sec^{-1} impinging on conidia and conidiophores were required to liberate spores in wind tunnel experiments (8,14,15). We eliminated the mechanical and vibrational affects of air movement in some of our experiments and found that *S. pannosa* discharged conidia in response to an abrupt decrease in relative humidity regardless of whether it was light or dark. This response occurred at constant temperature or with a synchronous increase in temperature. *E. pisi* discharged large numbers of conidia in response to abrupt decreases in relative humidity and coincident increases in temperature in still air. Likewise, in *E. graminis*, abrupt changes in relative humidity, whether an increase or a decrease, triggered spore release in wind tunnel experiments at a constant air velocity (0.5 m sec^{-1}). The actual change in relative humidity and temperature appeared to trigger the massive liberation of conidia. The response of the fungus to the abrupt relative humidity change often continued for approximately 3–40 min. Raising the relative humidity did not trigger spore release in *S. pannosa* and *E. pisi*, and spore discharge in all three fungi ceased at high relative humidity in nearly still air.

These results seem to contradict most previous research on liberation of conidia by powdery mildews. Earlier workers concluded that temperature and humidity had little epidemiological significance (5,6,34) and that photoperiod was the primary stimulant of release. Diurnal periodicity affects the sporulation process and the cyclical production and maturation of conidia and may mask the effects of temperature and humidity on liberation of conidia. Our results suggest that temperature and humidity are important triggering factors in spore discharge. The lack of sensitivity of most temperature and humidity sensors and spore traps tends to mask the microclimate factors that actually trigger spore liberation. This may have led researchers to represent spore catches as responding to constant low or high relative humidity and temperature. It is more likely that the catches were the accumulated discharges resulting from numerous fluctuations of relative humidity and/or temperature.

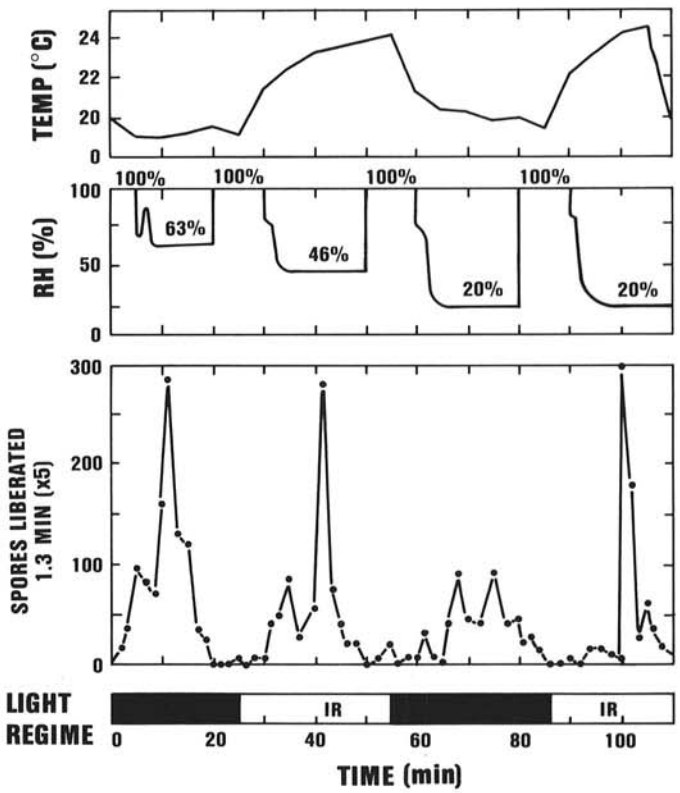

Fig. 8. Relationship of liberation of conidia by *Erysiphe graminis* to changes of relative humidity and exposure to red-infrared light. Air flow was a constant 0.5 m sec^{-1}.

Diurnal periodicity in spore catches may be explainable as exogenously initiated episodic liberations due to relatively consistent diurnal patterns of environmental changes. Conidia produced nocturnally are thus ready for dispersal at a time of day when temperature, relative humidity, wind, and solar radiation are actively fluctuating within the canopy microclimate. Further support for this argument comes from studies of spore catches of powdery mildews in the field (13,34,35). No diurnal periodicity of spore maturation or release is evident on overcast days, which cause a dampening of microclimate fluctuations in the plant canopy.

Spore discharge in response to sudden changes in relative humidity has been demonstrated to occur in dry-spored fungi in the Hyphomycetes (9,10,20,22), the Peronosporales (24,27), and now the Erysiphales. Among these fungi, differences in response to increasing or decreasing relative humidity have been noted. *Pyricularia* liberated greater numbers of spores during rising relative humidity, unlike the other fungi, which responded more pronouncedly to decrease in relative humidity. *E. graminis* liberated spores in response to an abrupt increase in relative humidity, but not *S. pannosa* and *E. pisi*.

The magnitude of fluctuations of relative humidity in the microclimate are primarily in response to the effect of solar radiation on plants. Leaf surface temperatures in bright sunlight are often 10 C above ambient and relative humidity is often 20% above ambient (32). Thus, as the solar radiation increases from dawn to midday then wanes toward dusk, so too does the active discharge of powdery mildew conidia. Wind also increases and wanes in the same diurnal pattern. In our glasshouse studies of *S. pannosa*, fluctuating temperature in the plant canopy always accompanied fluctuating relative humidity. It appears, therefore, that under natural conditions, abrupt changes in relative humidity are most commonly accompanied by, as well as initiated by, abrupt changes in temperature usually initiated by changes in solar radiation. Possibly any factor that causes sudden decreases in relative humidity will initiate the discharge of conidia and sporangia in fungal foliar pathogens. Such factors include a gust of drier or hotter air, an influx of solar radiation or a physical disturbance of the canopy.

Changes in solar radiation, IR, and relative humidity significantly influence the electrical charges on leaf surfaces (25,26). Pronounced increases in charge have been observed on overcast days when solar radiation increased after exposure of the sun from receding cloud cover (26). Abrupt increases in electrical charges on leaf surfaces correlate with massive liberation of spores by dry-spored foliar pathogens (25,26). The changes in electrical charge, particularly, are greater as related to relative humidity changes. The electrical field strength above leaf surfaces in a moving airstream (0.3 m sec^{-1}) range from 100–500V cm^{-1} whenever leaves are subjected to low humidities (35–50% RH) and drop to 0V in a saturated airstream (100% RH) (25). Measurements in the field are of the same order of magnitude (C. M. Leach, *unpublished data*). The magnitude of the force (F) involved in discharging powdery mildew conidia was calculated to be approximately 6×10^{-12} Newtons (4). The force exerted on a spore carrying a charge (q) in an electrostatic field of strength E is calculated using the formula $F = q\,E$. Because q is approximately 2×10^{-15} coulombs (29), E becomes 3,000 volts m^{-1} or 30V cm^{-1}. Thus, the electrical charge present on a plant leaf surface during a change from high to low humidity is in the range of the voltage required to remove conidia from conidiophores.

As early as 1925, Hammarlund (12) observed that conidia were forcibly discharged a distance of 10–20 conidial lengths in *S. Pannosa*, *E. polygoni* and other conidial chain-forming Erysiphaceae. Active discharge also was observed in *S. humuli* (17). The discharge of the powdery mildew conidia in nearly still air provides further evidence that an active discharge mechanism may be involved as proposed for *Drechslera turcica*, *Peronospora destructor* and other fungi (17,18,20,21,24). It has been argued that powdery mildew conidia are not actively discharged because if colonies are left undisturbed conidia accumulate in chains, topple, and become an entangled mat of mature spores (14,15). This phenomenon can be clarified in light of the knowledge of the triggering of discharge by naturally occurring fluctuation in relative humidity or temperature. Conidia would not discharge in an environment buffered from microclimate fluctuations as occurs at night or on foggy or continuously overcast days.

The hypothesis that wind velocities of approximately 1 m sec^{-1} are the force that directly dislodges powdery mildew conidia needs reexamining. Chains of conidia are usually within the 1–2 mm thick aerodynamic boundary layer on the surface of the leaf. In a plant canopy, ambient wind velocities usually range in magnitude from 0.1 to 1.0 m sec^{-1} (2,28). Such velocities are insufficient for penetrating a boundary layer (11,31). However, brief (10^{-3} sec) and energetic (2 m sec^{-1}) gusts of wind occur around plant leaves in the turbulent flow of the ambient wind (28,33). Mathematical models support the argument that the peak gusts successfully penetrate the boundary layer to impinge on conidia with sufficient force to cause removal (3). However, the complex behavior of wind flow around plant leaves and the effect of wind on the dynamics of the boundary layer are yet to be solved by fluid dynamicists (1,11,33). Experimental evidence for the gust hypothesis is based on observation of temperature changes occurring on a 15-cm plastic disk (3). Direct experimentation, demonstrating that gusts penetrate the boundary layer of leaves in a plant canopy and cause dislodgment of spores, is needed to support the hypothesis of passive dislodgment of spores. Experimental evidence favoring the alternate hypothesis of an active discharge of fungal spores is more extensive. This paper supports the conclusion that a sudden reduction in relative humidity is the main environmental variable that triggers active discharge of conidia in three species of powdery mildews.

LITERATURE CITED

1. Aylor, D. E. 1978. Dispersal in time and space: Aerial pathogens. Pages 159-180 in: Plant Disease: An Advanced Treatise II. J. G. Horsfall and E. B. Cowling, eds. Academic Press, New York. 436 pp.
2. Aylor, D. E., and Lukens, R. J. 1974. Liberation of *Helminthosporium maydis* spores by wind in the field. Phytopathology 64:1136-1138.
3. Aylor, D. E., and Parlange, J-Y. 1975. Ventilation required to entrain small particles from leaves. Plant Physiol. 56:97-99.
4. Bainbridge, A., and Legg, B. J. 1976. Release of barley-mildew conidia from shaken leaves. Trans. Br. Mycol. Soc. 66:495-498.
5. Cole, J. S. 1976. The formation and dispersal of *Erysiphe cichoracearum* conidia. Pages 185-198 in: Microbiology of Aerial Plant Surfaces. C. H. Dickenson and T. F. Preece, eds. Academic Press, New York.
6. Cole, J. S., and Fernandes, D. L. 1970. Effects of light, temperature and humidity on sporulation of *Erysiphe cichoracearum* on tobacco. Trans. Br. Mycol. Soc. 55:345-357.
7. Cole, J. S., and Geerligs, J. W. 1976. Time-lapse photography of formulation and release of conidia of *Erysiphe cichoracearum* on tobacco. Trans. Br. Mycol. Soc. 67:339-342.
8. Frinking, H. D. 1977. Research on wind dispersal of rose mildew spores (*Sphaerotheca pannosa*) in field, greenhouse and climate room. Grava 16:155-158.
9. Gottwald, T. R. 1982. Spore discharge by the pecan scab pathogen *Cladosporium caryigenum*. Phytopathology 72:1193-1197.
10. Gottwald, T. R. 1983. Factors affecting spore liberation by *Cladosporium carpophilum*. Phytopathology 73:1500-1505.
11. Grace, J., and Collins, M. A. 1976. Spore liberation from leaves by wind. Pages 185-198 in: Microbiology of Aerial Plant Surfaces. C. H. Dickenson and T. F. Preece, eds. Academic Press, New York.
12. Hammarlund, C. Von. 1975. Zur Genetik, Biologie und Physiologic einiger Erysiphaceen. Hereditas 6:1-120.
13. Hammett, K. R. W., and Manners, J. G. 1971. Conidium liberation in *Erysiphe graminis*. I. Visual and statistical analysis of spore trap records. Trans. Br. Mycol. Soc. 56:387-401.
14. Hammett, K. R. W., and Manners, J. G. 1973. Conidium liberation in *Erysiphe graminis*. II. Conidial chain and pustule structure. Trans. Br. Mycol. Soc. 61:121-133.
15. Hammett, K. R. W., and Manners, J. G. 1974. Conidium liberation in *Erysiphe graminis*. III. Wind tunnel studies. Trans. Br. Mycol. Soc. 62:267-282.
16. Hirst, J. M. 1953. Changes in atmospheric spore content: Diurnal periodicity and the effects of weather. Trans. Br. Mycol. Soc. 36:375-393.
17. Leach, C. M. 1975. Influence of relative humidity and red-infrared

radiation on violent spore release by *Drechslera turcica* and other fungi. Phytopathology 65:1303-1312.
18. Leach, C. M. 1976. An electrostatic theory to explain violent spore liberation by *Drechslera turcica* and other fungi. Mycologia 68:63-86.
19. Leach, C. M. 1980. An apparatus for precise control of humidity, temperature, air flow, and light in spore discharge studies. Phytopathology 70:189-191.
20. Leach, C. M. 1980. Influence of humidity and red-infrared radiation on spore discharge by *Drechslera turcica*–additional evidence. Phytopathology 70:192-196.
21. Leach, C. M. 1980. Vibrational release of conidia by *Drechslera maydis* and *D. turcica* related to humidity and red-infrared radiation. Phytopathology 70:196-200.
22. Leach, C. M. 1980. Influence of humidity, red-infrared radiation and vibration on spore discharge by *Pyricularia oryzae*. Phytopathology 70:201-205.
23. Leach, C. M. 1980. Evidence for an electrostatic mechanism in spore discharge by *Drechslera turcica*. Phytopathology 70:206-213.
24. Leach, C. M. 1982. Active sporangium discharge by *Peronospora destructor*. Phytopathology 72:881-885.
25. Leach, C. M. 1984. Leaf surface electrostatics. Response of detached leaves of beans and maize to humidity and red infrared radiation under controlled conditions. Phytopathology 74:695-701.
26. Leach, C. M., and Apple, J. D. 1984. Leaf surface electrostatics. Behavior of detached leaves of beans, maize, and other plants under natural conditions. Phytopathology 74:704-709.
27. Leach, C. M., Hildebrand, P. D., and Sutton, J. C. 1982. Sporangium discharge by *Peronospora destructor*: Influence of humidity, red-infrared radiation, and vibration. Phytopathology 72:1052-1056.
28. McCartney, H. A. 1985. Gust penetration into plant canopes. Atmos. Environ. 19:827-830.
29. McCartney, H. A., Bainbridge, A., Legg, B. J., and Jones, C. D. 1982. Electric charge on the deposition of spores of barley mildew *Erysiphe graminis*. Atmos. Environ. 16:1133-1143.
30. Packham, J. McC. 1969. Studies on the epidemiology of powdery mildew of greenhouse roses. (Abstr.) Phytopathology 59:1043.
31. Percier, E. R., Aston, A., and Aorkin, G. F. 1973. Wind flow characteristics on a soybean leaf compared with a leaf model. Physiol. Plant. 28:106-112.
32. Schnathorst, W. C. 1965. Environmental relationships in the powdery mildews. Annu. Rev. Phytopathol. 3:343-366.
33. Shaw, R. H., Ward, D. P. and Aylor, D. E. 1979. Frequency occurrence of fast gusts of wind inside a corn canopy. J. Appl. Meteorol. 18:167-171.
34. Sutton, T. B., and Jones, A. L. 1979. Analysis of factors affecting dispersal of *Podosphaera leucotricha* conidia. Phytopathology 69:380-383.
35. Yarwood, C. E. 1957. Powdery mildews. Bot. Rev. 23:235-300.