Evidence for an Electrostatic Mechanism in Spore Discharge by *Drechslera turcica*

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ABSTRACT

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Violent discharge of conidia by *Drechslera turcica* was studied visually and photographically in a specially designed Tyndall apparatus. Conidia were propelled into the air approximately at right angles to the sporulating lesion regardless of the orientation of the surface to gravity. When several spores were discharged simultaneously, their initial trajectories were parallel. Slight vibration of specimens caused synchronized release of conidia with trajectories identical to those of spores released in the absence of vibrations. Conidia discharged near two needle electrodes (400 V, DC) 10 mm apart consistently were attracted to the positive electrode whether liberated in response to vibration or in response to humidity changes. Conidia discharged near electrodes charged with an alternating current (115 V, 60 Hz) followed sinusoidal trajectories. When the potentials of sporulating specimens were artificially increased by applying negative voltages from 0 to 1,800, velocity of discharge increased with increase in voltage. The most convincing evidence for an electrostatic mechanism resulted from experiments on the electrical neutralization of sporulating lesions. Application of positive ions from a piezo-electric ion generator to the negatively charged sporulating lesion, stopped spore discharge. The results of these studies support the existence of an electrostatic mechansim for the violent discharge of conidia by *D. turcica*. Preliminary visual observations also were made on spore discharge by several other Fungi Imperfecti (*Drechslera maydis, Stemphylium botryosum,* and *Pyricularia oryzae*). All discharged conidia violently and the flight paths of liberated spores resembled those of *D. turcica*.

Conidia of a number of dry-spored plant pathogenic fungal species of the Fungi Imperfecti are violently discharged into the air (3,12). *Drechslera turcica* (Pass.) Subram. and Jain (conidial stage of *Trichometasphaeria turcica* Luttrell), the cause of northern leaf blight of maize, is an example. It discharges conidia violently in response to changes of humidity, exposure to red-infrared radiation (4,8,10), and in response to vibrations (9). Violent discharge of conidia can be observed under special illumination (Fig. 1). Spores are propelled into the air at right angles from the sporulating surface, and the trajectories of released spores are not noticeably influenced by the orientation of the surface relative to gravity. The flights of discharged conidia, whether triggered by changes of humidity, exposure to red-infrared radiation, or by vibrations, are indistinguishable suggesting the existence of a common mechanism. Meredith (12) postulated that violent discharge of conidia by *D. turcica* results from the rapid release of cellular tensions associated with the dehydration of conidia and conidiophores. More recently, I proposed an electrostatic mechanism (5,6) which involves the repulsion of unipolarly charged conidia from a charged surface of the same polarity.

The purpose of this study was to further investigate the possibility that violent discharge of conidia by *D. turcica,* whether triggered by humidity changes, exposure to red-infrared radiation, or by vibration, involves an electrostatic mechanism. Preliminary observations were also made on discharge of conidia by *Drechslera maydis, Stemphylium botryosum,* and *Pyricularia oryzae.*

MATERIALS AND METHODS

Preparation of specimens. Leaf lesions from maize with northern leaf blight (which is caused by *D. turcica*) were used in most experiments. These were collected from naturally infected maize, dried in a plant press, and stored at −20 C until needed. To induce sporulation, leaf lesions were soaked for 10 min in water and then incubated for 4 to 7 days under a daily cycling regime of near-ultraviolet light (20 W BLB "Black Light" fluorescent lamp 13 cm above specimens; 160 $\mu W/cm^2$) and temperature (12 hr dark, 12 hr NUV; 20 C night, 25 C day). Sporulating agar plugs were used in a few experiments. To obtain plugs, colonies were grown on potato dextrose agar (normally a poor medium for sporulation) for 7 days at 20 C in darkness; 12 mm diameter cylindrical plugs were removed from the actively growing peripheral mycelium and placed in an inverted position on filter paper (No. 3 Whatman) previously soaked in lactose, casein hydrolysate broth (15). Normally agar is included in this medium but it was excluded here. The fungus sporulated heavily on the plugs when exposed to the same conditions used for the leaf lesions.

Specimens of the three other fungi consisted of maize leaf lesions of *D. maydis*, rice culm lesions of *P. oryzae*, and cylindrical plugs from potato dextrose agar colonies of *S. botryosum*. To induce heavy production of conidia by these fungi, all were subjected to the same incubation conditions as described for *D. turcica.*

Specimens used in the Tyndall apparatus (Fig. 1) were trimmed to approximately 7 × 10 mm with a razor blade. In experiments in which the specimen voltage was artificially regulated, slightly smaller specimens were used (7 × 7 mm).

Tyndall apparatus. In 1909 Buller (2) recommended the use of a light beam to observe spore liberation by agarics. This technique involved the Tyndall effect (light scattering by small particles) and was the basis of the apparatus designed for these studies (Fig. 1). This apparatus, combined with a camera (Fig. 1A), was used to photograph flights of discharged conidia (Fig. 2). By removing the camera and combining it with a dissecting microscope (not shown), spore discharge could be followed visually.

Sporulating specimens were attached to a plastic, electrically nonconductive holder (Figs. 1-B,C,D) with Vaseline with the axes of conidiophores approximately horizontal (Fig. 1-D). In experiments requiring the modification of specimen voltages, a special brass holder was used. Specimens were attached to this by a thin film of sticky, highly conductive silver epoxy cement applied in the uncured state ("Epo-tek H31D," manufactured by Epoxy Technology Inc., Watertown, MA, USA). The specimen holder was adjustable and located within a cylindrical compartment to shield the specimen from extraneous light and drafts. The interior of this compartment was lined with black felt to minimize light reflection. Specimens were exposed to a uni-directional, approximately parallel light from a microscope lamp (American Optical, Model 350 microscope illuminator, 2.5–7.5 V incandescent lamp) (Fig. 1). Emission from this lamp included

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red-infrared radiation. The light beam was directed onto the specimen through an oval hole (2 × 3 cm) in the front of the cylindrical specimen compartment. An optically flat piece of clear glass was taped over the hole, and a piece of black cloth (not shown) was placed completely around the specimen compartment area to further reduce drafts. The complete elimination of drafts was important because the slightest air movement modified spore trajectories.

Camera and photographic procedures. A 35 mm single-lens reflex camera (Olympus OM-1 MD) with extension bellows (Fig. 1A) and a close-up lens (Olympus f3.5 automatic macro) was used in all experiments in which spore discharge was photographed. A high-speed and fairly fine-grain black-and-white film (Kodak Tri-X, ASA 400) were used, with the camera aperture set at f5.6. Film was developed for 5 min at 20 C (Acufine developer, Acufine Inc., Chicago, IL, USA). The camera was operated by an electrical remote-control button and a motor-driven winder capable of taking several exposures per second. To photograph the flights of discharged conidia, synchronized liberation was triggered by a single light tap on the specimen platform (Fig. 1) with a metal rod. The camera shutter was opened manually immediately prior to and closed within 0.5 sec after tapping. Length of exposure was not critical in recording the flight of conidia (Fig. 2).

A different procedure was used to photograph spore discharge for velocity measurements. At shutter speeds of either 1/4, 1/8, 1/15, or 1/30 sec, the specimen holder was first tapped (single tap) to liberate spores and then almost simultaneously the camera shutter was tripped. By measuring the length of the trajectories on the negatives (Fig. 3D). I could determine the velocity of spore discharge. Mean velocities were determined for 25 measurements, randomly distributed among four or more releases. The accuracy of the camera's shutter speeds (1/4, 1/8, 1/15, and 1/30 sec) was tested with a selenium photocell, placed in the camera's focal plane to

TABLE 1. Polarity of charge on conidia of *Drechslera turcica* released in response to humidity changes

Position of positive[a] electrode	Relative humidity regime[b]	Spores trapped[c,d]			
		Positive electrode		Negative electrode	
		%	No.	%	No.
right	lowered (100% → 40%)	76.8	239.2	23.2	72.2
right	raised (40% ← 100%)	80.7	8.4	19.3	2.0
left	lowered (100% → 41%)	87.2	224.0	12.8	32.6
left	raised (41% ← 100%)	86.6	5.2	13.4	0.8
right	lowered (100% → 41%)	81.9	42.8	18.1	9.4
right	raised (41% ← 100%)	85.7	3.6	14.3	0.6
left	lowered (100% → 40%)	86.8	56.8	13.2	8.6

[a] Electrode polarity (2,000 V DC) reversed after humidity cycle.
[b] A single specimen was subjected to alternate cycles of humidity change. Lowering or raising humidity took approximately 2 min (7).
[c] Averaged from five random counts across electrode surfaces; each count covered an area 50 × 1 mm.
[d] Electrodes counted and replaced after each change of humidity.

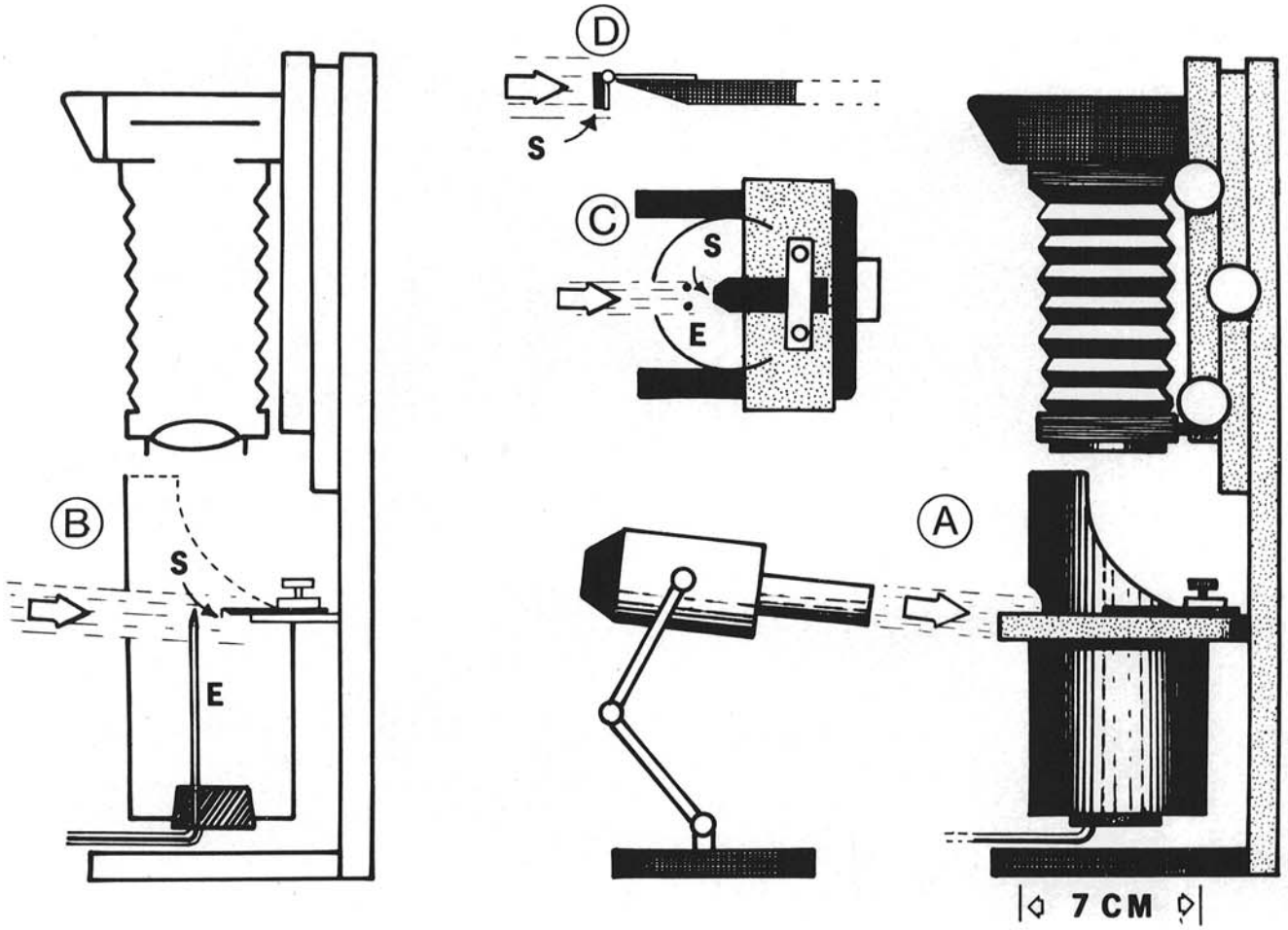

Fig. 1. Tyndall apparatus for photographing fungal spore discharge. **A,** Side view showing cylindrical specimen compartment, 35-mm camera with bellows and a microscope lamp; **B,** Sectional drawing showing location of specimen (S) and electrodes (E); **C,** Top view of specimen platform showing specimen holder and the tips of the two needle electrodes, 10 mm apart; **D,** An enlarged side view of the hinged end of the specimen holder (All drawings are schematic and not to scale).

receive light from a microscope illuminator directed onto the lens. On opening the shutter, an electrical signal was generated by the photocell, and this was recorded in a storage oscilloscope accurate to 0.1 μsec (Model 511, Tektronix Inc., Beaverton, OR, USA). Repeated tests showed the shutter speeds to be extremely accurate and reliable.

Polarity of charges on conidia. The polarity of charges on conidia was determined with (i) the Tyndall apparatus (Fig. 1) and (ii) a previously described spore release apparatus (7). Specimens were positioned in the Tyndall apparatus 10 to 15 mm from two parallel needle electrodes 1 mm diam. and 10 mm apart as depicted in Figs. 1B–D. The electrodes were connected to either a high-voltage DC source (Model 245 high-voltage supply, Keithley Instruments Inc., Cleveland, OH, USA), or to alternating current from a laboratory wall outlet (115 V, 60 Hz). The flights of discharged spores near the DC and AC electrodes were followed both photographically and visually.

Using the spore release apparatus (7), release of conidia was triggered by changes of humidity (4,8,9) as indicated in Table 1. Air temperature (20 C) and air velocity (0.5 m/sec) were kept constant. Released spores were directed through a large rectangular orifice (8 × 30 mm) between two thin, rectangular copper electrodes, each measuring 12 × 50 mm. The electrodes were slightly angled to each other. The 50 mm leading edges of the electrodes were 10 mm apart while the trailing edges were only 4 mm apart. The 50 mm length of the electrodes were aligned with the 30 mm length of the orifice. The exposed surfaces of the electrodes were coated with a thin layer of uncured, sticky, silver epoxy cement (Epo-tek H31D). The electrodes were connected to a high-voltage DC supply. Following each humidity change, the electrodes were replaced and the spores trapped on the electrodes were counted microscopically using overhead illumination (Nikon epi-illuminator). Polarity of electrodes was reversed after each complete humidity cycle (RH lowered, then raised) as shown in the Table.

Modification of specimen voltages. Specimen voltages were regulated in the Tyndall apparatus by placing them on a brass specimen holder (Figs. 1B–D). Specimens were attached to the holder by means of a thin film of uncured silver epoxy cement.

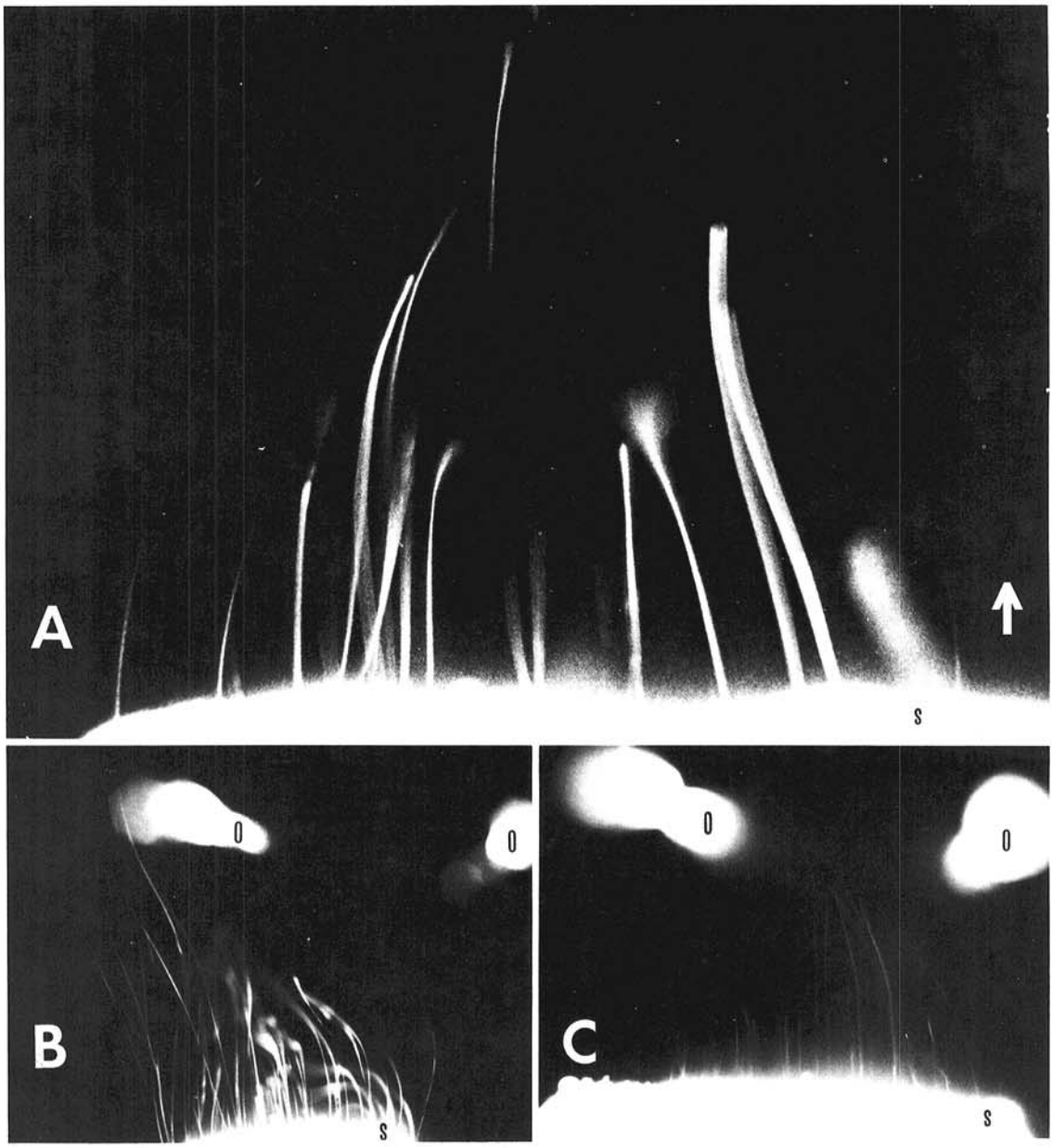

Fig. 2. Trajectories of conidia violently discharged in response to vibration. **A,** *Drechslera turcica;* **B,** *D. maydis;* and **C,** *Stemphylium botryosum.* (Photographs are time exposures; tips of uncharged electrodes (0) 10 mm apart; specimen (S); arrow indicates direction of discharge; approximate magnifications are × 8 for A, and × 4 for B and C).

The 7 × 7 mm holder was either grounded (connected to a 1.5-m copper rod driven into the ground) or connected to the negative lead of the high-voltage DC supply (Keithley, Model 245).

RESULTS

Spontaneous liberation of conidia. When *D. turcica* was transferred directly from the incubator to the Tyndall apparatus following a period of darkness (air temperature 20 C, humidity uncontrolled), no spore discharge was evident at first; then after a few seconds of exposure to light (Fig. 1) conidia began to discharge randomly into the air. Within minutes many conidia could be observed discharging. Specimens of *D. maydis, S. botryosum,* and *P. oryzae* behaved similarly. Discharged conidia of *D. turcica* were violently propelled for approximately 5–10 mm after which they floated haphazardly off into the air. Trajectories were initially straight and parallel with each other and approximately at right angles to the sporulating surface irrespective of its gravitational orientation. Photographing this spontaneous discharge was difficult because it was random and because the vibration caused by the camera's focal plane shutter and mirror were sufficient to trigger vibrational release (next section). Visually and photographically the trajectories of spontaneously discharged conidia of all four fungi were identical to those triggered by vibration (Fig. 2).

Incubation conditions prior to placing specimens of *D. turcica* in the Tyndall apparatus influenced subsequent spore discharge. Maximal discharge always followed incubation in darkness; least discharge occurred when specimens were removed from the incubator while exposed to near-ultraviolet radiation. In addition, spore discharge was most abundant from young, moist specimens and least from old and dry specimens.

I concluded that *D. turcica, D. maydis, P. oryzae,* and *S. botryosum* are all capable of violently discharging their spores into the air in the absence of vibration.

Liberation of conidia by vibration. I discovered accidentally that a slight vibration of the specimen in the Tyndall apparatus caused massive discharge of conidia, and the longer specimens were exposed to light, the more sensitive they became to vibration (9). To investigate this form of spore liberation, specimens of each of the four fungi were individually placed in the Tyndall apparatus (Fig. 1) and the release of conidia was triggered by vibration (single taps) and photographed. Individual specimens were subjected to a sequence of 10–30 taps within several minutes and the spore release associated with each tap was photographed.

All four fungi discharged conidia in response to vibration. Photographs of release of conidia by *D. turcica, D. maydis,* and *S. botryosum* are shown in Fig. 2, and are typical of the many photographs taken. *P. oryzae* behaved similarly, but could not be photographed because too little light was reflected by its small conidia.

During vibration experiments with specimens of *D. turcica,* as

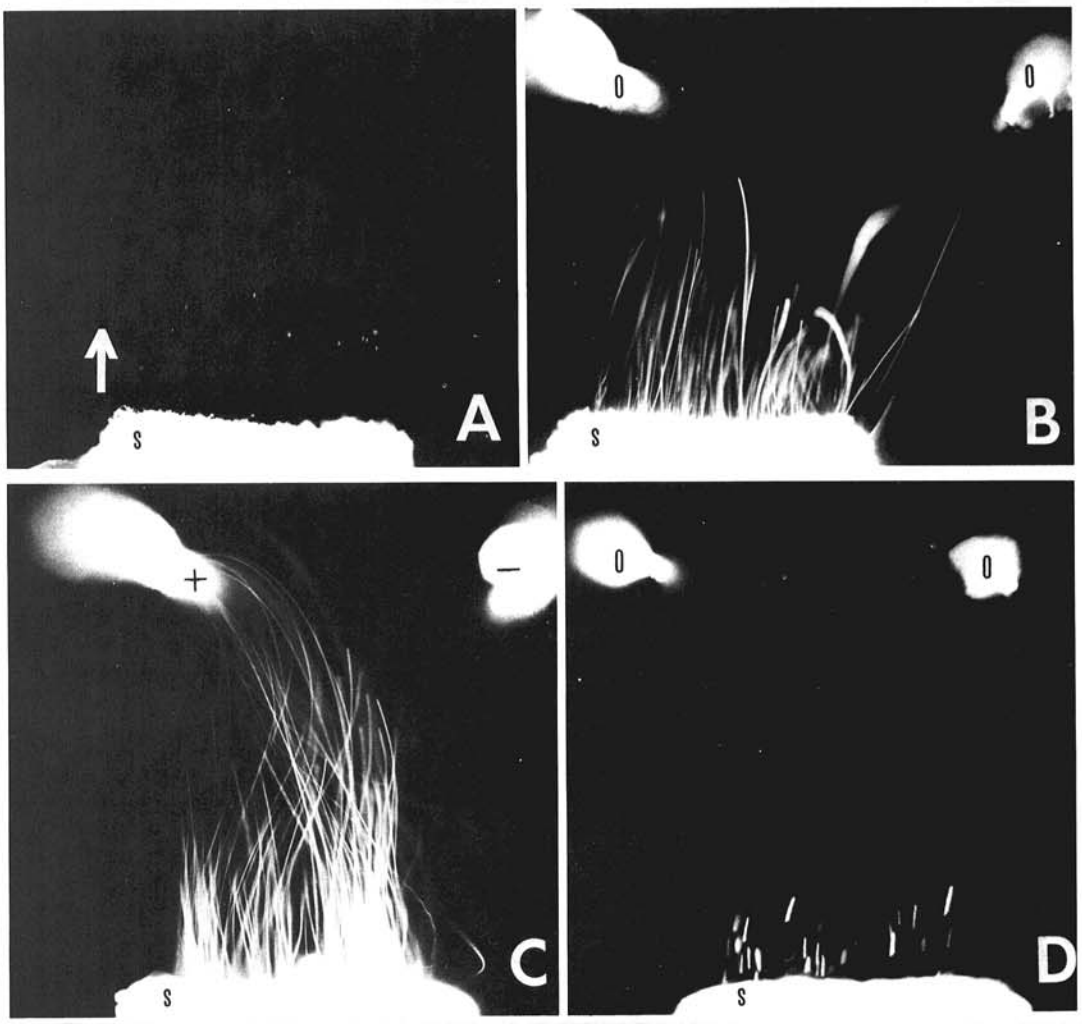

Fig. 3. Violent discharge of conidia of *Drechslera turcica* in response to vibration. **A,** Exposure of 1/60 sec showing discharged conidia as white spots above the specimen (S); arrow indicates direction of flight); **B,** Trajectories (time exposure) of discharged conidia near the tips of two uncharged needle electrodes (0); **C,** Trajectories of conidia attracted to the positive electrode (400 V DC); **D,** Flight of conidia during 1/30 sec used to determine velocity of discharge. (Magnification of all photographs approximately × 5).

well as the other fungi, I observed that not all conidia were discharged at once, and a sequence of taps always resulted in repeated releases of conidia. The numbers of conidia discharged in response to vibration varied considerably from specimen to specimen. Usually most of the released conidia were propelled into the air (Fig. 2) but in some specimens a proportion of spores appeared to be merely mechanically dislodged; that is, they fell off. I was unable to record this mechanical dislodgement photographically.

Electrically charged conidia. If conidia are violently discharged into the air by an electrostatic mechanism as postulated (5), it is axiomatic that released spores must be both charged and of the same polarity. Two series of experiments were conducted with *D. turcica* to determine whether this was so. In one series, conidia were liberated in response to humidity changes under controlled conditions; in the other, vibrationally in the Tyndall apparatus in the presence of charged electrodes.

An average of 84% of the spores liberated by humidity changes (as shown in Table 1) and trapped in repeated experiments of trapped spores were negatively charged; ie, they were found on the positively charged electrode. Though some spores also were trapped on the negative electrode, it was not known whether these were positively charged or merely trapped mechanically. Further studies are needed to resolve this question. I concluded that spores liberated in response to humidity changes are mainly negatively charged, irrespective of the form of the humidity change (ie, increasing or decreasing).

In the Tyndall apparatus, with 400 V DC electrodes, vibrationally released conidia were consistently attracted to the positive electrode and were therefore negatively charged (Fig. 3C). Spores liberated vibrationally near electrodes charged with an alternating current followed sinusoidal trajectories (Fig. 4) also indicating that they were charged. When the electrode voltage was varied from 0 to 1,200 V DC, velocity of discharge at take-off remainded constant for all voltages indicating no effect of electrode field on velocity of spore discharge.

Influence of specimen voltage on spore velocity during discharge. Velocity of discharge was consistently greater in grounded than in nongrounded specimens (Fig. 5A). In Fig. 5, a measure of the velocity of discharge is the length of the 1/4 sec trajectories, ie, they are longer in the grounded than in the nongrounded specimens. Although the specimen voltages were unknown in either, the results did suggest that specimen potential influences the velocity of spore discharge.

Artificial modification of specimen potential (100–1,600 V DC) had a very marked effect on velocity of spore discharge. As the voltage was increased, the velocity of discharge increased as shown photographically in Fig. 5B (1/4 sec exposures) and graphically (Fig. 6). Characteristically, the velocity of discharge increased up to a maximum beyond which voltage increases had no further effect. Where single specimens were used for the complete experiment (Fig. 6, I and II), specimens had begun to dry by the end of the experiment which probably resulted in a loss of conductivity. Maximal spore velocities were lower in these experiments than when a fresh specimen was used for each voltage increase in (Fig. 6, III).

Effect of neutralizing specimen of spore discharge. If violent spore release is an electrostatic phenomenon as proposed, neutralization of specimen charge should cause a cessation of spore discharge. To test this hypothesis, specimens of *D. turcica* were placed on an electrically grounded specimen holder, and conidia were again liberated vibrationally by a sequence of taps and photographed as previously described (time exposures). The needle electrodes in front of the specimen holder (Fig. 1B–D) were

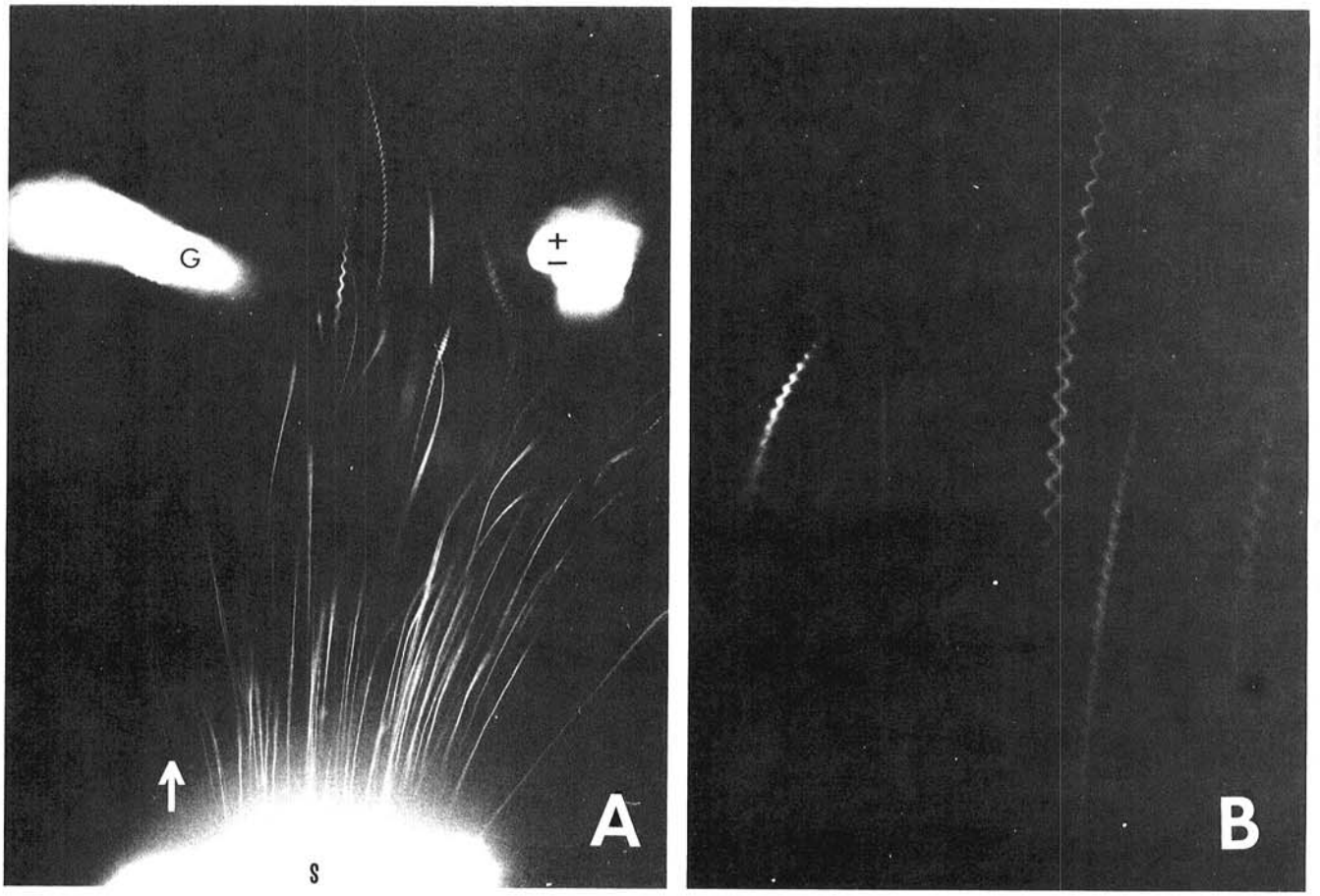

Fig. 4. The effect of an alternating current (115 V, 60 Hz) on the trajectories (time exposures) of conidia of *Drechslera turcica* liberated by vibration. **A,** Flights of conidia showing sinusoidal trajectories near electrodes (10 mm apart). Approximate magnification is ×5. S = specimen, G = grounded electrode, arrow indicates direction of conidial discharge. **B,** Trajectories enlarged.

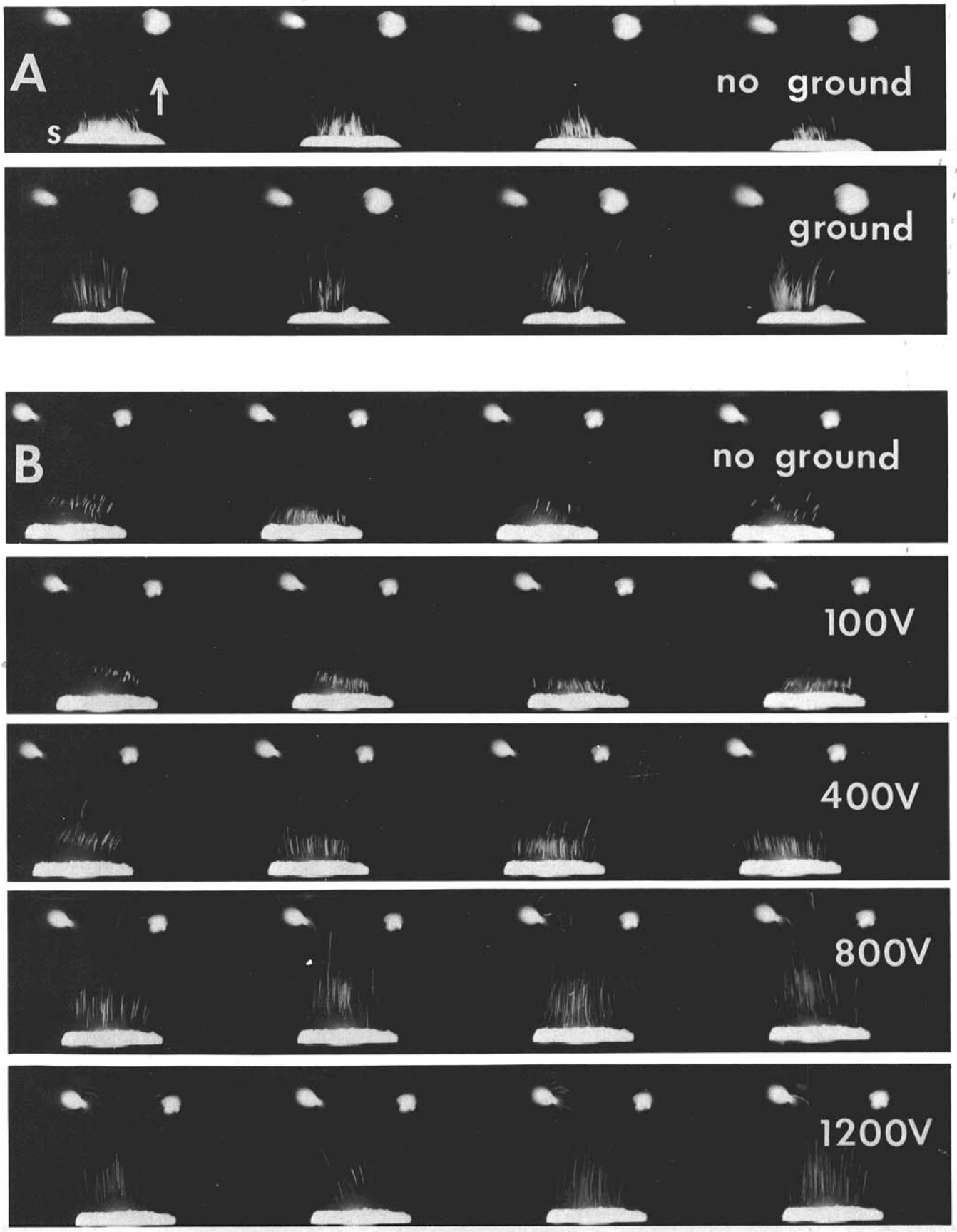

Fig. 5. The effect of specimen (*Drechslera turcica*) voltage on velocity of spore discharge triggered by vibration. **A,** Effect of grounding specimen, versus nongrounding; **B,** Effect of different negative voltages on specimen (S, specimen; arrow, direction of discharge; exposures 1/8 sec; though electrodes were uncharged some residual charge is evident in B.

regulated at 400 V DC so that the polarity of charge on discharged spores could be determined. Partway through the series of taps, the specimen was electrically neutralized by applying positive ions. Source of the positive ions was a piezo-electric ion generator (Zerostat Instruments Co., St. Ives, Cambridge, England), a device normally used to neutralize electrostatic charges on phonograph records. The ion generator emitted either positive or negative ions and was hand-held a few centimeters from the specimen. Ions were applied for a few seconds only.

Neutralization of the specimen caused an immediate and almost complete cessation of spore discharge triggered by vibration. Figure 7 (photos 1-4) shows spore release resulting from a sequence of single taps in which initially all spores were negatively charged. After the fourth tap (photo 4), the specimen was neutralized with positive ions, resulting in a dramatic cessation of spore discharge (photos 5 and 6). After the sixth tap (photo 6), the specimen was again exposed to positive ions; it lost its neutrality and became positively charged, sufficient to cause conidia to be violently released when the specimen was again tapped (photos 7 and 8) but with a reversal of the charge on spores.

The cessation of spore discharge after neutralization of specimens was the most convincing evidence that violent liberation of conidia by *D. turcica* involves an electrostatic mechanism.

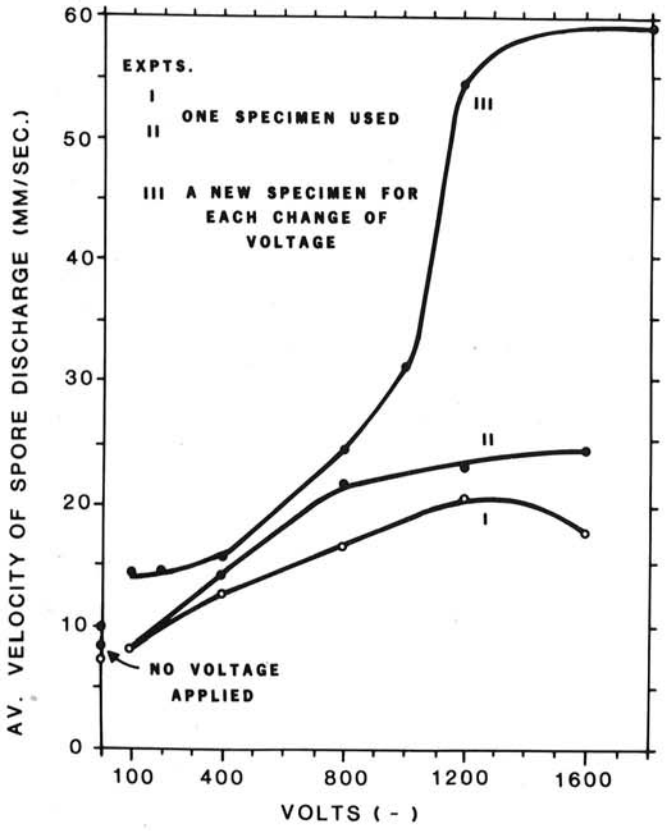

Fig. 6. Effect of artificially increasisng the specimen voltage on velocity of spore discharge by *Drechslera turcica* when triggered by vibration (Voltage negative; velocities were averaged from 25 measurements per voltage level).

DISCUSSION

Buller (2) observed 70 yr ago that basidiospores allowed to fall between electrically charged plates, were mainly negatively charged, and his comments about this observation were "that the spores bear electric charges during their passage through the air may be regarded as a physical fact of no apparent biological importance;" he considered further investigations of the phenomenon unnecessary. In 1965 Savile (14) proposed a unified mechanism to explain violent discharge of basidiospores. He postulated that the force propelling basidiospores into the air might involve the repulsion of charges centered in the spore from similar charges below the sterigma. He suggested an endogenous origin for these charges but did not provide evidence to support that hypothesis. In 1976, on the basis of my experimental studies on *Drechslera turcia,* I proposed (5) an electrostatic theory to explain violent discharge of fungi having exposed, dry spores. This theory suggests that the conidia and the sporulating surface become unipolarly charged and this initiates an electrostatic repulsive force between conidia, conidiophore, and surface. Under suitable conditions this force causes spores to be propelled into the air. I also suggested that the origin of these charges was probably not endogenous but rather external and associated with changes in surface-atmospheric moisture relations.

The research described here, along with the results of earlier studies (5), supports the involvement of an electrostatic mechanism in violent discharge of conidia whether the discharge is triggered by humidity changes (4,8), exposure to red-infrared radiation (4,8), or in response to vibration (9). The evidence for an electrostatic mechanism in spore discharge by *D. turcica* is as follows: For spores to be discharged by an electrostatic mechanism triggered by humidity changes, significant changes of surface potentials must occur and these should correlate with the humidity changes. Earlier studies (5) demonstrated this relationship. For an electrostatic mechanism to exist it is axiomatic that the conidia must be unipolarly charged. Conidia were found to carry unipolar charges when liberated (Figs. 3C and 7). If conidia are discharged

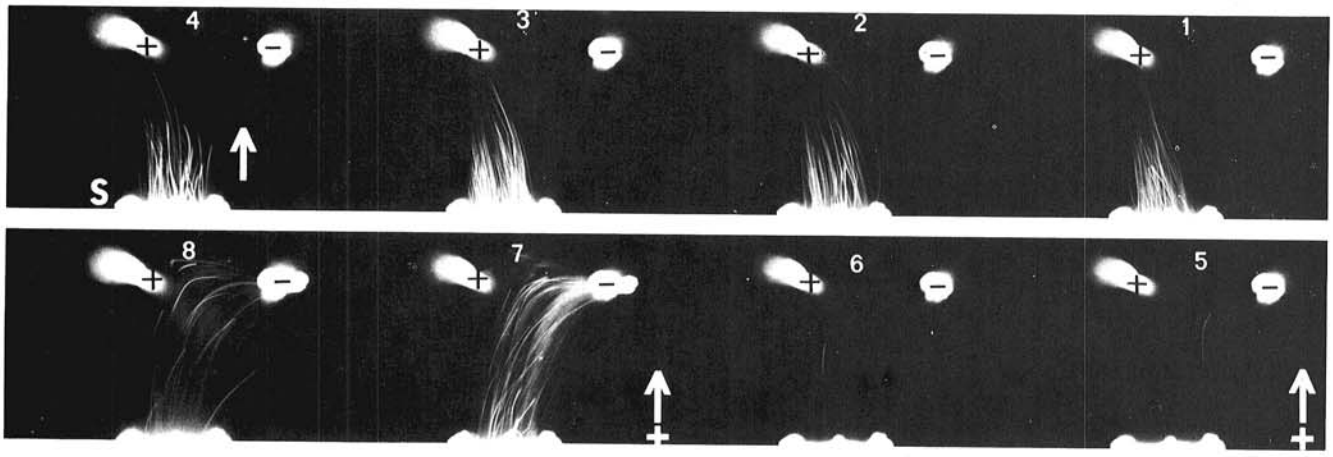

Fig. 7. The effect of neutralizing charges on specimens of *Drechslera turcica* with positive ions on violent discharge triggered by vibration (Specimens were grounded; two electrodes were at 400 V DC). Conidia liberated by a succession of single taps, were first negatively charged (photos 1–4). Just before photo 5, the specimen's charge was neutralized by applying positive ions, which caused spore discharge to stop (photos 5 and 6). More positive ions were applied after photo 6, causing the specimen to become positively charged with a resultant reversal of charge on conidia.

by an electrostatic mechanism, the trajectories of spores must relate to an electrical field associated with unipolarly charged specimens. The parallel take-off of conidia at right angles to the specimen surface irrespective of its gravitational orientation (Figs. 2, 3B–C) can be explained only by an electrostatic mechanism. If conidia are propelled into the air by an electrostatic mechanism, it is also axiomatic that the velocity of release will relate directly to the surface potentials of the specimen. Artificial modification of surface potentials demonstrated this to be true (Figs. 5 and 6). If the propulsion of conidia depends on an electrostatic repulsive force between spore, conidiophore, and spore-bearing surface, the neutralization of surface charges should stop spore discharge. This indeed happened when the specimen was neutralized with positive ions (Fig. 7).

The behavior of charged particles in an AC field, as shown in Fig. 4, has been used to determine the size of the charges associated with the particles (11,16). Before the charges on *D. turcica* conidia can be determined accurately, it will be necessary to modify the Tyndall apparatus and this has still to be done. This apparatus has been most useful in demonstrating spore liberation but unfortunately it cannot be used to study humidity effects on spore release.

A slight vibration of a northern leaf blight lesion under favorable conditions of humidity and light will cause many conidia to be released into the air (9), and this also appears to be true of other fungi (1,9,13). When vibrationally released conidia of *D. turcica* are photographed in flight by means of the Tyndall apparatus (Fig. 1), it becomes evident that they are actively propelled into the air at right angles to the surface of the specimen (Fig. 2), the spores are charged (Fig. 3C) and their velocity at take-off relates to the electrical potential of the lesion (Figs. 5,6,7). This, along with other evidence presented in this article, suggests that under certain conditions vibrational discharge of conidia involves an electrostatic mechanism. However, in a few experiments, the number of conidia actively discharged in response to vibration was small and many appeared to be merely mechanically dislodged from their conidiophores. The relative importance of mechanical dislodgement of conidia versus an electrostatic mechanism in vibrational spore release has yet to be determined.

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