# Leaf Surface Electrostatics: Response of Detached Leaves of Beans and Maize to Humidity and Red-Infrared Radiation Under Controlled Conditions

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## ABSTRACT

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The electrical fields associated with leaf surfaces of beans (*Phaseolus vulgaris*) and maize (*Zea mays*) were measured under controlled conditions to determine if detached leaves become charged and whether this relates to the environmental factors that trigger active spore release. Electrical field intensities were measured with the measuring instrument (field mill) positioned 10 mm above the adaxial surfaces of leaves placed within a special apparatus. In saturated still air, leaf electrical field intensities were high (2,700V cm$^{-1}$ maximum); however, any movement of the saturated air caused a rapid loss of surface charge. A saturated air velocity as low as 0.07 m/sec caused a slight loss of charge, with much greater losses occurring at velocities of 0.21 m/sec and higher. When leaves in saturated still air were briefly connected to an electrical ground, electrical field strength diminished rapidly but was partially regained when the ground was disconnected. In a moving airstream (1 m/sec), highest field intensities (100–500V cm$^{-1}$) were measured whenever the leaves were subjected to low humidities (35–50% RH), with lowest intensities (near 0V) in a saturated airstream (100% RH). Exposure of leaves to red-infrared radiation (IR) in a saturated airstream had a profound effect on field intensities; eg, in one experiment, an 11-min exposure caused a 312V cm$^{-1}$ increase that rapidly diminished when the IR lamps were switched off. If IR was transmitted through water (20 cm deep), it lost much of its effectiveness in causing changes in field intensity. Repeated exposure of leaves to IR in a moving, saturated airstream indicated that the IR had caused relatively long-lasting changes in the electrical characteristics of leaf surfaces. The polarity of leaves detached from growth-chamber plants was consistently positive, whereas leaves from mature field-grown plants collected during a period of unsettled weather were all negative. The reason for these polarity differences is not yet known.

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If dry-spored, foliar, pathogenic fungi actively discharge their spores into the atmosphere by an electrostatic mechanism (3), leaf surfaces must become electrically charged and this should relate to the physical factors that trigger spore liberation. Do leaves become electrostatically charged and does this relate to changes of humidity and exposure to IR, factors known to trigger spore discharge (1,2,5,6,7,10)? Because there are no known published reports on the electrostatic behavior of leaf surfaces, to resolve these questions, leaves of beans (*Phaseolus vulgaris*) and maize (*Zea mays*) were investigated under controlled conditions, using a special instrument (field mill) capable of measuring electrical fields associated with surfaces without actually physically touching the surfaces. The sensor of the instrument was positioned 10 mm above adaxial leaf surfaces. Beans and maize were investigated because the sensor's large sensing area (47 mm diameter) required relatively large leaves and because maize had been used in earlier spore discharge studies (5,6,8).

## MATERIALS AND METHODS

**Sources of leaves.** Detached leaves used in experiments were mainly from the bean cultivar Light Red Kidney grown in silica sand (20-mesh) and periodically watered with Hoagland's solution. Seedlings were grown in 9-cm-diameter clay pots (three seedlings per pot), which were irrigated from a water reservoir below by means of cotton wicks. Plants were grown in a constant-temperature room (23–25 C) under fluorescent lamps (eight 40W fluorescent lamps, four warm-white and four cool-white, 150 $\mu$Einsteins m$^{-2}$ sec$^{-1}$ with a cycle of 14 hr light/10 hr darkness). Atmospheric humidity within the constant-temperature room was not controlled. Unifoliolate bean leaves used in experiments were obtained from 14- to 30-day-old plants (days from sowing). Trifoliolate leaves from mature field-grown beans, as well as leaves from maize, were also used in some experiments. Leaves from these unknown cultivars were collected early in the morning and immediately brought into the laboratory and used for experiments within 30 min. These field-grown plants were collected during a period of unsettled weather (overcast skies and precipitation), which may have affected their polarity (12).

**Instrumentation.** Electrical field intensities associated with leaf surfaces were measured with a special instrument known technically as a "field mill" (model 107, MK II, Industrial Development Bangor-UCNW, Ltd., Bangor, Wales, U.K.). The instrument's sensor was positioned horizontally 10 mm above adaxial leaf surfaces. The arrangement of the sensor and the apparatus used in this study are described separately (11). Because electrical field intensity decreases with increased distance from a charged surface, the approximate attenuation at 10 mm from the leaf surface (position of the electrostatic sensor) was determined experimentally as follows: A 55-mm-diameter brass disk, approximating the size of a leaf, was attached to a high-voltage regulator and field strengths were determined at several distances from the disk. From these measurements, an attenuation factor of 1.59 was calculated for the 10-mm distance. This factor, used as a multiple, is noted on the abscissae of graphs in Figs. 1–12. To obtain an approximation of electrical field strengths at the leaf's surface, plotted intensities must be multiplied by this factor. Where field intensities have been cited in the text, they have already been multiplied by this factor.

**Apparatus.** To regulate humidity and expose leaves to IR, leaves were placed in a specially designed apparatus (11). This apparatus allowed leaf surface electrical fields to be monitored continuously under controlled conditions. Within the apparatus, a standardized leaf disk 55 mm in diameter was exposed to the electrostatic sensor.

**Precautions for handling leaves.** Touching leaf surfaces with bare fingers and other foreign objects can cause drastic changes in a leaf's surface charge and polarity. To reduce introduced errors, insulated procedures were used both in removing leaves from

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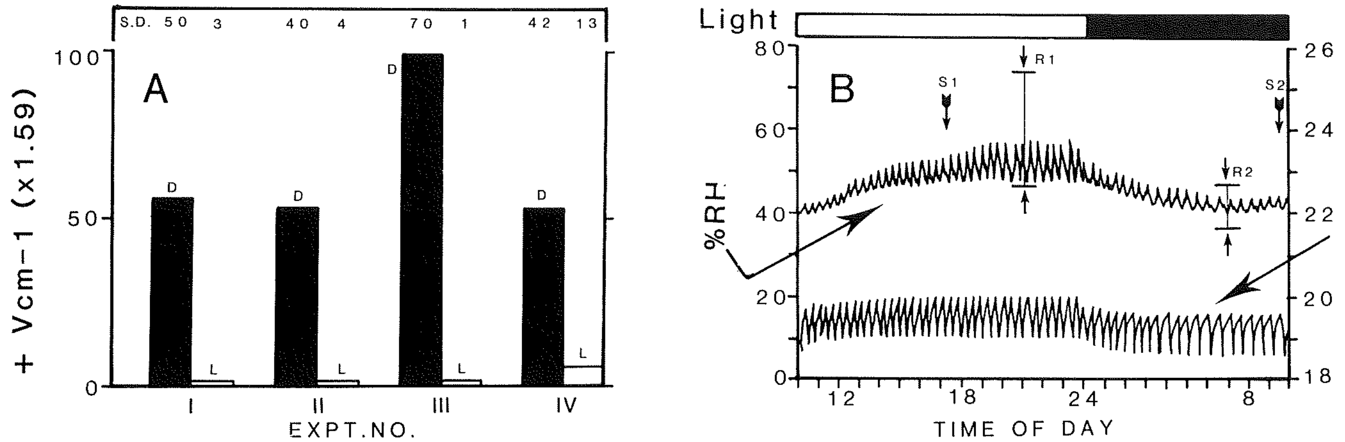

**Fig. 1. A,** A comparison of the electrical field intensities of the surfaces of detached bean leaves taken from plants subjected to either 7 hr of darkness before sampling (D) or 7 hr of light before sampling (L). Four experiments were conducted over a period of 10 days (average of 10 leaf measurements per treatment). **B,** Growth-room conditions during experiments. R1 and R2 = variation of humidity for light and dark periods during the 10 days, S1 and S2 = times of sampling, and S.D. = standard deviations.

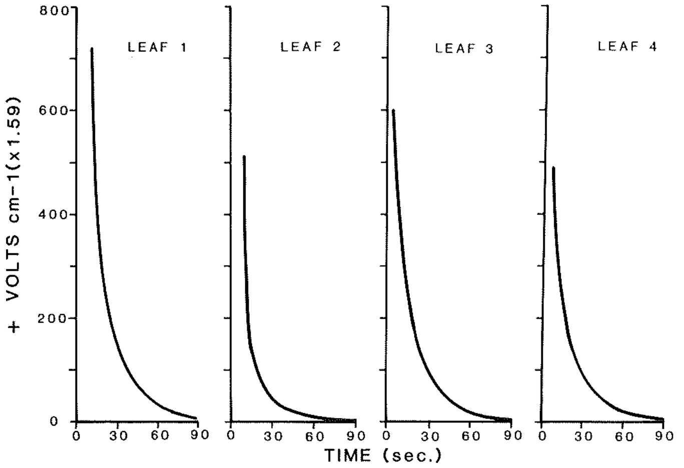

**Fig. 2.** Evanescent nature of electrical field intensities associated with the surfaces of bean leaves detached from growth-room plants and measured within 60 sec (growth room conditions: 22 C, 14 hr light/10 hr dark, 35-45% RH).

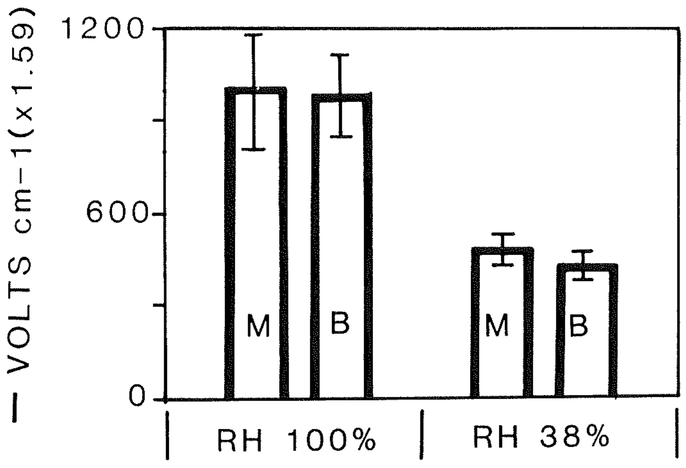

**Fig. 3.** Field intensities of detached leaves of beans (B) and maize (M) incubated in darkness either in saturated still air (100% RH) or at the ambient RH of 38%. Incubation was for 99–126 min. Each bar is the average of six leaf measurements.

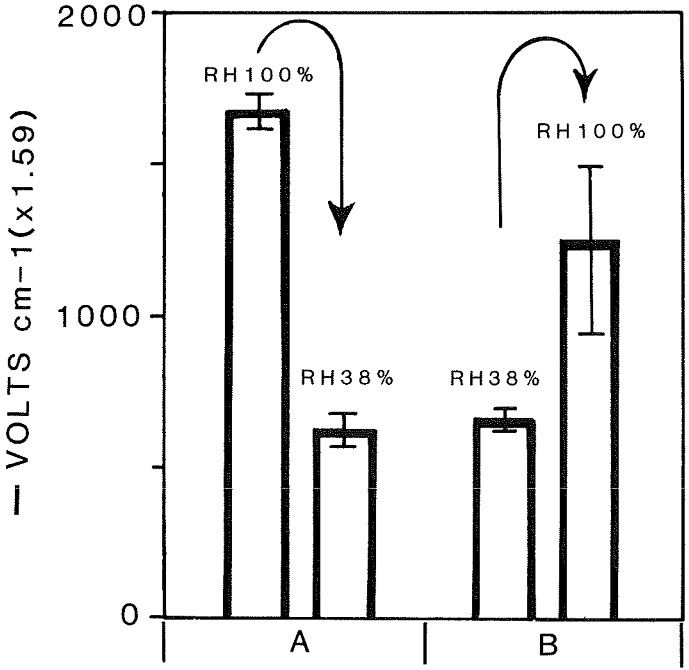

**Fig. 4.** Field intensities of detached leaves of maize in still air. **A,** Leaves incubated in saturated air, then transferred to 38% RH, and **B,** vice versa. Each bar is the average of four leaf measurements.

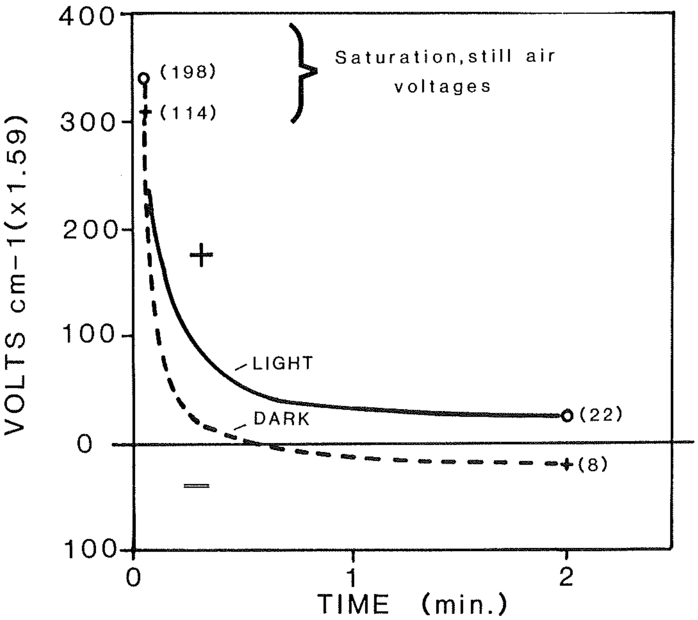

**Fig. 5.** A comparison of field intensities of detached leaves of beans incubated in saturated still air for 24 hr in either light or darkness (average of nine leaves per treatment). Figures in parentheses are standard deviations for beginning and end of measurements at 20 C. Note rapid loss of field intensities caused by air movement from the field mill's rotor.

plants and in their subsequent handling. Details of these procedures have been described separately (11).

**Still air studies.** To investigate the effect of saturated still air on leaf field intensities (Figs. 3–7), replicated leaves were mounted individually in "leaf chambers" specially modified to act as moist chambers (11). The RH within these chambers was about 100% as determined with an electrical humidity probe. Both incubation and measurement of leaves in the chambers were at 20 C.

**Moving air studies.** The effects of humidity and exposure to IR in a moving airstream were determined by mounting leaves in the specially designed apparatus (11) and subjecting them to different humidity and IR regimes. Precise humidity changes were provided by an apparatus developed for spore discharge studies (4). Atmospheric humidity could be quickly (<2 min) and precisely changed anywhere within the range of 20–100% RH. In all experiments, unless noted otherwise, air temperature was at a constant 20 C and air velocity was constant at 1 m/sec. The leaf chambers (11) were not designed for uniform airflow, and airspeeds over a leaf surface actually varied from 0.5 to 1.5 m/sec, depending on the position of the anemometer. Airspeed was measured periodically during experiments, using a hot-wire-type anemometer (4). Air temperature was measured with thermocouples and humidity (moving air) with a wet-wick-type thermocouple psychrometer (4). Both temperature and humidity were recorded continuously during experiments on a multichannel recorder.

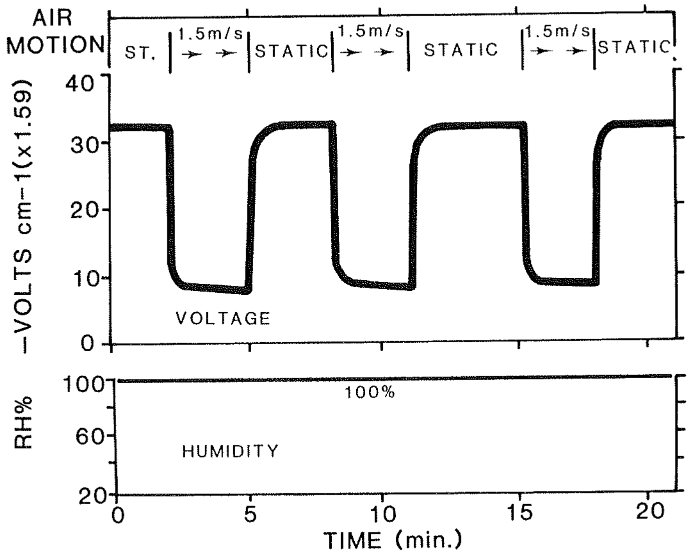

**Fig. 6.** Bean leaf field intensities for a single leaf repeatedly exposed to saturated still air followed by saturated moving air (20 C; trifoliolate leaflet from a field-grown plant).

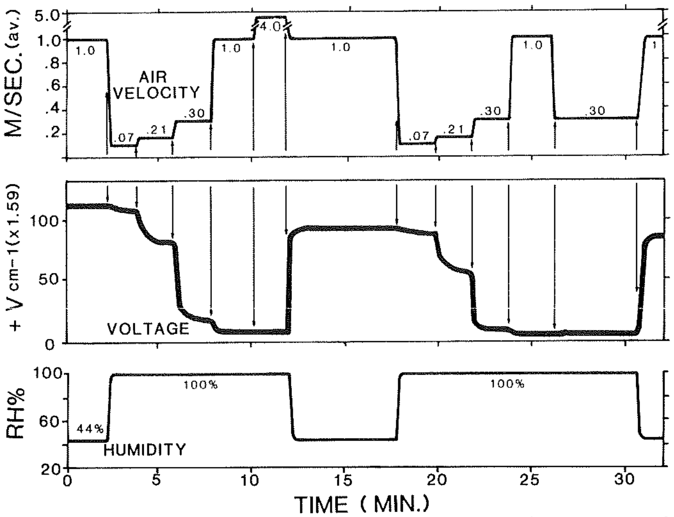

**Fig. 7.** Effect of air velocity on field intensities for a single bean leaf incubated in saturated air at 20 C in darkness.

In the IR experiments, leaves mounted in the apparatus (11) were exposed to reflected radiation from an unfiltered IR lamp (Sylvania 250W, 115V). The front surface of the lamp was 47.5 cm from the leaf (11). In one experiment (Fig. 12), IR was transmitted through a 20-cm-deep, distilled water filter in a Pyrex beaker. Intensity of IR at the leaf surface was measured with a radiometer (1). The intensity of the unfiltered IR was 7,150 $\mu W/cm^2$ and 511 $\mu W/cm^2$ after transmission through the water filter.

**Electrical grounding of leaves.** The effect of electrically grounding the surface of a leaf incubated in saturated still air was determined by incorporating a small insulated ground wire (22 gauge) into several leaf chambers (11). The exposed tip of the wire was bent to make contact with the edge of the mounted leaf and this contact was improved by adding a small amount of electrode paste (DB Electrode Paste, Day-Baldwin, Inc., Hillside, NJ 07205). The wire could be electrically grounded by touching it to another wire connected to an outside copper rod driven 1.5 m into the soil.

## RESULTS

Experiments were first conducted to learn whether leaves of bean plants raised hydroponically in a growth room became charged,

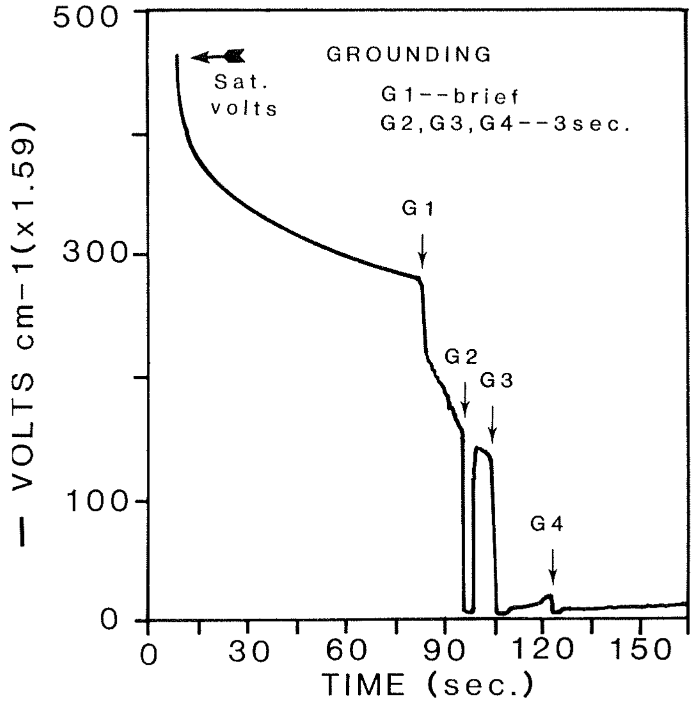

**Fig. 8.** Effect of electrically grounding a detached bean leaf incubated in saturated still air in darkness at 20 C. Note that the decline of field intensities beginning at the arrow is caused by air movement from the field mill's rotor.

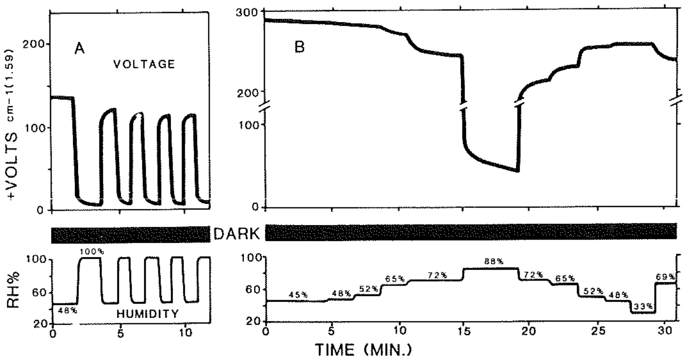

**Fig. 9.** Effect of relative humidity on field intensities for a detached bean leaf placed in a moving airstream. **A,** Repeated cycling of humidity between 100 and 48% RH. **B,** Stepwise reductions and increases of RH (air temperature 20 C, air velocity 1 m/sec, darkness).

and these were followed by experiments to determine the electrical behavior of leaves kept in saturated still air. Finally, the effects of humidity and exposure to IR on the electrical behavior of leaf surfaces were followed in a moving airstream.

**Exploratory experiments.** To determine if leaves of bean plants become electrostatically charged when grown under artificial conditions, plants were grown in a growth room under a daily cycle of illumination alternating with darkness at a constant temperature. These conditions, for a single 24-hr period, are summarized in Fig. 1B. Leaf field intensities were measured on four occasions when the plants were from 20 to 30 days old (Fig. 1A). On each of these occasions, one group of leaves was measured after 7 hr of darkness, and these were compared with others measured after 7 hr of illumination (Fig. 1A).

Consistently, leaves measured after a period of darkness (Fig. 1A) were electrically charged with field intensities (avg. 112V cm$^{-1}$) considerably higher than for those leaves removed from plants illuminated for the preceding 7 hr (avg. 6.4V cm$^{-1}$). Polarity of leaves from both treatments was positive. This experiment revealed that detached leaves of bean plants were electrostatically charged when removed from plants grown under artificial conditions, also that lighting conditions seemed to influence the intensity of leaf surface charges.

The reason for the differences in size of field intensities between leaves sampled after 7 hr of exposure to light versus those sampled after 7 hr of darkness only became apparent after later humidity studies revealed that highest charges in moving air are associated with low humidities and lowest charges with high humidities. In the growth room, when the lamps over three shelves of plants were turned on, the room humidity was significantly higher than during periods of darkness (Fig. 1). It was assumed that this resulted from greater transpiration from the illuminated plants as well as from greater evaporation from the hydroponic system feeding the plants. The marked difference in leaf field intensities was probably an effect of humidity rather than of direct light.

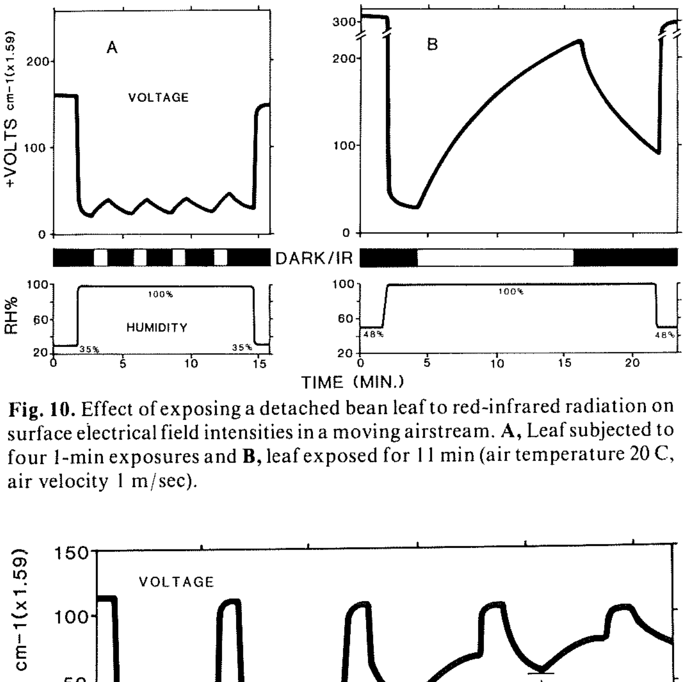

**Fig. 10.** Effect of exposing a detached bean leaf to red-infrared radiation on surface electrical field intensities in a moving airstream. **A,** Leaf subjected to four 1-min exposures and **B,** leaf exposed for 11 min (air temperature 20 C, air velocity 1 m/sec).

When leaves were removed from bean plants from the growth room and the field intensity was measured immediately, there was usually a rapid loss of intensity after the initial measurement. To explore this phenomenon more fully, eight leaves were removed one at a time from growth-room bean plants at the end of a dark cycle (14 hr darkness/10 hr light, 22 C, 35–45% RH) and quickly measured within 30 sec of removal. Field intensities for the eight leaves started with an initial maximum intensity ranging from 429 to 1,161V cm$^{-1}$, and all were positive. After the initial measurement, all showed a rapid loss of charge, as indicated for the four examples illustrated in Fig. 2. Within 30 sec of the initial measurement, intensities had decreased into the range of 28–35V cm$^{-1}$, and after 90 sec, most leaves had almost completely lost their charges. It was suspected that this rapid loss of surface charge resulted from air movement caused by the electrostatic field mill's rotor. To test this possibility, the field mill was compared with another instrument, a tuning fork-type electrostatic sensor (Isoprobe Model 244 electrostatic voltmeter, Monroe Electronics, Inc., Lydonville, NY), which causes much less air movement. The results indicated that air movement was responsible for the rapid loss of charge illustrated in Fig. 2.

**Comparison of bean leaves and maize in saturated still air.** Leaves of beans and maize were collected (0830 hours) from flowering field-grown plants and brought to the laboratory; experiments began within 30 min of collection. Six leaves of each species were individually mounted in the small moist chambers (11) and incubated in darkness under saturated still air conditions at 20 C for a minimum of 90 min. Another group of leaves was also mounted in leaf chambers but these were left open to ambient air (38% RH). After 90 min of incubation, measurements of field intensities were begun, with the last measurement completed after 126 min. It was found that both bean and maize leaves incubated in saturated still air had significantly higher field intensities than those incubated at the ambient humidity of 38% RH (Fig. 3). The polarity of leaves from both groups was negative.

To further examine effects of alternating high and low RH, six maize leaves were incubated in saturated still air, then electrostatic fields were measured; these same leaves were then transferred to room ambient humidity (38% RH), incubated, and measured again (Fig. 4). This was then done in reverse, with six leaves incubated first at 38% RH, then transferred to saturated still air. Contrary to expectations, field intensities in saturated still air were always much higher than those for leaves incubated in still ambient air at the ambient RH of 38%.

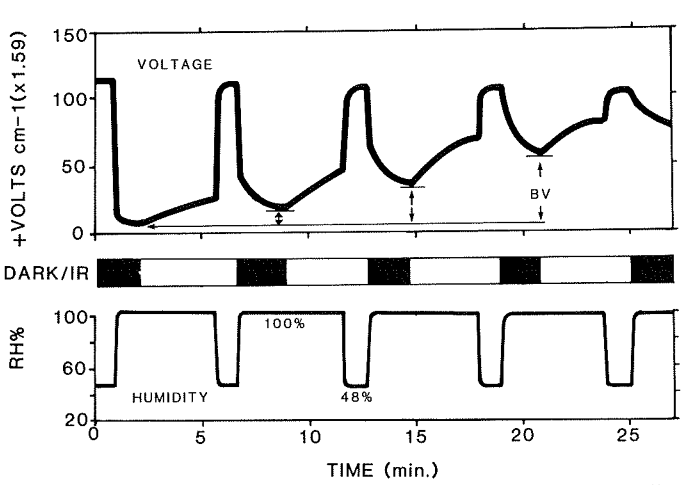

**Fig. 11.** Evidence of a "carryover effect" when a bean leaf was repeatedly exposed to red-infrared radiation. Exposures were 6, 5, 5, and 5 min, respectively (air temperature 20 C, air velocity 1 m/sec; BV = base voltage).

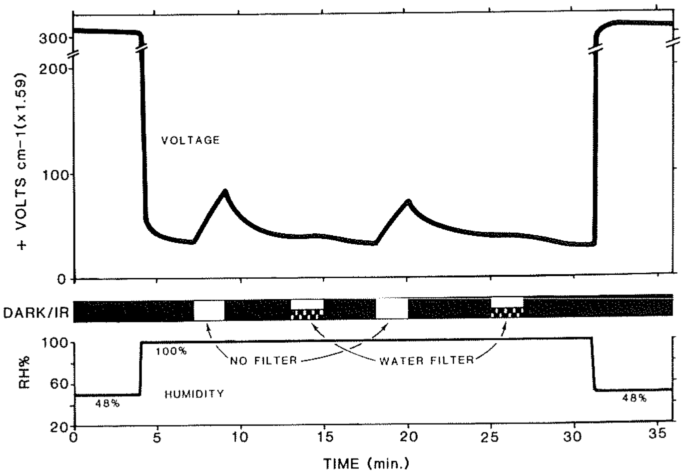

**Fig. 12.** A comparison of the effect of filtered (20 cm distilled water) versus unfiltered red-infrared radiation on bean leaf field intensities (a single leaf; temperature and air velocity constant at 20 C and 1 m/sec, respectively).

**Effect of light versus darkness on bean leaves in saturated still air.** To determine if light might influence surface-charging of leaves, eight bean leaves were removed from growth-room plants and incubated in moist chambers (100% RH) while exposed for 24 hr to light (four 40W warm-white and four 40W cool-white fluorescent lamps, 150 $\mu$Einsteins m$^{-2}$ sec$^{-1}$). Another eight leaves were incubated in darkness for 24 hr under similar conditions. Although initial field intensities for both treatments were not significantly different (Fig. 5), there were major differences in polarity following the loss of charge attributable to air movement from the field mill's rotor. After 2 min of continuous measurement, polarity of leaves from the illuminated plants was consistently positive, whereas polarity of those incubated in darkness was consistently negative (Fig. 5).

**Saturated still air versus saturated moving air.** On several occasions, I observed that when leaves were placed in saturated still air, field intensities were high, but as soon as the air was put in motion, leaf surface charges were lost. To compare more precisely the effect of still air versus moving air, leaves from field-grown beans were mounted in a leaf chamber (11) connected to a controlled-air humidification system (4). Moistened filter paper was placed inside the chamber to maintain saturation when the air was still. The experiment, conducted in darkness at 20 C, consisted of comparing leaf voltages for saturated still air versus saturated flowing air (1.0 m/sec) using the same leaf (Fig. 6). This experiment was repeated several times, always with the same results, ie, the magnitude of leaf voltages related directly to air movement. Highest voltages always occurred when the saturated air was static and lowest voltages when the saturated air was in motion (Fig. 6).

To determine the relationship of rate flow of saturated air on leaf surface electrostatics, a leaf was mounted in the chamber (11) in darkness at 20 C and field intensities were measured for different airspeeds at 20 C (Fig. 7). Airspeeds were 0.07 m/sec (range 0.05–0.10 m/sec), 0.21 m/sec (range 0.10–0.23 m/sec), 1.0 m/sec (range 0.5–1.5 m/sec) and 4.0 m/sec (range 3.0–5.0 m/sec). The experiment was started with the RH at 44% and the airspeed at 1.0 m/sec, with an initial field intensity of 191 V cm$^{-1}$). After an initial period of a few minutes at low humidity, the RH was raised to 100% while simultaneously reducing the airspeed to 0.07 m/sec. This was then followed by a sequence of airflow increases with the RH remaining at 100% (Fig. 7). The whole sequence of events was then repeated a second time after another period of reduced humidity.

The results of this experiment (Fig. 7) again demonstrated that leaf surfaces become charged in saturated air but only when the air remains relatively still. Even the lowest air motion (0.07 m/sec) caused a slight reduction of field intensity. Airspeeds of 0.3 m/sec and higher caused an almost complete loss of charge. Dielectric materials normally lose their charges at high humidities (17), just the reverse of my results for an electrically isolated leaf in saturated still air, which becomes highly charged under these conditions.

**Grounding leaves in saturated still air.** When dielectric materials are exposed to high humidities, they lose their capacity to act as insulators; their surfaces become electrically conductive because of the absorption of a layer of moisture (17). Are leaf surfaces good conductors at high humidities? To test this possibility, bean leaves were mounted in leaf chambers (11) under saturated still air conditions. They were then electrically grounded to determine if there was a loss of charge as measured by field intensities. The results of one experiment are shown in Fig. 8. In this experiment, the leaf's field intensity in saturated still air was initially at −731 V cm$^{-1}$, and this decreased fairly rapidly because of air movement caused by the field mill's rotor. The first grounding, which consisted of a quick touch of wire in contact with leaf to the ground wire, caused an immediate 60V cm$^{-1}$ loss of field strength followed by a continuing but less rapid loss after the ground had been disconnected. A second grounding for 3 sec caused the field intensity to drop rapidly to zero, which on disconnecting the ground, increased back to almost its former level. Grounding the leaf a third and fourth time caused the leaf's charge to fall to near zero, with only slight increases of field strength on disconnecting the ground. The results indicated that under saturated still air conditions, leaf surface charges are good conductors, which indicates that under natural conditions with plants growing in soil (ie, electrically grounded), there would be little likelihood of leaves becoming charged under conditions favorable to charging in the laboratory, ie, when the atmosphere is still and saturated. When plants are grown in plastic containers (ie, isolated from ground), there remains a possibility that leaves might become charged in saturated still air.

**Humidity changes in darknesss in a moving airstream.** In moving air, certain types of humidity changes, particularly lowering the humidity, will trigger active spore liberation of a number of foliar pathogens (1,2,5,6,10). If active release of spores involves an electrostatic mechanism, then one would expect a direct relationship between these humidity changes and the electrical behavior of leaf surfaces. To determine whether humidity changes influenced leaf surface electrical fields, a bean leaf was subjected to repeated cycles of raising and lowering the RH from 48 to 100% in a moving airstream (1.0 m/sec) in darkness while continuously monitoring leaf field intensities (Fig. 9A). In this experiment, leaf field intensities correlated directly with humidity changes. Maximum field intensities occurred in dry air (48% RH) and ranged from 175 to 227V cm$^{-1}$ for the five humidity cycles, whereas minimum voltages ($<$16V cm$^{-1}$) corresponded with periods of saturation. During the repeated humidity cycles, a gradual decline in maximum voltages occurred with each successive period of low humidity.

To ascertain more precisely the influence of humidity on electrical field intensities, a bean leaf was subjected to a series of stepwise increases and decreases of humidity at 20 C, again in darkness at a constant airspeed of 1.0 m/sec (Fig. 9B). The experiment began at 45% RH, with the leaf's voltage at about 77V cm$^{-1}$. As the RH was first increased from 45 to 48% and through the second step from 48 to 52%, there was no marked loss of voltage. However, with each subsequent increase in humidity, there was a corresponding reduction in field intensity. Greatest reduction occurred for the increase of humidity from 72 to 82%. In a reversal of the series, ie, stepwise decreases of RH, the first reduction from 88 to 72% caused a major increase in field intensity, with smaller increases associated with succeeding decreases of RH. The last reduction from 48 to 33% RH had no effect. In this and other similar experiments, highest field intensities in moving air in darkness were always associated with low humidities. Conversely, lowest field intensities were associated with high humidities.

**Effects of IR in a moving airstream.** Exploratory experiments on bean leaves exposed to IR in a moving airstream indicated an increase in field intensities but only when leaves were exposed to IR at high humidities. To determine more precisely the effect of IR on leaf voltages in a saturated airstream (1.0 m/sec, 20 C), leaves were repeatedly subjected to short, 1-min exposures to unfiltered IR (Fig. 10A). The first exposure caused a noticeable increase in field intensity, which immediately began to decrease as soon as the lamp was switched off, and this pattern was repeated for each of the subsequent exposures. In another experiment under similar conditions, the effect of a longer, 11-min exposure was determined (Fig. 10B). As soon as the IR was switched on after the RH level had been increased to 100%, the field intensity began to increase and this continued over the 11-min exposure, though at a gradually decreasing rate. During this longer exposure, there was an increase in field intensity of 312V cm$^{-1}$ over the base voltage of 57V cm$^{-1}$. As soon as the IR lamp as switched off, the field intensity decreased quite rapidly.

In several experiments in which bean leaves were repeatedly exposed to IR followed by darkness (eg, Fig. 10A), it was observed that after each successive exposure, the lowest intensity ("base voltage" of Fig. 11) never quite decreased to the level that preceded the exposure. Thus, in the results of the experiment shown in Fig. 10A, the electrical field intensity after the last period of darkness was 24V cm$^{-1}$ higher than the base voltage measured before the first exposure. In another experiment on this phenomenon (Fig. 11), a leaf was irradiated on four occasions with respective exposures of 6, 5, 5, and 5 min, again using an airstream at 1.0 m/sec and 20 C. In this experiment, each of the IR exposures was begun when the RH was at 100% and continued on into the dry periods. Base voltages were again appreciably higher after each succeeding exposure, with the last base intensity about 80V $cm^{-1}$ higher than before the first exposure (Fig. 11). These results suggest that the IR must be causing a fundamental change to the electrical characteristics of the leaf surface that is carried over after the IR irradiation has been terminated.

When IR is filtered through water, its effectiveness in triggering spore discharge is greatly reduced (5). To learn if this might also influence the effect of IR on leaf field intensities, a bean leaf under the conditions of the preceding experiments was exposed to IR (four 2-min exposures) with and without a water filter (20 cm of distilled water), as shown in Fig. 12. The unfiltered IR caused a typical increase in field intensity; in contrast, filtered IR caused only negligible increase in intensity. There was considerable disparity between intensities of filtered and unfiltered IR (refer to Materials and Methods), and further studies are needed before the significance of this experiment can be judged.

The IR experiments clearly demonstrated that exposure of leaves to IR can markedly influence a leaf surface's electrical characteristics, though these changes were only observed when leaves were exposed in air near saturation. The experiments also revealed a carryover effect of IR (Fig. 10 and 11), which suggests that the IR is causing fundamental changes in the electrical characteristics of leaf surfaces.

## DISCUSSION

If spores are actively discharged from leaf surfaces by an electrostatic mechanism, then one must assume that the leaves themselves become electrostatically charged and that this must relate to the environmental factors known to trigger spore liberation. The experiments described in this article support this hypothesis, at least under the controlled conditions of the laboratory. Leaf voltages were found to relate to humidity changes and they were also affected by exposure to IR. The electrical fields associated with the surfaces of detached leaves were found to be relatively large and frequently exceeded those found to influence velocity of spore discharge in earlier experimental studies on *Drechslera turcica* (8) and *Peronospora destructor* (9).

In spore discharge studies conducted under controlled conditions on a number of dry-spored fungi (1,2,5,6,10), lowering the humidity from saturation to about 40% RH consistently triggered spore discharge. A comparable lowering of the humidity for bean leaves caused major increases in electrostatic field intensities (Fig. 9). At high humidities, liberation of spores by dry-spored fungi is negligible, ie, a at time that corresponds to negligible field intensities, at least in a moving airstream. In general, exposure of sporulating leaves to IR triggers or enhances spore liberation; correspondingly, exposure of leaves to IR causes a significant increase in field intensities but only at high humidities. This effectiveness of IR in causing electrical changes at high humidities is not consistent with most spore discharge studies in which IR is most effective in triggering spore liberation at relatively low humidities. An exception is *P. destructor* (10), which can liberate spores at high humidity but only when exposed to IR; however, the IR is far more effective in triggering spore discharge by *P. destructor* at lowered humidities. The role of IR in spore liberation is not understood, but it seems likely that it could be involved in causing humidity changes within the atmosphere, it causes electrical changes of sporulating leaf surfaces, and it may well influence the strength of juncture between sporophore and spore through dehydration of cell wall components. The discovery that the surfaces of detached leaves can become highly charged in saturated still air was quite unexpected; however, it would appear to be of little consequence where plants are grown under natural conditions. The fact that merely touching leaves with a grounded wire while in a saturated atmosphere caused them to rapidly lose their charge suggests that in nature where plants are naturally grounded, it would be unlikely for a charge to build up. Also against the charging of leaves under high humidities in nature is the fact that slight air movement causes a loss of charge. In nature, the air is rarely still for long. There is the possibility that leaves could be charged in still, saturated air in glasshouses where plants are electrically isolated in plastic containers.

The electrical charging of leaf surfaces revealed in this study supports the involvement of an electrostatic mechanism in active spore discharge by dry-spored foliar pathogens; yet there are some conundrums that remain to be resolved. For example, although spore discharge is triggered by decreasing humidities (5,6,7,10), which corresponds to increase of leaf field intensities, yet spores can also be liberated, though in relatively fewer numbers, when the RH is raised from a lower level back to saturation. If an electrostatic mechanism is valid, why should spores be released at a time when a leaf's field intensities are decreasing?

Why do leaves become electrostatically charged? At this moment, the biophysical characteristics of leaf surfaces have not been explored. The response of leaves to humidity and IR suggests the possible involvement of bioelectrets. An electret is "... a piece of dielectric material exhibiting quasi-permanent electrical charge" (15). Some of the earliest studies on bioelectrets were on a Carnauba wax obtained from the leaves of the South American palm *Copernica prunifera*. Because waxes have good dielectrical properties and are important surface components of cuticles (13), they may be involved in the electrical charging of leaf surfaces. Tribe et al (16) have reported a direct relationship between light intensity and leaf wax formation and this may explain the low field intensities I have measured in glasshouse plants in midwinter when light intensities were low. Dielectric materials act as electrical insulators at low humidities but they lose this ability as the humidity increases above 50% (approximately), and this has been attributed to their absorption of surface-layer moisture (17). Mascaranhas (14) has stated, "One of the most important aspects of electret research in biophysics is that of water bound to polymers in the so-called structured form (also called bound water or biowater) may also be involved in the electret state." Could the charging of leaf surfaces involve this type of relationship?

Finally, one cannot escape the question of the relevance of electrostatic studies conducted on detached, electrically isolated leaves in the laboratory to the leaves of plants grown in their natural environment, where they are rooted in the soil. Field studies on beans and maize and miscellaneous other plant species have revealed that both detached (12) and attached (Leach, *unpublished*) leaves do become charged in nature in much the same manner as they do in the laboratory.

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