# Leaf Surface Electrostatics: Behavior of Detached Leaves of Beans, Maize, and Other Plants Under Natural Conditions

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## ABSTRACT

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To determine if leaves become charged under natural conditions, the electrical fields associated with leaf surfaces of beans (*Phaseolus vulgaris*) and maize (*Zea mays*) were measured over periods ranging from 1 to 5 days during both fine and unsettled weather. Electrical fields were measured with an electrostatic sensor (field mill) positioned 10 mm above adaxial leaf surfaces. Surfaces of leaves became charged, with average field intensities $<500 \mathrm{V\,cm^{-1}}$. The highest field intensity measured was $1{,}600 \mathrm{V\,cm^{-1}}$. The size of electrostatic fields appeared to relate directly to changes of humidity and was also influenced by intensity of solar radiation. As relative humidity decreased, field intensities increased; conversely, as humidity increased, leaf surface charges were dissipated. Highest field intensities were recorded on warm, sunny, and dry days, and wind apparently had no effect. At night, when the humidity was high, leaves remained uncharged. During cloudy periods with rain, field intensities were small or nonexistent. Polarity of leaves was consistently positive on sunny, dry days; but on several cloudy days with intermittent rain, leaves were of mixed polarity and predominantly negative on one occasion. A direct comparison of electrical field intensities of beans and maize leaves over several 3- to 5-day periods revealed essentially identical behavior. Detached leaves of eight other plant species were also electrically charged under sunny, warm, and dry conditions. Field intensities for the eight species ranged from 100 to 400V $\mathrm{cm^{-1}}$, all with positive polarity.

An electrostatic mechanism to explain active spore liberation by dry-spored foliar pathogens has been proposed (6) and challenged (1). Using photographic techniques and other procedures, it has been demonstrated (10,11) that both conidia and sporangia can be electrically charged when liberated and their trajectories conform to what would be expected if an electrostatic mechanism were involved. It has also been reported (10,11) that artificial manipulation of leaf surface potentials can modify spore discharge velocities and that neutralization of leaf surface charges will stop spore discharge. These findings suggest that it is perhaps too early to discard an electrostatic mechanism.

If an electrostatic mechanism is involved in the active discharge of spores by foliar pathogens in nature, leaf surfaces must become electrostatically charged. In addition, charging should relate directly to the environmental factors that are important in triggering spore discharge, namely atmospheric humidity changes and exposure to red-infrared radiation (IR) (2,4,7–11,14), and surface electrostatic forces must be of sufficient magnitude to propel spores away from the leaf surface. Controlled laboratory experiments on detached leaves of beans and maize (13) have demonstrated that leaves in a moving airstream become electrostatically charged in response to humidity changes and that exposure of leaves to IR causes a profound increase in field intensities. Because controlled experiments on electrically isolated leaves are quite different from experiments on plants growing in soil in their natural environment, the objective of this investigation was to determine if detached leaves of bean (*Phaseolus vulgaris* L.) and maize (*Zea mays* L.) plants growing in soil under natural conditions become electrostatically charged.

## MATERIALS AND METHODS

Three cultivars of beans (*Phaseolus vulgaris*), Light Red Kidney, Red Kidney and Blue Lake, and one cultivar of maize (*Zea mays*), Golden Cross Bantam, were planted in Linn County, OR, in rows 61 cm apart, fertilized, and sprinkler-irrigated during dry periods. The beans and maize were sown on 21 May 1982, with a second sowing of Light Red Kidney beans on 28 July 1982.

To determine influence of shade on leaf field intensities, sun shades 0.9 m high × 2.4 m × 1.5 m were placed over rows of beans and maize shortly after the seedlings emerged. Light intensity at the center of the shades and 20 cm above the ground was 44% of full sunlight, as measured with a radiometer (Model 65A radiometer, YSI-Kettering, Yellow Springs Instrument Co., Yellow Springs, OH 45378).

Electrostatic field intensities associated with the adaxial surfaces of detached leaves of miscellaneous plant species present on the field station and in the first author's home garden were measured under relatively dry and sunny conditions (Fig. 1). Selected leaves were all large enough to be measured under the Model 107 field mill. They included apple (*Malus sylvestris* Mill. cv. Johnathon), rose (*Rosa* sp. cv. Camelot), grape (*Vitis vinifera* L. cv. Seneca), table beet (*Beta vulgaris* L.), English laurel (*Laurus nobilis* Linn.), thornless loganberry (*Rubus* sp.), cherry (*Prunus avium* L. cv. Royal Anne), and rhododendron (*Rhododendron* sp.).

Continuous recordings were made of atmospheric humidity, air temperature, wind velocity, and barometric pressure. Rain and clouds were observed visually. Dew was recorded by a water-soluble, pencil/mechanical-type recorder (C. M. Leach, *unpublished*) and by visual observations. Relative humidity was measured at a height of 40 cm with a relative humidity indicator (Model HM111 with an HMP 14U sensor, Weathermeasure, Sacramento, CA 95841) and at a height of 28 cm with a hair-type hygrometer (M701 Meterograph, Weathermeasure). Air temperature in the shade was measured at a height of 40 cm with a shielded copper-constantan thermocouple and a millivolt recorder, also at a height of 28 cm, with a thermograph (M701 Meterograph, Weathermeasure). Barometric pressure was recorded at a height of 8 cm with the Meterograph. Horizontal wind velocity was monitored at a height of 1.5 m with a cup anemometer (modified Model W200SI, Weathermeasure) and an air velocity meter (Model 241M, Weathermeasure).

Leaves were removed from plants using insulated procedures

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and quickly (<60 sec) placed in a special holder 10 mm below the front surface plate of the electrostatic sensor (field mill, Model 107 MK II, Industrial Development Bangor-UCNW, Ltd., Bangor, Wales, U.K.). A more detailed description of the leaf holder and handling and measurement procedures have been reported separately (12). Single leaflets from trifoliolate leaves of beans were measured. For maize, a section of leaf about 7 cm long was removed using electrically nonconductive scissors (12). Only upper leaf surfaces (adaxial) were measured, except during a comparison of upper and lower leaf surfaces in beans.

Because earlier controlled studies (13) on beans had been confined to unifoliolate leaves of seedlings, a comparison was made between field intensities of unifoliolate leaves and leaflets of trifoliolate leaves of mature plants. No discernable differences were detected and all other sampling of bean was done with trifoliolate leaves.

Considerable variability of measurements of leaf field intensities existed from leaf to leaf under identical conditions. Although the causes of this variability were not fully understood, standardized sampling procedures were adopted to minimize experimental error and allow valid comparisons among treatments (cultivars, etc.).

In comparisons between beans and maize, the minimum number of leaves sampled at any one time was normally 20, with each taken from a different plant. Considerable temporal variation (Fig. 2) appeared when sampling a sequence of 20 leaves within a relatively short period (60 min). To minimize experimental error attributable to time, particularly in comparative experiments, two procedures were adopted. The first procedure involved sampling five leaves from one species (or treatment), each leaf from a different plant, with measurements made in rapid succession. Immediately after the last measurement, five leaves from another species (or treatment) were measured in a similar manner. This alternating procedure was continued until a minimum of 20 leaves were measured. In the second procedure, a leaf from one species (or treatment) was measured, followed quickly by a leaf measurement of the other species. This was also repeated until a minimum of 20 leaves were measured for each species (or treatment). Because only a single electrostatic field mill was available, it was never possible to compare two leaves simultaneously. An examination of field intensity measurements revealed variance to be a multiplicative function, eg, as measured field intensity increased, so did corresponding variance. A logarithmic transformation was performed to meet the requirement of constant variance in analysis of variance. Logarithmically transformed data were analyzed by analysis of variance, with cultivar, shading, or leaf side as treatments in respective experiments. Each set of treatment measurements was blocked to separate variation due to time.

CONDITIONS

| DATE | Aug.19 | | | Sept.5 | | | | |
|---|---|---|---|---|---|---|---|---|
| TIME | 0929 | 1300 | 1335 | 1540 | 1554 | 1606 | 1722 | 1741 |
| RH% | 40 | 32 | 32 | 25 | | | | |
| TEMP. | 22 | 27 | 27 | 27 | | | | |
| WIND(m/s) | 3 | 1.5 | 1.5 | 3 | | | | |
| LEAF WET.% | 0 | 0 | 0 | 0 | | | | |
| CLOUD COVER | Thin cirrus(100%) | | | Sunny and clear | | | | |

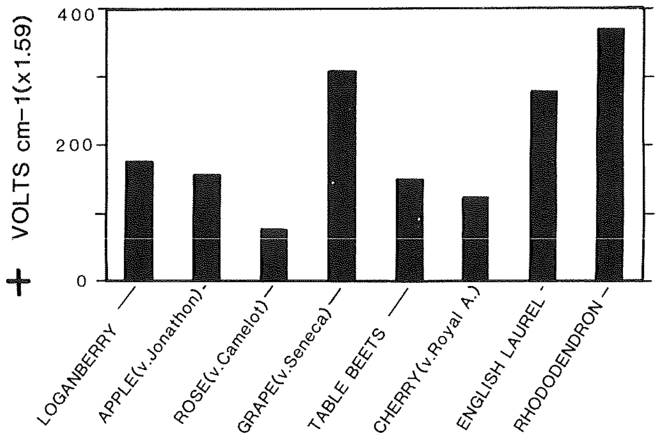

**Fig. 1.** Electrostatic fields associated with the adaxial surfaces of leaves of eight plant species (each bar averaged from 20 leaves).

During an attempt to measure dew on bean leaves with an electrical sensor (C. M. Leach, *unpublished*), it was found that although the sensor was ineffective in measuring dew, it was effective in measuring changes in leaf surface conductivity. The sensor consisted of a series of parallel strands of nichrome wire (32-gauge) 1 mm apart, with the wires held in a small plastic frame (22 × 22 mm). Each alternating wire was of opposite polarity and at a potential of 10 mV. Whenever a conductive material bridged the wires, a small current (20 $\mu$A) flowed and this was recorded. A 6V battery was used as a power supply. The sensor wires were tightly pressed to the leaf surface with a temporary clamp and held in place with a quick-drying glue (Duro Super Glue). The circuitry was derived from an unpublished dew sensor designed by K. Young (D.S.I.R., Auckland, New Zealand).

## RESULTS

**Exploratory studies on beans.** To address the question whether leaves of field-grown beans become electrically charged, detached leaves of Light Red Kidney beans were measured periodically over a period of 4 days (26–30 July 1982). The preceding few days had been cloudy, with scattered periods of rain. The first day of sampling, however, was warm, dry, and sunny and this was followed by three heavily overcast days with much higher humidities. Leaves measured the first day (31 C max.; 31% RH min.) were electrostatically charged, with maximum field intensity

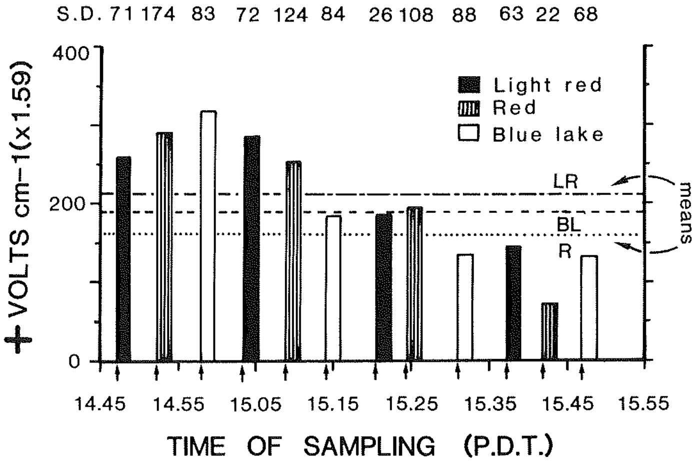

**Fig. 2.** A comparison of the electrostatic fields associated with leaf surfaces of three cultivars of beans, Light Red Kidney, Red Kidney, and Dwarf Blue Lake (sequential sampling with each bar averaged from five leaves; arrows indicate start of sampling; weather: clear, 29.5 C, wind ≤2 m/sec, RH 29%, leaves dry).

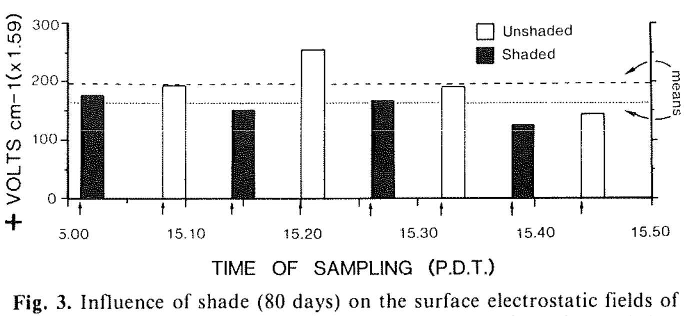

**Fig. 3.** Influence of shade (80 days) on the surface electrostatic fields of leaves of Light Red Kidney beans (sequential sampling with each bar averaged from five leaves; arrows indicate start of sampling; weather: clear, 28 C, wind ≤2 m/sec, RH 30%, leaves dry).

about 160V $\text{cm}^{-1}$. During the next few overcast days, field intensities were very small or nonexistent during early morning and early evening. During the 4-day period, 220 leaves were measured, with 73% positive, 5% negative, and the remainder neutral. This exploratory study was the first to reveal that under field conditions, detached leaves were electrically charged. In this and subsequent studies, there was considerable variation in field intensity measurements among different leaves, and this contributed to the large standard deviations.

To determine whether there might be significant differences in leaf surface electrical behavior of different cultivars of beans, Light Red Kidney, Red Kidney, and Dwarf Blue Lake were grown under identical conditions and sampled sequentially on the same day when all were at the same age. The differences of leaf field intensities among the three cultivars were weakly significant at $P = 0.07$ (Fig. 2). During the relatively short sampling period (1445–1555 hours), there were significant transitory changes of leaf voltage measurements for all three cultivars. Thus, field intensities between 1445 and 1505 hours were considerably larger than those between 1535 and 1555 hours. To separate the effect of this temporal variation from cultivar variation, each complete set of treatment readings was blocked in time (eg, four time blocks of 15 field intensity measurements, five measurements on each cultivar). This did not remove the confounding order of cultivar measurement in time, but it did separate somewhat the effects of time and treatment. Temporal variation (between time blocks) was highly significant ($P < 0.05$), indicating the need to study more carefully the changes in measured leaf field intensities as they relate to transitory changes of humidity and temperature and, possibly, to other temporal variables.

When leaves from shaded bean plants (Light Red Kidney) were compared with leaves from unshaded plants of the same age (Fig. 3), field intensities of the plants grown in full sunlight were consistently larger ($P = 0.09$) than those measured from plants grown in shade (44% reduction of light intensity). Transitory temporal variation did not contribute significantly to the total variation. The results of this experiment are weakly indicative of a light intensity effect and they indicate the need for further investigation using even lower light intensities.

During exploratory studies, the possibility of electrical differences between adaxial and abaxial leaf surfaces was determined for 30-day-old Light Red Kidney beans (Fig. 4). Leaves were sampled and measured sequentially under the weather conditions included in Fig. 4. An analysis of field intensities revealed no significant differences between the two surfaces.

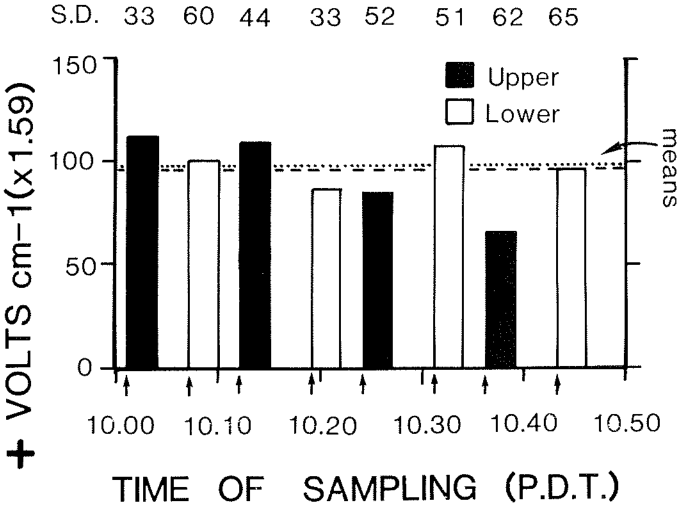

**Fig. 4.** A comparison of the electrostatic fields associated with adaxial versus abaxial leaf surfaces of Light Red Kidney beans (sequential sampling with each bar averaged from five leaves; arrows indicate start of sampling; weather: 100 light cirrus clouds, 23C, wind ≤2 m/sec, RH 38%, leaves dry).

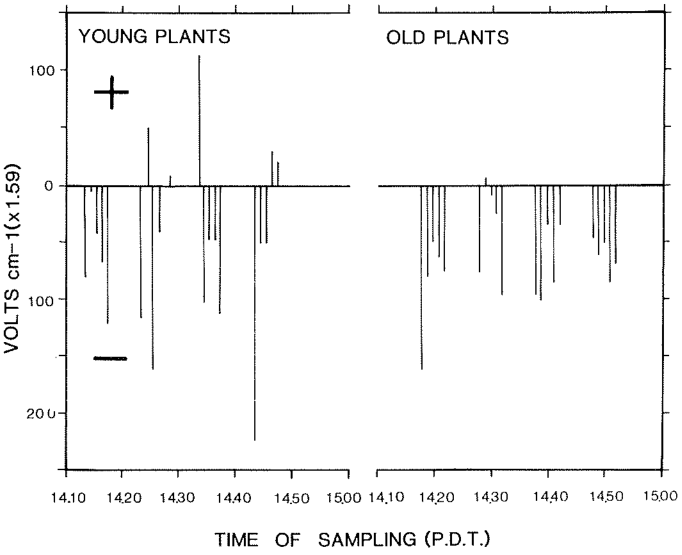

**Fig. 5.** A comparison of the electrostatic fields associated with leaf surfaces of young (33 days) and old (99 days) Light Red Kidney bean plants (sequential sampling; each bar from a single leaf; weather: 85% cloud cover, 23 C, wind ≤2 m/sec, RH 58%, leaves dry, measurements preceded by rain).

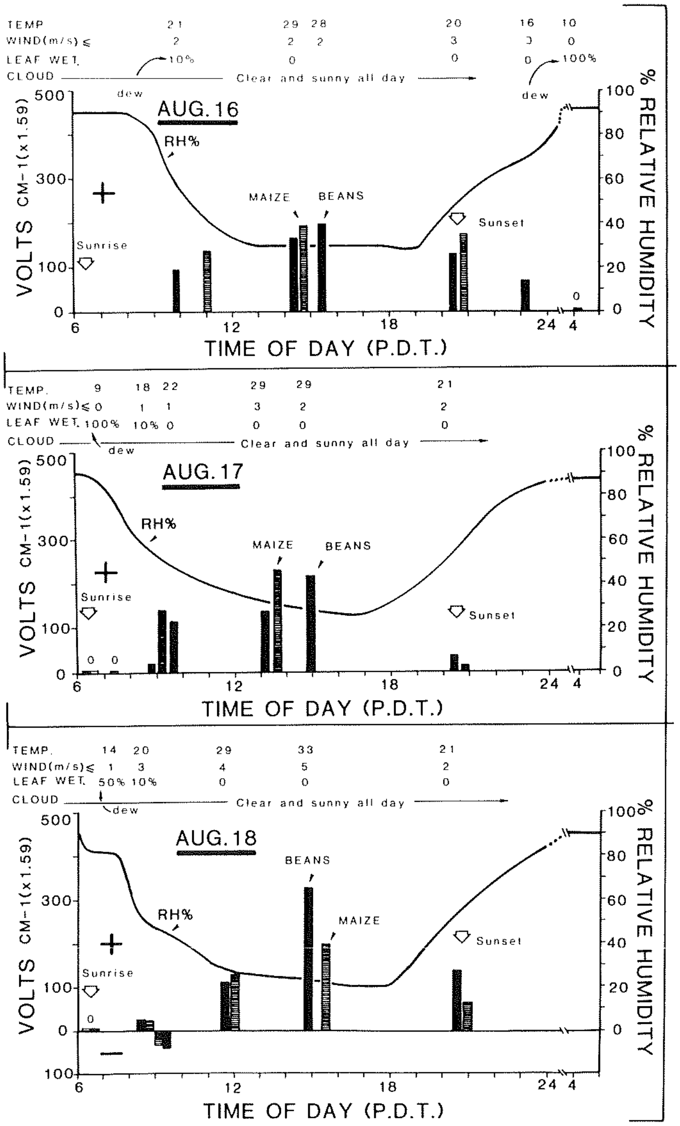

**Fig. 6.** A comparison of the electrostatic field of leaf surfaces of Light Red Kidney beans and Golden Cross Bantam maize over a 3-day period of fair weather (each bar averaged from 20 leaves).

As earlier studies under controlled conditions (13) were mainly confined to unifoliolate (seedling) leaves, these were also examined under natural conditions. Twenty leaves were sampled and field intensities measured from 13-day-old plants. The sampling was begun at 1125 hours (P.D.T.) when the sky was 100% overcast, air temperature was 23 C, RH was 42%, wind velocity was $\leq 3$ m/sec, and the leaves were dry. The unifoliolate leaves were all positively charged and averaged 108V $cm^{-1}$ (SD = 47V).

To determine if differences existed between leaves of young and old plants, field intensities of lower leaves from 33- and 99-day-old Light Red Kidney beans were measured. Leaves from old and young plants were alternately sampled from plants grown in the same location (Fig. 5). The weather on the day of sampling was initially overcast (85% cloud cover) with intermittent rain, then the rain stopped and at the time of sampling (1411 hours), the leaves were dry, air temperature was 23 C, wind velocity was <2 m/sec, and RH was 58%. Variation in leaf field intensities for young plants was significantly greater ($P = 0.05$) than for older plants; however, an analysis revealed no significant differences between the field intensities of the two groups (Fig. 5). These results were noteworthy in that leaves were of mixed polarity with negative field intensities predominating. This was one of the few occasions during our study that leaves were predominantly negatively charged, and we speculated that it might have related to the preceding unsettled weather.

**Comparison of bean and corn leaves.** To determine if the behavior of bean leaves might be characteristic of other plant species, beans and maize were compared over several extended periods, which included both fair and unsettled weather. Light Red Kidney beans were grown side by side in parallel rows with Golden Cross Bantam maize. Leaves of the two plant species were sampled within seconds of each other for the two periods 16–18 August and 30 August–3 September. In addition, a late-season sampling was made for beans on about 7–9 September.

During the first comparisons of beans and maize (16–18 August), the weather was warm, sunny, and dry, with dew formation each night (Fig. 6.). Leaves were measured periodically beginning around sunrise and finishing after dusk. On one occasion, leaves were measured during the early morning (0400 hours, 16 August). The general electrical patterns of the two plant species were very similar (Fig. 6). Field intensities were consistently near zero around sunrise when the relative humidity was high and leaves were covered with dew. First evidence that leaves were becoming charged was not until after sunrise and coincided with evaporation of dew and decreasing atmospheric humidity. Although small field intensities (<10V $cm^{-1}$) could be first detected when the relative humidity was in the range of 60–70%, it was not possible to establish the precise onset of leaf charging because of lack of sensitivity of the field mill. Highest electrostatic field intensities were usually measured during the afternoon. In late afternoon, as the humidity began to increase, field intensities decreased, eventually reaching zero at 100% RH. Electrical fields were consistently positive except for a brief period on 18 August (discussed later). On one evening (16 August), the air remained relatively dry and the leaves remained charged until well after dusk. Leaves measured during the early morning (0400 hours, 16 August) were uncharged and this was typical of other measurements made at night when the humidity was near saturation and leaves were covered with dew. On 18 August, between 0800 and 1000 hours (Fig. 6), a unique polarity reversal was observed. This day dawned clear with dew and high relative humidity, similar to the preceding 2 days, and leaves measured at sunrise were uncharged. At 0815 hours, 20 leaves of beans were measured and all were positive with an average field intensity of 40V $cm^{-1}$; 19 leaves of maize were then measured and they too were positive with an average field intensity of 37 V $cm^{-1}$. Measurement of the 20th maize leaf was negative, indicating an erroneous measurement or a polarity reversal; however, the next 19 maize leaves were also negative. Another 20

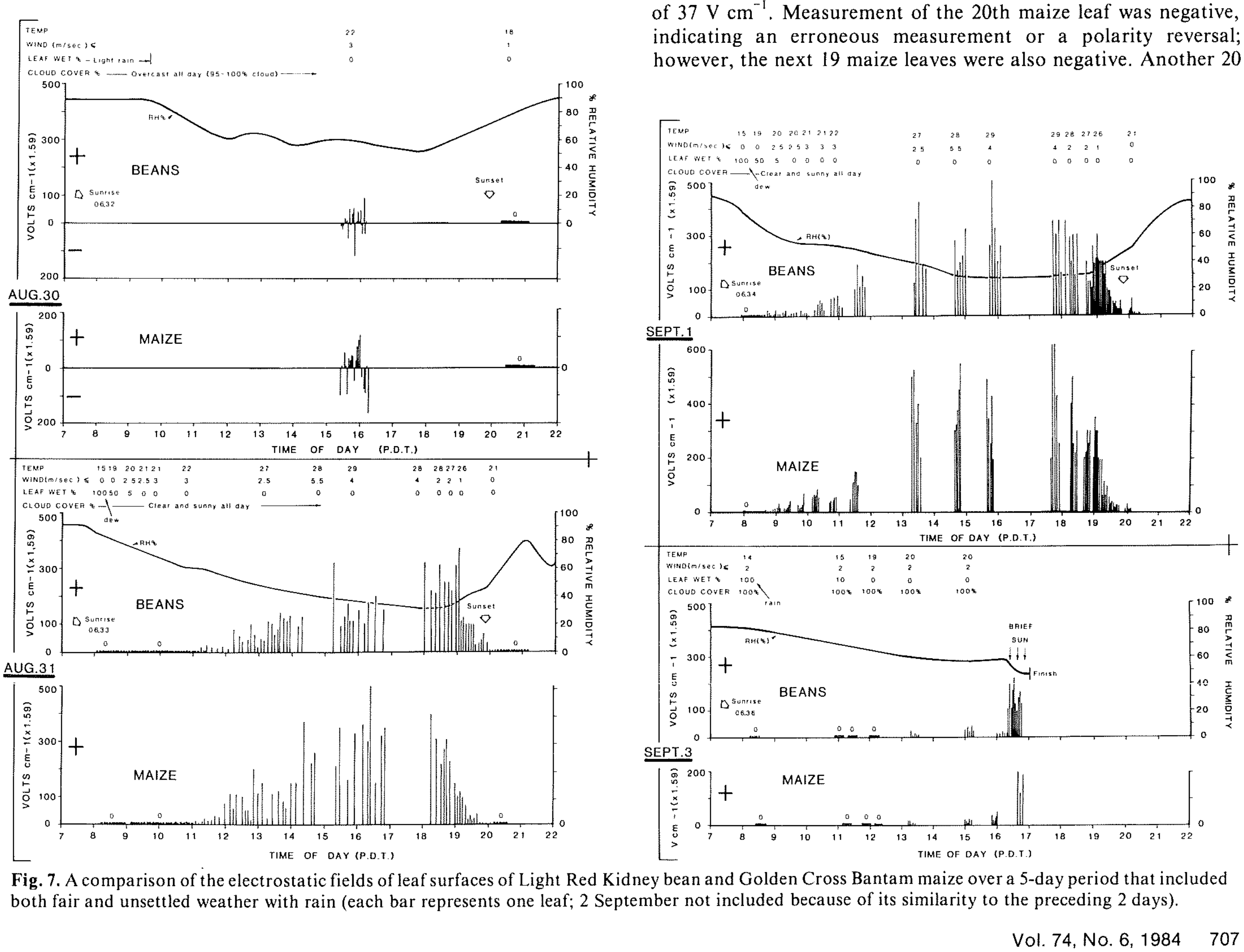

**Fig. 7.** A comparison of the electrostatic fields of leaf surfaces of Light Red Kidney bean and Golden Cross Bantam maize over a 5-day period that included both fair and unsettled weather with rain (each bar represents one leaf; 2 September not included because of its similarity to the preceding 2 days).

bean leaves were then measured and they too were all negative. The next series of measurements made at 1125 hours revealed another polarity reversal, with leaves of both plant species back to positive and similar to the preceding 2 days. Accompanying this brief reversal of polarity on 18 August was a pronounced change in wind pattern.

The comparative study from 16–18 August revealed a similar pattern of electrical behavior for detached leaves of beans and maize. The leaves of both species became charged as the humidity decreased and both species lost their charges as the relative humidity increased toward saturation. At night when relative humidity was near saturation, leaves of both species remained unchanged.

Bean and maize were again compared from 30 August to 3 September, a period of 5 days that included both fair and unsettled weather (Fig. 7). The first day was heavily overcast with periods of rain, but the next three days were warm, dry, and sunny. The last day (3 September) was overcast with rain. On 30 August, the humidity was fairly high (>60%) and field intensities for both species were low and of mixed polarity. During the next 3 days (31 August–2 September), which were clear, sunny, and warm with about 30% RH each day, leaves were uncharged during the early morning when the air was saturated (100% RH). Then for each of these days, as the humidity decreased so field intensities increased with maxima measured early to late afternoon, rapid loss of leaf charges occurred as the humidity increased each evening, eventually reaching zero at the higher humidities. On each of these sunny, warm, and dry days, the leaves of both species were consistently positively charged. The last day of the series (3 September) was overcast with intermittent rain and fairly high humidity (<60%). Field intensities were very small all day until 1620 hours, when there was a brief period of sunshine. This was accompanied by a fairly rapid fall in humidity and a significant increase in field intensities. During this 5-day comparison, the electrical behavior of both species of plants was again very similar.

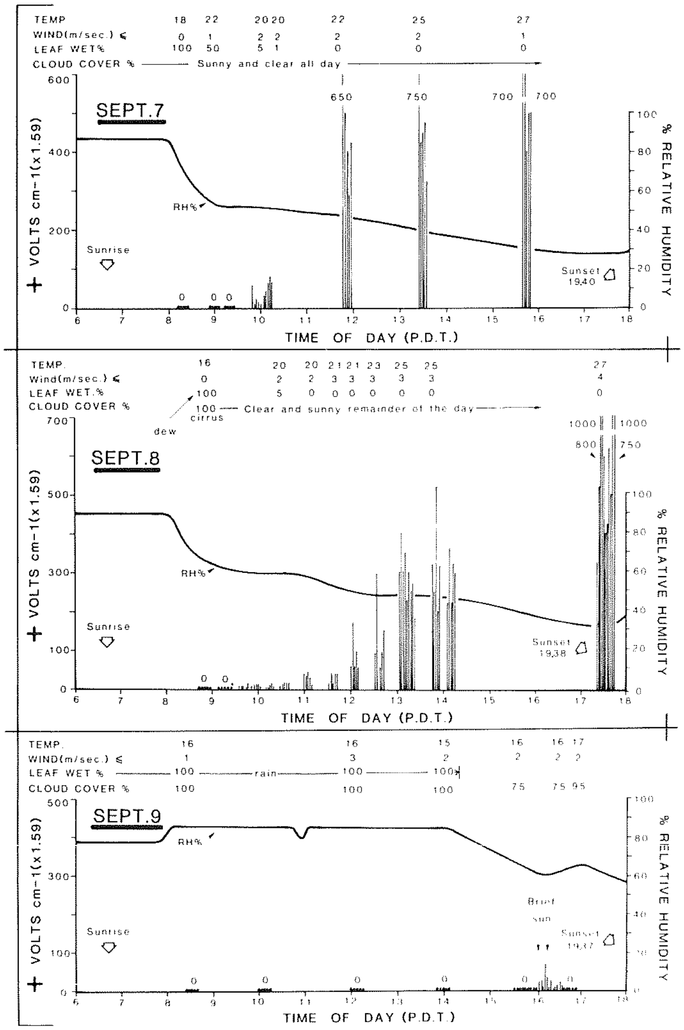

**Fig. 8.** Electrostatic fields of leaf surfaces of Light Red Kidney beans over a 3-day period in late season (each bar represents a single leaf).

A final series of measurements restricted to Light Red Kidney beans was made late in the growing season (Fig. 8). The weather was warm, sunny, and dry the first 2 days, then cool with intermittent rain and high humidity on the last day. The electrical behavior of bean leaves (Fig. 8) was consistent with the earlier comparative studies. Leaves were positively charged during the fair weather, with maximum field intensities measured during the afternoons when the humidity was low. Negligible charging of leaves was evident during the day of unsettled weather, accompanied by rain. Again, a brief burst of sunshine caused a significant increase in field intensity (9 September). It was during this period that the highest field intensities of the entire summer were measured (about 1,600V cm$^{-1}$).

**Miscellaneous.** The similarity of electrical behavior of bean and maize leaves indicated that surface charging of leaves might be a widespread phenomenon. To explore this possibility, the electrical fields of leaves of a number of unrelated species of plants (Fig. 1) were measured. As the plants were scattered over various locations, it was not possible to make direct comparisons from one species to another. Leaves of all eight plant species were positively charged, with average field intensities ranging from 70V cm$^{-1}$ for rose to 550V cm$^{-1}$ for rhododendron. These results indicate that the electrical charging of leaves is a common phenomenon.

During a comparative study of bean and maize, the surface electrical conductivity of an attached bean leaf was measured over several days, and this was repeated for several other leaves. Figure 9 shows the conductivity changes that occurred for one of these leaves. On this day, electrical conductivity of the leaf was high throughout the night until about 0820 hours in the morning, at which time the conductivity of the leaf began to fall. By midmorning, the leaf surface was no longer a conductor. This change in conductivity appeared to be inversely proportional to the leaf's increase in electrostatic field intensity. Later in the afternoon (not shown in Figure 9), as field intensities decreased with rising humidity, the electrical conductivity of the leaf began to increase again. Similar observations have been made by P. D. Hildebrand of the University of Guelph (*personal communication*).

## DISCUSSION

If an electrostatic mechanism is involved in the active discharge of spores by dry-spored foliar pathogens (6), then it is axiomatic that leaves become electrostatically charged and that this should relate to changes of atmospheric humidity and exposure to IR

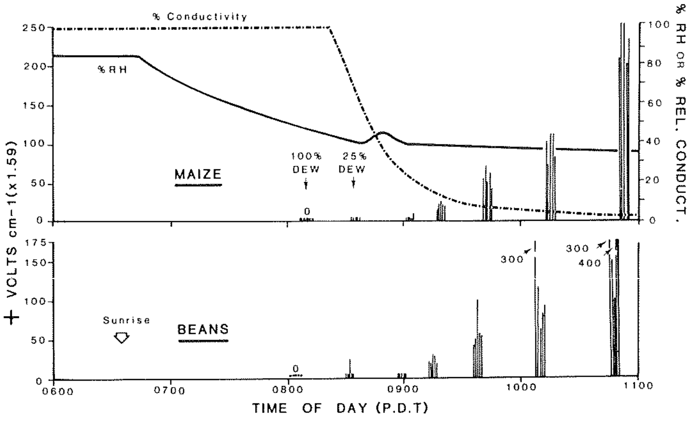

**Fig. 9.** Surface electrical conductivity (relative) of a single bean leaf related to the electrostatic fields associated with the surfaces of leaves of surrounding bean plants (each bar represents one leaf; weather: clear, 27 C at 1100 hours; wind ≤1 m/sec).

factors known to trigger spore release (2–4,7–9). Controlled studies on detached leaves of beans and maize (13) revealed that leaf surfaces become charged in response to humidity changes and exposure to IR, and this has been found to be true for detached leaves of field-grown plants, particularly as related to humidity changes. A major difference between the controlled and field studies was the behavior of leaves in saturated atmospheres. In the controlled studies, leaves exhibited large electrostatic field intensities in saturated still air, but not when the saturated air was in motion. In contrast, in nature, leaves remained uncharged when the humidity was near saturation. Preliminary evidence (Fig. 9) indicates that leaf surfaces become electrically conductive at high atmospheric humidities but not at low humidities. If this can be confirmed, then under conditions of high humidity, plants growing under natural conditions would be electrically grounded and therefore would not be expected to build up surface charges.

In controlled experiments on leaves in a moving airstream (13), detached leaves of beans and maize always became charged whenever the atmospheric humidity was reduced below a certain level; this was also true in nature. Conversely, in the laboratory, leaves rapidly lost their charges when the humidity was raised from a low level back to saturation; likewise, in nature, loss of charge consistently occurred during the early evening as the humidity began to increase. On several evenings when the humidity remained low well after sunset (eg, Fig. 6, 16 August), leaves remained charged for several hours into the night. In arid regions where nocturnal humidities may remain fairly low, it seems likely that leaves could remain charged well into the night.

The effect of IR on spore discharge has been reported in a number of studies (2–4,7–9). Exposure of sporulating leaf lesions to IR both triggers and enhances spore liberation, and it also affects leaf surface charging (13). Under field conditions, it is difficult to demonstrate the effect of the IR component of solar radiation, yet in the field studies on bean and maize, highest field intensities were always recorded on sunny days. Pronounced effects of solar radiation were observed on several days when the sun's direct radiation briefly broke through overcast skies, eg, on 3 September (Fig. 7) and 9 September (Fig. 8). These brief bursts of sunshine were accompanied by marked increases in field intensities as well as significant lowering of relative humidity.

The polarity of leaves grown under sunny, warm, and dry conditions were consistently positive, except briefly on 18 August between 0800 and 1000 hours (Fig. 6). On this day, there was a double reversal of polarity associated with detached leaves of beans and maize. Leaves measured in early morning were positively charged; this later changed to negative and then back to positive several hours later. This unusual polarity reversal was accompanied by a major shift in wind direction and velocity. The early-morning prevailing wind was a westerly, moist, ocean breeze (<1 m/sec), which changed at the time of the polarity reversal to a fairly strong (⩽3 m/sec) northeasterly wind from the hot, dry regions of eastern Oregon and Washington. Possible explanations for this polarity reversal relate to electrical events that can occur in the atmosphere. Electrostatic charging of surfaces can be induced from blowing dust (18). Normally, dust storms introduce negative space charges, but on some occasions, they are known to result in positive space charges. Hot, dry winds can also be preceded by air masses carrying excessive positive air ions (5), and this type of phenomenon could have caused the short, negative polarity reversal of 18 August.

On several occasions after periods of unsettled weather, which included rain, leaves were measured with mixed polarity (Fig. 5). This was in contrast to the warm, dry periods, when leaves were consistently positive. These polarity differences remain unexplained.

The possibility that wind, rain, dew, and temperature might influence the electrical behavior of leaves was not ignored during the studies on beans and maize. After extended periods of rain, leaves were uncharged, although there were numerous instances when small field intensities were measured on leaves still covered with dew. There was no indication that temperature was involved in electrostatic relationships, yet humidity and temperature changes closely parallel each other and temperature can significantly influence electret phenomena (16). There was no evidence that wind influenced leaf surface charges.

A major weakness of the study on beans and maize under natural conditions was the use of detached leaves to follow the electrical behavior of leaf surfaces. It can be argued that detached leaves are unlikely to represent what happens to leaves attached to plants rooted in soil, ie, electrically grounded. The shortcomings of this approach are recognized, but we were unable to overcome the technical problems associated with the measurement of leaves still attached to growing plants. More recently, these obstacles have been overcome.

The nature of leaf surface charging is not understood. The phenomenon could involve electrets (16), with epicuticular waxes (15) the logical choice. An early report on electrets concerned the electrical properties of carnauba wax from the leaves of a Brazillian palm (16). Tribe et al (17) reported that leaf wax formation is directly related to light intensity, a report that caused an examination of the effect of shade on the field intensities of leaves. Our finding that the electrical conductivity of bean leaf surfaces can change with humidity indicates that during the day, a leaf's cuticle may act both as a conductor and insulator.

This investigation was begun seeking evidence that an electrostatic mechanism might be involved in the active discharge of spores by certain foliar plant pathogens. If these observations for detached leaves represent what happens on the surfaces of leaves attached to growing plants, then the case for an electrostatic spore discharge mechanism is fairly strong.

## LITERATURE CITED

1. Aylor, D. E., and Pau K. T. U. 1980. The role of electrostatics in spore liberation by *Drechslera turcica*. Mycologica 72:1213-1219.
2. Gottwald, T. R. 1982. Spore discharge by the pecan scab fungus, *Cladosporium caryigenum*. Phytopathology 72:1193-1197.
3. Gottwald, T. R. 1983. Factors affecting spore liberation by *Cladosporium carpophilum*. Phytopathology 73:1500-1505.
4. Gottwald, T. R., and Tedders, W. L. 1982. Studies on conidia release by the entomogenous fungi *Beauvaria bassiana* and *Metarhizum anisopliae* (Deuteromycotina: Hyphomycetes) from adult weevil (Coleoptera: Curculionidae) cadavers. Environ. Entomol. 11:1274-1279.
5. Krueger, A. P. 1982. Air ions as biological agents—fact or fancy? Immunol. Allerg. Practice 4:129-140.
6. Leach, C. M. 1976. An electrostatic theory to explain violent spore liberation by *Drechslera turcica* and other fungi. Mycologia 68:63-86.
7. Leach, C. M. 1980. Influence of humidity and red-infrared radiation on spore discharge by *Drechslera turcica*—Additional evidence. Phytopathology 70:192-196.
8. 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.
9. Leach, C. M. 1980. Influence of humidity, red-infrared radiation, and vibrational spore discharge by *Pyricularia oryzae*. Phytopathology 70:201-205.
10. Leach, C. M. 1980. Evidence for an electrostatic mechanism in spore discharge by *Drechslera turcica*. Phytopathology 70:206-213.
11. Leach, C. M. 1982. Active sporangium discharge by *Peronospora destructor*. Phytopathology 72:881-885.
12. Leach, C. M. 1984. Leaf surface electrostatics: Apparatus and procedures used under controlled and natural conditions. Phytopathology 74:701-703.
13. 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.
14. 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.
15. Martin, J. T., and Juniper, B. E. 1970. The Cuticles of Plants. Edward Arnold (Pub.) Ltd. 347 pp.
16. Sessler, G. M., ed. 1980. Electrets. Springer-Verlag (Topics in Applied Physics), New York. 365 pp.
17. Tribe, I. S., Gaunt, J. K., and Parry, D. W. 1968. Cuticular lipids in the Gramineae. Biochem. J. (Proc.). 109:8.
18. Vonnegut, B. 1973. Atmospheric electrostatics. Pages 391–423 in: Electrostatics and Its Applications. A. D. Moore, ed. John Wiley & Sons, New York.