Available online at www.sciencedirect.com
ScienceDirect
Atmospheric Environment 41 (2007) 1587–1595
ATMOSPHERIC ENVIRONMENT
www.elsevier.com/locate/atmosenv

Electrostatic forces in wind-pollination—Part 1: Measurement of the electrostatic charge on pollen ☆

George E. Bowker[a,*], Hugh C. Crenshaw[b]

[a]National Exposure Research Laboratory, United States Environmental Protection Agency, Research Triangle Park, NC 27711, USA
[b]GlaxoSmithKline, Technology Development Department, RTP, NC 27709, USA

Received 10 March 2006; received in revised form 6 September 2006; accepted 26 October 2006

Abstract

Under fair weather conditions, a weak electric field exists between negative charge induced on the surface of plants and positive charge in the air. This field is magnified around points (e.g. stigmas) and can reach values up to $3 \times 10^6\,\mathrm{V\,m^{-1}}$. If wind-dispersed pollen grains are electrically charged, the electrostatic force (which is the product of the pollen's charge and the electric field at the pollen's location) could influence pollen capture. In this article, we report measurements of the electrostatic charge carried by wind-dispersed pollen grains. Pollen charge was measured using an adaptation of the Millikan oil-drop experiment for seven anemophilous plants: *Acer rubrum, Cedrus atlantica*, *Cedrus deodara*, *Juniperus virginiana, Pinus taeda, Plantago lanceolata* and *Ulmus alata*. All species had charged pollen, some were positive others negative. The distributions (number of pollen grains as a function of charge) were bipolar and roughly centered about zero although some distributions were skewed towards positive charges. Most pollen carried small amounts of charge, 0.8 fC in magnitude, on average. A few carried charges up to 40 fC. For *Juniperus*, pollen charges were also measured in nature and these results concurred with those found in the laboratory. For nearly all charged pollen grains, the likelihood that electrostatics influence pollen capture is evident.

Keywords: Electrostatic field; Fair-weather electricity; Pollen; Wind pollination

1. Introduction

For many plant species, successful reproduction depends on the release, the movement, and the deposition of pollen on the stigma of a receptive conspecific plant. Electrostatic fields are pervasive in the environment and electrostatic forces possibly influence the dispersal and deposition of wind-dispersed pollen grains. Electrostatic forces have been suggested to be involved in insect pollination (Corbet et al., 1982; Gan-Mor et al., 1995), and have been shown to influence deposition in agricultural wind-pollination settings when the pollen is artificially charged (Bechar et al., 1999; Vaknin et al., 2000, 2001; Law et al., 2000; Law, 2001; Gan-Mor et al., 2003).

This is the first in a series of two articles exploring the role of electrostatic forces in the capture of wind-dispersed pollen grains. The electrostatic force experienced by a charged wind-dispersed pollen

☆The United States Environmental Protection Agency through its Office of Research and Development partially supported and collaborated in the research described in this paper. It has been subjected to Agency review and approved for publication.

*Corresponding author.
E-mail address: bowker.george@epa.gov (G.E. Bowker).

1352-2310/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.atmosenv.2006.10.047

grain is the product of two factors; its electrostatic charge and the electric field at its location. In this article, we explore the first of these factors, determining the electrostatic charge on wind-dispersed pollen grains. In the companion article (Bowker and Crenshaw, 2006), we develop a model of the electric fields around plants and then estimate the forces experienced by charged pollen grains and simulate their trajectories as they pass near plants.

While explored in detail by Bowker and Crenshaw (2006), during fair weather electric conditions (relatively clear skies, calm winds) when pollination typically occurs, a vertical electric field averaging roughly $100\,\mathrm{V\,m^{-1}}$ is present in nature. Negative charge is present on the ground (and on plants) while an equal positive charge is present in the air. The negative charge on plants is asymmetrically distributed, concentrated on points (e.g. the tips of branches, the edges of leaves, and the feathery stigmatic female reproductive structures) that extend above their surroundings. The electric field surrounding these charged features is distorted and magnified; sometimes reaching values $>100\,\mathrm{kV\,m^{-1}}$ (Law, 1987, 2001; Dai and Law, 1995; Bechar et al., 1999). Positively charged pollen grains encountering these regions would be strongly attracted to the plant and negatively charged pollen grains would be repelled.

The electrostatic charge of naturally released wind-dispersed pollen is not known. Investigators have suggested pollen charge distributions can be primarily positive (Erickson and Buchmann, 1983), primarily negative (McWilliam, 1959), or bipolar (Bowker and Crenshaw, 2003). However, at electrostatic equilibrium with the air, the charges on pollen grains are likely small ($<0.002\,\mathrm{fC}$), resulting from Boltzmann charging (Hinds, 1982) and from incurring a charge per volume equal to the ambient space charge (Chalmers, 1967). The electrostatic force acting on a airborne pollen grain with such a small charge, in a $200\,\mathrm{kV\,m^{-1}}$ electric field, is small ($4\times10^{-13}\,\mathrm{N}$) relative to gravity ($4\times10^{-11}\,\mathrm{N}$) (assuming $10\,\mu\mathrm{m}$ radius and a density of $1000\,\mathrm{kg\,m^{-3}}$).

The neutralization process, by which airborne pollen grains lose their charge and reach electrostatic equilibrium with the air, takes substantial amounts of time due to the low conductivity of air. The time for an object to lose 63% of its charge, is approximately 440 s (Bowker and Crenshaw, 2003). If pollen grains are charged at release, they may carry substantial charge through dispersal, if the dispersal time is short relative to the neutralization time.

Wind pollination is usually a localized process, with most pollen grains released from one plant traveling short distances (centimeters to meters depending on release height) and settling on neighboring plants. To a first approximation, the dispersal time is simply the time required for the pollen to fall through the air to the ground, depending on pollen settling velocity (typically 0.02–$0.06\,\mathrm{m\,s^{-1}}$) and plant height (Crane, 1986; Young and Schmitt, 1995). Consequently, dispersal times are relatively short (a few seconds to a few minutes). Because the electrostatic neutralization time for an airborne pollen grain is long relative to its short average dispersal time, most pollen charged during release will retain a substantial charge throughout dispersal. They will not be at electrostatic equilibrium with the air and will not have sufficient time to become uncharged. Consequently, if pollen grains are charged at release, an electrostatic interaction with the plants in the environment is possible (Niklas, 1985; Crane, 1986).

The object of this paper was to determine the electrostatic charges on pollen grains immediately upon release (the non-equilibrium charges) for seven species of wind-pollinated plants: *Plantago lanceolata* (Bowker and Crenshaw, 2003), *Cedrus deodara*, *Cedrus atlantica*, *Juniperus virginiana*, *Acer rubrum*, *Pinus taeda*, and *Ulmus alata*. To corroborate the laboratory experiments, the charges on juniper pollen grains (*J. virginiana*) were also measured in nature immediately upon release from the plant. For the electrostatic force to be functionally significant in pollen capture, it must be comparable in magnitude to other active forces, such as the gravitational force. Thus, for pollen grains of various sizes with differing charges, we determined the electric field necessary for the electrostatic force to equal gravity. In the companion paper (Bowker and Crenshaw, 2006), we used the charges measured here to estimate the electrostatic force experienced by pollen grains and simulate their motion as they encounter the electric field around a plant.

2. Materials and methods

2.1. Estimating pollen radius and charge from velocity measurements

Pollen charge can be determined by measuring its deflection and velocity in a uniform horizontal electric field (Swinbank et al., 1964; Leach, 1976). A pollen grain moving through the air experiences a drag force that depends on the Reynolds number ($\mathrm{Re} = L\mathbf{U}\rho_a/\mu$, where L is the diameter of a pollen grain, $\mathbf{U}$ is the relative velocity of the pollen grain, ρ_a is the density of air, and μ is the dynamic viscosity of air). The Re of a typical wind-dispersed pollen (e.g. radius 10 μm) settling at $0.03\,\mathrm{m\,s^{-1}}$ in air is 0.02. For low Re flows ($\mathrm{Re} < 1$), the drag of a sphere is given by Stokes' Law, $\mathbf{F}_D = 6\pi\mu\mathbf{U}a$, where $\mathbf{F}_D$ is the drag and a is the radius of the pollen (Vogel, 1994).

In the absence of an electric field, the pollen grain falls straight down under the influence of gravity at a constant velocity ($\mathbf{U}_y$). At terminal velocity, the drag force balances the gravitational force,

$$6\pi\mu\mathbf{U}_y a = M\mathbf{g} = \rho_p \tfrac{4}{3}\pi a^3 \mathbf{g}. \tag{1}$$

The gravitational force equals the acceleration of gravity ($\mathbf{g}$) multiplied by the mass (M) of the pollen. The pollen grains are assumed to be spherical in shape (radius a) with a density (ρ_p) equal to that of water ($1000\,\mathrm{kg\,m^{-3}}$), a primary constituent within the pollen. This pollen grain density is comparable to that measured for ragweed (*Ambrosia artemisiifolia*, $840\,\mathrm{kg\,m^{-3}}$, by Harrington and Metzger, 1963) and corn (*Zea mays*, $1100\,\mathrm{kg\,m^{-3}}$, by van Hout and Katz, 2004). Rearranging Eq. (1), the radius of the pollen can be determined from the observed settling velocity

$$a = \sqrt{\frac{9\mu\mathbf{U}_y}{2\rho_p\mathbf{g}}}. \tag{2}$$

Errors result when the actual pollen density is different than assumed (e.g. *Pinus taeda*) or is non-spherical (e.g. *Acer rubrum* and *Pinus taeda*).

When a horizontally aligned electric field is imposed, the charged pollen grains migrate toward either the positive or negative plate. The pollen experiences an electrostatic force ($\mathbf{F}_E$), equal to the product of its charge (q) and the strength of the electric field ($\mathbf{E}$), $\mathbf{F}_E = \mathbf{E}q$. The pollen accelerates until the electrostatic force is balanced by drag and the pollen grain moves with a constant horizontal velocity ($\mathbf{U}_x$). The horizontal velocity ($\mathbf{U}_x$) is reached by 0.1 s and is frequently faster than 0.01 s. Setting the electrostatic force equal to drag, then solving for the pollen's charge,

$$q = \frac{6\pi\mu\mathbf{U}_x a}{\mathbf{E}}. \tag{3}$$

In this experiment, pollen grains were videotaped as they settled vertically under gravity and moved horizontally in a known electric field. The electrostatic charges on the pollen were calculated from the observed velocity measurements by substituting Eq. (2) for the pollen's radius a,

$$q = \frac{6\pi\mu\mathbf{U}_x\sqrt{9\mu\mathbf{U}_y/2\rho_p\mathbf{g}}}{\mathbf{E}}. \tag{4}$$

The accuracy of the charge calculations were limited by the validity of the assumptions of pollen density and shape and on the measurement accuracy for the electric field and the terminal velocities. The accuracy of the electrostatic velocity component was limited by parallax in the optical system, due to variations in the distance of the pollen grain from the camera, leading to a possible 4% error.

2.2. Measuring pollen charge

Branches or spikes containing pollen-filled flowers from trees and herbs (*Juniperus virginiana, Acer rubrum, Ulmus alata, Plantago lanceolata,* and *Pinus taeda*) were harvested from the Duke University campus during the spring of 2001. The cut ends of the stems were placed in water for about 24 h. This allowed the flowers to develop fresh pollen. Additionally, pollen grains were collected from two cedar species located on campus (*Cedrus atlantica* and *Cedrus deodara*) by picking cones directly from the tree. Between one and three individual trees per species were used. Multiple branches, flowers, or cones were taken from the lower portion of each tree. To minimize direct charging of the pollen-laden branches and cones during the experiment, they were electrically connected to ground (at a potential of 0 V). Furthermore, to minimize charge induced by external electric fields, they were placed between a set of vertically positioned grounded parallel plates (13 cm tall × 9.7 cm wide, separated by 5.2 cm) serving as a partial electrical shield (Fig. 1).

The pollen-laden branches and cones were positioned about 5 cm above a second set of aluminum plates, the "measurement" plates, (19.9 cm tall × 13.2 cm wide) held vertically and separated by 1.89 cm (Fig. 1) by ceramic standoffs. The stem of each plant was lightly tapped to release the pollen. To minimize the movement of air between the measurement plates, the top and the two open sides of the vertical plates were covered by Plexiglas. The top cover had a quarter inch hole drilled

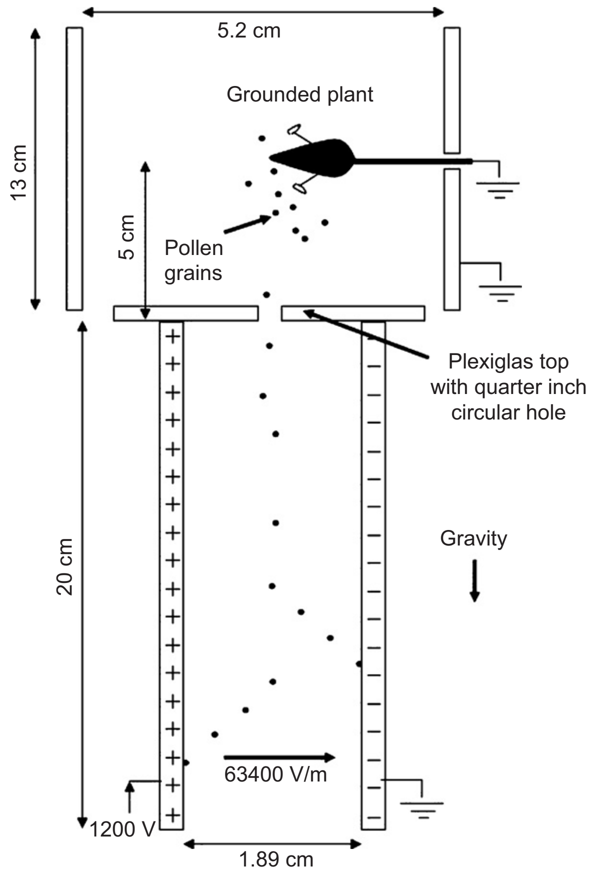

Fig. 1. A cross-section of the apparatus used to measure the electrostatic velocity and settling velocity for pollen. Pollen released from the electrically grounded plant fell through a circular quarter inch hole into the region between the bottom parallel plates. An electric field of $6.34 \times 10^4\,\mathrm{V\,m^{-1}}$ was created between the plates and the velocity in the horizontal and vertical direction was measured.

through it, permitting a small fraction of the released pollen to enter the measurement apparatus as it drifted down. The plates were connected to the positive and negative poles of a 1200 V dc power supply by a homemade switching device. When switched on, there was a horizontal "measurement" electric field of $6.34 \times 10^4\,\mathrm{V\,m^{-1}}$ between the plates. The "measurement" field was only switched on (for roughly 1 s time periods) after the settling pollen grains entered the field of view between the measurement plates. When the "measurement" field was off, both plates were grounded.

The pollen motion was videotaped at 60 fields $\mathrm{s^{-1}}$ (30 frames $\mathrm{s^{-1}}$) on SVHS videotape using a model 4900 COHU video camera equipped with a macro lens. The observational area began about 0.01 m from the top of the plates and covered the plate separation (resolution 210 pixels $\mathrm{cm^{-1}}$). The pollen grains were visualized using dark-field illumination. The fiber optic lights used to illuminate the pollen grains were equipped with infrared filters (minimizing heat transfer to the system and thereby minimizing convection). Pollen charge was calculated from measurements of pollen velocity using Eq. (4).

To verify the laboratory results, measurements of pollen charge were made in nature using a single juniper tree after sunset on a relatively windless evening. To increase the number of pollen grains, the juniper tree was periodically shaken. The Plexiglas top was removed from the measurement plates, allowing more pollen to settle between them. The earth's ambient electric field was not measured, but was probably negligible because the pollen-shedding branches were located on the lower side of the tree and were electrically shielded by the upper part of the tree. We videotaped the pollen as it moved and calculated charge using the same techniques described for the charge measurements in the laboratory.

2.3. Analysis and pollen tracking

Analysis of the videotaped data was performed using a particle tracking program contained in the freeware flow visualization package FLOWVis (Tennakoon, Bowker, Katz, and Crenshaw) using Image Acquisition (NI-IMAQ) Version 2 and IMAQ Vision software (National Instruments). For each pollen grain, the program recorded its instantaneous position in each video field, determined its position in the subsequent field, and then calculated instantaneous vertical and horizontal velocities. These were averaged to give a single value for the vertical and horizontal velocities for each pollen grain. Not all pollen grains were subjected to both the presence and the absence of the "measurement" electric field. The velocities of some grains were only measured for one of the conditions.

Since typical pollen grains moved only a few pixels per video field, the program successfully tracked most pollen grains. Errors were present when there were too many pollen grains in the field of view (the distance the pollen moved was greater than the spacing between pollen grains). Thus, for some species with high pollen counts (approximately 55 of 125 pollen releases for *Plantago*), the uncharged pollen grains were undercounted.

Similarly, pollen grains with high velocities were susceptible to being tracked incorrectly. In a few cases, for extremely high velocity *Pinus* pollen, pollen tracks were created by hand from the raw particle position data. From the position data, pollen velocities were measured and the radii and charges were calculated.

3. Results

A total of 13,465 average velocities were calculated for 9489 pollen grains from seven plant species. Most pollen grains carried a measurable electrostatic charge. Collectively, for all species in the laboratory, the average pollen grain carried a charge of positive 0.32 fC. The average of the absolute value of all charges was 0.84 fC. For all species and all trials, positively and negatively charged pollen grains were present (Fig. 2).

When the measurement electric field was off, the pollen grains fell nearly straight down, suggesting that the horizontal movement observed when the field was present resulted from the electrostatic force on the charged pollen grains and not from air currents. The mean (two-tailed *t*-test) and the variance (two-tailed *F*-test) of intraspecific on and off horizontal velocities were almost always significantly different (Statview 5.0).

With one exception, the charge distributions were all slightly positively shifted. *Acer rubrum* was the only species to have a net negative average pollen charge −0.56 fC (Fig. 2). However, most species had charge distributions with tails approximately equal in the positive and negative directions (*Acer rubrum*, *Ulmus alata*, *Cedrus deodara* and *Cedrus atlantica*). The charge distributions for *Pinus* and *Plantago* had tails elongated in the positive and negative directions, respectively (Fig. 2). *Cedrus deodara,* and *Cedrus atlantica* had a substantial number (0.5% and 5%) of pollen grains with charges greater than 8 fC in magnitude. Five percent of the *Pinus* pollen grains carried positive charges greater than 10 fC. The entire distribution for *Juniperus* was heavily skewed in the positive direction with relatively few negatively charged pollen grains, suggesting that its pollen is consistently positively charged (Fig. 2). The charge distributions for *Juniperus virginiana* were similar in the laboratory and in nature, with positive charges averaging 0.29 fC inside, and 0.33 fC outside (Fig. 2).

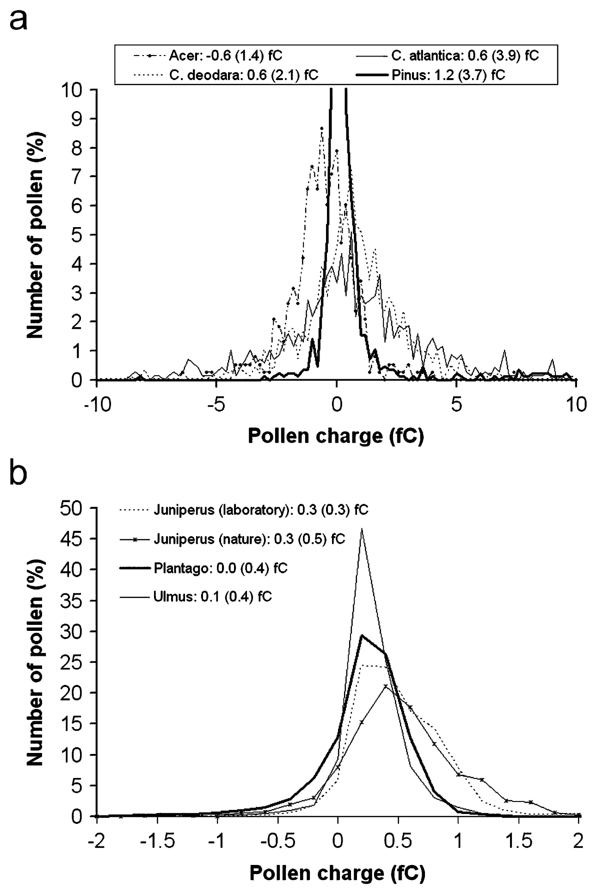

Fig. 2. Frequency distributions of pollen grains as a function of pollen charge (fC). The charges are in increments (0.2 fC in size) centered about the number. The numbers following the name of each species are the average and standard deviation of the charge (fC) for the distribution. For clarity, two points in panel A (0 fC, 23.6%, and 0.2 fC, 17.8%) for *Pinus* are omitted.

4. Discussion

The release, transport, and capture of wind-dispersed pollen are mechanical processes of great importance to many plant species which depend on successful pollen transfer for reproduction. Aerodynamic and gravitational forces govern the process, yet other forces such as electrostatic may be important, perhaps even dominating in some circumstances. Bechar et al. (1999), Law et al. (2000), Vaknin et al. (2000, 2001), and Gan-Mor et al. (2003) have shown that electrostatic forces can dramatically increase deposition of artificially charged pollen grains, with preferential deposition on flower stigmas.

The electrostatic force experienced by an airborne pollen grain passing by a plant is the product of the pollen's charge and the local electric field around the plant. For an artificially produced electric field, Vaknin et al. (2001) and Bechar et al. (1999) have shown that floral morphology magnifies the local electric field around the stigma, thereby directly increasing charged pollen deposition. While the origin of the ambient electric field is different under natural conditions, the magnification of the electric field around flowers is similar. During natural fair-weather conditions (when the $100\,V\,m^{-1}$ ambient electric field is present), the field around pointed features like the edges of leaves and the tips of spiky stigmas can, typically, be $10–100\,kV\,m^{-1}$ (Bowker and Crenshaw, 2006) Charged pollen grains encounter the natural electric fields around plants and experience an electrostatic force. Positively charged pollen grains are attracted toward plants while negatively charged pollen grains are repelled from plants.

For the pollen grains examined here, nearly all were electrostatically charged (average 0.33 fC) some being negative while others positive. The magnitude of charge (the average of the absolute value) carried by a typical pollen grain was 0.84 fC. Some pollen grains carried charges up to 40 fC. The magnitudes of charge carried by individual pollen grains of various sizes are shown in Fig. 3.

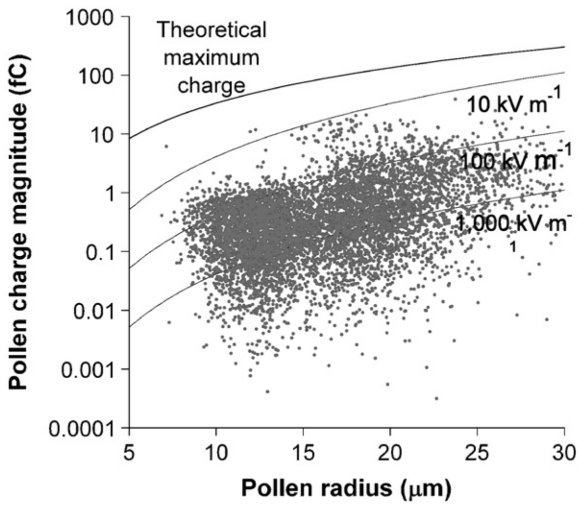

Fig. 3. The measured electrostatic charge magnitudes (fC) for individual pollen grains (gray dots) for the eight species as a function of size. The solid lines show the magnitude of charge necessary as a function of pollen grain size (radius) for electrostatic forces to equal gravitational forces at three electric field values. The dark "maximum charge" line shows the theoretical maximum possible charge for a pollen grain of particular size (Eq. (6)).

Generally, each species had a bipolar distribution of pollen charges, often roughly centered about zero. Some of the distributions were tightly centered, while others (particularly the cedars) had a wide spread of charges. Other distributions (e.g. *Juniperus* and *Pinus*) were skewed toward the positive.

The charge distributions measured in the laboratory are comparable to the charge distributions in nature based on the similarity of charge distributions for *Juniperus virginiana*. The differences seen in these two distributions are, in part, traceable to differences in settling velocity (laboratory $0.016\,m\,s^{-1}$, nature $0.024\,m\,s^{-1}$) resulting from relative absence of bulk air movement in the laboratory.

The charge distributions measured and reported here are not equilibrium charge distributions, where presumably the pollen grains would be essentially uncharged, but were measured seconds after release. Since the dispersal time is often short relative to the neutralization time, pollen grains will retain a substantial proportion of this initial charge during pollen transport. The charges reported here ($\sim$0.3 fC) are several orders of magnitude larger than those ($<$0.002 fC) expected at electrostatic equilibrium due to Boltzmann charging or those incurred from the small positive space charge present in the air (Hinds, 1982; Chalmers, 1967).

If electrostatic forces are large enough to influence pollination, the nature of the pollen charge distributions is relevant in pollination. An estimate of the charge necessary to influence pollen capture can be obtained by equating the electrostatic and gravitational forces for a spherical pollen (radius a and density ρ_p equal to water, $1000\,kg\,m^{-1}$) in a known electric field ($\mathbf{E}$) and then solving for the pollen's charge (q).

$$q = \frac{4/3\pi\rho_p \mathbf{g} a^3}{\mathbf{E}}, \tag{5}$$

where $\mathbf{g}$ is the acceleration of gravity. Electrostatic forces will be most important for small pollen grains carrying large charges. The fine lines on Fig. 3 show the charge necessary for electrostatic and gravitational forces to balance for pollen grains of increasing size for three electric field magnitudes (10, 100, and $1000\,kV\,m^{-1}$). For the majority of pollen grains examined here, electric fields from 100 to $1000\,kV\,m^{-1}$ in magnitude are necessary for electrostatic forces to equal gravity (Fig. 3). For a pollen grain of particular size, this electric field can

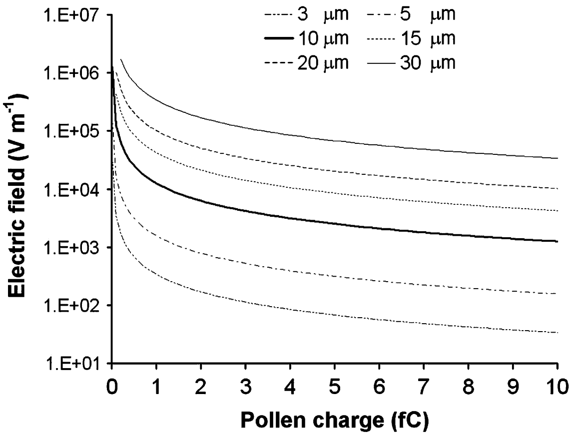

Fig. 4. The electric field ($V\,m^{-1}$) necessary to balance the electrostatic force and gravity as a function of pollen grain charge (fC), for spherical "pollen grains" ranging from 3 to 30 μm in radius.

be found directly by rearranging Eq. (5) and solving for **E** (Fig. 4). For pollen grains ($>15\,\mu m$ radius with <0.4 fC of charge), electric fields larger than $100\,kV\,m^{-1}$ are necessary for the electrostatic force to equal gravity. Relatively weak electric fields ($\sim 10\,kV\,m^{-1}$) will influence the motion of pollen grains (10 μm radius) carrying more than 1 fC of charge (Fig. 4). For very small pollen grains ($<5\,\mu m$ radius), electrostatic forces are significant relative to gravity for nearly all pollen grain charges. The consequences of the electrostatic, wind, and gravitational forces on pollen capture are explored in the companion article.

How did the pollen grains charge, why are the charge distributions bipolar, and what limits the charge? While it is possible that pollen grains may charge while suspended in the air through an active charging mechanism such as the photoelectric effect, in this experiment, most pollen grains appeared to be charged and to move at constant velocity in the presence of the electric field. This suggests that there were no appreciable changes in their charges during the measurement (several tenths of a second) and that the pollen grains were charged during the pollen-release process. These results are consistent with a long neutralization time.

The actual charging mechanism of wind-dispersed pollen during release remains unclear, though we suspect there two primary mechanisms: First, the pollen acquires a charge by triboelectric charging (a combination of frictional and contact charging) when it separates from the anther and the other pollen contained within the anther. Second, negative charge is induced on the plant by the fair weather electric field and is then transferred to the pollen (Bowker and Crenshaw, 2003).

The charge imparted to pollen by triboelectric charging is quite variable, depending on environmental conditions and the chemical and physical nature of the pollen and anther. Upon separation of two objects composed of the same material, an equal and opposite charge develops. The magnitude of the charge varies with each separation, but is usually small for similar materials. Consequently, assuming the pollen and anther are composed of similar materials, we expect a zero-centered Gaussian distribution of charges on pollen grains, with equal numbers of positively and negatively charged pollen grains (Swinbank et al., 1964; Hendricks, 1973; Wahlin, 1986). Biases in the pollen charge distributions (e.g. *Juniperus*, in the positive direction) may indicate differences in composition materials between the pollen and anthers. Whether there is any regulation (chemical composition or microenvironment within the anther) of pollen charging by plants is uncertain.

Bowker and Crenshaw (2003) have shown that negative charge induced on plants by the Earth's $100\,V\,m^{-1}$ fair weather electric field is partially transferred to pollen as demonstrated by the extension and strengthening of the negative side of the charge distributions for *Plantago lanceolata*. However the anther, which encloses the pollen prior to release, may electrically shield the pollen, thereby mitigating the possible effects. This suggests that the charge distributions presented here, derived from electrically neutral plants, may be characteristic of the pollen charge distributions in nature.

The theoretical maximum charge (q_{max}) carried by a pollen grain is determined by the electric field generated at pollen grain's surface which, in turn, is limited to the breakdown field strength of air (roughly $3\times10^6\,V\,m^{-1}$). If exceeded, ionization of the surrounding air occurs, leading to rapid neutralization. q_{max} depends on pollen size and shape. Charge is maximal for smooth spheres, a consistent shape for most wind-dispersed pollen grains. Pollen grains with spiky exines (e.g. ragweed, *Ambrosia artemisifolia*), would have smaller q_{max} because the electric field would be enhanced around the spikes. For a smooth spherical pollen grain of radius a,

$$q_{max} = 12\times10^6\pi\varepsilon_a a^2, \tag{6}$$

where ε_a is the electric permittivity of air (8.854×10^{-12} farads m^{-1}) (Bowker and Crenshaw, 2003). The pollen charges measured in this study were consistently below q_{max} averaging 1% (and maximally 35%) of the limit (Fig. 3).

How might the charge on pollen influence dispersal and capture? Since pollen grains are charged and assuming that they experience sufficient electrostatic forces to influence their motion, the bipolar nature of the charge distributions could influence the dispersal and capture of pollen. This is explored in the companion article. Positively charged pollen would tend to be attracted to plants, particularly the feathery stigmas with their correspondingly large surrounding electric fields. Positively charged pollen may even have difficulty escaping from the parent plant. Some pollen grains, such as a few *Pinus taeda* with charges up to 40 fC would experience significant electrostatic forces meters away from a tree, where the electric fields are a few hundred volts per meter.

All species examined had a considerable number of negatively charged pollen grains, which would be repelled from the negatively charged plants, presumably a maladaptive strategy. However, negatively charged pollen could ensure that some pollen escapes from the parent plant, ensuring travel to another plant and the possibility of cross-fertilization.

A negative charge does not necessary imply that pollen is not capturable. In fact, pollen with a charge of either polarity may experience enhanced capture if it can get within micrometers of the plant. A charged pollen grain will induce an opposite charge or an "image" charge on the plant's electrically conductive surface and, thus, will experience an attractive force that dramatically increases with proximity to the plant, eventually becoming larger than any other force. The relative importance of the self-induced image force on pollen capture is explored in the companion paper (Bowker and Crenshaw, 2006).

Since pollen grains with negative and positive charges are simultaneously released, it is possible that electrostatic forces could enhance conglomeration of pollen—presumably a maladaptive occurrence because it limits dispersal. The charges on pollen grains are small enough that attraction between grains is important only if they are almost touching (a few micrometers).

Clearly, the possibility that electrostatic forces are involved in pollination under natural conditions requires further study. Direct measurements in nature in combination with computer simulations of pollen capture are necessary to explore how variability in the polarity and magnitude of the pollen's charge may influence capture. Direct measurements are complicated by the fact that the electrostatic fields are quite variable (both temporally and spatially) and are easily disturbed by the presence of measurement equipment. Coupled with the small size of pollen grains, the large electrostatic pollen charges measured here present the possibility that electrostatic forces play a role in wind-pollination.

Acknowledgements

The authors thank the Duke University Department of Zoology, the National Science Foundation, Sigma Xi, and Keithley Electronics for financial and equipment support, and S.E. Law, S. Vogel, G. Ybarra, and S. Perry for advice and assistance. This work was submitted in partial fulfillment of a Ph.D. in Zoology at Duke University (G.E.B.)

References

Bechar, A., Shmulevich, I., Eisikowitch, D., Vaknin, Y., Ronen, B., Gan-Mor, S., 1999. Modeling and experiment analysis of electrostatic date pollination. Transactions of the ASAE (American Society of Agricultural Engineers) 42 (6), 1511–1516.

Bowker, G.E., Crenshaw, H.C., 2003. The influence of fair weather electricity on the charging of wind-dispersed pollen. In: Proceedings of the 12th International Conference on Atmospheric Electricity, vol. 1, Versailles, France, pp. 361–364.

Bowker, G.E., Crenshaw, H.C., 2006. Electrostatic forces in wind-pollination—Part 2: Simulations of pollen capture. Atmospheric Environment, in press, doi:10.1016/j.atmosenv.2006.10.048.

Chalmers, J.A., 1967. Atmospheric Electricity, second ed. Pergamon Press, Oxford, UK, 515pp.

Corbet, S., Beament, J., Eisikowitch, D., 1982. Are electrostatic forces involved in pollen transfer? Plant, Cell and Environment 5, 125–129.

Crane, P.R., 1986. Form and function in wind dispersed pollen. In: Blackmore, S., Ferguson, I.K. (Eds.), Pollen and Spores: Form and Function. Academic Press, London, UK, pp. 179–202.

Dai, Y., Law, S.E., 1995. Modeling the transient electric field produced by a charged pollen cloud entering a flower. IEEE/IAS Conference Record 2, 1395–1402.

Erickson, E.H., Buchmann, S.L., 1983. Electrostatics and pollination. In: Jones, C.E., Little, R.J. (Eds.), Handbook of Experimental Pollination Biology. Scientific and Academic Edition, New York, NY, pp. 173–183.

Gan-Mor, S., Schwartz, Y., Bechar, A., Eisikowitch, D., Manor, G., 1995. Relevance of electrostatic forces in natural and artificial pollination. Canadian Agricultural Engineering 37 (3), 189–194.

Gan-Mor, S., Bechar, A., Ronen, B., Eisikowitch, D., Vaknin, Y., 2003. Improving electrostatic pollination inside tree canopy via simulations and field tests. Transactions of the ASAE (American Society of Agricultural Engineers) 46 (3), 839–843.

Harrington, J., Metzger, K., 1963. Ragweed pollen density. American Journal of Botany 50 (6), 532–539.

Hendricks, C.D., 1973. Charging marcroscopic particles. In: Moore, A.D. (Ed.), Electrostatics and Its Applications. Wiley, New York, NY, USA, pp. 57–85.

Hinds, W.C., 1982. Aerosol Technology. Wiley, New York, NY, USA, 424pp.

Law, S.E., 1987. Basic phenomena active in electrostatic pesticide spraying. In: Brent, K.J., Atkin, R.K. (Eds.), Rational Pesticide Use: Proceedings of the Ninth Long Ashton Symposium. Cambridge University Press, New York, USA, pp. 81–105.

Law, S.E., 2001. Agricultural electrostatic spray application: a review of significant research and development during the 20th century. Journal of Electrostatics 51&52, 25–42.

Law, S.E., Wetzstein, H.Y., Banerjee, S., Eisikowitch, D., 2000. Electrostatic application of pollen sprays: effects of charging field intensity and aerodynamic shear upon deposition and germinability. IEEE Transactions on Industry Applications 36 (4), 998–1009.

Leach, C.M., 1976. An electrostatic theory to explain violent spore liberation by *Drechslera turcica* and other fungi. Mycologia 68, 63–86.

McWilliam, J.R., 1959. Bioelectric phenomena in relation to pollination in *Pinus*. Silvae Genetica 8, 59–61.

Niklas, K., 1985. The aerodynamics of wind pollination. Botanical Review 51 (3), 328–386.

Swinbank, P., Taggart, J., Hutchinson, S.A., 1964. The measurement of electrostatic charges on spore of *Merulius lacrymans* (Wulf.) Fr. Annals of Botany 28 (110), 239–249.

Vaknin, Y., Gan-Mor, S., Bechar, A., Ronen, B., Eisikowitch, D., 2000. The role of electrostatic forces in pollination. Plant Systematics and Evolution 222, 133–142.

Vaknin, Y., Gan-Mor, S., Bechar, A., Ronen, B., Eisikowitch, D., 2001. Are flowers morphologically adapted to take advantage of electrostatic forces in pollination? New Phytologist 152, 301–306.

van Hout, R., Katz, J., 2004. A method for measuring the density of irregularly shaped biological aerosols such as pollen. Journal of Aerosol Science 35, 1369–1384.

Vogel, S., 1994. Life in Moving Fluids. Princeton University Press, Princeton, NJ, USA, 467pp.

Wahlin, L., 1986. Atmospheric Electrostatics. Research Studies Press Ltd. (Wiley), New York, NY, 130pp.

Young, K.A., Schmitt, J., 1995. Genetic variation and phenotypic plasticity of pollen release and capture height in *Plantago lanceolata*. Functional Ecology 9, 725–733.