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The role of electrostatic forces in pollination

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Abstract. This paper reviews research on the role of electrostatic forces in pollination, both in natural and in agricultural systems. Researchers from various fields of biological studies have reported phenomena which they related to electrostatic forces. The theory of electrostatically mediated pollen transfer between insect pollinators and the flowers they visit is described, including recent studies which confirmed that the accumulated charges on airborne honey bees are sufficient for non-contact pollen detachment by electrostatic forces (i.e., electrostatic pollination). The most important morphological features in flower adaptiveness to electrostatic pollination were determined by means of two theoretical models of a flower exposed to an approaching charged cloud of pollen; they are style length and flower opening. Supplementary pollination by using electrostatic techniques is reported, and its possible importance in modern agriculture is discussed.

Key words: Electric charges, electrodeposition, electrostatic pollination, electrostatic powder coating, flower morphology.

Introduction

Electrostatics deals with the electric forces which involve electrons and ions, and with the related electric fields and potentials. In electrostatic charging, electrons remain relatively stationary and are spread on the surface of the object and concentrated on sharp edges. An object becomes electrostatically charged either by having electrons added to it, thus becoming "negatively" charged or by having them removed from it, thus becoming "positively" charged. Charges of the same sign repel each other and of opposing signs attract each other. The electrostatic force between two charged bodies (F) is described in Coulomb's equation: $F = K(q_1 q_2/r^2)$. This force is dependent on the magnitude of the charges (q_1 and q_2), the distance between the charged bodies (r), and on the dielectric coefficient (K). Electrostatic interactions play a major role in a variety of biological processes (Honig and Nicholls 1995), including the pollination of plants, both in nature and in agriculture.

Normally plants possess small negative surface charges under clear fair-day conditions, and are, therefore, surrounded by electric fields of low intensity (Maw 1962). Under unstable weather conditions, as on a cloudy or rainy day, the electric fields can change their polarity and the surface charges become positive (Warnke 1977). The magnitude of the electric fields depends in part on the chemical composition of the plant, its height and the environment (Erickson and Buchmann 1983). The distribution of the electric field around the plant varies with its shape, and the plant's electrical fields should be greatest near sharp points such as plant terminals including flowers (Dai and Law 1995).

Foraging bees usually possess electrically positive surface charges (Erickson 1975, Yes'kov and Sapozhnikov 1976, Warnke 1977, Schwartz 1991, Gan-Mor et al. 1995). When a bee flies through the air it is confronted with electrical currents and its body will be electrostatically charged with "frictional electricity" (Warnke 1977). Warnke (1977) and Thorp (1979) suggested that in the case of pollen-seeking insects, accumulation of pollen on the surfaces of the insects and pollen distribution by the insects are enhanced by the forces of attraction between the insect's positively charged body surface and the generally negatively charged plant with its pollen.

Electrostatic pollination in natural systems

Stanley and Linskens (1974), suggested that while there was no evidence to support the view that electropotential gradients between pollen carried by insects and flower stigmas were involved in pollination, it was possible that long-distance transport of pollen to the flowers was influenced by electrical relationships. Several researchers in various fields of pollination study reported the possible involvement of electrostatics in natural pollination mechanisms.

Wind pollination is associated with the aerodynamics of particle transport and capture (Whitehead 1969, Niklas 1985). It involves airflow patterns which bring conspecific pollen to stigmas of wind pollinated flowers, and is influenced by various factors, including the overall shape of the plant (Niklas and Buchmann 1985, Niklas et al. 1986), the size and shape of the inflorescence (Niklas and Buchmann 1988), and flower morphology and position on the branch (Niklas and Buchmann 1985). Electrostatic forces have also been shown to influence pollen separation or clumping, which could affect its aerodynamic properties (Erickson and Buchmann 1983). It was later speculated that as pollen grains were carried through the air they acquired a strong positive charge and were thereby electrostatically attracted to the negatively charged female flowers that were concentrated on the terminals of the plants they reached (Erickson and Buchmann 1983). Therefore, together with airflow, electrostatic attraction could form an efficient mechanism for pollen capture by anemophiles (Erickson and Buchmann 1983). However, most reports on the possible involvement of static electricity in wind pollination are speculative, since it is very hard to distinguish between aerodynamic and electrostatic forces in the direction of pollen grains towards the receptive stigma.

Buchmann and Hurley (1978) described the probable role of electrostatics in buzz pollination (vibrational pollination); they considered the attachment of the small, light and dry pollen grains of buzz-pollinated plants (e.g. senna *Cassia* sp., shooting star *Dodecatheon* sp., deadly nightshade *Solanum* sp. and many others) to the body of the pollen-collecting female bee to be largely electrostatic in nature. Pollen deposition on the stigma of these plants is also assumed to be mediated electrostatically (Buchmann 1983, Erickson and Buchmann 1983). However, the actual process of pollen transfer and adhesion to the dry stigmatic surface is as yet unknown.

Eisikowitch (1981) observed that sometimes, under sunny conditions, bumble bees leaving the flowers of oilseed rape (*Brassica napus* L.) created clouds of pollen grains which burst out of the flowers. Some of this pollen was assumed to have reached and adhered to the bumble bee's body, drawn by electrostatic attractive forces (Eisikowitch, personal information). Although wind or spontaneous selfing was considered as the main agent of pollination of oilseed rape, seed yield increased when flowers were subjected to insect pollination.

Corbet et al. (1982) experimented with a living bumble bee (*Bombus* sp.) held down to a cork on a wax block with silken threads. Oilseed rape pollen was sprinkled over the bee and some of the pollen grains that were falling near the bee rapidly drifted towards it and adhered to its body. Electrostatic forces of attraction were thought to be responsible for this phenomenon also.

In avocado (*Persea americana* Mill.), in the pistillate stage, the style is erect and receptive, while the anthers bend up towards the style and dehiscence occurs. Ish-Am and Eisikowitch (1993) found that bees collecting nectar, or nectar and pollen, visited both pistillate and staminate flowers, and, because of the flower structure, they were forced to touch both pistil and anthers. Their visits to flowers in the staminate stage were very short, and they touched the anthers for less than 1 s while hovering, or while landing instantaneously on the flower on the top most position. During these visits, their buzzing sounded lower than usual, and a small cloud of pollen sometimes surrounded them. The possible role of this phenomenon was not discussed, although it is likely that electrostatic forces assisted pollen precipitation (Ish-Am and Eisikowitch, personal information).

Schroeder (1995), stated that electrostatic forces may be associated with the movement of the avocado pollen within a given flower and in the subsequent transfer of pollen grains to other flowers by the honey bee. He conducted simple studies on the effects of electrostatic forces on pollen collection from avocado flowers, and proposed that it is most probable that the pollen adheres to insect bodies not only by the stickiness of the pollenkit but also by the action of electrostatic forces.

Endress (1997) who worked on pollination of *Dillenia* (Dilleniaceae), suggested that the pointed ends of the stylar branches with the stigmas may also be seen as an adaptation to enhance the efficacy of the electrostatic forces involved in the transfer of the dry pollen from anthers to bees and from bees to stigmas.

Theory of electrostatic pollination

The theoretical basis for electrostatic induction suggests that when a charged body is brought into the vicinity of an earthed electrode, a charge of the opposing sign is induced to flow from earth up onto the electrode, to ensure that the electrode remains at ground potential in the presence of the charged body (Law 1975) (Fig. 1A).

Based on this theory, a detailed mechanism of pollination involving electrostatics has been suggested (Hardin 1976, Corbet et al. 1982, Erickson and Buchmann 1983). As an insect carrying an electrical charge approaches a flower, charge of opposite polarity flows into the plant stem and flowers and induces an electric field between the insect and the flower. This electric field grows in strength as the gap between them narrows, and the forces of attraction temporarily created between the airborne insect and the flower initiate the detachment of pollen grains from the anther and their deposition on the body of the insect; the same forces initiate the detachment of the pollen grains from the insect's body and their deposition on various flower parts, including the stigma (Fig. 1B). These processes depend upon physical variables such as the magnitude and spacing of the charge source, the dielectric properties of the media, and the geometry of the flower (Dai and Law 1995). It also depends upon environmental variables such as atmospheric ion concentrations and mobility, and local components of the earth's ambient electric field (Law et al. 1996). Other factors such as flower size, size and hairiness of the bee, level of bee activity and relative humidity are yet to be tested.

The electrostatic force can also function as a short-term sticking factor, especially if the pollen grain is deposited on a dry stigma, enabling it to remain on the receptive surface long enough for proper germination (Woittiez and Willemse 1979).

Chaloner (1986) suggested the possibility that features of exine ornament in pollen of

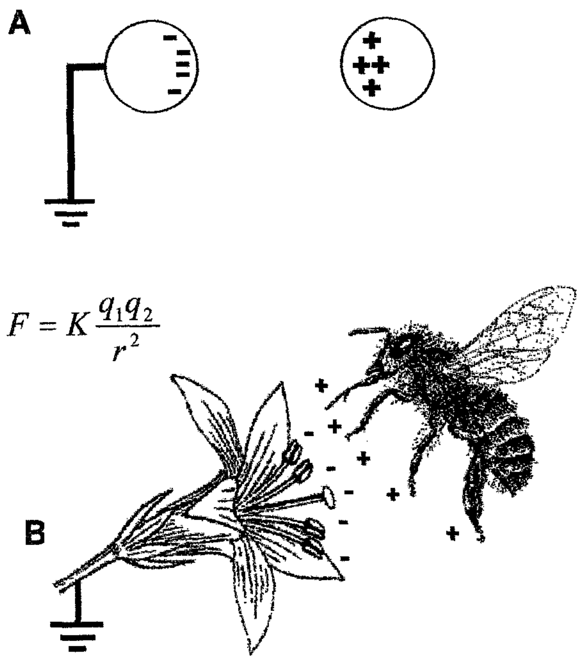

Fig. 1. A scheme of electrostatic induction. (**A**) A positively charged sphere approaches an earthed sphere and induces an opposite charge; (**B**) a positively charged bee, carrying pollen grains on its body, approaches an earthed flower and induces an opposite charge, especially on the edges of the flower. In both cases the induction causes temporary forces of attraction between the charged bodies (F). These forces are dependent on the magnitude of the charges (q_1 and q_2) and on the distance between the charged bodies (r). K the dielectric coefficient

entomophilous flowers may have some functional significance in the context of electrostatically assisted pollination. According to this, the exine ornament could function to separate the charged pollen from either the surface of the bee or the flower, to which it is attracted. Accordingly, this would delay charge sharing, and so prolong adherence of pollen to an oppositely charged surface. However, this is pure speculation and requires experimental validation.

Hardin (1976) and Corbet et al. (1982) suggested that when stigmas protrude from the flower and provide the lowest-impedance path to earth, the electric field induced by an approaching charged bee will be the strongest around the stigma. Such a field may enhance pollen transfer from the bee to the stigma because the stigma will provide the strongest attraction for the charged pollen grains on the body of the insect.

However, on the basis of calculations of relaxation time (the time it takes the charges to flow from the ground through the plant and into the flowers) conducted by Dai and Law (1995) the authors of the present paper do not agree with this statement. Experimental measurements of style and petal conductivity of yellow crooked-necked summer squash (13 mΩ (Ohm) and 100 mΩ, respectively) revealed that the relaxation times were 3 ns for the style and 25 ns for the petals (Dai and Law 1995). This difference in relaxation time is so small that it is negligible since the charged body covers the last millimeters in few tenths of a second.

Measurements of the forces involved in electrostatic pollination

Several attempts have been made to measure the forces of attraction induced by the foraging honey bee as it approaches the flower (Corbet et al. 1982, Schwartz 1991, Gan-Mor et al. 1995). In a series of experiments, Corbet et al. (1982) subjected pollen grains of oilseed rape (*Brassica napus* L.) on anthers and honey bees to electrostatic potentials of hundreds of volts as suggested by the measurement of Yes'kov and Sapozhnikov (1976). They showed that a dead honey bee connected to a potential of 750 V (Volt) could cause detachment of oilseed rape pollen from an earthed anther to the bee's body over a distance of 630 μm. Under the same potential, pollen on the bee's body jumped to an earthed stigma over a distance of 376 μm.

In the case of the honey bee, Gan-Mor et al. (1995) were able to show that the average charge on a honey bee after active flight through the air was 23.1 pC (pico Coulomb), with a maximum of 93 pC. The forces required for detaching pollen were 4×10^{-10} N (Newton), 3×10^{-10} N, and 39×10^{-10} N for avocado, *Eucalyptus camaldulensis*, and lisianthus (*Eustoma grandiflo-*

rum), respectively. Mathematical modeling showed that there were cases when the accumulated charge on the honey bee was sufficient for non-contact pollen detachment (Gan-Mor et al. 1995).

Electrostatic pollination and flower morphology

The geometries involved in electrodeposition processes of pollen grains are very complex and difficult to model mathematically. Nevertheless, two mathematical models have been developed in order to describe the complex system of a charged body (insect or pollen cloud) approaching a flower which has a protruding stigma.

A 3-D finite-element model for the analysis of the transient electric field produced by a cloud of charged pollen particles as it approaches and enters a model squash flower was constructed by Dai and Law (1995). The model was coupled with the dynamic space charge and the resulting transient boundary potential on the flower surface. Exactly modeling the charged cloud and its neighboring flower becomes difficult because of the extremely complex geometry of the flower. Therefore, several assumptions were made to simplify the physical model: (1) the cloud's space charge was represented by a uniform space charge density; (2) the charged cloud had a cylindrical shape; (3) the flower consisted of a style surrounded by five segmented cone petals. For instantaneous introduction of a charged pollen cloud, results showed that the electric field immediately above the flower stigma was approximately three times that above the petal edges. The model also showed that the electric field near a flower was affected by the geometry of the flower: as the opening angle between the petals and the style increased, the electric field near the stigma rose while the one near the petals decreased. According to this model, the greater electric fields which prevail when the flower is more open and exposed enable pollen electrodeposition onto the stigma to be maximized.

In another model, the electric field in a system comprising a charged cloud approaching an earthed date (*Phoenix dactylifera* L.) flower was calculated (Bechar 1996, Bechar et al. 1999). A 3-D finite element model was constructed, and a pollen-grain trajectory initiated from the cloud and ending on the flower was simulated. The model flower was simplified by defining its geometry as a 4 mm diameter sphere with a cylindrical pistil, 0.4 mm in diameter attached to its top. It was found that the maximal electric field was concentrated on the pistil top, and it increased as the pistil length increased. The simulation also showed that when electrostatic charging was applied, the pollen density on the pistil top was much higher (up to 225%) than without charging. Two experimental systems were set up, in order to test this model. One experiment with an artificial flower used a 19-mm-diameter steel sphere with a 1.9-mm-diameter, and 19-mm-long rod to represent the style (on a scale of 4.75:1). The artificial flower was exposed to three treatments: It was dusted with uncharged date pollen; with pollen charged by electrostatic corona at 40 kV and 11 mA (for more details see Bright et al. 1978); and with pollen charged by electrostatic corona at 80 kV and 27 mA. It was found that as the voltage and the electrostatic charge density in the pollen cloud increased, the density of pollen on the pistil increased, and the ratio of the pollen density on the pistil to that on the corolla also increased. In another experiment, almond flowers were exposed to the same pollination regimes as those above and similar differences in pollen densities on the stigma were obtained (Fig. 2; Vaknin 1999).

Electrostatic pollination in agricultural systems

Pollination of crop plants is a major factor in achieving sufficient crop set. Crop plants are pollinated by various means: most of them, such as almond (*Amygdalus communis* L.) and apple (*Malus sylvestris* Mill.) by insects (mainly honey bees, *Apis mellifera* L.) (McGregor

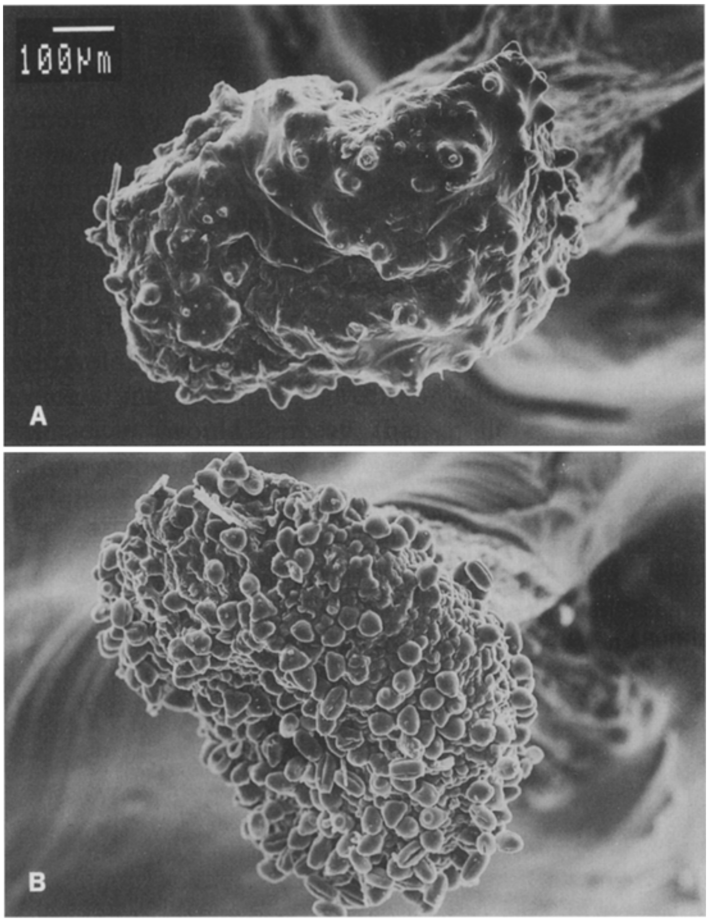

Fig. 2. Pollen grains of almond deposited on the stigmas of almond flowers. (**A**) The flower was dusted with uncharged pollen; (**B**) the flower was dusted with pollen charged at 80 kV and 27 mA

1976, Free 1993), others, such as date, olive (*Olea europea* L.) and pistachio (*Pistacia vera* L) by wind.

In recent years, insufficient pollination has been found to be one of the important causes of low yields in many field and orchard species (Shivanna and Sawhney 1997). Some species require management of pollinating agents, while others benefit from artificial means of pollination, one of which is pollen supplementation (Hopping and Jerram 1980a, b), involving three major steps: (1) pollen collection; (2) pollen storage; (3) pollen deposition on receptive stigmas.

Over the past 35 years, electrostatic forces have been employed in numerous technologies, including the transportation, collection, or separation of materials in the form of powder or small droplets (Bright et al. 1978).

Law et al. (1996), stressed the need for an efficient mechanized pollination method as a solution for pollination deficiencies in modern agriculture. They suggested using the techniques used in electrostatic deposition of powders and liquids, which were available in both industry and agriculture. These techniques generally comprise three distinct operations: (1) the generation and electrification of a charged particulate cloud or stream; (2) the conveyance of these particles to the vicinity of the desired target object; and (3) deposition of the charged particulates on the target (Law 1989).

Law and Cooper (1989) had shown that for plants growing directly in the soil, electrical conduction must be adequate to establish the appropriate distribution of charges to maintain the plant at earth potential during its interaction with an incoming electrostatic charge. Also, several experiments showed that electrical grounding of plants is adequate for the satisfactory development of electrostatic crop-spraying.

Three widely used particle charging methods are suggested for electrostatic pollen supplementation: (1) electrostatic induction of charge onto a conductive liquid dispersion medium containing suspended pollen grains (Banerjee and Law 1996); (2) triboelectrification (i.e. frictional charging) of pollen grains (Banerjee and Law 1988); and (3) ionized-field charging of the pollen grains by feeding them in an air stream past a high-voltage electrode which incorporates spikes at which corona discharges are formed by the locally intense electric field (Bright et al. 1978). Emerging pollen grains are charged by ion bombardment in the corona region, and are then transported by both aerodynamic and electrostatic forces towards the flowering plant. As the mass of negatively charged pollen grains approaches the targeted plant, they induce positive charging by creating an electron flow inside the plant down into the soil, which keep the earthed plant at zero potential, leaving all the exposed plant surfaces with a temporary positive charge. The resulting electric field forces the negatively charged pollen grains in the cloud front towards the positively charged plant parts.

In the last 20 years, several groups of researchers have tried various techniques for supplementary pollination.

Although experiments on mechanical dusting of flowering apple trees with apple pollen succeeded in increasing fruit set, when the pollen grains were electrostatically charged, pollen deposition in the trees did not increase (Legge 1975, cited by Williams and Legge 1979).

Oltman (1997) described, in a commercial paper, mechanical dusting techniques for various commercially grown plants, including almond, plum (*Prunus* spp.), apple, olive, walnut (*Juglans regia* L.), and pistachio. The machinery consisted of pollen blowers with discharge nozzles that induced an electrostatic charge on the pollen. Although no scientific experiment was carried out, it seems that farmers in California are now beginning to use this technique regularly, and some even report increases in yield (Vaknin, personal communication).

Electrostatic dusting of larch (*Larix eurolepis* Henry.) was described by Philippe and Baldet (1997). In this experiment, electrostatically charged pollen was blown to the flowering trees by an electrostatic gun and its effectiveness was compared with that of conventional pollen blowing. Results showed that electrostatic dusting deposited three times more pollen on the flowers (15 vs five pollen grains per bract) and enhanced full seed percentage (32 vs 23%) without reduction in pollen viability, although the amount of pollen used was much smaller in the electrostatic procedure.

Bechar et al. (1999) used electrostatic dusting techniques in pollination experiments on dates, and found that by applying electrostatically charged pollen they could raise fruit set by an average of 85 to 175%. SEM analysis of date flowers which were dusted electrostatically or non-electrostatically showed that the stigmas which were dusted electrostatically were totally covered with pollen grains whereas the ones which were dusted non-electrostatically received fewer pollen grains. Similar results were observed with almond flowers (Fig. 2; see also Bechar 1996).

Detailed experiments on several aspects of pollen supplementation in almond and pistachio were conducted by the authors of this paper. They included pollen collection and storage (Vaknin and Eisikowitch 2000) and pollen dilution prior to its application (Vaknin et al. 1999). They had also shown that the use of electrostatic techniques in pollination of almond and pistachio could raise yields by an average of 10 and 20% respectively (Vaknin et al. a, Vaknin et al. b, in preparation). Usually, an increase of 10% or more in fruit set is sufficient to cover all expenses of pollen supplementation and it leaves the growers with a substantial profit. However, an excess of pollen supplementation could be detrimental as it has been found in walnuts (*Juglans regia* L.; McGranahan et al. 1994). The balance between sufficient and excess pollen supplementation requires further investigation for each crop individually. These studies have just begun to reveal the potential of this technology. More research on this subject will not only lead to improved crops in agriculture, but will also add valuable information on the intricacies of electrostatics in pollination biology.

Summary

The possible involvement of electrostatic phenomena in pollination processes in nature has been a subject of discussion and speculation for the last 20 years. The theory of the electrostatic aspect of pollination describing the effect of a charged bee approaching a flower, has been widely known for many years, but only recently has its occurrence in nature been partially confirmed. It was shown that the accumulated charge on airborne honey bees is sufficient to achieve non-contact pollen detachment by electrostatic forces. Two mathematical models were constructed to describe the complex system of a charged body such as a honey bee approaching a flower. The models predicted that the electric field near a flower and its stigma should depend mostly on the geometry of the flower. The electrical field above the flower stigma was predicted to be much greater than those above the petal edges. Also, as flower opening and style length increased, the electrical field above the stigma increased and that above the petal edges decreased. Harnessing these electrostatic forces by using them as the basis of a method of pollen supplementation in agriculture could prove to be a major breakthrough in modern management of pollination processes. However, much more research is required, to elucidate the relevant phenomena, in both natural and agricultural systems.

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