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Diurnal variation in settling velocity of pollen released from maize and consequences for atmospheric dispersion and cross-pollination

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ABSTRACT

Settling velocity of maize (*Zea mays L.*) pollen plays an important role in its dispersal and, therefore, cross-pollination. Estimated probability density functions (PDFs) of settling velocity based on experimental measurements show strong variation between early morning and noon. The variation is correlated to the time-integrated vapor pressure deficit (VPDT) and reflects the drying of pollen grains. A model for the decrease in germination rate of pollen grains exposed to atmospheric conditions suggests that the decrease in settling velocity is accompanied by a decrease in pollen viability. A simple dispersion model is used to illustrate the possible consequences of changes in settling velocity and germination rate for pollen dispersal and cross-pollination of maize. Results suggest that current models of pollen dispersal that do not account for these changes overestimate cross-pollination rates.

1. Introduction

Quantifying and predicting gene flow and rates of cross-pollination in maize (*Zea mays L.*) have been the focus of much research in the past few decades. This information is important in the development of strategies for gene flow management, which are required to ensure maximum kernel set and high levels of genetic purity in hybrid seed production (Aylor, 2003; Fonseca and Westgate, 2005) and to minimize risks associated with the spread of genetically modified traits (Wolfenbarger and Phifer, 2000). A complete model of cross-pollination has to account for pollen production and release at the source, pollen entrainment into the turbulent atmosphere, pollen dispersion and deposition, pollen viability, competition with local pollen at the receptor plant, and fertilization (e.g., see Aylor et al., 2003). The entrainment, dispersion and deposition processes are governed by the characteristics of atmospheric turbulence and physical properties of pollen grains such as shape, size, density and surface characteristics (Chamecki et al., 2007). Pollen properties determine the inertia of pollen grains and, therefore, their response to turbulent motion. Typically, dispersion models neglect pollen inertia using its settling velocity in still fluid to represent the effects of the pollen properties on dispersion (Jarosz et al., 2004; Dupont et al., 2006; Chamecki et al., 2009; Viner and Arritt, 2010). In this simplified modeling approach, the value adopted for the settling velocity has a critical impact on the model results.

Experimental measurements of settling velocity of maize pollen grains range roughly between 0.20 and 0.31 $\mathrm{m\,s^{-1}}$, depending on the natural variation of pollen sizes and pollen water content (Raynor et al., 1972; Di-Giovanni et al., 1995; Aylor, 2002; Loubet et al., 2007). Pollen water content has a profound effect on pollen size, shape and density, and consequently on its settling velocity. Aylor (2002) found a reduction of 34% in settling velocity of dry pollen compared to fresh pollen. This large variation can have dramatic consequences for dispersion. Therefore, the initial water content when pollen is entrained by the turbulent wind, as well as the rate of dehydration during exposure to atmospheric conditions, become important in assessing transport distances.

Maize pollen release is controlled by biological and environmental factors and three key steps take place before dispersion. The first step in the process is anthesis, which consists of the formation of a pore on the tip of the anther due to anther dehydration (Keijzer et al., 1996). The second step is the mechanical vibration of the anther caused by the wind, which drives pollen grains out of the anther (Aylor et al., 2003). Once pollen is shed from the anther, it may be immediately entrained or it may temporary sit on a tassel or leaf until a strong turbulent motion entrains it. In the pollen dispersion literature, the term “pollen release” is usually employed without making any distinction between these three processes. However, the distinction between the three processes may be critical since the water content and settling velocity may vary significantly from one step to the next.

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Gene flow and cross-pollination in maize require transport of viable pollen. Fresh pollen grains are generally considered viable and the probability that a grain maintains viability decreases as it dries. Consequently, the water content of "fresh" pollen has been studied by several authors. The water content is typically quantified as the difference in weight between a fresh pollen sample and an oven dried sample, expressed as a percentage of sample fresh weight. Estimates of fresh water content vary depending on the methods used to collect and dry pollen. Barnabás (1985) reports a variation between 40 and 50% for pollen collected "after anthesis". Kerhoas et al. (1985) obtained 57–58% for pollen "regularly collected in the morning at anthesis". To ensure that freshly produced pollen was collected, Aylor (2002) removed the pollen remaining in the anthers at the end of the previous day and obtained a range of 40–56%. Fonseca and Westgate (2005) followed Aylor's procedure and obtained a tighter fresh water content range of 54.2–60.2%. It is important to note that all measurements of water content discussed are based on the average weight of millions/billions of pollen grains (using this approach, variability within each sample can not be quantified).

In a recent paper, Loubet et al. (2007) proposed a new technique to measure settling velocity of large particles such as maize pollen grains. As an example of application, the authors presented measurements of the distribution of settling velocity for four samples of maize pollen freshly collected at different times/days. A very strong bi-modal distribution was found, suggesting that two populations with markedly different water content were present.

In this paper we present experimental estimates of the probability density function (PDF) of settling velocity of maize pollen and its change between early morning and noon. In addition, we use simple models of pollen viability and dispersion to investigate the consequences of these changes for atmospheric transport and cross-pollination.

2. Materials and methods

2.1. Pollen source and field sampling

Experimental plots of maize varieties Bodacious (RM GCP) and Pioneer (34M78) were established at the Russell E. Larson Research and Education Center in Rock Springs, PA during the summer of 2010. The Bodacious maize plot (20 m × 80 m) and Pioneer maize plot (30 m × 65 m) were planted in rows of 0.76 m at population densities of 65, 000 plants ha^{-1} on days of the year 140 and 150, respectively. The plots were maintained using standard production practices for the region[1] and irrigated during dry weather conditions. Bodacious and Pioneer maize plants were approximately 1.5 and 2.5 m high, respectively at the time of pollen shed and sampling.

Data reported here were sampled on three days (07/22 for Bodacious and 08/02 and 08/06 for Pioneer). On each day, several experimental runs were conducted to capture the time evolution of the pollen properties. Each run consisted of sampling pollen for size characterization and performing settling velocity measurements, as described below. In addition, an experimental run using oven dry pollen grains (i.e. with zero water content) was performed for comparison.

2.2. Pollen characterization

Pollen grain size distribution was determined in the laboratory using a microscope at 100 × magnification. Tassel branches from multiple runs were tapped over microscope slides coated with petroleum jelly, and digital images were recorded for multiple fields of view. These digital images were analyzed using IMAGE J software[2] with a procedure similar to Loubet et al. (2007). Outliers were visually removed if they were not single or whole grain values. Both the major and minor principal diameters for each pollen grain were recorded. The number of sampled pollen grains for Bodacious and Pioneer maize was 156 and 218, repectively.

2.3. Measurements of settling velocity

Pollen grain settling velocity was determined using the method described by Loubet et al. (2007). A portable settling velocity chamber was positioned immediately adjacent to the maize plots. Fresh pollen samples were collected at each sample time point by randomly excising pollen producing tassel branches. Tassel branches were handled carefully to limit pollen loss from wind and excess shaking. Fresh pollen was released from branches within 1–2 min after excision by tapping them over the chamber drop tube at the top of the 1 m high tower. Pollen grains then passed through a small opening into the narrow focal plane of the camera, and grain trajectories were captured using a digital camera with a maximum continuous shooting speed of 4.5 frames per second. A total of six branches were collected for each run which provided a minimum of 800 pollen settling velocity measurements per run. The shutter speed of the camera was set to a fixed value (1/100 s), and trajectory distances were converted to velocity using this value (images were analyzed with IMAGE J). The entire procedure was calibrated using glass spheres with results equivalent to those obtained by Loubet et al. (2007).

The objective was to sample the pollen cloud that would be entrained if a strong turbulence gust had passed by at the moment of the experiment. Therefore, the samples do not represent pollen conditions at anthesis or necessarily that of freshly shed pollen. Pollen grains may remain inside anthers for long periods after anthesis and may sit on tassels for a few hours before being entrained by turbulence. Visual inspection during the experiments suggests that there were not large quantities of pollen attached to the tassels used, but no action was taken to eliminate these if they existed. Consequently, the procedure adopted here is appropriate for characterizing the population of pollen grains that are available for dispersal at each time of the day.

2.4. Meteorological data

During the field experiment, a temperature and relative humidity probe (HMP45C, Vaisala, Woburn, MA, USA) was deployed at tassel height inside both maize fields. Data were collected continuously at a frequency of 0.1 Hz and averaged over 10-min periods with a CR1000 datalogger (Campbell Scientific, Logan, UT, USA). For each 10-min period, average temperature (T) and relative humidity (RH) were used to determine the average vapor pressure deficit (VPD). Mean wind speed was measured at a height of 10 m above an oat field located next to the corn fields (no wind measurements were made above the corn field) using a light cup anemometer (014A, Met One, Grants Pass, OR, USA).

2.5. Pollen germination rate model

Aylor (2004) found a strong effect of environmental conditions on germination rate of pollen grains, and developed a model to predict the decrease in germination rate based on environmental conditions and pollen water content. Measurements of pollen

[1] PSU Agronomy Guide – http://agguide.agronomy.psu.edu/.

[2] National Institutes of Health, USA – http://rsb.info.nih.gov/ij/.