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Numerical modeling of meteorological and topographical effects on pollen shed, dispersion, and viability

Brian Viner
Iowa State University

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For open-pollinated species, the success of a pollen grain pollinating a receptive plant is a function of when it is shed, its dispersion in the atmosphere, and the chance of germination upon deposition. Most studies of pollen dispersion have focused on a source and surrounding fields in relatively flat terrain, but dispersion to distances over 20 km has been reported in regions of complex terrain. For this reason, a more detailed examination of atmospheric dispersion over long distances and the components of dispersion – shed, transport, and successful pollination – was undertaken. This dissertation uses numerical models to predict these components in order to improve simulations of dispersion over long distances. Chapter One provides an overview of work previously done in pollen dispersion. Chapter Two describes a model that uses empirical relationships between pollen release and meteorological variables to predict diurnal variations in maize pollen shed. The model captured the general pattern of shed and predicted the time of peak shed on most days. In Chapter Three, a meteorological model was combined with a Lagrangian dispersion model to predict bentgrass pollen dispersion over complex terrain. The models predicted pollen deposition in locations where outcross was previously reported over 20 km from the source. However, pollen was not predicted to be deposited on upwind slopes of mountains or in valleys more than a few kilometers from the source. Chapter Four examines how thermally-generated updrafts resulting from surface sensible heat flux and mechanically-generated updrafts associated with complex topography affect dispersion. We determined the gaps in pollen dispersion found in Chapter Three resulted from additional lift created by convergence on the windward side of mountains and thermally-induced flow that traveled up valley walls and mountain slopes. Chapter Five examines how maize pollen viability is affected when pollen grains are lifted higher in the atmospheric boundary layer. Viability was predicted to be as much as 30% higher when the atmospheric conditions along a pollen grain’s trajectory are used compared to estimates of viability using conditions at the Earth’s surface. Chapter Six summarizes the dissertation. The results of this work are expected to improve future models of pollen dispersion, leading to more accurate predictions of outcrossing. Also, the methods described here are not limited to maize or bentgrass pollen, but can be modified for applications to other biological particles that rely on atmospheric conditions for dispersion.
CHAPTER 1. GENERAL INTRODUCTION

1.1 Introduction

The creation of genetically-modified plants has created concern that the foreign genes they contain will spread to conventional or wild relatives, leading to unintended economic or social consequences. In anemophilous plants such as maize, the spread of genetic material typically occurs through the dispersion of pollen in the atmosphere. Whether a pollen grain successfully pollinates a receptive plant is a function of when it is shed, the atmospheric conditions that determine its dispersion, and the chance that it contacts a receptive surface while remaining viable when it is deposited. Each of these steps has a distinct relationship with the atmosphere. Pollen shed, though it is a biological function, has been linked to atmospheric moisture (Jarosz et al., 2004) and solar radiation (van Hout et al., 2008). Dispersion is largely determined by wind. Pollen is typically transported in the direction of the horizontal wind while vertical winds from thermally- or mechanically-generated turbulence is important for lifting particles. Pollen viability, the likelihood that a pollen grain will germinate when it lands on a receptive flower, is related to the water content of the pollen grain and is modified by the atmospheric demand for moisture. When the atmosphere is warmer and drier, pollen grains lose water to the air more quickly than when the atmosphere is cooler and more moist, and thus lose viability more quickly.

Quantifying the potential for the unintended spread of genetic material has been the motivation of many pollen dispersion studies both in the field (Raynor et al., 1972; Luna et al., 2001; Jarosz et al., 2003; Ma et al., 2004; van Hout et al., 2008) and through the use of numerical models (Jarosz et al., 2004; Dupont et al., 2006; Arritt et al., 2007; Chamecki et al., 2009). These studies have noted similar behaviors of maize pollen dispersion and cross-pollination:

- Pollen shed typically begins after sunrise and continues through the afternoon (Jarosz et al., 2004; van Hout et al., 2008). Pollen shed does not continue overnight, though some pollen remains in the atmosphere (Jarosz et al., 2004)
- Pollen dispersion generally occurs in the direction of the mean wind, though some pollen is seen to be transported against the wind and may be the result of turbulent motions (Arritt et al., 2007).
The amount of pollen deposition decreases rapidly with distance from the source (Raynor et al., 1972) with a dispersive tail that can extend many kilometers (Aylor et al., 2003). Correspondingly, the occurrence of outcross also decreases with distance from the source (Luna et al., 2001). While differences in the shedding behavior may exist in other open-pollinated plants, the characteristics of pollen dispersion are generally consistent.

Maize produces one of the largest pollen grains (~90 µm) which has a terminal velocity of ~20-30 cm s\(^{-1}\) (Aylor, 2002). As a result, studies have found that most pollen grains are deposited within a few tens of meters from the source (Raynor 1972; Emberlin et al., 1999) and measurable outcross in maize has been limited to a few hundred meters (Luna et al., 2001). Consequently, isolation distances as small as a few tens of meters have been suggested for maize (Gustafson et al., 2006; Kuparinen, 2007). Since most maize pollen is deposited near its source, studies of dispersion and outcross in maize have generally been limited to a source and its surrounding fields.

Studies of pollen dispersion need to be extended to a larger scale for plants that produce smaller pollen grains. Watrud et al. (2004) reported outcross in bentgrass occurring on the order of kilometers. Bentgrass pollen is smaller than maize pollen (~20 µm) and has a smaller terminal velocity (~2 cm s\(^{-1}\)). Smaller particles may travel greater distances and potentially pollinate receptive flowers farther away because they can be more easily lifted by turbulent eddies and fall more slowly. For this reason, a greater understanding of atmospheric dispersion over long distances and the components contributing to the outcome of a pollen grain – shed, transport, and successful pollination – is necessary.

The biological signals that result in pollen shed have not been identified. Some simulations of maize pollen dispersion have assumed a constant rate of pollen shed (Dupont et al., 2006; Arritt et al., 2007) but this contrasts with observations of pollen shed that show a diurnal variation that peaks in mid-morning to early afternoon (Ogden et al., 1969; Jarosz et al., 2003). Another method is to diagnose the strength of the pollen source based on measurements of airborne concentration (Aylor and Flesch, 2001; Jarosz et al., 2004). While effective, this method requires measurements of pollen concentration that are impractical to make often and lacks the ability to predict a shed event. Although the biological signals are
not known, it has been suggested that shed could be modeled as a function of local meteorological conditions including vapor pressure (Jarosz et al., 2005) or solar radiation (van Hout et al., 2008). A predictive model for pollen shed that makes use of widely available meteorological data would allow for realistic variations in pollen shed rather than assuming a specific pattern of shed.

The long-distance cross-pollination of bentgrass reported by Watrud et al. (2004) also indicates the need for accurate pollen dispersion modeling over complex terrain. While pollen dispersion models have been applied to regions of flat terrain (Arritt et al., 2007), they have not been tested in complex terrain which may have local topographically-induced circulations. Gaseous dispersion has been studied extensively in complex terrain with both thermally- and mechanically-induced turbulence identified as promoting dispersion. For example, Turnipseed et al. (2009) identified thermally-driven upslope winds created by mountain-valley flow as a primary influence on ozone dispersion while Kim and Stockwell (2008) concluded that local topography was a stronger lifting force than convection for the dispersion of nitric acid. Successes in using Lagrangian dispersion models to simulate gaseous dispersion (Carvalho et al., 2002; Anfossi et al., 2010) are encouraging because simulating pollen dispersion relies on the same principles, though additional terms are required for inertial drift and settling velocity (Csanady, 1963).

Successful pollination is dependent on pollen grain viability. In maize, viability decreases as the pollen grain moisture content decreases (Fonseca and Westgate, 2005; Aylor, 2003). Once pollen is released from the anther, the rate of moisture loss from the pollen grain to the atmosphere is determined by the vapor pressure deficit (VPD) of the atmosphere (Aylor, 2003). When the atmosphere is warm and dry, VPD is large so that pollen grains rapidly lose moisture and viability. Conversely, cool and humid conditions promote moisture retention and increased viability. Estimates of pollen viability are often based on surface conditions (e.g., Luna et al., 2001) but pollen has been observed hundreds of meters high in the atmospheric boundary layer where meteorological conditions can differ substantially from the surface (Brunet et al., 2004; Boehm et al., 2008). Pollen lifted to these heights may remain viable longer since moisture will not be lost as quickly.
1.2 Thesis Organization

This dissertation consists of four manuscripts. Chapter Two describes the creation of a model to predict pollen shed in maize. The model is based on relationships between pollen shed and meteorological variables that were derived in laboratory and field experiments. Chapter Three reports the results of combining a meteorological model with a Lagrangian dispersion model to predict bentgrass pollen dispersion. Predictions of dispersion are compared to outcross events reported by Watrud et al. (2004) and a modeling analysis by Van de Water et al. (2007). Chapter Four examines how pollen dispersion is affected by two lifting processes: thermally-generated lifting resulting from surface sensible heat flux and mechanically-generated lifting resulting from complex topography. Chapter Five discusses how the rate of viability loss is affected in maize pollen grains when they are lifted higher in the atmospheric boundary layer. Pollen viability is calculated based on the changing conditions pollen experiences during its flight and based on the surface measurements at the pollen source. Chapter Six gives a summary of the dissertation.

1.3 References


CHAPTER 2. A MODEL TO PREDICT DIURNAL POLLEN SHED IN MAIZE

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Brian J. Viner, Mark E. Westgate, and Raymond W. Arritt

Abstract
We have developed a mathematical model to predict the diurnal pattern of maize (Zea mays L.) pollen shed based on local meteorological conditions. Our goal is to improve simulations of maize pollen dispersion that have typically released pollen at a constant rate in contrast with measurements of pollen shed that show diurnal variation in the rate of shed. Measurements coupling pollen shed and local meteorological variables were made during controlled experiments and a 2004 field experiment to examine the influence of meteorological conditions on pollen shed. From these data, a model was developed to predict the diurnal pattern of pollen shed as a function of vapor pressure deficit, solar radiation, temperature and the amount of pollen remaining to be shed. The model was validated by predicting the rate of pollen shed, normalized by the daily total of pollen shed, that occurred hourly for days during a 2003 field study (RMSE = 0.061 hr⁻¹) and results from van Hout et al. (2008; RMSE = 0.089 hr⁻¹). The model captured the general trend of pollen shed and predicted the time of peak shed within an hour of the measured peak on most days. The model, however, tended to underpredict the magnitude of the normalized peak rate of shed and did not account for secondary peaks in pollen shed that were occasionally observed. Thus, future model refinements will depend on identifying additional biological or environmental factors that impact the instantaneous rate of pollen shed.

2.1 Introduction
With the development of genetically modified maize, concerns regarding cross-pollination between genetically modified varieties and wild or conventional relatives have prompted the development of dispersion models to predict pollen movement and the likelihood of cross-pollination. Previous simulations of maize pollen dispersion have usually assumed a
constant rate of pollen shed (e.g., Aylor and Flesch, 2001; Dupont et al., 2006; Arritt et al., 2007), but observations of pollen shed show a diurnal variation with a peak in mid-morning to early afternoon (Ogden et al., 1969; Jarosz et al., 2003). From a quantitative perspective, the rate of pollen shed within a source field is determined by the number of anthers beginning to shed pollen and the rate of pollen release from those actively shedding anthers. However, the mechanisms controlling when anthers begin to shed pollen and those controlling pollen release are not well understood. Improved understanding of these mechanisms and how they interact should lead to more accurate evaluations of dispersion and cross-pollination.

For wind-pollinated crops such as maize, the biophysical factors affecting pollen shed and the weather conditions affecting pollen dispersal interact to determine the amount of pollen that reaches a receptor plant. Processes on three temporal scales determine the instantaneous rate of pollen shed at a specific time:

• Seasonal population dynamics that determine the number of plants that have reached the flowering stage.

• Daily flowering dynamics that determine how many anthers are recruited for pollen shed on individual days.

• Hourly dynamics of pollen shed from recruited anthers on each day.

The first process has been documented (Westgate et al., 2003) and can be used to estimate the amount of pollen that will be shed on any given day. The factors that govern the recruitment of anthers, both on individual plants and across a field, and the rate of pollen shed from recruited anthers have not been examined in depth. We define anther recruitment as the process of anthers beginning to shed pollen; i.e., when an anther begins to release pollen, we consider it recruited. Before pollen can be shed, anthers must be exserted from the florets, at which time they are exposed to the atmosphere and begin to dehydrate. Once an anther has lost sufficient moisture, the structure opens at its tip, releasing the mature pollen grains within (Keijzer et al., 1996). Previous studies have suggested that the mechanism for anther recruitment could be modeled as a function of vapor pressure (Jarosz et al., 2005) or solar radiation (van Hout et al., 2008).

We conducted field studies and experiments in controlled environments to study how meteorological factors affect the recruitment of anthers and the rate of pollen shed. Using
data collected from a 2004 field study and the controlled experiments, we developed an empirical model that simulates the diurnal pattern of pollen shed by predicting the fraction of the total daily amount of pollen shed during a time interval. A 2003 field experiment and published results from van Hout et al. (2008) were used to validate the model. Our goal is to predict the general trend of pollen shed under a variety of weather conditions. Of particular importance is predicting the time when peak shed occurs since the pollen released within one hour of this peak typically accounts for most of the pollen dispersed during a day.

2.2 Materials and Methods

2.2.1 Data collection

2.2.1.1 Field studies

Diurnal pollen shed was monitored in commercial maize fields at three Iowa State University research farms located approximately 12 km west of Ames, IA (42.02°N, 93.77°W) in 2003 and 2004. At each location, two fields in the midst of pollen shed were selected for monitoring (Table 1). The distance between sampling fields was at least 100 m to ensure the pollen collectors monitored local pollen shed density. Three passive pollen collectors designed according to Fonseca et al. (2002) were placed within each field approximately 10 m apart and 1 m above the ground to capture pollen passing through a plane at normal ear height. Pollen collectors were placed at each location at 0730 Local Daylight Time (LDT) and replaced approximately each hour in the morning and at two-hour intervals in the afternoon until pollen shed was near completion around 1600 LDT. Collectors were covered prior to being removed from the field to prevent contamination from other pollen sources during transport.

The number of grains collected on each pollen collector was quantified by fluorescence microscopy and image analysis (Fonseca et al., 2002). The amount of pollen collected during each sampling period was normalized by the total amount of pollen collected each day. This approach eliminated developmental and genetic differences in daily pollen shed and also corrected for weather dependent variation in total daily pollen shed. Further, this allows a generic model to be developed that could be applied to a range of weather conditions and maize varieties.
Fifteen-minute averages of relative humidity, temperature and wind speed were collected using weather stations (Campbell Scientific Inc., CR-10) placed within 50 m of the pollen collection sites. The weather stations were placed in maize at least 300 m away from obstructions and at a height of 2 m which was approximately tassel height. All five days in 2003 had similar conditions, with a temperature range between 15.1°C and 28.7°C, an average temperature of 24.0°C and winds generally from the southwest between 1 and 2.5 m s⁻¹. The temperature in 2004 ranged between 9.1°C and 26.3°C, with an average temperature of 18.6°C and winds generally from the north between 1 and 4 m s⁻¹. Solar radiation measurements were taken as hourly averages from the Iowa Environmental Mesonet station for Ames, IA located about 1 km from the field at a height of 2 m, which is sufficiently nearby to provide estimates of the hourly mean solar radiation incident at the testing site (Su et al. 2008).

2.2.1.2 Controlled Environment Experiments

Experiments conducted in controlled environments were used to examine how the rate of anther recruitment was affected by varying the meteorological conditions around the tassel. We examined how varying temperature, vapor pressure deficit (VPD) and incident radiation affected the length of time between the recruitment of the first and last exserted anther to shed pollen. Conditions tested were chosen based on the measurements taken between sunrise and 1200 LDT in 2004 which showed a temperature range from 9°C to 24°C, a VPD range of 0.2 to 11.6 mbar and a range of solar radiation from 0 to 773 W m⁻². We tested conditions comprising a combination of VPD of 0.085, 4.26, and 9.37 mbar and temperature of 15°C; or VPD of 1.17, 5.84, and 10.51 mbar and temperature of 20°C. These VPD values correspond to relative humidity values of 95%, 75%, and 55% at the specified temperature. Incident radiation was varied using values of 0, 122, 383 and 530 W m⁻² at a constant temperature of 20°C. Tests examining variations of temperature were conducted at a constant light intensity of 530 W m⁻².

Maize plants were grown in a greenhouse until tassels began to exsert anthers. Once pollen shed began, individual tassel branches were collected for study. Branches were cut around sunset and placed with their cut ends in water into sealed desiccators maintained at
near-saturated conditions like those that persist overnight in the field and stored in dark incubator chambers (Percival Scientific Inc., I-36LLVL) which maintained a constant temperature. Previously exerted anthers were removed to ensure only newly exerted anthers were observed during testing conditions. Prior to sunrise (chamber lights on), the branch was placed into a new desiccator preconditioned to the desired environmental conditions of light intensity, temperature and VPD (Figure 2.1). Holes were cut in the closed-cell foam between the desiccator body and lid to allow manual observation for pollen shed without altering the conditions within the desiccator. Testing for pollen shed was done approximately each hour by placing double-sided sticky tape on a rod and touching the rod to the end of newly exerted anthers. The tape was then visually examined for pollen to determine whether an individual anther was shedding pollen. When an anther was observed to be shedding pollen, it was manually removed from the branch.

The VPD of the desiccator was varied by placing salt solutions of known osmotic pressure in the desiccator (Table 2) and mixing the atmosphere with a battery powered fan. Data loggers (Onset Computer Corp., H032 Hobo Pro) continuously monitored temperature and VPD to confirm that atmospheric conditions in the desiccator remained unaffected during the testing process. Light intensity was varied from 0 W m$^{-2}$ to 530 W m$^{-2}$ using dual fiber optic light sources (Dolan-Jenner Industries, Fiber-Lite Series 180) directed at tassel branches. Incident light intensity was measured using a spectrometer (Decagon Devices, Accupar LP-80) placed inside the desiccator next to the tassel branch in the direction of the light source.

2.2.1.3 Other Data Sources

Published results from van Hout et al (2008) were used in addition to our own field data for model validation. Their study measured the concentration of pollen grains captured by rotorod samplers at four heights between $z/h = 1$ and $z/h = 2$, where $h$ is the height of the canopy, at 1 hour intervals between 0600 LDT and 1200 LDT and at 2 hour intervals between 1200 LDT and 1800 LDT. Meteorological variables were measured at the center of their sampling field. Measurements of wind direction, wind speed and solar radiation were taken at $z/h = 3$ and temperature and relative humidity were measured at $z/h = 2$. 
The pattern of pollen emission in van Hout et al. (2008) consisted of an increase in pollen shed after sunrise with a peak approximately 2 to 3 hours after sunrise and a general decline in shed through the afternoon. On four of the six days, a second peak of pollen shed was measured approximately 2 hours after the initial peak. No obvious relationships between pollen emission and either solar radiation or temperature were observed. For days that exhibited two peaks of pollen shed, the authors noted that the decrease in pollen shed between the peaks may be due to a corresponding decrease in wind speed during that period.

The authors point to two primary factors determining pollen shed: the diurnal solar cycle and a sufficiently dry atmosphere to allow for anther dehiscence. Minimal pollen was collected overnight or when the atmosphere was near saturation. When the atmosphere remained sufficiently dry that pollen shed could be expected to occur, pollen was not collected until after sunrise, suggesting that a light signal was necessary for anther maturation.

2.2.2 Statistical Tools

The statistical package ‘R’ was used to fit mathematical models to the data collected for this study. ‘R’ calculates statistical measures, including values of adjusted $R^2$ and significance values, to evaluate the ability of the models chosen to represent the processes related to pollen shed.

To evaluate model accuracy comparing predicted values to measured data, we used root mean square error (RMSE) as:

$$RMSE = \left[ \frac{1}{n} \sum_{i=1}^{n} (P_i - O_i)^2 \right]^{1/2},$$

where $P_i$ and $O_i$ are the predicted and observed rates of pollen shed and $n$ is the number of observations during each field trial.

2.2.3 Model development

Our goal was to develop a model consistent with the biology of pollen shed that was general enough to be applied to a wide range of conditions. We modeled the maize field as a
single entity, rather than simulating the behavior of individual plants. Also, we predict pollen shed from the entire field based on the average conditions measured by our sensors. This approach ignores potential differences in pollen shed between the borders of the field and its interior, but allows for a model consisting of few equations to simulate the average pollen shed over the field.

### 2.2.3.1 Field Study Relationships

In both 2003 and 2004, pollen shed typically began about an hour after sunrise followed by a rapid increase and gradual decline through the remainder of the day (Figure 2.2). In 2003, the peak rate of shed occurred between 0900 and 1000 LDT and was generally greater in magnitude than in 2004 when the peak rate of shed occurred shortly after 1000 LDT. We hypothesize the later occurrence of peak shed in 2004 was due to lower average temperature during anthesis, causing anther recruitment to occur more slowly. Slower recruitment also may have caused the rate of shed to decline more slowly in 2004. The 2004 field study was chosen as the developmental data set because it contained a wider range of conditions as described previously and should provide for more robust relationships in the model.

We used VPD rather than relative humidity to measure the water content of the air around exserted anthers because VPD is more directly related to atmospheric water demand and therefore to the rate of water loss from anthers. VPD is the difference between saturation vapor pressure ($e_s$, mbar) and ambient vapor pressure ($e$, mbar); $e_s$ is solely dependent on the temperature ($T$, °C) following Bolton (1980) and $e$ varies with $e_s$ and relative humidity (RH):

$$e_s = 6.11 \exp \left( \frac{17.67T}{243.50 + T} \right)$$  \hspace{1cm} (2)$$

$$e = e_s \cdot RH$$  \hspace{1cm} (3)$$

$$VPD = e_s - e$$  \hspace{1cm} (4)$$

There was a consistent relationship between the observed rate of pollen shed and the amount of pollen remaining to be shed each day (Figure 2.3) using observations at and after the peak pollen shed when all anthers were assumed to be recruited for pollen shed. The
equation fit to the data relating the rate of pollen shed (RoS, hr\(^{-1}\)) to the amount of pollen remaining (R, dimensionless) is given by:

\[
RoS = 0.2335R^{0.65}
\]  

(adjusted \(R^2 = 0.70, p < 0.01\)). Since the measurements of pollen shed were normalized to the total amount of pollen collected, RoS is defined as the fraction of the total daily amount of pollen shed per hour. Correspondingly, \(R\) varies from 1 (no pollen has been shed) to 0 (all of the day’s pollen has been shed). Both can be converted to an actual number of pollen grains by multiplying by the measured or estimated total amount of pollen to be shed on each day. These estimates are available in studies such as Fonseca et al. (2004) which measured the total amount of pollen shed on each day during flowering.

The observed rate of pollen shed during each sampling period was also compared to the prevailing meteorological conditions during the period. Very little pollen was shed when the VPD was less than 0.350 mbar or when the temperature was below 15°C at tassel height (Figure 2.4). On days when these conditions persisted, the peak rate of shed was delayed, suggesting that cool, wet conditions slow the recruitment of anthers.

Pollen shed exhibited a parabolic relationship with VPD, temperature and solar radiation. However, it is not clear whether these relationships actually exist or merely coincide with the diurnal pattern of pollen shed. Field measurements indicated pollen shed builds in the morning to a peak and decays through the afternoon. Typical conditions on a clear day follow a diurnal pattern with VPD, temperature and solar radiation also increasing through the early afternoon and decreasing after. We believe that the apparent relationships are indirect and reflect the similar diurnal trends of the atmospheric variables and pollen shed rather than the direct effect of each variable on the amount of pollen being shed.

An unexpected result was the absence of a relationship between wind speed and pollen shed in our observations. We expected to find such a relationship on intuitive grounds, as had been previously suggested (Ogden et al., 1969). However, we measured the same range of pollen shed rates at 1 m s\(^{-1}\), the lowest reliable measurement of wind speed by our anemometer, and 5 m s\(^{-1}\), indicating that only a light wind is necessary for pollen shed and stronger winds may not necessarily cause more pollen to be shed. It appears that there may be a drop in RoS at wind speeds greater than 3 m s\(^{-1}\), but we attribute this feature to high
wind speeds generally occurring only in the afternoon when RoS was decreasing and daily pollen shed was coming to an end. Even in the absence of mean wind, sufficient wind speeds to dislodge pollen could be provided by the turbulent motions induced by free convective turbulence in the atmospheric boundary layer (Aylor et al. 2003, Arritt et al. 2007).

2.2.3.2 Controlled Experiment Relationships

Earlier studies examined both the presence of light and the drying of the atmosphere as necessary for pollen shed (Jarosz et al. 2004; van Hout et al. 2008). To test whether these conditions were necessary for shed, we monitored pollen shed from anthers maintained in a saturated atmosphere and in the dark. Tassel branches maintained at $VPD = 0$, or saturation, exserted anthers but they were not recruited for pollen shed. Branches placed in darkness also exserted anthers and were recruited for pollen shed after many hours. Although every effort was taken to maintain the samples in darkness, it is possible that exposure to a small amount of light during sampling periods may have been sufficient to initiate recruitment.

The length of time needed for full anther recruitment, defined as the time between the first and last anther to begin shedding pollen on a given day, was found to depend on the atmospheric conditions (Figure 2.5). Anthers placed in drier environments with high VPD reached full recruitment more rapidly than those placed in more humid environments. The time required for full recruitment also decreased rapidly with increasing light intensity. The largest change occurred between 0 and 125 W m$^{-2}$ while further increasing the light intensity decreased the time required for recruitment but did not have as strong an effect. Increasing temperature also decreased the amount of time required for recruitment. A first-order polynomial equation was fit to the data:

$$LoR = -4.38 \times 10^{-3} S - 9.46 \times 10^{-1} T - 1.70 \times 10^{-1} VPD + 23.97$$

(adjusted $R^2 = 0.91$, all coefficients are significant at $p < 0.01$) where $LoR$ is the length of time for all anthers to be recruited (h), $S$ is the flux of incident radiation (W m$^{-2}$) and $T$ is temperature ($^\circ C$). A lower limit of 0.01 h was placed on $LoR$ to prevent division by zero within the model or meaningless negative values. A second order term in $S$ was initially considered in the model since the relationship between solar radiation and $LoR$ is not perfectly linear, but it was not considered significant and lowered the adjusted $R^2$ of the
model to 0.84. The influence of temperature on LoR in this model is greater than it might appear since temperature also affects VPD.

2.2.3.3 The Pollen Shed Model

To determine the rate of pollen shed at any time during a day, the model combines a recruitment function based on meteorological conditions and a depletion function based on empirical observations of the rate of pollen shed (Figure 2.6). The recruitment of anthers and the rate of pollen shed from actively shedding anthers are predicted using the relationships developed in the previous sections, assuming anther recruitment across the field follows a normal distribution. This model also assumes that the processes that initiate pollen shed begin at sunrise, which was between 0600 to 0615 LDT for the days examined in the field studies.

The relationship for determining the start of anther recruitment after sunrise was found by calculating the accumulated vapor pressure deficit (\(VPDT\), mbar·hr) between sunrise and the estimated start of anther recruitment on each day in 2004 as

\[
VPDT = \sum_{i=0}^{n} VPD_i dt
\]

where \(i = 0\) is the first time increment starting at sunrise, \(n\) is the time increment when anther recruitment begins, and \(dt\) is the time between increments \(i\) and \(i-1\). The estimated start of anther recruitment was determined by initiating the modeled recruitment of anthers at various times and choosing the time that minimized the RMSE between the predicted rate of pollen shed to the observed rate for each day in 2004 (Figure 2.7). Temperature was taken as the average temperature between sunrise and the estimated start of pollen shed.

Using the relationship derived from data in Figure 2.7, we predict when the first anthers will dehisce according to:

\[
VPDT_{tar,i} = 104.8 \exp(-0.24T)
\]

where \(VPDT_{tar,i}\) is the value of VPDT necessary to cause anthers to begin dehiscing. The fraction of the total drying that is necessary to begin anther recruitment (\(FoD\)) that occurs during each time increment is determined as
\[ \text{FoD}_i = \frac{\text{VPD}_i dt}{\text{VPDT}_{\text{tar},i}}, \quad (9) \]

where \( \text{VPD}_i \) is the vapor pressure deficit during the \( i^{\text{th}} \) time interval. The model begins recruiting anthers for pollen shed when \( \text{VPDT} \geq \text{VPDT}_{\text{tar}} \).

We assume the recruitment of anthers represents a typical biological process for a population that follows a normal distribution whose time duration between \( \sigma = -3 \) and \( \sigma = 3 \) is \( \text{LoR} \) (Figure 2.8). \( \text{LoR} \) was calculated in the previous section as the time necessary for all anthers to be recruited on a given day if the atmospheric conditions around the tassels remain unchanged. Since atmospheric conditions may change, the fraction of anthers recruited during a given time under the present conditions is calculated. We use the definition of \( \text{LoR} \) to estimate the mean (\( \mu \)) and standard deviation (\( \sigma \)) of the recruitment curve as

\[ \mu = \frac{\text{LoR}}{2}, \quad \sigma = \frac{\text{LoR}}{6}, \quad (10) \]

The fraction of anthers recruited for pollen shed (\( A \)) at a time increment is predicted as the probability that the statistical Z-value is less than \( Z_i \)

\[ A_i = P(Z < Z_i), \quad (11) \]

where \( Z_i \) at each time increment is calculated as

\[ Z_i = Z_{i-1} + dZ_i, \quad (12) \]

with

\[ dZ_i = \frac{dt}{\sigma}, \quad (13) \]

and \( Z_0 = -3 \). As \( \text{LoR} \) increases or decreases throughout the day, \( \sigma \) will increase or decrease and a smaller or larger fraction of the remaining anthers will be recruited during the time increment.

The rate of shed from actively shedding anthers is modeled following the relationship given in Eq. 5. Since this relationship was derived for conditions when all anthers were shedding pollen, we include the fraction of anthers recruited at the \( i^{\text{th}} \) timestep, \( A_i \), to adjust \( \text{RoS} \) for the gradual recruitment of shedding anthers over time. The new equation is

\[ \text{RoS}_i = 0.2335 A_i R_i^{0.65}, \quad (14) \]
where $R_i$ is the fraction of total daily pollen remaining to be shed at time increment $i$. At $i = 0$, no pollen has yet been shed ($R_i = 1$) and at all other times

$$R_i = R_{i-1} - RoS_i dt$$

(15)

The predicted rate of shed will increase as more anthers are recruited for pollen shed (so $A_i$ increases in Eq. 14) and decrease as more pollen is shed following Eq. 15. The dynamics of $A$ and $R$ typically act to produce an increase in $RoS$ in the morning as anthers are recruited for shed and a slower decrease in $RoS$ throughout the afternoon as the pollen source is depleted.

Graphical representations for the model’s individual components are presented for 29 July 2003 to illustrate how the model works (Figure 2.9). On this day, temperature, solar radiation and VPD steadily increased from sunrise. This caused anthers to dry at an increasing rate after sunrise until the first anthers were predicted to dehisce at 0800 LDT. The rate of anther dehiscence increased as $LoR$ decreased and all anthers were predicted to be shedding by 1030 LDT. The combination of the increasing amount of anthers shedding and the amount of pollen remaining produced a peak in pollen shed around 1015 LDT, shortly before the last anthers began shedding pollen. After the peak, the rate of pollen shed was predicted to steadily decrease through the remainder of the day as the amount of pollen remaining to be shed decreased.

## 2.3 Results and Discussion

### 2.3.1 Model Validation

To determine how well the model fits the data used to create it, the model was applied to the 2004 field study and compared to the observations (Figure 2.10; Min. $RMSE = 0.040$ hr$^{-1}$, Max. $RMSE = 0.114$ hr$^{-1}$, $\overline{RMSE} = 0.076$ hr$^{-1}$). On each day, the model predicted the same general behavior that was observed in the field studies with a peak in pollen shed occurring shortly after the beginning of pollen shed. This was followed by a decrease in the rate of pollen shed through the rest of the day. On four days, the predicted peak in pollen shed occurred within the sampling period that contained the peak for the day. The two days when peak pollen shed was predicted later than the observed peak were cooler, with temperatures staying below 15°C for most of the morning.
The model was validated against the diurnal patterns of pollen shed measured in 2003. The model predicted the general trend and predicted the peak rate of shed to occur within an hour of the observed peak on each day (Figure 2.11; Min. \( RMSE = 0.031 \ \text{hr}^{-1} \), Max. \( RMSE = 0.103 \ \text{hr}^{-1} \), \( \overline{RMSE} = 0.061 \ \text{hr}^{-1} \)). Prior to peak shed, the predicted intensity of pollen shed was generally within one standard deviation of the measured intensity of pollen shed. After the peak, the model predicted the gradual decline in shed that occurred on most days and remained within a standard deviation of the measured rate of shed at most sampling times. On three of the five days tested, peak pollen shed was predicted to occur earlier than was measured. The meteorological conditions in 2003 were much less variable than in 2004 and temperatures were generally higher than those in the 2004 data used to create the model; morning temperatures during sampling dates in 2003 were generally near 20°C, which was higher than the morning temperatures in the calibration data set.

The model was also validated against six days of pollen shed from a field in Baltimore, MD, reported by van Hout et al. (2008; described in the Materials and Methods section) using the meteorological data reported in their paper. The model predicted both the timing and the magnitude of the peak rate of pollen shed on most days (Figure 2.12; Min. \( RMSE = 0.042 \ \text{hr}^{-1} \), Max. \( RMSE = 0.183 \ \text{hr}^{-1} \), \( \overline{RMSE} = 0.089 \ \text{hr}^{-1} \)). The late prediction of peak pollen shed on 14 July 2004 is likely due to the persistence of high humidity on this day, with VPD of less than 1 mbar until 0930 LDT, resulting in a slow accumulation of VPDT and delaying the initiation of pollen shed.

From 15 to 17 July, peak pollen shed was predicted earlier than observed. Conditions during anther recruitment on these days were much warmer (25 to 28°C) between sunrise and 1200 LDT compared to the days used for development and beyond the range of values used in the controlled experiments. The timing of peak shed is more closely matched by the model on days when the morning temperatures are nearer the range used in model development.

Although the timing of peak pollen shed was predicted fairly well across a range of conditions, the magnitude of the peak pollen shed was underpredicted in many cases. The model has an inherent limitation in the magnitude of peak pollen shed, which will not exceed the coefficient of 0.2335 in Eq. 5 (assuming \( A_i \) and \( R_i \) equal 1). The data used to develop Eq.
5 contains greater variability in $RoS$ when $R$ is high suggesting other factors should be included, either meteorological or biological, that influence $RoS$ more strongly than $R$ when $R$ is large such as turbulence or wind speed at the time of dehiscence.

Errors in predicting the time of peak shed may be caused by sensitivity to temperature in the anther recruitment portion of the model. Anther recruitment in the model tended to occur too quickly on warmer days, resulting in an early prediction of peak shed, and too slowly on cool days, resulting in a late prediction of peak shed. In most cases, the peak shed was predicted to occur within an hour of the measured peak. Exceptions occurred when temperatures were more than 5°C warmer than the controlled conditions used to model anther recruitment. Despite these errors in predicting the time and magnitude of peak pollen shed, allowing for generality in the model creates a better tool for predicting pollen shed in a range of conditions than restricting model application to a specific set of conditions.

### 2.3.2 Secondary Peaks in Pollen Shed

During each set of trials there were days that had secondary peaks in pollen shed. These secondary peaks may have been caused by meteorological factors not taken into account in this model or may reflect a second wave of anther exsertion or re-deposition of pollen shed earlier in the day. When a secondary peak occurred, the model tended to underpredict the rate of shed since it did not generate a secondary peak. Secondary peaks were not observed in our controlled experiments and no meteorological relationship was found using observed data from the field studies. Van Hout et al. (2008) suggested that a decrease in wind speed may have been responsible for the secondary peaks by causing a lull in pollen shed and a second peak when wind speeds increased again. Comparison of wind speeds and shed rates from our field studies showed some days, such as 29 July 2003 and 17 August 2004 that may support their hypothesis, but other days, such as 5 Aug 2004 and 12 Aug 2004, did not show a concurrence of low shed rates with lower wind speeds (Figure 2.13). To examine the relationship between wind speed and the rate of pollen shed, studies that sample pollen at higher temporal rates may be necessary. Fluctuations in wind speed can occur on scales ranging from seconds to minutes while the sampling methods in available studies examine hourly averages of pollen shed and correlate their measurements to hourly
averages of wind speed. To examine a direct relationship between wind speed and the rate of pollen shed, both pollen collection and wind measurements will need to be made at higher frequency.

Other causes of secondary peaks may include spatial variability in either the meteorological conditions across the field or in the biological processes of the individual plants within the field. This model treats the entire field as a single unit, using a single measurement of temperature at the center of the field, and predicts the recruitment of anthers and shedding of pollen as if conditions are identical across the field. As a hypothetical shortcoming of the approach, it is possible that plants near the edges of a field could respond differently to atmospheric conditions than plants located at the center of a field or may be affected by a different set of conditions than those in the center of the field. For instance, winds will tend to be more variable at the field edges where changes in surface characteristics generate turbulence. On certain days, such as 29 July 2003, a secondary peak was measured in one field but not in the other. This may be explained by processes such as the re-entrainment of pollen deposited on plants described by Aylor (2005). Strong gusts could potentially lift pollen off of the plants and re-deposit it on the pollen collectors.

Despite the failure of the model to predict secondary peaks in pollen shed, it did capture the general trend of pollen shed observed in 2003 and the van Hout et al. (2008) study characterized by pollen shed starting after sunrise, peaking during the late morning and generally decreasing through the afternoon. The general diurnal pattern of pollen shed was similar in all cases, implying that the model captures the most important biological and atmospheric variables controlling the diurnal pattern of pollen shed. Further work will be needed to determine whether these secondary peaks occur often enough to warrant special consideration in predicting pollen shed or if predicting the general trend is sufficient.

2.4 Conclusions

We have developed a quantitative model for the diurnal pattern of pollen shed based on meteorological conditions around the tassels. The use of this model in combination with pollen dispersion models is intended to provide more accurate simulations of pollen dispersion and concentration in the atmosphere compared with the assumption of a constant
rate of shed throughout the day. Potential applications of the model include predicting pollen shed from individual fields or large regions using the available network of meteorological data. The conceptual approach used here may also be extended beyond predicting the shed of maize pollen, such as the shed of pollen from grasses.

One of our primary goals was to calculate the timing of the peak rate of pollen shed accurately since this represents the time when the majority of pollen is shed. The model predicted the timing of the peak rate of pollen shed within thirty minutes of the measured peak for our 2004 data which was used to develop the model. Similar performance was observed when predicting the timing of the peak rate of pollen shed for the 2003 field site and some days reported by van Hout et al. (2008). In all tests, the model was able to predict the time of peak pollen shed within an hour of the measured peak when conditions remained between 10°C and 25°C during anther recruitment.

VPD was a primary component in the model for determining how quickly anthers are recruited for pollen shed. The ability of the model to capture the general trend of pollen shed and predict the timing of the peak rate of shed implies that these measurements may be important in future applications of this model or similar models. Accumulation of VPD over time (VPDT) indicates the cumulative atmospheric demand for water vapor and could be used to estimate the drying of anthers. The calculation of VPD requires only measurements of temperature and a suitable moisture variable such as relative humidity or dew point. Since these measurements are often readily available, the model may be of a practical use as well as provide a basis for future research.

The primary areas of improvement in the model are the prediction of the magnitude of peak pollen shed and predicting the occurrence of secondary peaks in pollen shed that were observed in the afternoon. While the peak rate of shed, normalized to the total amount of pollen shed, was accurately predicted on some days, there were many instances when the normalized peak exceeded the predicted peak rate of shed. The underprediction may have been caused by the difference in meteorological conditions between the developmental data from 2004 and the validation data; the days when pollen shed was measured in 2004 tended to be cooler than the days used to validate the data.
The presence of secondary peaks was noted on multiple days within our studies as well as in the studies of van Hout et al. (2008) and Jarosz et al. (2004). We were unable to determine a cause for these peaks and hypothesize that sampling pollen shed more frequently or the inclusion of biological processes may be necessary to predict them.

VPD, temperature and solar radiation were the primary components in the model for determining how quickly anthers are recruited for pollen shed. The ability of the model to capture the general trend of pollen shed implies that these measurements may be important in future applications of this model or similar models. Since these measurements are often readily available, the model may have practical uses in a number of locations as well as providing a basis for further research.

2.5 Acknowledgements
This research was supported by the USDA Biotechnology Risk Assessment Program and by the Iowa Home Economics and Experiment Station. The lead author is supported by a Research Training Fellowship from Iowa State University, Ames, IA.

2.6 References


Figure 2.1. The chamber system used to control environmental conditions while observing the onset and duration of pollen shed from a tassel branch. Vapor pressure deficit was varied using saturated salt solutions at the base of chamber. The system was placed in an incubator to control temperature. The ring of closed-cell foam with stoppers provided access to the exserted anthers. Mixing fan and instruments used to monitor atmospheric conditions are not shown.
Figure 2.2. The average daily pattern of the rate of pollen shed (RoS) in 2003 and 2004, expressed as the fraction of the total daily amount of pollen shed. Pollen shed typically peaked about one hour earlier in 2003, and declined more rapidly in the afternoon.
Figure 2.3. The relationship between the current rate of pollen shed ($\text{RoS}$) and the fraction of total daily pollen remaining to be shed ($R$) derived from observations of diurnal pollen shed taken during the 2004 field study. Each point represents approximately two hours of pollen shed. These data were used to define the pollen depletion function in the diurnal pollen shed model.
Figure 2.4. The relationships between the measured rates of pollen shed and hourly average wind speed \((U)\), temperature \((T)\), vapor pressure deficit \((VPD)\), and solar radiation \((S)\). Meteorological data were collected in the field within 50 m of the pollen collection sites with the exception of solar radiation, which was measured at a location approximately 1 km from the collection sites.
Figure 2.5. The effects of light intensity (top) and temperature (bottom) on the length of time necessary for full recruitment of anthers for pollen shed at 55%, 75% and 95% relative humidity. Variations in light intensity were tested at a temperature of 20°C and variations in temperature were tested at a light intensity of 530 W m$^{-2}$. 
Figure 2.6. Description of the anther recruitment function (top) and the pollen depletion function (bottom) used to model diurnal pollen shed. The fraction of anthers recruited ($A$) depends on meteorological conditions encountered from sunrise to peak shed. The depletion function ($RoS$) is dependent on the amount of daily pollen remaining to be shed ($R$).
Figure 2.7. The effect of air temperature (T, °C) on the accumulated vapor pressure deficit after sunrise necessary to initiate the anther recruitment function ($V_{PDT_{tar}}$, mbar·hr). The progress of anther ‘drying’ is calculated as the percentage of $V_{PDT_{tar}}$ achieved at each time increment. The relationship was determined by forcing anther recruitment to begin at a time providing the lowest root mean square error for each day in the model calibration set. The temperature is the average for recorded values between sunrise and the predicted start of pollen shed.
Figure 2.8. Statistical approach for recruiting anthers for pollen shed. Recruitment follows a normal distribution curve with a width of three standard deviations equal to time for full recruitment (LoR; top). The percentage of anthers recruited at each time increment equals the area under the curve corresponding to the interval $dZ_i$ (center). The interval $dZ_i$ increases as LoR decreases, accounting for a larger fraction of the normal curve (bottom).
Figure 2.9. Example model simulation of the diurnal progress of anther drying (FoD), anther recruitment for pollen shed (A), pollen depletion (R), and hourly fraction of total pollen shed (RoS; top) and the recorded meteorological data for 29 Jul 2003 (bottom). All simulation units are dimensionless except for the RoS which is hr$^{-1}$. 
Figure 2.10. An example of how the pollen shed model fits the collected data from the six dates in 2004 that were used for model calibration. Measured rates of pollen shed in the field are the mean ± one standard deviation of three replicates. The simulated rates of shed (RoS) are presented as the fraction of total daily pollen shed per hour and the RMSE values are the average for the two field sites. Time is given in Local Daylight Time and S denotes the time when sunrise occurred.
Figure 2.11. Comparison of predicted and measured patterns of diurnal pollen shed. Data points represent pollen shed rates as measured in the field study in 2003 and the solid line is the model prediction. Measured data are the mean ± one standard deviation of three replicates. The simulated rates of shed (RoS) are presented as the fraction of total daily pollen shed per hour and the RMSE values are the average for the two field sites. Time is given in Local Daylight Time and S denotes the time when sunrise occurred.
Figure 2.12. Predicted patterns of diurnal pollen shed for field measurements of pollen shed published by van Hout et al. (2008). The predicted rate of shed \((RoS)\) is presented as the fraction of total daily pollen shed per hour. Time is given in Local Daylight Time and \(S\) denotes the time when sunrise occurred.
Figure 2.13. Meteorological conditions on days when pronounced secondary peaks occurred two sampling periods after the first peak. The vertical line in each plot indicates the sampling period between measured peaks.
Table 2.1. Hybrids sampled at each field site.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Field</th>
<th>Hybrids</th>
</tr>
</thead>
<tbody>
<tr>
<td>29-Jul-03 to 02-Aug-03</td>
<td>Brunner Farm</td>
<td>Pioneer 35Y55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fontanelle 4693</td>
</tr>
<tr>
<td>23-Jul-04</td>
<td>Brunner Farm</td>
<td>Fontanelle 4741</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DKL 58-78</td>
</tr>
<tr>
<td>05-Aug-04 to 06-Aug-04</td>
<td>Marsden Farm</td>
<td>Fontanelle LL 5L819</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mycogen 2A672</td>
</tr>
<tr>
<td>11-Aug-04 to 12-Aug-04</td>
<td>Agronomy Farm</td>
<td>Pioneer 36B08</td>
</tr>
<tr>
<td>17-Aug-04</td>
<td>Agronomy Farm</td>
<td>IRF311 male inbred</td>
</tr>
</tbody>
</table>
Table 2.2. The salt solutions used to create specific conditions of Vapor Pressure Deficit in closed environments. Enough salt was added to 100 mL of water to ensure the solution remained saturated by the salt so that the desired conditions would persist.

<table>
<thead>
<tr>
<th>Salt Solution</th>
<th>Target VPD at 20°C (mbar)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lithium Chloride</td>
<td>19.0</td>
</tr>
<tr>
<td>Calcium Chloride</td>
<td>14.5</td>
</tr>
<tr>
<td>Magnesium Nitrate</td>
<td>10.0</td>
</tr>
<tr>
<td>Sodium Chloride</td>
<td>5.5</td>
</tr>
<tr>
<td>Sodium Sulfate</td>
<td>1.0</td>
</tr>
</tbody>
</table>
CHAPTER 3. MODELING POLLEN FLOW OVER COMPLEX TERRAIN USING A LAGRANGIAN DISPERSION MODEL

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Brian Viner and Ray Arritt

**Abstract**

Movement of particles in the atmosphere is dependent on the wind speed and direction which can be influenced by local meteorological patterns caused by mountains and valleys. We combined a high-resolution atmospheric dynamical model and a Lagrangian dispersion model to assess whether these models can predict the movement of bentgrass pollen over complex terrain. We simulated six days (22 Jun – 24 Jun 2003) from a case reported by Watrud et al. (2004) who found outcross in bentgrass could occur at distances greater than 20 km near Madras, OR (44.74°N, 121.15°W). The days chosen were based on a modeling study by Van de Water et al. (2007) that back-predicted pollen trajectories from outcross locations using mean hourly winds. Our model simulated pollen dispersion to distances over twenty kilometers from its source and matched observed locations of outcross from Watrud et al. (2004). We also observed that pollen was not deposited in large quantities within valleys or on the windward sides of mountains in our simulations, suggesting possible topographic effects that may warrant further examination. We conclude that combining a large-scale meteorological model with a Lagrangian dispersion model can be used to simulate dispersion in complex terrain and may be a useful tool in future applications.

**3.1 Introduction**

Local meteorological patterns caused by mountains and valleys make predicting pollen dispersion in complex terrain challenging. As an example, mountains influence local conditions by blocking winds, causing higher wind speeds at mountain tops than farther downslope (Raichle and Carson, 2009). In valleys, air flow can differ from the mean regional wind if a strong temperature inversion exists within the valley (Banta et al., 1999).
The inversion prevents mixing between the valley and the surrounding environment by creating a stable layer at the top of the valley.

Diurnal circulations also exist in complex terrain such as upslope flow during the day, due to surface heating and convection, and downslope flow during the night, due to surface cooling (Allwine, 1993). Such circulations can exist when there is only a small gradient in slope (Whiteman and Zhong, 2008). These small-scale circulations present a challenge because they are often not resolved on local sensor networks and cannot be accurately simulated if the model grid is too coarse.

Studies examining the effects of mountain- or valley-induced circulations on the transport of atmospheric gases have discussed the influence of these local circulations on dispersion. Turnipseed et al. (2009) identified thermally-driven upslope winds created by mountain-valley flow as a primary influence on ozone dispersion. Kalthoff et al. (2000) and Wang and Starzewski (2007) also identified thermally-driven winds as promoting the dispersion of gaseous tracers. Kim and Stockwell (2008) concluded that convection was not a strong force for lifting particles but found that local topography induced sufficient lifting with taller peaks creating more lift. McBride et al. (2001) found that mountains affected dispersion by forcing particles to move laterally around them or channeling winds through gaps between mountains. They also suggested that particles could be trapped within the wake zone on the lee side of hills. Simulating pollen dispersion relies on the same principles as simulating gaseous dispersion but must add terms for inertial drift and settling velocity that are negligible in gaseous tracers (Csanady, 1963).

While studies simulating gas dispersion in complex terrain are available, studies predicting pollen dispersion are sparse. One motivation for accurate dispersion modeling in complex terrain is the presence of genetically modified (GM) plants being grown in mountainous regions. Potential for conventional or wild varieties of crops to be pollinated by GM plants threatens their purity. In response to these concerns, purity threshold levels have been established in some regions, leading to economic consequences for growers if cross-pollination occurs beyond the threshold. One example of cross-pollination in a mountainous region was reported by Watrud et al. (2004) who found cross-pollination occurred over 20
km from the nearest GM sources. The outcross was potentially linked with the GM sources using backward-prediction methods based on hourly mean winds (Van de Water et al., 2007).

We have combined the Weather Research and Forecasting (WRF) model with a Lagrangian dispersion model to simulate the dispersion of bentgrass pollen in complex terrain from the GM sources described in Watrud et al. (2004). Although this case was previously simulated by Van de Water et al. (2007), they used mean hourly winds to predict pollen trajectories. Our model uses simulated wind fields that include resolved turbulence fields and a dispersion model that adds a turbulent component to the particle motion to simulate the unresolved portion of turbulence.

Six days were selected for simulation based on the analysis of Van de Water et al. (2007). Predictions of pollen deposition were made to determine if simulated pollen could be transported to the location of the sentinel plots where outcross was reported on any one of these days. These simulations provided a test for whether a predictive model for pollen dispersion, shown to produce reasonable predictions of dispersion in flat terrain (Arritt et al., 2007), can provide reasonable predictions in complex terrain.

### 3.2 Methods and Materials

#### 3.2.1 Overview of Simulated Case

We have simulated a case reported by Watrud et al. (2004) who observed outcross between a bentgrass source and sentinel plots. Outcross was determined by testing for the existence of the \textit{CP4 EPSPS} gene. Eight source plots were located in a plateau region along the Deschutes River, north of Madras, Oregon (44.75°N, 121.15°W; Figure 3.1). 79 resident bentgrass plots plus additional sentinel plants – deployed for the purpose of providing a regular grid to detect pollen flow from the source plots – were located up to 21 km from the source fields. The arrangement of potential receptors was designed based on knowledge of typical wind patterns in the region.

The number of outcross events decreased with distance from the source. The frequency of outcross was highest within 2 km of the source but still occurred at distances greater than 20 km. Watrud et al. (2004) pointed out the role of flowering time on their
results by suggesting the measured outcross frequencies may have been higher if some receptors had not flowered 2-3 weeks after the source.

Van de Water et al. (2007) simulated the dispersion of pollen for this case using HYSPLIT-4. HYSPLIT-4 can make use of both Eulerian and Lagrangian techniques to simulate dispersion (Draxler and Hess, 1999), but was used as a purely Lagrangian model by Van de Water et al. (2007). Particles were modeled backwards-in-time from the receptor plots for three hours to assess when the pollen responsible for the outcross events may have been released. The three-hour limit was imposed based on measurements of bentgrass pollen viability conducted by Fei and Nelson (2003). Periods when the trajectories crossed over the source region were considered most favorable for pollination. The period of 22 Jun through 27 Jun 2003 was concluded to be the most likely period for pollination at the majority of the receptors; in particular, the wind field on 24 Jun was found to potentially account for outcross at most receptor fields.

3.2.2 Meteorological Simulation

The Weather Research and Forecasting model, available from the National Center for Atmospheric Research, was used to predict meteorological conditions for the dispersion model. A detailed description of the WRF model can be found on the WRF homepage (www.wrf-model.org).

The WRF model uses compressible, nonhydrostatic Euler equations to predict horizontal and vertical winds, turbulence kinetic energy, atmospheric moisture in various states, and perturbations of potential temperature and pressure on constant-η surfaces. The ability of WRF to predict mesoscale circulations was important to ensure smaller domains received updated information regarding large-scale flow. Topography was represented at 3-second (~90 m) resolution using data from the Shuttle Radar Topography Mission conducted by the Consultative Group for International Agricultural Research’s Consortium for Spatial Information (http://srtm.csi.cgiar.org/index.asp; Figure 3.2).

Initial and lateral boundary conditions for WRF were taken from the North American Regional Reanalysis (NARR) available from the National Centers for Environmental Prediction (Mesinger et al., 2006). NARR data is available at 3-hour intervals and a
horizontal resolution of ~32 km which was linearly interpolated to the WRF model grid. Three-dimensional wind and turbulence kinetic energy were output from WRF at 1-minute intervals for use as input to the dispersion model.

### 3.2.3 Particle Dispersion Model

The Lagrangian dispersion model of Arritt et al. (2007) was used to simulate pollen dispersion. Since the principles of modeling gas dispersion and pollen dispersion are similar with the exception of additional terms for modeling particles, we expect that the Lagrangian framework should provide reasonable simulations of pollen dispersion in complex terrain (Jarosz et al. 2004; Holmes and Morawska 2006).

Van de Water et al. (2007) used HYSPLIT-4 to predict dispersion in a Lagrangian sense. Many of the predictive equations in HYSPLIT-4 are similar to those in our model. The primary differences between our model and Van de Water et al. (2007) is that we updated our meteorological conditions at a faster rate [1-minute intervals in our study compared to 1-hour intervals in Van de Water et al. (2007)] and that we predicted the movement of particles forward-in-time as opposed to backwards-in-time. The use of a smaller timestep in our model means that the Lagrangian timescale in each direction cannot be assumed constant as they are in HYSPLIT-4.

Three-dimensional movement of a hypothetical tracer particle is simulated using mean and turbulent wind components,

\[
x_{ik}(t + dt) = x_{ik}(t) + dt[u_{ik}(t) + u_{0ik}(t)], \quad k = 1,2,3, \tag{1}
\]

where \(x_{ik}\) is the position of the \(i^{th}\) particle in the \(k\) direction, \(u_{ik}\) is the mean wind speed that the particle experiences, and \(u_{0ik}\) is a simulated random component of the wind to account for unresolved turbulence. The model timestep was \(dt = 2\) s. \(u_{0ik}\) was calculated as a first-order Markov process

\[
u_{0ik}(t + dt) = \nu_{0ik}(t)R_{ik}(dt) + \left[1 - R_{ik}(dt)^2\right]^{1/2} q\sigma_{ik}, \quad k = 1,2,3 \tag{2}
\]

where \(R_{ik}\) is the autocorrelation value, \(q\) is a normally distributed random number with the distribution \(N(0,1)\), and \(\sigma_{ik}\) is the standard deviation of the wind speed in the \(k\) direction. The standard deviation is derived from the turbulence kinetic energy field predicted by WRF. \(R_{ik}\)
acts as a memory of turbulence at the previous timestep and is determined by the particle’s Lagrangian timescale in the $i$th direction, $\Gamma_i$:

$$R_{ik}(dt) = \exp\left(-\frac{dt}{\Gamma_{ik}}\right)$$  \hspace{1cm} (3)

As $R_{ik}$ decreases from 1 to 0, a particle’s turbulent motion goes from constant in time to completely random.

In the horizontal directions, we assume that the particle timescale equals the fluid timescale, and is given by

$$\Gamma_{ik} = \frac{x_{i3}(t)}{2\sigma_{ik}} \quad \text{for } k = 1, 2$$  \hspace{1cm} (4)

In the vertical direction, the particle timescale will not be equal to the fluid timescale because heavy particles lose memory faster than the flow (Csanady, 1963). Instead, the particle timescale in the vertical direction is given as

$$\Gamma_{i3} = \frac{x_{i3}(t)}{2\sigma_{i3}\sqrt{1 + (\beta v_T/\sigma_{i3})^2}}$$  \hspace{1cm} (5)

following Csanady (1963) where $v_T$ is the particle’s terminal fall speed in still air and $\beta$ is a dimensionless coefficient set to 1.5. The terminal fall speed of bentgrass pollen was set to 0.019 m s$^{-1}$ (Pfender et al. 2007).

A drift correction term ($w_c$) was added to the vertical component of the particle’s motion and defined following Legg and Raupach (1982)

$$w_c = \frac{x_{i3}(t)}{2\sigma_{i3}} \frac{\partial(\sigma_{i3}^2)}{\partial z} \left[1 - R_{i3}(\Delta t)\right]$$  \hspace{1cm} (6)

Since turbulence is not homogeneous in the vertical direction, particles will accumulate in regions of low turbulence (Legg and Raupach, 1982; MacInnes and Braco, 1992). The drift correction term corrects this behavior and preserves the well-mixed condition, which requires that a mixed tracer remain mixed. With the above additions, Eq. 1 becomes

$$x_{ik}(t + dt) = x_{ik}(t) + \left[u_{ik}(t) + u_{0ik}(t) + \delta_{ik}(w_c - v_T)\right]dt$$  \hspace{1cm} (7)

A pollen grain was removed from the model under three conditions:

- If it was less than 1 m above the ground, it was considered deposited.
• If it was suspended in the air longer than 3 hours, it was considered to have lost viability and would not pollinate a receptive plant.
• If it left the model domain.

The viability constraint was chosen because bentgrass pollen has been shown to remain viable for no more than three hours after exposure to ambient air (Fei and Nelson, 2003). Since pollen will not fertilize a receptive plant after this period, it could not produce an outcross event. Pollen leaving the domain accounted for only a few percent of all pollen grains.

3.2.4 Statistical Methods for Assessing Errors in Predicted Winds

Errors in wind speed and direction are presented as the difference between the analyzed wind from the NARR and the predicted wind in WRF using vector subtraction. The mean ($\bar{u}_{e,k}$) and standard deviation ($\sigma_{u_{e,k}}$) of wind speed errors were calculated as

$$\bar{u}_{e,k} = \frac{1}{N} \sum u_{e,ik} \quad (8)$$

$$\sigma_{u_{e,k}} = \sqrt{\frac{1}{N-1} \sum (u_{e,ik} - \bar{u}_{e,k})^2} \quad (9)$$

where $u_e$ is the difference between the observed wind speed and the predicted wind speed and $N$ is the number of measurements of $u_e$.

Errors in wind direction were calculated using vector subtraction between the observed and simulated wind. The mean ($\bar{\theta}$) and standard deviation ($\sigma_\theta$) of wind direction was calculated following Skibin (1984) and accounts for the discontinuity between 0° and 360° that complicates the calculation of wind direction statistics (Verrall and Williams, 1982). Measurements of wind direction error are categorized into bins of $\theta < 180^\circ$ (represented by the suffix 1) and $\theta > 180^\circ$ (represented by the suffix 2) and grouped by their sums ($A1$ and $A2$) and their sum of squares ($S1$ and $S2$):

$$A1 = \sum \theta_i , \quad S1 = \sum \theta_i^2 \text{ if } \theta \leq 180^\circ \quad (10)$$

$$A2 = \sum \theta_i , \quad S2 = \sum \theta_i^2 \text{ if } \theta > 180^\circ \quad (11)$$
N1 and N2 are defined as the number of measurements in each bin. If the quantity \((A2/N2 - A1/N1) < 180^\circ\),

\[
\bar{\theta} = (A1 + A2)/(N1 + N2)
\]

\[
\sigma_\theta = \left\{ (S1 + S2 - \bar{\theta}^2 (N1 + N2))/(N1 + N2 - 1) \right\}^{1/2}
\]  \hspace{1cm} (13)

If the quantity \((A2/N2 - A1/N1) > 180^\circ\),

\[
\bar{\theta} = [A1 + A2 - N2(360^\circ)]/(N1 + N2)
\]

\[
\sigma_\theta = \left\{ (S1 + S2 + N2(360^\circ) - 2A2/N2 - \bar{\theta}^2 (N1 + N2))/(N1 + N2 - 1) \right\}^{1/2}
\]  \hspace{1cm} (14)

3.3 Results and Discussion

3.3.1 Simulated Wind Patterns

We simulated the period of six days (22 Jun 2003 through 27 Jun 2003) considered the most likely period for long-range outcross by Van de Water et al. (2007). WRF was run using four nested domains (Figure 3.3). The innermost domain had a grid spacing of 200 m while the outermost domain had a grid spacing of 5400 m and encompassed an area 1080 km by 1080 km to capture the evolution of mesoscale features. The grid spacing and timestep were scaled with a ratio of 1:3 between domains. Simulations began prior to sunrise (0518 Local Daylight Time (LDT)) and ended near sunset (2053 LDT).

Simulated winds on 24 Jun were representative of the diurnal wind pattern during the six-day period (Figure 3.4). Morning winds were generally from the northwest. Weaker winds were present over the source because the valley wall located northwest of the source impeded the mean flow from lower terrain. The westerly flow over the source turned laterally north or south when it reached the mountains east of the source. As convective turbulence strengthened after noon, air moved up the valley wall northwest of the source and up the mountain slopes. Wind during this time was variable over the domain, but wind speeds were lower over the plateau in the center of the domain and higher moving up the slopes. The prevailing northwest flow returned in the evening over the entire domain. Mean differences in wind speed between the WRF simulation and the NARR analysis were generally about 1.5 m s\(^{-1}\) or less while differences in wind direction were varied (\(\sigma_\theta > 90^\circ\); Figure 3.5).
Simulated 10 m wind speeds in the region of Madras, OR (Figure 3.6) showed 22 – 23 Jun and 27 Jun had much higher wind speeds while those on 25 Jun had low wind speeds all day. 24 and 26 Jun had low simulated wind speeds during the morning which increased during late afternoon. These results agreed with weather station data reported by Van de Water et al. (2007). Predicted 10 m wind speeds tended to be lower than the NARR analysis during the morning and early afternoon and greater than the NARR analysis during late afternoon. For example, predicted wind speeds deviated -3.28 m s\(^{-1}\) to -0.52 m s\(^{-1}\) from the NARR analysis at 1100 LDT and -1.55 m s\(^{-1}\) to 7.16 m s\(^{-1}\) at 1700 LDT. Differences between the WRF predictions and NARR analysis are due in part to errors in WRF and may also be due to errors in the NARR analysis.

### 3.3.2 Simulated Dispersion

The Lagrangian model used predicted three-dimensional wind and turbulence fields from WRF to simulate dispersion. Pollen was released from 275 points in the source region described in Watrud et al. (2004; Figure 3.3) at a rate of one grain per timestep between 0800 and 1600 LDT. While measurements of pollen shed may exhibit diurnal variation, we were not concerned with the actual concentration of pollen being deposited downwind. Rather, we were attempting to determine whether it is possible to predict the potential for long-range transport using this modeling approach. If future applications are concerned with specific pollen concentrations, the results could be scaled by the known or estimated varying rate of shed.

Accumulated pollen deposition over each day was predicted by our model (Figure 3.7). Pollen was predominantly transported in the direction of the mean wind. The highest deposition was immediately around the sources and decreased with distance, becoming nearly constant at low values over many kilometers. Most of the pollen released during the morning was deposited within the source region because vertical motions from thermally-induced turbulence were not strong during the morning and not yet developed to a scale large enough to be explicitly resolved in our model. Thermally-driven turbulence created stronger lifting in the afternoon, lifting pollen higher into the boundary layer and allowing it to move farther downwind before settling.
Pollen generally moved southeast and was transported over 20 km on five of the six days, but was limited to within 3 km of the source on 25 Jun when wind speeds were lower. Some pollen was predicted to move upwind of the source most days, possibly due to thermal or mechanical turbulence generated along the steep slope upwind of the source. The range of upstream dispersion was limited to a few hundred meters on 25 and 26 Jun but was as large as a few kilometers on 24 and 27 Jun.

Pollen deposition followed the local terrain, particularly at longer distances from the source. Gaps in pollen deposition were found on the windward sides of hills and mountains. The convergence of wind on the windward side may have created additional lift that prevented pollen from settling, while the divergence in the lee of the mountain may have allowed pollen to be deposited. Pollen deposition was also absent within most of the valley along the north and west sides of the pollen source; it would seem intuitive that the valley would be a likely spot for deposition based on its proximity to the pollen source. The steep valley walls may have generated mechanical turbulence which would have prevented pollen from settling in the valley.

On four of the six simulated days (22-24, 26 Jun), pollen was predicted to reach the farthest receptor plots with reported outcross (marked with an X in Figure 3.7). The simulation of 24 Jun predicted pollen deposition in the vicinity of each receptor plot greater than 15 km from the source. The wind direction on 24 Jun was more northerly than other days. The north wind was necessary to transport pollen to the farthest receptor directly south of the source that was missed on other days. On 27 Jun, pollen was predicted to be deposited near two of the fields with outcross, but the wind did not transport pollen far enough to the south to reach the locations of outcross. Only on 25 Jun was no pollen predicted to be deposited in the vicinity of the observed outcrosses since the simulated wind speeds were very small.

The presence of updrafts and downdrafts could be identified when following the trajectories of individual pollen grains and appeared to be a characteristic of long-distance dispersion (Figure 3.8). The trajectories of the particles follow the well-known convective boundary layer behavior of small but strong updrafts and broader but weaker downdrafts (Letzel and Raasch, 2003); particles were lifted quickly and settled more slowly. Pollen
grains dispersed over 20 km were lifted multiple times during their flight, representing the grain being lifted by multiple turbulent eddies, and none of these grains remained near the surface for more than a few minutes. The lack of time spent near the ground indicates that updrafts capable of lifting pollen many hundred meters are necessary for pollen to move greater distances.

Our results agree with Van de Water et al. (2007) that 24 Jun appeared to be the most likely day for long-range pollen transport to the most distant receptors. Pollen was transported tens of kilometers on most days, but only on 24 Jun was it predicted to reach the vicinity of all the receptor fields farther than 15 km from the sources.

### 3.4 Conclusions

We combined a high-resolution atmospheric model with a Lagrangian particle model to simulate bentgrass pollen dispersion in a region where outcross was observed. Our simulations exhibited the characteristics of pollen dispersion that have been previously identified:

- Most pollen was deposited within and immediately around the sources.
- Dispersion followed the primary wind direction.
- Pollen concentration decreased away from the source with a dispersal tail that extended many kilometers.

Our results also matched the same general conclusions given by Van de Water et al. (2007):

- The period of 22 June to 27 June 2003 was sufficient to transport pollen to all of the surrounding receptor fields where outcross was observed.
- The wind fields on 24 Jun 2003 appeared ideal for long-range transport to the receptor plants monitored by Watrud et al. (2004)

The predictive nature of our simulations suggests that it may be possible to use the framework of a dynamical meteorological model with a Lagrangian dispersion model to study patterns of pollen dispersion in complex terrain.

Compared to similar methods, the Lagrangian approach provides a more detailed examination of dispersion that allows the environmental conditions along each point of the particle’s trajectory to be evaluated. This capability may be beneficial in future applications,
particularly since viability loss in pollen grains may be highly variable depending on atmospheric conditions and will be discussed in Chapter 5. The drawback of this approach is the computing resources necessary for the simulation of millions of individual particles; each simulation reported here required about 40 hours of computing time. However, as computing resources continue to improve, this drawback will be reduced.

A question that arises from our simulations is how topographic features can influence dispersion. Gaps in pollen deposition were found on the windward sides of mountains and in the valley north and west of the pollen source. This behavior was seen on multiple days, suggesting that local circulations may be hindering deposition in these regions. With further study, it may be possible to use regions such as these to isolate crops requiring greater genetic purity from adventitious pollen flow from genetically-modified sources.

3.5 References


Figure 3.1. Location of the bentgrass pollen source and sentinel plots in Watrud et al. (2004). Figure taken from van de Water et al (2007).
Figure 3.2. Topography in Domain 4 of WRF (top). The large box represents the region examined by Watrud et al. (2004). Topography data was obtained from the Shuttle Radar Topography Mission at 3 s resolution. Sources were evenly spaced at 400 m intervals (bottom) within the approximate boundaries of the outlined control region in Watrud et al. (2004).
Figure 3.3. Graphical representation of the four domains used by the Weather Research and Forecasting model. Predicted meteorological conditions in the innermost domain (D4) are used to simulate the movement of bentgrass pollen. All latitude and longitude values are in degrees.
Figure 3.4. Evolution of the wind field over Domain 4. Longer vectors indicate stronger wind speeds and contours mark lines of constant terrain height at 100 m intervals.
Figure 3.5. Wind errors on 24 Jun 2003 expressed as the vector difference between the predicted wind from the WRF model and analyzed winds from the NARR (a-d) and the modeled topography of the second domain (e). Vectors indicate the magnitude and direction of the error vector. Contours mark lines of constant terrain height at intervals of 200 m.
Figure 3.6. Modeled 10 m wind speeds over the center of the pollen source (solid line) and observed NARR 10 m wind speed (boxes).
Figure 3.7. Concentration of deposited pollen grains. Each ‘X’ represents the location of a sentinel plot farther than 15 km from the source where outcross was detected according to Watrud et al. (2004). Contours indicate 100 m intervals of terrain height.
Figure 3.8. Examples of pollen grain height as a function of time for grains traveling farther than 20 km from their source point within the imposed 3-hour viability limit on 24 Jun 2003.
CHAPTER 4. EXAMINING THE IMPACT OF SURFACE SENSIBLE HEAT FLUX AND COMPLEX TERRAIN ON POLLEN DISPERSION

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Brian Viner and Ray Arritt

Abstract

Pollen dispersion has been modeled in regions of flat terrain but has not been applied to complex terrain until recently. Studies examining gaseous dispersion in the atmosphere have identified thermally- and mechanically- induced flows resulting from surface sensible heat flux and complex topography as the primary lifting mechanisms that promote dispersion. To understand how these flows may affect pollen dispersion, we simulated bentgrass pollen dispersion for three days in a region of complex terrain using a model capable of predicting the effects of surface sensible heat flux and complex topography. Simulations with no surface sensible heat flux or flat terrain were also performed to examine how dispersion differed in these conditions. When both surface sensible heat flux and complex terrain were included, gaps in pollen deposition were present in valleys and on windwind mountain slopes. Removing surface sensible heat flux limited dispersion but topography produced sufficient lift to transport pollen 20 km from its source. Flat terrain extended dispersion and allowed pollen grains to travel farther while remaining close to the surface. We found surface sensible heat flux and complex terrain were each capable of generating sufficient lift to transport pollen tens of kilometers. However, neither process alone was able to reproduce the dispersive pattern that was predicted when both were present. We conclude that both surface sensible heat flux and complex topography must be adequately modeled to obtain accurate predictions of dispersion. Our results also indicate potential locations where pollen deposition may be reduced. These regions could be strategically used to isolate crops that require greater genetic purity from adventitious pollen flow.
4.1 Introduction

Evidence for pollen dispersion over long distances in complex terrain has been reported by Watrud et al. (2004) who observed outcross in bentgrass over 20 km from the nearest source. Bentgrass pollen has a terminal velocity of ~ 2 cm s$^{-1}$ (Pfender et al., 2007) and must be lifted to prevent it from settling within a few tens of meters of its source. In complex topography, three lifting processes have been identified: mechanically-generated flow due to the presence of complex terrain (Kim and Stockwell, 2007; McBride et al., 2001), thermally-generated turbulence resulting from surface sensible heat flux (Westbrook and Isard, 1999), and organized thermally-driven flows resulting from warm air rising upslope or cold air moving downslope (Turnipseed et al., 2009; Kalthoff et al., 2000; Wang and Starzewski, 2007). The effects of these circulations on pollen dispersion have not been studied but their impacts on the dispersion of atmospheric pollutants and gaseous tracers have been documented.

Mechanically-generated flow due to complex terrain can result from wind moving up and down sloping terrain. Other vertical motions are created by mountains blocking the wind, reducing the wind speed causing convergence on the windward side of the mountain. Convergence forces air to move laterally around the mountain and creates additional lift. Likewise, diverging winds which create downward motion may be the cause of increased deposition that has been observed on the leeward sides of mountains (McBride et al., 2001). Uchida and Ohya (2003) used Large Eddy Simulation to model dispersion in the lee of a mountain. They found that the increased turbulence in this region enhanced horizontal and vertical movement of particles.

Thermally-induced turbulence results from buoyant instability caused by surface sensible heat flux. As the sun warms the surface, the surface heats the lowest level of the atmosphere and creates an unstable layer. The result of this instability is the formation of turbulent eddies that transport heat, with upward motion in one location that is balanced by downward motion in another. As the Earth’s surface warms through the day, vertical motions increase and build a boundary layer that can be over a kilometer deep. Thermally-generated turbulence has been identified as lifting pollen and extending the distance it can potentially travel (Westbrook and Isard, 1999).
Thermally-induced flow that is more organized than buoyant instability can occur in regions of complex terrain. These circulations typically occur on a diurnal cycle with upslope flow during the day, caused by surface warming, and downslope flow during the night, caused by surface cooling (Allwine, 1993). Turnipseed et al. (2009) identified thermally-driven upslope winds as a primary influence on ozone dispersion. Kalthoff et al. (2000) and Wang and Starzewski (2007) also identified thermally-driven slope winds lifting gaseous tracers and increasing the distance they were dispersed.

Modeling pollen dispersion in complex terrain was not attempted until recently (Van de Water et al., 2007) but has been performed over flat terrain for many years (Raynor et al., 1972; Luna et al., 2001; Jarosz et al., 2003; Ma et al., 2004). Characteristics of pollen dispersion that have been identified in these studies include:

- Pollen dispersion tends to follow the wind direction,
- Most pollen is deposited within and immediately around its source
- The amount of deposited pollen decreases rapidly away from its source with an extended dispersal tail that may extend many kilometers

Similar characteristics were described in Chapter 3 when modeling dispersion in complex terrain, but the dispersive tail was broken by the presence of valleys and mountains. These breaks indicate that other processes affecting dispersion are occurring that are not present in flat topography.

To better understand how pollen dispersion is affected by complex topography, we examined the lifting processes that potentially extend the distance pollen can be transported. We have used numerical models to examine the individual effects of surface sensible heat flux and topography on the dispersion of bentgrass pollen. Bentgrass pollen was chosen because the ability of the model framework used here to simulate patterns of pollen dispersion similar to the observed pattern of outcross reported by Watrud et al. (2004) was demonstrated in Chapter 3.

Simulations which included surface sensible heat flux and complex topography were performed for three days for pollen dispersion from a genetically-modified bentgrass source described by Watrud et al. (2004). The days were chosen so that each had a different prevailing wind direction. These simulations were repeated with either topography or
surface sensible heat flux removed from the simulation. Comparisons of these simulations with the original simulations will indicate how these mechanisms affect dispersion.

4.2 Methods and Models

4.2.1 Meteorological Simulation

The Weather Research and Forecasting (WRF) model, a meteorological model that is available from the National Center for Atmospheric Research, was used to predict meteorological conditions for the dispersion model. WRF uses compressible, nonhydrostatic Euler equations to predict horizontal and vertical winds, turbulence kinetic energy, atmospheric moisture in various states, and perturbations of potential temperature and pressure on constant-\(\eta\) surfaces. A detailed description of WRF can be found on the WRF homepage (www.wrf-model.org).

Topography was represented at 3-second (~90 m) resolution using data from the Shuttle Radar Topography Mission conducted by the Consultative Group for International Agricultural Research’s Consortium for Spatial Information (http://srtm.csi.cgiar.org/index.asp). Initial and lateral boundary conditions for WRF, including soil properties, horizontal wind, pressure, potential temperature, and atmospheric moisture were taken from the North American Regional Reanalysis (NARR) available from the National Center for Environmental Prediction (Mesinger et al., 2006). NARR data is available at 3-hour intervals with a horizontal resolution of ~32 km which was linearly interpolated to the WRF model grid. Three-dimensional wind and turbulence kinetic energy were output from WRF at 1-minute intervals to be used by the dispersion model.

4.2.2 Particle Dispersion Model

The Lagrangian dispersion model of Arritt et al. (2007) was used to simulate dispersion. Three-dimensional movement of a hypothetical tracer particle is simulated using mean and turbulent wind components,

\[
x_{ik}(t + dt) = x_{ik}(t) + dt\left[ u_{ik}(t) + u_{0ik}(t) \right], k = 1, 2, 3,
\]

where \(x_{ik}\) is the position of the \(i^{th}\) particle in the \(k\) direction, \(u_{ik}\) is the mean wind speed that the particle experiences, and \(u_{0ik}\) is a simulated random component of the wind that
represents turbulent motions on scales too small to be resolved on the WRF model grid. The particle model timestep was $dt = 2$ s. $u_{0ik}$ was calculated as a first-order Markov process

$$u_{0i}(t + dt) = u_{0i}(t)R_{ik}(dt) + \left[1 - R_{ik}(dt)^2\right]^{1/2} q \sigma_{ik}, k = 1,2,3$$

where $R_{i,k}$ is the autocorrelation value, $q$ is a normally distributed random number with the distribution $N(0,1)$, and $\sigma_{i,k}$ is the standard deviation of the wind speed in the $k$ direction derived from the turbulence kinetic energy field predicted by WRF. $R_{i,k}$ acts as a memory of turbulence at the previous timestep and is determined by the particle’s Lagrangian timescale in the $k$ direction, $\Gamma_{p,i}$

$$R_{ik}(dt) = \exp\left(-\frac{dt}{\Gamma_{ik}}\right)$$

As $R_{i,k}$ decreases from 1 to 0, a particle’s turbulent motion goes from constant in time to completely random.

In the horizontal directions, we assumed that the particle timescale equals the fluid timescale

$$\Gamma_{ik} = \frac{x_{i3}(t)}{2\sigma_{ik}} \quad \text{for } k = 1,2$$

In the vertical direction, the particle timescale will not equal the fluid timescale because heavy particles lose memory faster than the flow (Csanady, 1963). Instead, the particle timescale in the vertical direction is given as

$$\Gamma_{i3} = \frac{x_{i3}(t)}{2\sigma_{i3}\sqrt{1 + (\beta v_T/\sigma_{i3})^2}}$$

following Csanady (1963) where $v_T$ is the particle’s terminal velocity in still air and $\beta$ is a dimensionless coefficient set to 1.5. The terminal velocity of bentgrass pollen was specified as 0.019 m s$^{-1}$ (Pfender et al., 2007).

A drift correction term ($w_c$) was added to the vertical component of the particle’s motion and was defined following Legg and Raupach (1982)

$$w_c = \frac{x_{i3}(t)}{2\sigma_{i3}} \frac{\partial(\sigma^2_{i3})}{\partial z} \left[1 - R_{i3}(\Delta t)\right]$$
Since turbulence is not homogeneous in the vertical direction, particles will accumulate in regions of low turbulence (MacInnes and Braco, 1992). The drift correction term counteracts this behavior and preserves the well-mixed condition, which requires that a mixed tracer remain mixed. With the above additions, Eq. 1 becomes

\[ x_{ik}(t + dt) = x_{ik}(t) + dt[u_{ik}(t) + u_{0ik}(t) + \delta_{k3}(w_c + v_T)] \]  

(7)

A pollen grain was removed from the simulation under three conditions:

- If it was less than 1 m above the ground, it was considered deposited.
- If it was suspended in the air longer than 3 hours, it was considered to have lost viability so that it could not pollinate a receptive plant.
- If it left the model domain.

The viability constraint was chosen because bentgrass pollen has been shown to remain viable for no more than three hours after exposure to ambient air (Fei and Nelson, 2003). Since pollen will not fertilize a receptive plant after this period, it could not produce an outcross. This is consistent with the work of Van de Water et al. (2007) who examined 3-hour windows for dispersion. Pollen leaving the domain accounted for only a few percent of all pollen grains.

### 4.3 Results

#### 4.3.1 Simulations with Surface Sensible Heat Flux and Complex Topography

WRF was run using four nested domains (Figure 4.1). The grid spacing of the outermost domain was 5400 m and encompassed an area 1080 km by 1080 km to capture the evolution of mesoscale features. The grid spacing and timestep were scaled using a 1:3 ratio corresponding to grid spacings of 1800 m, 600 m, and, in the smallest domain, 200 m. Simulations began prior to sunrise (0518 LDT) and ended near sunset (2053 LDT).

17, 24, and 28 Jun 2003 were simulated because they represented three days with differing wind fields based on analysis of the NARR data (Figure 4.2). The morning of 17 Jun had south winds which slowed and became north winds after a front passed in the late morning. A surface low pressure system was over the region during the morning of 24 Jun and moved to the east during the day. This resulted in winds turning around the low during the morning and northwest winds throughout the day with faster wind speed in the morning.
and afternoon, but slower wind speeds around noon. On 28 Jun, the region was between a surface high pressure center to the east and a surface low pressure center to the west. The day began with southerly winds which became northeasterly in the afternoon. Wind speed decreased in the afternoon on 17 and 28 Jun and increased in the afternoon on 24 Jun. On each day, the wind direction within the valleys was different from the wind direction over the surrounding region, indicating that our model was able to resolve the flow within the valleys and its potential effects on dispersion. There are no observations of this valley flow to compare with, however, so we cannot say with certainty that this result is accurate.

Vertical winds near the surface followed a similar evolution on each day (Figure 4.3). In the morning, most vertical motions were small in magnitude but regions of stronger motion existed along steep slopes. During the afternoon, vertical wind speeds became more varied and were characterized by regions of downward motion surrounded by upward motion. Stronger vertical motions were present along mountain and valley slopes where additional lifting processes existed. 400 m above the surface, turbulent motions from buoyant instability covered most of the domain (Figure 4.4). Over the southeastern region of the domain, broader upward motion existed due to the air being lifted over the mountains.

Pollen was released at a rate of one grain per timestep between 0800 and 1600 LDT from 275 points located in a source region designed to represent the control region described in Watrud et al. (2004). While measurements of pollen shed may exhibit diurnal variation, we were not concerned with predicting actual concentration of pollen being deposited downwind. Rather, our goal is to evaluate how predicted patterns of deposited pollen differed between the simulations.

On each day, most pollen was deposited near the sources and decreased with distance in the predominant wind direction (Figure 4.5). On 17 Jun, pollen was deposited south and southwest of the source field. Near the source field, pollen was deposited within and around the Deschutes River Valley. Farther downwind of the source, pollen was only deposited on the higher elevations surrounding the valley but not within the valley (Figure 4.6).

This behavior may be explained by the evolution of the wind flow within the valley. Early in the simulations there was downslope flow along the valley walls that allowed pollen to be transported into the valley. In the afternoon, upslope flow existed along the valley
walls as a result of surface heating and may have lofted pollen over the valley. Close to the source, pollen could enter the valley while downslope flow was occurring. Farther from the source, deposition in the valley would be hindered since pollen would likely not be transported farther down the valley until after upslope flow would have begun.

On 24 Jun, deposition occurred mostly south and southeast of the source. Pollen that reached the mountains to the east of the source was deposited only on the lee side of the mountain (Figure 4.6). Wind speeds on the windward sides of the mountains were lower than over the plateau, indicating converging winds which would produce upward motion, following the conservation of momentum simplified to two dimensions:

\[
\frac{\partial u}{\partial x} = -\frac{\partial w}{\partial z}
\]

This is supported by the broad regions of upward motion both at the surface and at 400 m.

On 28 Jun, pollen was deposited in all directions from the source. In the morning, pollen was transported to the west and north. Downslope flow along the valley walls that ran along the source region allowed pollen to be deposited in the valley. In the afternoon, pollen was transported to the southwest and deposition followed the topography with little pollen being deposited in the narrow valley to the southwest where upslope flow prevented pollen from moving into the valley. Pollen was instead deposited on the higher elevations surrounding the valley.

### 4.3.2 Effects of Surface Sensible Heat Flux

Removing sensible heat flux from the simulation did not create many differences in the horizontal winds until the afternoon (Figure 4.7). On 17 Jun, the movement of the front was delayed and on 28 Jun the winds remained from the southeast in the afternoon. The similarity of the morning wind fields to the original simulations may have been because
thermally-induced turbulence resulting from surface sensible heat flux is not strong enough to be resolved by our model until later in the simulation.

Turbulent vertical motion was still present due to mechanical generation of turbulence, but vertical winds did not form the pockets of downdrafts surrounded by updrafts that characterized the daytime boundary layer in the previous simulations (Figure 4.8). Instead, vertical motions remained generally small in magnitude with regions of stronger motion along steep slopes. Vertical motions along the slopes were due to air moving along the surface; as the surface sloped up or down, air moved up or down with it, creating the stronger vertical motions that were modeled. These motions only occurred near the surface and were not present higher in the atmosphere as they were in the original simulations since surface sensible heat flux was absent (Figure 4.9). At 400 m, vertical motions were small and never evolved into strong regions of upward or downward motion.

Pollen transport was reduced when sensible heat flux was removed (Figure 4.10). Pollen deposition was mostly confined to the source region on 17 Jun and confined to a few kilometers on 28 Jun. The reduced movement of pollen was likely caused by a lack of upward motion over the source region to prevent pollen from settling to the surface quickly. Winds on these days were generally from the southeast and crossed a long stretch of relatively flat terrain that did not induce much vertical motion due to the lack of thermally-induced turbulence. On 24 Jun, pollen transport was also reduced, but some pollen grains traveled over 20 km. On this day, winds from the northwest traveled up the valley wall before reaching the source, creating mechanical turbulence which was able to loft some pollen grains, allowing them to move farther with the horizontal wind before settling.

The trajectories of pollen grains that were transported more than 20 km from their source differed from those in the simulations including sensible heat flux. Pollen grains in these cases remained closer to the surface until they were subject to a single burst of lifting caused by mechanical turbulence generation from the valley wall. There is still some evidence of eddy-like behavior but the random motions used by the dispersion model to represent small-scale turbulence appear to dominate the particles’ trajectories.
4.3.3 Effects of Terrain

Removing terrain resulted in smoother and more homogeneous wind fields across the domain (Figure 4.11). Wind direction and speed were nearly uniform over the model domain in the morning. As convective turbulence increased through the day, the wind direction varied but remained generally uniform. Wind speeds also varied and weakened slightly in the afternoon. Wind speeds over the pollen source were typically faster than in simulations containing complex terrain, likely because the wind was unimpeded by variations in surface height. On 28 Jun, winds remained from the northeast throughout the day rather starting as southerly winds as they did in the original simulations.

Vertical motions were similar over the entire domain and exhibited none of the strong motions that were previously observed along steep slopes (Figure 4.12). In the morning, updrafts and downdrafts were weak due to the lack of resolved buoyant instability. The few vertical eddies that did exist extended over broad regions spanning many kilometers. In the afternoon, these motions became stronger as buoyant instability increased as a result of surface sensible heat flux and turbulent eddies became more resolved. Vertical motions at 400 m were much stronger than at the surface (Figure 4.13). The stronger motions indicate the presence of large turbulent eddies that characterize the boundary layer. Without complex terrain, these motions existed throughout the domain. The only exceptions existed along the upwind side of the model boundary which artificially prevented turbulent eddies from forming there.

Pollen was transported tens of kilometers along flat terrain on each day (Figure 4.14). Less pollen was deposited within the source region and more pollen was deposited downwind compared to the first simulations. This was due to faster wind speeds that were not slowed down by complex terrain. The direction of dispersion differed from previous simulations as a result of the difference in mean wind direction during the day.

Pollen traveling more than 20 km was still lifted by turbulent eddies similar to the full simulations. Since wind speeds were generally faster, less time was required to reach distances greater than 20 km. The maximum height of pollen trajectories was reduced slightly with only a couple of the selected pollen grains reaching heights of 1 km or more.
Most of these pollen grains remained below 500 m and a few remained below 100-200 m for most of their flight.

### 4.4 Conclusions

We examined the effects of surface sensible heat flux and complex topography on lifting and transporting pollen. Vertical motions from surface sensible heat flux or complex topography alone are capable of lifting pollen grains and allowing them to be transported many kilometers from their source. However, dispersion without one of these mechanisms did not produce similar results to the full simulations or to observed outcrossing reported by Watrud et al. (2004). Accurate understanding and modeling of both surface sensible heat flux and complex topography are necessary to create realistic simulations of pollen dispersion in complex terrain.

On each day, pollen deposition tended to follow local terrain, particularly far from the sources. Near the source field, patterns were less clear because pollen was deposited prior to upslope flow developing in the valleys around the source. Later in the day, after upslope flow was established, pollen was prevented from settling in the valleys and instead was deposited along the valleys following the terrain contours.

Pollen that was transported to the vicinity of the mountains south and east of the source was generally only deposited on the leeward side of the mountains. The updrafts along the windward side of the mountains, created by the sloping terrain and the convergence of winds, were sufficient to lift pollen over the mountain. The downdrafts on the lee of the mountain tended to force pollen to be deposited.

In simulations including both surface sensible heat flux and complex topography, pollen traveling greater than 20 km was lifted many hundred meters. Pollen grains were still lifted when sensible heat flux was removed, but the maximum height of pollen grains was reduced by more than half. The vertical motions created by complex topography were sufficient to prevent pollen grains from settling but could not lift pollen as high as vertical motions caused by buoyant instability. Removing complex terrain reduced the maximum height of pollen grains only by a few hundred meters. A surprising result was that some pollen grains remained within a couple hundred meters of the surface for longer spans, which
was not noticed in simulations that included complex terrain. This suggests that complex terrain may enhance deposition for pollen that remains low in the atmosphere. Small turbulent eddies created by surface wind shear may contribute to this behavior.

Surface sensible heat flux appears to be the dominant lifting mechanism in this study, perhaps because the pollen source was located in a broad plateau with only the steep valley walls to the north and west providing topographic influences. The presence of topography can add additional lift that may help pollen move over mountains. The lack of pollen spending long periods near the surface in the original simulations suggests complex terrain may inhibit the flow of pollen low in the atmosphere.

Pollen deposition in and around valleys was affected by the presence of thermally-induced turbulence while deposition around mountains was affected by mechanically-induced turbulence. Very few pollen grains were deposited on the upwind slopes of mountains or within valleys that were sufficiently removed from the pollen source. The mountains’ blocking effect slows the wind, forcing winds to move laterally around the mountain and strengthen upward motion due to convergence. This suggests that pollen reaching the windward slopes would more likely be directed around or over the mountain rather than be deposited on the windward side. In the case of valleys, if pollen transport to the valley takes long enough that upslope flow can begin the valley may be adequately isolated from adventitious pollen. These results suggest possible locations for planting crops that have greater purity requirements.

Bentgrass pollen is about 20 µm in diameter and has a small terminal fall speed of approximately 0.02 m s⁻¹ (Pfender et al., 2007). We have described the effects of surface sensible heat flux and complex topography on the dispersion of bentgrass pollen and expect that similar effects would be noticed on other particles, although differences in particle size may create different results. For example, heavier particles such as maize pollen which have greater terminal velocities may be more easily deposited in valleys or on the windward sides of mountains since greater vertical velocities would be necessary to prevent them from settling.
4.5 References


Figure 4.1. Model domains (left) and the topography of the innermost domain (right) used by WRF. The outlined region on the topography map is the region pollen was released from.
Figure 4.2. Horizontal wind fields predicted by WRF for the original simulations including surface sensible heat flux and complex terrain. Longer vectors indicate stronger wind speed and contours indicate 100 m intervals of terrain height.
Figure 4.3. Vertical wind speed (m s\(^{-1}\)) just above the surface for the original simulations including surface sensible heat flux and complex terrain.
Figure 4.4. Vertical wind speed (m s\(^{-1}\)) 400 m above the surface for the original simulations including surface sensible heat flux and complex terrain.
Figure 4.5. Pollen deposition for each day in the original simulations including surface sensible heat flux and complex topography and sample pollen trajectories for pollen grains that traveled at least 20 km (lower right). Contours on the deposition plots indicate 100 m intervals of terrain height.
Figure 4.6. Examples of pollen deposition around a valley on 17 Jun and around a mountain on 24 Jun. Shaded regions indicate pollen deposition, contours indicate 100 m intervals in topography height, tick marks on the contours indicate the downhill direction, and arrows indicate wind direction and relative speed.
Figure 4.7. Horizontal wind fields predicted by WRF for the simulations with surface sensible heat flux (SSHF) removed. Longer vectors indicate stronger wind speed and contours indicate 100 m intervals of terrain height.
Figure 4.8. Vertical wind speed (m s\(^{-1}\)) just above the surface for the simulations with surface sensible heat flux (SSHF) removed.
Figure 4.9. Vertical wind speed (m s$^{-1}$) 400 m above the surface for the simulations with surface sensible heat flux (SSHF) removed.
Figure 4.10. Pollen deposition for each day in the simulations with surface sensible heat flux (SSHF) removed and sample pollen trajectories for pollen grains that traveled at least 20 km (lower right). Contours on the deposition plots indicate 100 m intervals of terrain height.
Figure 4.11. Horizontal wind fields predicted by WRF for the simulations with flat terrain. Longer vectors indicate stronger wind speed.
Figure 4.12. Vertical wind speed (m s$^{-1}$) just above the surface for the simulations with flat terrain.
Figure 4.13. Vertical wind speed (m s$^{-1}$) 400 m above the surface for the simulations with flat terrain.
Figure 4.14. Pollen deposition for each day in the simulations with flat terrain and sample pollen trajectories for pollen grains that traveled at least 20 km (lower right).
CHAPTER 5. INCREASED POLLEN VIABILITY RESULTING FROM TRANSPORT TO THE UPPER BOUNDARY LAYER

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Brian J. Viner and Raymond W. Arritt

Abstract

Previous studies have examined the rate of viability loss in pollen grains based on surface conditions but some pollen grains are lifted throughout the atmospheric boundary layer to heights where temperature and moisture differ markedly from near the surface. This transport may affect pollen viability, as pollen viability in maize is linked to its moisture content. Using Large-Eddy Simulation, we have examined the effect of boundary layer transport on pollen viability. We compared viability diagnosed using surface measurements at the pollen source to viability diagnosed using the atmospheric conditions following the pollen grain’s trajectory as it moves through the atmospheric boundary layer. Use of surface values provides a reasonable prediction of viability for pollen grains that travel less than a kilometer from the source field, but underpredicts pollen viability by as much as 20% for pollen that travels several kilometers. The difference is attributed to the tendency for longer range transport to require lofting of pollen grains into the upper part of the atmospheric boundary layer, where cooler temperature and higher relative humidity are conducive to increased viability. We conclude that pollen grains traveling many kilometers may be more likely to pollinate a receptive silk than would be expected based on atmospheric conditions at the pollen source.

5.1 Introduction

The adoption of genetically modified (GM) crops has raised concern that GM plants may pollinate compatible non-GM varieties to produce undesired hybrids. One crop of concern is maize (Zea mays L.), which is anemophilous; it relies predominantly on atmospheric dispersion by wind to transport pollen from source to receptor plants. When
pollen reaches a silk, it must be viable for fertilization to take place. Therefore, knowledge of atmospheric conditions during dispersion is necessary to make accurate predictions of viability upon deposition.

Viability decreases as a pollen grain’s moisture content decreases (Fonseca and Westgate, 2005; Aylor, 2003). Once pollen is released from the anther, the rate of moisture loss from the pollen grain to the atmosphere is determined by the vapor pressure deficit (VPD) of the atmosphere (Aylor, 2003). When the atmosphere is warm and dry, VPD is large so that pollen grains rapidly lose moisture and viability. Conversely, cool and humid conditions promote moisture retention and increased viability.

The length of time that pollen remains viable and the maximum isolation distance to prevent cross-pollination have been estimated using surface conditions near a source field (e.g., Luna et al., 2001) but such estimates do not account for movement of pollen to heights well above the surface. Boehm et al. (2008) measured pollen concentration up to 1 grain m\(^{-3}\) at 200 m above ground level under convective conditions, while Brunet et al. (2004) observed pollen distributed throughout the daytime boundary layer, which is around 1000 m deep on typical clear summer days in the temperate mid-latitudes. Meteorological conditions at heights of several hundred meters or more can differ substantially from conditions at the surface. For example, on a typical clear summer day, the atmospheric water vapor mixing ratio remains nearly constant throughout the depth of the boundary layer while temperature decreases at approximately the dry adiabatic lapse rate, so that VPD decreases with height (Figure 5.1). Pollen grains lifted to heights where VPD is lower than at the surface may remain viable longer since moisture will not be lost as quickly. Horizontal winds at these heights may also be stronger than surface winds, transporting pollen farther from its source. These differences may result in inaccurate predictions of viability and isolation distance.

To examine the effects of changing atmospheric conditions on pollen grains lifted throughout the boundary layer, we have combined a Large-Eddy Simulation (LES) model with a Lagrangian particle dispersion model to simulate the movement of pollen and predict pollen viability upon deposition for a typical summer day. This approach has been previously used to predict pollen dispersion (Viner, 2007). Within this framework, we have diagnosed and compared pollen viability upon deposition using two approaches. The first
approach diagnoses viability using only conditions at the pollen source, corresponding to the method used in some field studies. The second approach diagnoses viability based on changing conditions encountered by pollen grains as they move through the atmosphere.

### 5.2 Predictive Models

#### 5.2.1. Large Eddy Simulation

Large eddy simulation (LES) was used to predict the atmospheric conditions for pollen dispersion by predicting the turbulent atmospheric eddies that redistribute heat, moisture and momentum in the daytime boundary layer. The smallest eddies that can be resolved are around 4 to 8 times larger than the model grid spacing; turbulent motions from eddies too small to be resolved are parameterized by a closure scheme that estimates subgrid quantities in the turbulence equations (Stull, 1988).

We used the Advanced Regional Prediction System (ARPS) as an LES model to simulate conditions at a field site near Ankeny, IA for 9 Aug 2003. This date was chosen because it was known to exhibit the temperature and moisture characteristics of a typical clear summer day described above and had been previously shown to exhibit long-distance dispersion in simulation (Viner, 2007). ARPS is a three-dimensional, time-dependent, compressible and non-hydrostatic atmospheric model developed at the Center for Analysis and Predictions of Storms at the University of Oklahoma and is described in Xue et al. (2000; 2001). Our domain was 10 km x 10 km with 100 m grid spacing in the horizontal directions and 5 km with 50 m spacing in the vertical direction. A vertical sounding was used to provide horizontally homogenous initial conditions. Since there is no radiosonde site in central Iowa, soundings from Davenport, IA and Omaha, NE at 12 UTC were averaged to estimate a vertical sounding near Ankeny. The surface was modeled as a homogeneous cultivated region with roughness length of 0.06 m and vegetation fraction of 0.7. These parameters were chosen to represent general surface characteristics of a large expanse of mature maize.

ARPS modeled the atmospheric variables necessary to predict dispersion and viability: three dimensional winds, turbulence kinetic energy, potential temperature and specific humidity. Subgrid-scale turbulence was parameterized using the 1.5 order closure
option. Results were recorded at one minute intervals of simulated time and used to drive the dispersion model.

### 5.2.2 Pollen Dispersion Model

The pollen dispersion model used for this study has been described in Arritt et al. (2007) where its predictions were compared to observations. Three-dimensional movement of pollen is simulated using the mean and turbulent wind components,

\[ x_{ik}(t + dt) = x_{ik}(t) + dt\left[ u_{ik}(t) + u_{0ik}(t) \right], \]

where \( x_{ik} \) is the position of the \( i^{th} \) particle in the \( k \) direction, \( u_{ik} \) is the mean wind speed and \( u_{0ik} \) is the simulated random component of the wind to account for unresolved turbulence. The timestep used in the model was \( dt = 2 \) s. \( u_{0ik} \) was calculated following a first-order Markov process as

\[ u_{0ik}(t + dt) = u_{0ik}(t)R_{ik}(dt) + \left[ 1 - R_{ik}(dt)^2 \right]^{1/2} q\sigma_{ik}, k = 1,2,3 \]

where \( R_{i,k} \) is an autocorrelation value, \( q \) is a normally distributed random number with a mean of 0 mean and variance of 1, and \( \sigma \) is the standard deviation of the wind speed in the \( k \) direction. \( R_{i,k} \) acts as a memory of the turbulence at the previous timestep and is determined by the particle’s Lagrangian timescale in the \( i \)th direction, \( \Gamma_{p,i}: \)

\[ R_{ik}(dt) = \exp \left( \frac{-dt}{\Gamma_{p,i}} \right) \]

As \( R_{i,k} \) decreases from 1 to 0, a particle’s turbulent motion goes from constant in time to completely random.

In the horizontal directions, we assume that the particle timescale equals the fluid timescale, given by

\[ \Gamma_{p,k} = \frac{z}{2\sigma_k} \]

In the vertical, the particle timescale will not be equal to the fluid timescale because heavy particles lose memory faster than the flow (Csanady, 1963). Instead, the particle timescale in the vertical direction is given as
where \( v_T \) is the particle’s terminal fall speed in still air and \( \beta \) is a dimensionless coefficient set to 1.5. The terminal fall speed was set to 0.2 m s\(^{-1}\) following Arritt et al. (2007).

A drift correction term \( (w_c) \) was added to the vertical component of the particle’s motion and defined following Legg and Raupach (1982)

\[
\Gamma_{p,3} = -\frac{\Gamma_{L,3}}{\sqrt{1 + \left( \frac{\beta v_T}{\sigma_w} \right)^2}}
\]  

(5)

With the above additions, Eq. 1 becomes

\[
x_{ik}(t + dt) = x_{ik}(t) + dt[u_{ik}(t) + u_{0ik}(t) + \delta_{k,3}(w_c + v_T)]
\]

(7)

The pollen source was assumed to be a 75 m by 75 m field located near the upwind boundary of the model domain. Since winds were from the east, the source field was placed two kilometers away from the eastern boundary of the model and equidistant from the northern and southern boundaries to provide a large region to evaluate pollen dispersion. Pollen was released continuously between 0800 and 1600 Local Daylight Time (LDT) from 625 point sources evenly spaced within the source field. The pollen source strength was assumed to be constant during the day, with pollen grains being released from each point source every timestep between 0800 and 1600. Pollen grains were tracked until they either left the model domain or dropped below a height of one meter, the typical height of receptive silks, when they were considered to be deposited. The distance traveled and the length of time a grain was suspended in the atmosphere were recorded by the model, and the grain’s viability was diagnosed using conditions encountered along its trajectory from the source following the procedure described in the next section.

### 5.2.3 Viability Model

Viability of the \( i^{th} \) pollen grain was calculated following Fonseca and Westgate (2005) as a function of pollen moisture content \( (PMC_i) \)

\[
V_i = 100\% \left( \frac{PMC_i - 0.288}{0.632 - 0.288} \right)
\]

(8)

where \( PMC_i \) is given as a function of the accumulated vapor pressure deficit \( (VPDT_i) \).
\[ PMC_i = 0.632 \exp\left(-1.5 \times 10^{-5} VPDT_i\right) \]  

The accumulated vapor pressure deficit over time \((VPDT_i, \text{mbar} \cdot \text{s})\) is

\[ VPDT_i = \int_{t=0}^{t_{dep}} VPD_i(t) \, dt \]  

\(VPD\) was calculated using saturation vapor pressure, which is a function of temperature (Bolton, 1980), and vapor pressure, which was determined by the amount of water vapor in the atmosphere (here described as relative humidity),

\[ e_{sat,i} = 6.11 \exp\left(\frac{17.67T}{243.50 + T}\right) \]  

\[ e_i = \frac{w}{w + 0.622} p \]

\[ VPD_i = \left(e_{sat,i} - e_i\right) \]

where \(T_i, w, p, VPD, e_{sat,i}\) and \(e_i\) are the temperature \(^\circ\text{C}\), water vapor mixing ratio, atmospheric pressure (mbar), vapor pressure deficit (mbar), saturation vapor pressure (mbar) and vapor pressure (mbar) of the air surrounding the \(i^{th}\) pollen grain.

The value of \(VPDT\) upon pollen deposition was calculated two ways. The first used

\[ VPD_{i,t} = VPD_{src,i} t_{dep,i} \]  

In this approach, \(VPD_{src,i}\) is a constant value taken as the VPD at the pollen grain’s source when it is released and \(t_{dep}\) is the length of time the particle is suspended in the atmosphere. Predicting viability by tracking a grain along its flight was done in a similar manner, but instead of using a constant \(VPD\), a new value was determined for each timestep \((VPD_{i,t})\) and \(VPDT_i\) is given as

\[ VPDT_i = \sum_{t=0}^{t_{dep}} VPD_{i,t} \, dt \]

where \(dt\) is the timestep of the dispersion model. This method allows for changing atmospheric conditions encountered along the pollen grain’s trajectory to influence accumulated vapor pressure deficit and thereby alter the rate of viability loss.
Summarizing the procedure above, we interpret pollen viability following Fonseca and Westgate (2005) as the percent chance that an individual pollen grain from a sample of similar grains is capable of pollinating a silk. Viability in turn depends on pollen moisture content, which gradually decreases at a rate determined by the atmospheric demand for water vapor reflected by VPD. Pollen grains are assumed to have a PMC of 63.2% when they are first released (Fonseca and Westgate, 2005; Kerhoas et al., 1987; Roeckel-Drevet et al., 1995) and are not expected to pollinate a silk when their PMC is below 28.8%.

5.3 Results and Discussion

5.3.1 Large Eddy Simulation

Horizontally averaged profiles of wind, temperature and mixing ratio for four selected times show their simulated evolution (Figure 5.2). Mixing ratio remained nearly constant through the boundary layer and changed little through the day. Temperature increased with time at the surface due to surface heating from solar radiation and decreased with height to the top of the boundary layer. The vertical gradient of vapor pressure deficit was found to increase through the day, reflecting the exponential dependence of saturation vapor pressure on temperature.

Since water vapor mixing ratio, analogous to vapor pressure ($e$), was nearly constant with height while the saturation mixing ratio, analogous to saturation vapor pressure ($e_{sat}$), is proportional to temperature and decreased with height, VPD decreased with height to the top of the boundary layer following Eq. 10. The simulated atmospheric profile is consistent with the typical profile discussed earlier (Figure 5.1) and the boundary layer reached a height of 1100 m in late afternoon.

5.3.2 Pollen Dispersion

The height of the boundary layer is determined by the action of turbulent motions originating near the surface. Since these motions are the primary mechanism lifting pollen, vertical dispersion is typically limited to the boundary layer. Horizontally-averaged profiles of pollen concentration at three times (Figure 5.3) are consistent with measured profiles taken
by Brunet et al. (2004) who found that pollen concentration decreased rapidly with height in the late morning and became greater and more uniform with height during the afternoon.

As turbulent mixing increased, the boundary layer increased in height and pollen was lifted higher. Pollen concentration throughout the boundary layer also increased since updrafts were sufficient to prevent pollen from settling to the surface. Late in the afternoon, pollen concentration was well-mixed in the upper-half of the boundary layer. The concentration at most heights above 400 m was approximately 1% of the concentration near the surface. Since wind speed in the boundary layer typically increases with height, this suggests that a few percent of pollen grains released may reach heights where strong winds will cause them to travel farther, as seen in our simulation (Figure 5.4).

### 5.3.3 Pollen Viability

To determine the relationship of pollen height to the rate of viability loss for individual pollen grains, we selected individual particles that were lifted to heights greater than 400 m and predicted their rate of viability loss using either conditions at the source when they were released or changing atmospheric conditions encountered during its flight. Figure 5.5 shows an example of one such particle that is representative of the general results. The pollen grain followed the turbulent motions of the atmospheric boundary layer and the broad updrafts and downdrafts that affected it can be identified. Using the surface conditions at the source to diagnose the rate of viability loss yields a constant rate of viability loss such that pollen grains become completely non-viable within 1.75 hours.

Viability diagnosed following conditions along the pollen trajectory typically produced a rate of loss less than that diagnosed using constant values of temperature and humidity. The rate of viability loss varied inversely with height, with rates greater near the surface and lower rates aloft. This is attributed to changes in VPD as the pollen grain increased or decreased in height. As pollen was lifted, VPD around the grain was reduced and the rate of viability loss decreased; the opposite was true as the pollen grain fell. In this example, the pollen grain remained viable for 2.5 hours. When examining all simulated pollen grains, a consistent relationship was found between the maximum height a pollen grain reached and its viability upon deposition (Figure 5.6). At each height, viability was
greater when predicted following the pollen trajectory. This difference increased for pollen grains that reached greater heights.

Evaluations of viability for pollen grains deposited within a few hundred meters of their source showed little difference between the two approaches for diagnosing viability (Figure 5.7). This is explained by these grains not being lifted to heights greater than 100-150 m (Figure 5.4). As a result, they were not subject to conditions appreciably different from the surface for a long period of time. Differences were greater for pollen grains deposited farther from their source. Pollen dispersed over 5 km was diagnosed to have viability as much as 20% higher using conditions following the pollen trajectory rather than constant conditions taken at the source. These pollen grains were lifted at least 100 m into the atmosphere and experienced temperature and humidity different from the source for most of their transit time from source to receptor.

While lifting pollen into the atmosphere should increase its lifetime, pollen lifted higher than 500 m and deposited within the model domain was still diagnosed to have lost its viability despite the reduced rate of viability loss (Figure 5.6). This result suggests that while pollen viability at distances of several kilometers from a pollen source may be greater than expected based on surface meteorological conditions, an upper limit still exists for the dispersion of viable pollen. The value of this limit will vary depending on the meteorological conditions prevailing in a particular circumstance: strong winds, cool temperatures, and vigorous turbulence will tend to promote long-distance transport of viable pollen.

5.4 Conclusions

Our results suggest that pollen viability upon deposition may be higher than estimated using methods based on surface meteorological measurements, particularly for pollen traveling more than a kilometer from its source. Since the upper region of the boundary layer tends to have stronger winds and lower VPD, the turbulent transport of pollen to this region may extend the distance pollen can travel and reduce its rate of viability loss. This suggests that predictions of viability for pollen traveling many kilometers may be inaccurate if only atmospheric measurements at the pollen source are considered.
The meteorological variables necessary to predict VPD – water vapor mixing ratio and temperature – do not typically vary greatly on horizontal scales of a few hundred meters. Since particles landing within a few hundred meters of their source are generally not lifted high in the boundary layer and are not suspended long before being deposited, they are not subject to conditions that appreciably differ from those at their source. Thus, predictions of pollen viability using only temperature and water vapor mixing ratio measurements at the source are appropriate to determine viability for pollen traveling distances up to a few hundred meters. Pollen traveling farther is usually lifted and subject to lower VPD than at the surface. Diagnosis of viability following the trajectory of a pollen grain predicted the average pollen viability to be as much as 20% higher compared to values obtained using surface meteorological conditions.

Aylor (2003) suggested that different methods of modeling dispersion are required for short- and long-distance pollen transport. A similar idea can be proposed for viability, identifying a short-distance regime where pollen is not lifted into the boundary layer and source measurements are sufficient to predict pollen viability and a long-distance regime where pollen is lifted throughout the boundary layer and conditions at the pollen source may not be able to adequately predict pollen viability. Taking both the results obtained here and the recommendations of Aylor (2003) into account, we recommend that methods used to predict short-distance pollen dispersion and outcross likely cannot be extrapolated to situations involving longer distances.

Finally, we note that direct verification data for our viability computations presently are unavailable. The great majority of previous field studies of pollen dispersion and viability have focused on distances less than 1 km from source to receptor. Our results are consistent with the observations of Brunet et al. (2004), who measured maize pollen concentration and viability using aircraft flights. They found viable pollen present at all levels of the boundary layer. Their observations, combined with our modeling results, suggest that field studies should be undertaken to measure maize pollen transport and viability over distances of at least 5 km.
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5.6 References


Figure 5.1. Measurements of temperature (thin line) and mixing ratio (dashed line) taken from a sounding at Davenport, IA at 00 GMT, 16 August 2006. The vapor pressure deficit (VPD; thick line) was calculated from these variables. The boundary layer height at this time was approximately 1150 m.
Figure 5.2. Simulated profiles of temperature (thin line), mixing ratio (dashed line) and vapor pressure deficit (thick line) for 0800 LDT (top-left), 1100 LDT (top-right), 1400 LDT (bottom-left) and 1700 LDT (bottom-right).
Figure 5.3. Vertical profiles of pollen concentration at 1000 LDT (solid line), 1300 LDT (dashed line) and 1600 LDT (dot-dash line). The boundary layer height is ~ 400 m at 1000, 900 m at 1300 and 1100 m at 1600 LDT. Pollen concentration was averaged over the model domain ($10^4$ km$^2$) and over 20 m vertical increments.
Figure 5.4. Comparison of the maximum height and the distance traveled by pollen grains. Shading indicates the number of pollen grains at each height and distance.
Figure 5.5. Variations in the rate of viability loss using only source conditions (thin dashed line) and changing conditions (thick dashed line) as the height of the pollen grain changes (solid line).
Figure 5.6. Comparison between the average predicted viability upon deposition and the maximum height reached using meteorological measurements only at the source and changing conditions along the pollen grain’s trajectory. The dashed lines indicate one standard deviation of predicted viability for the pollen grains reaching a certain height.
Figure 5.7. Comparison between the average predicted viability upon deposition and the distance traveled using meteorological measurements only at the source and changing conditions along the pollen grain’s trajectory. The dashed lines indicate one standard deviation of predicted viability for the pollen grains reaching a certain distance.
CHAPTER 6. GENERAL CONCLUSIONS

The potential for cross-pollination of conventional or wild plants by genetically-modified relatives has prompted field studies and the creation of numerical models to examine the potential for unintended spread of genetic material. Attention has been given to cross-pollination occurring within hundreds of meters but recent evidence has suggested that outcross could occur at greater distances. This dissertation presented methods of improving predictions of pollen shed, dispersion, and viability in an effort to improve the prediction of pollen movement and the identification of non-target fields that may be at risk for outcross.

The pollen shed model uses measurements of temperature, solar radiation and atmospheric moisture to predict diurnal variations in shed. The model was created using data from a field study and controlled experiments. The model captured the diurnal range of pollen shed and predicted the time of peak pollen shed on most days. One feature of measured pollen shed that the model cannot predict in its current form is the occurrence of secondary peaks. Sampling more frequently may be necessary to determine if a meteorological relationship exists to predict when secondary peaks will occur.

Lagrangian dispersion models have been used to predict dispersion of atmospheric gases and pollutants in complex terrain but using them to predict pollen dispersion in complex terrain is a new application. We demonstrated that combining a mesoscale meteorological model with a Lagrangian dispersion model was able to predict pollen transport to locations where outcross had been previously reported. Pollen deposition followed the terrain and gaps in pollen deposition patterns were noticed in valleys and on the windward slopes of mountains. These results indicate that pollen dispersion is affected by processes that are not present over flat terrain.

These results prompted an examination of the effects of topography and surface sensible heat flux on pollen dispersion. Surface sensible heat flux generated thermally-driven eddies that lift pollen and extend the distance it can potentially travel. Topography caused mechanically-generated flow which has a strong effect near the surface but less impact higher in the boundary layer. The primary effect of topography was to create convergence on the windward sides of mountains, creating additional lift that prevented
pollen from settling on the windward side. Pollen deposition was also absent in valleys more than a few kilometers from the pollen source. It is thought that by the time pollen was transported to these valleys, thermally-driven upslope flow prevented the pollen from settling into the valley and instead deposited it along the edges of the valley.

When pollen reaches a receptive plant, the chance that it will successfully pollinate the plant is described by its viability. Current methods of estimating pollen viability are typically based on surface measurements at the pollen source. This was found to be inadequate for pollen that is transported more than a few kilometers from the source. When viability was predicted for maize pollen using the changing conditions experienced along its trajectory, it was expected to be as much as 30% higher than if surface measurements were used.

The methods used here are not limited to predicting the behavior of maize or bentgrass pollen. They can potentially be used to predict the movement of pollen from other plants, seeds, or other particles that are transported through the atmosphere by making small changes to the characteristics of the simulated particle. This versatility makes the models used in this research and the conclusions reached applicable to a variety of situations.
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