



Quantifying maize pollen movement in a maize canopy

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Abstract

An accurate assessment of the amount of pollen released in a cornfield that reaches the female flowers (silks) is important for determining both the amount and purity of seeds produced. A method for making this assessment is presented. In this method, the movement of maize pollen in and above a crop canopy is evaluated using a combination of measurements and modeling. In particular, concentrations, C (grains m^{-3}), and downward vertical fluxes, F_v (grains $\text{m}^{-2} \text{s}^{-1}$) of pollen were measured at several heights inside and above a flowering maize canopy, and a Lagrangian stochastic (LS) simulation model was used to calculate concentrations and fluxes of pollen at these locations. Model estimates for the average release rate of pollen grains per area of crop, Q (grains $\text{m}^{-2} \text{s}^{-1}$) were deduced by comparing measured and modeled values of C . Using these determinations of Q , the model predicted well ($r^2 = 0.73$) the measured pollen fluxes in the canopy. On average, about 20% of the pollen released by the tassels reached the height of the silks in the canopy. Fluxes of pollen at silk height were highly variable, however. This variability was mainly due to the faster wind speeds and higher levels of turbulence in the upper canopy, which led to greater amounts of rebound and re-entrainment of pollen grains from leaves. The results of this study underscore the importance of rebound and re-entrainment processes in the amount of maize pollen reaching the silks.

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1. Introduction

In order to design seed production fields for both optimum yield and seed purity, it is important to be able to predict the fraction of pollen released by the male parent that will reach the female flower (silks) of the female parent plants. This is important not only for evaluating fertilization potential for pollen

released within the seed production field itself but also for evaluating the potential competition for the silks between locally produced pollen and pollen arriving at the top of the canopy from an outside source, which might contribute unwanted genetic material to the seeds. Understanding pollen movement in crop canopies is also clearly important for evaluating potential genetic contamination in conventional production fields.

In maize, pollen is released near the top of the plant. In order to fertilize the ovules it must reach the silks,

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which are typically located near mid-canopy height and lie below half or more of the canopy leaf area. By intercepting pollen drifting toward the silks, plant leaves compete strongly with the silks for the available pollen (Aylor et al., 2003). Thus, to evaluate seed set and purity, it is important to be able to quantify pollen movement in the canopy and to understand how crop and environmental factors might affect it.

The purpose of this study is to quantify pollen movement in a maize canopy, with an emphasis on evaluating the fraction of pollen released in the field that reaches the silks. The approach taken was to first measure pollen concentrations and fluxes in and above a field of maize and to then compare the results with a Lagrangian stochastic (LS) simulation model (Aylor and Flesch, 2001). The combination of measurement and modeling presented here offers a new approach for evaluating pollen fluxes to silks. Important components of the model are rebound and re-entrainment (Paw U, 1983; Aylor and Ferrandino, 1985; Aylor et al., 2003) which are shown here to have an important effect on the amount of pollen reaching the silks.

2. Methods

2.1. Crop canopy and pollen source

Experiments were conducted in two adjacent plots of maize (*Zea mays* L.) located on Lockwood Farm in Mt. Carmel, CT. The plots were 24.4 m wide in the N–S direction (perpendicular to the rows) and 65 m long in the E–W direction (along the rows) and were planted next to one another (along the long axis of the plots) with a 1.5-m alleyway between them. Within these plots, commercially available hybrid maize (37M81, Pioneer Hi-Bred International, Des Moines, Iowa) was planted in rows spaced 0.76 m apart and grown using standard agronomic practices. The first (southernmost) plot was planted on 17 May and the second plot was planted on 2 June 2004. Measurements were conducted during flowering in two successive periods in July–August 2004. During both periods of pollen shed, the height of the canopy in both plots was approximately the same, resulting in a nearly uniform height canopy 50 m by 65 m block of maize. The field containing both plots is almost flat and is

situated at the top of a slight (1–2°) rise from the northerly, westerly, and southerly directions. Low crops (0.5 m or less) were planted about 25 m from the southerly edge of the field. The wind direction was generally either northerly or southerly when pollen dispersal measurements were made.

The leaf area of the maize canopy was determined for each planting at the time of flowering (26–27 July in Planting 1 and 3 August in Planting 2). Randomly selected plants were destructively sampled to determine leaf area (one-sided) per plant. The leaf area index (*LAI*) for the crop was estimated by multiplying the average leaf area per plant by the number of plants per unit ground area in the field. The average plant density (N_p) was 12.1 plants m^{-2} in both plantings. *LAI* was 5.81 ± 0.57 in Planting 1 and 5.87 ± 0.66 in Planting 2. Canopy height, h , (measured to the top of the fully extended tassels) was 2.89 (± 0.17) m in Planting 1 and 2.95 (± 0.12) m in Planting 2. The top of the foliage was at 2.56 (± 0.2) m in Planting 1 and 2.59 (± 0.12) m in Planting 2. In the model simulations (described below), we let the source height vary along the vertical extent of the tassel (2.72 ± 0.15 m). Silk height was at 1.5 m and the stem area index (*SAI*) was 0.4 in both plantings.

An estimate for the potential number of pollen grains released per plant per day during sampling was obtained by enclosing the tassels on five to eight randomly chosen plants in breathable plastic bags (Pantek, Montesson, France) on the preceding evening. The bagged tassels were collected intact following the sampling runs, and were stored upside down and allowed to dry. Pollen was recovered from the samples and weighed. For a subset of these samples, counts were made for a known weight of pollen and a relationship between the number of pollen grains and weight of the sample was determined using regression analysis.

2.2. Airborne concentrations of pollen

Aerial concentrations of maize pollen, C (grains m^{-3}), were measured in and above the crop canopy using rotorod samplers with retracting-type sampling heads (Model 82, Sampling Technologies, Inc., Los Altos Hills, CA). A vertical sampling array of five rotorods was supported by a pole located near the center of the source areas (Fig. 1). The pollen

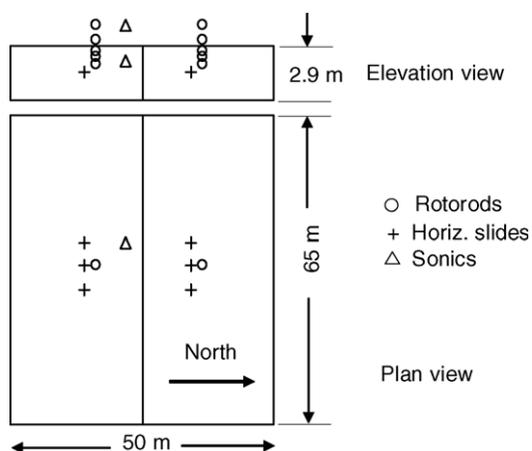


Fig. 1. Schematic of the elevation and plan views of the experimental plots showing the locations of the rotorods, horizontal slides and the sonic anemometers (elevation view not drawn to scale).

collection rods were located at heights of 1.9, 2.3, 2.6, 3.2, and 4.0 m above the ground. Pollen sampling periods were generally begun between 08:00 and 09:35 local standard time (LST) and lasted for 1 h. Three to four 1-h periods were carried out on each of eight days of sampling during pollen shed (24 July–4 August), giving a total of 29 sampling periods.

The sampling surfaces of the rotorods were coated with a thin layer of high vacuum silicone grease (Dow Corning Corp., Midland, MI). Maize pollen grains deposited on the sampling surfaces were counted using a microscope at 50 \times magnification. These counts were converted to pollen concentrations by accounting for the sampling rate (38 L min⁻¹), the duration of the sampling period, and the efficiency of the sampler. The capture efficiency of the rotorod samplers for maize pollen was taken to be 0.8 (Aylor, 1993; May and Clifford, 1967; Noll, 1970).

2.3. Vertical fluxes of pollen in the canopy

Three replicate sets of greased photographic slides (35 mm) were placed at each of four heights (total of 12 slides) in the canopy during the 29 sampling periods (Fig. 1). The slides were oriented horizontally with the greased side facing upwards at heights of 0.05, 0.50, 1.00, and 1.50 m above the ground. The slides were supported by a narrow metal stake using a spring clip to grip the end. Deposited

pollen grains were counted at 40 \times in three 2.5-mm wide \times 23-mm long transects for a total of 174 mm² per slide. Fluxes of pollen (grains m⁻² s⁻¹) at the location of the slides were estimated by dividing the deposition per unit area by the duration of the exposure (usually 60 min). By virtue of their being solid, the horizontal slides impede vertical flow and do not precisely measure unimpeded pollen flux. However, at mid-canopy and below (where the slides were used) the vertical pollen flux is dominated by sedimentation (McCartney and Aylor, 1987), and the measured values should give a reasonable approximation for the flux.

2.4. Meteorological conditions

Wind speed and direction, air temperature, relative humidity, and solar irradiance were monitored continuously adjacent to the test site using a data logger (Model 21X, Campbell Scientific, Inc., Logan, UT). Wind speed and direction were measured using a cup anemometer and a vane (Model 014A and 024A, Met-One, Inc., Grants Pass, OR), both located at a height of 3.25 m above the ground. Temperature and relative humidity were measured with a probe (Model CS 500, Campbell Scientific, Inc.) that was shielded from the sun and located at a height of 2.2 m. Solar insolation was sensed by a pyranometer (Model LI-200S, LI-COR, Lincoln, NE) at a height of 2.4 m. These instruments were sampled at 10-s intervals and averaged for 20 min.

Turbulence statistics during the pollen release periods was characterized using a three-dimensional sonic anemometer (Model 81000, R.M. Young Co., Traverse City, MI) placed near the center of the maize blocks at a height of 4.0 m above the ground (Fig. 1). A second sonic anemometer, located on the same tower at a height of 2.1 m, was used to estimate 'cup' wind speed in the upper canopy. The sonic anemometers were sampled at 5 Hz. Average values of the horizontal, lateral, and vertical components of the vector wind velocity (u , v , w , respectively) and the variances and covariances between these velocity components were recorded every 20 min using a data logger (Model 23X, CSI, Logan, UT). The friction velocity, u^* (m s⁻¹), derived from the covariance of u and w , was used to scale wind velocity profiles in and above the canopy. Vertical profiles of average 'cup'

wind speed were measured during selected periods inside the canopy using a hotwire anemometer (VelociCalc[®], Model 8353-3, TSI, St Paul, MN). Additional information on wind statistics inside the canopy was obtained from the literature (Raupach et al., 1991; Wilson et al., 1982).

2.5. Lagrangian stochastic simulation model calculations

The aerial concentrations of pollen, C (grains m^{-3}), at the heights of the rotorods and the downward fluxes of pollen, F_V (grains $\text{m}^{-2} \text{s}^{-1}$), at the heights of the sticky slides in the canopy were calculated using a two-dimensional Lagrangian stochastic dispersion model. The basic LS model used here has previously been described in detail (Aylor and Flesch, 2001; Aylor et al., 2003) and is based, in large part, on several previous studies (Flesch and Wilson, 1992; Flesch et al., 1995; Rodean, 1996; Sawford and Guest, 1991; Thomson, 1987; Wilson, 2000; Wilson and Sawford, 1996). Briefly, the model numerically simulates the trajectories of pollen grains released from the tassels into a vertically inhomogeneous turbulent wind field. The location of a pollen grain in two dimensions (x, z) as it is carried along by the wind is obtained by integrating the equations that describe the increments in the alongwind and vertical air velocities (u, w) surrounding a pollen grain over a time step dt , viz.:

$$\begin{aligned} du &= a_u dt + b_u d\xi_u \\ dx &= u dt \end{aligned} \quad (1)$$

$$\begin{aligned} dw &= a_w dt + b_w d\xi_w \\ dz &= (w - v_s) dt \end{aligned} \quad (2)$$

where the Langevin coefficients $a_u, b_u, a_w,$ and b_w are functions of velocity and position; $d\xi_u$ and $d\xi_w$ are random numbers selected from independent Gaussian distributions, each having average 0 and variance dt ; and v_s is the settling velocity of the pollen grain in still air. The wind statistics used in the model were treated as horizontally uniform, so that the mean average vertical velocity (W) was set equal to zero. Details about how the Langevin coefficients are evaluated are given in Flesch and Wilson (1992) and Aylor and Flesch (2001). The model equations were solved numerically using a simulation time step $\Delta t = 0.025\tau$,

where τ is a local turbulent decorrelation timescale for heavy particles (Aylor and Flesch, 2001, Eq. (7)).

The deposition and retention of pollen on plant elements play an important role in determining how many pollen grains reach the silks. As a pollen grain drifts through the canopy, it encounters stems, leaves, ears, and silks. The probability that a pollen grain will be deposited during a model time step depends on two things: (1) the probability that a pollen grain will encounter an element of vegetation during that time step and (2) the probability that the vegetation will capture the pollen. The probability of pollen-plant encounters is calculated as a matter of course by the LS model during the calculation of pollen trajectories. The probability of pollen deposition, P_D , during the small time interval dt can be expressed as: $P_D = G \times dt$, where $G(z)$ (s^{-1}) is the relative rate of deposition per unit depth of canopy (Aylor et al., 2003).

Deposition of pollen on areas orientated at an angle α (measured from the horizontal) is calculated by assuming that particles settle onto the horizontally projected area and impact onto (or are intercepted by) the vertically projected area (McCartney and Aylor, 1987). Since in any given differential time step, these probabilities are both small, it is reasonable to assume that they act independently. The G function is written to explicitly include the retention of pollen as part of the deposition process (Aylor and Flesch, 2001):

$$G(z, t') = f_{R_1} v_P f_X a_P + f_{R_2} u_P E_1 f_Z a_P, \quad (3)$$

where v_P (m s^{-1}) is a local rate of pollen deposition (assumed here to be equal to v_s), a_P is the area density of the plant element in question (e.g., leaf area density), f_X and f_Z are the projections of a_P onto the horizontal and vertical plane, respectively, E_1 is impaction efficiency (given by Eq. (9) in Aylor and Flesch, 2001), u_P is the speed of the pollen grain (wind) approaching the target leaf or stem, and f_{R_1} and f_{R_2} are retention coefficients, which account for rebound and re-entrainment of particles from the target surfaces. G depends on t' because of the loss of water from the pollen grain and its effect on the settling speed of pollen. Through proper selection of the parameters in Eq. (3), the LS model can be readily formulated to describe deposition for different plant

parts and canopy architectures, as well as different crops and pollen species (Aylor and Flesch, 2001; Aylor et al., 2003).

When freshly released from the anthers, maize pollen is prone to rebound and re-entrainment from plant surfaces (Aylor et al., 2003). The deposition algorithm, given in Eq. (3), was parameterized to allow for the specific rebound and re-entrainment characteristics of maize pollen on maize leaves and stems. Fresh maize pollen was assumed to be re-entrained from plant leaves and stems whenever the calculated velocity at impact, V_i , was greater than a critical velocity, V_{crit} . Based on an earlier study (Aylor et al., 2003), re-entrainment of freshly released maize pollen occurs over a range of V_{crit} values from 0.3 to 0.6 m s^{-1} . Model runs conducted with V_{crit} equal to 0.45 m s^{-1} showed good overall agreement between the shapes of modeled and measured vertical profiles of pollen concentration, and V_{crit} was set equal to 0.45 m s^{-1} for all model runs compared with data (for purposes of later discussion, some model runs were also done for a wide range (0–60 m s^{-1}) of V_{crit} values). The effects of rebound and re-entrainment were modeled here by simply setting both f_{R1} and f_{R2} equal to 1 if particle speed at impact was $<V_{crit}$ and setting them both equal to 0 if u_p was $>V_{crit}$. Although more complicated formulations can easily be constructed, this simple rule captures the main effects while not succumbing to reductionism beyond our knowledge of micro particle-surface interactions.

In the model, it was assumed that rebound and re-entrainment occurred more or less instantaneously with deposition and, therefore, interactions with foliage were considered to be just another part of the particle trajectory. Based on this assumption, the pollen source was treated as a volumetric source at tassel height (simulated pollen was released from the vertical extent of the tassel). The model did not consider any of the re-entrainment to originate from previously deposited pollen, which could act as a volumetric source from within the canopy.

The LS model requires several input parameters including the settling velocity of the pollen grains, the size and area distribution of plant elements in the canopy, and several wind statistics in and above the canopy. The value of the settling velocity, v_s , of *Z. mays* pollen used in the model was 0.3 m s^{-1} (Aylor, 2002; Di-Giovanni et al., 1995). The canopy was

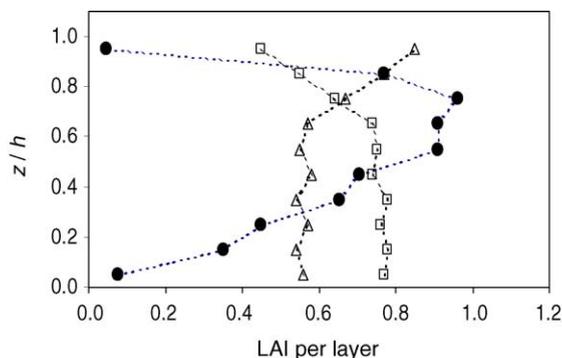


Fig. 2. Leaf area per ground area, LAI, per 0.1*h*-thick crop layer (solid circles), the fraction of horizontally projected leaf area, f_x (squares), and the fraction of vertically projected area, f_z (triangles) vs. normalized height, z/h , in the canopy. The LAI of the crop was 5.83 ± 0.58 . To obtain values for leaf area density (LAD) (m^{-1}) multiply the abscissa values by $10/h$, equal to 3.46.

conceptually divided into 10, equally-thick ($h/10$ m), vertically-stacked, horizontal slices. The vertical distribution of leaf area densities ($\text{m}^{-2} \text{m}^{-3}$) and average leaf orientation within each of these layers were determined by measurement (Fig. 2). The leaf area index for the crop was $\sim 5.8 \text{ m}^2 \text{ m}^{-2}$ in both plots. The characteristic widths of leaves (used for calculating inertial impaction of pollen onto plant parts) varied with height in the canopy and ranged from 0.015 m near the bottom to 0.064 m near the top. The characteristic width of stems was taken to be a constant 0.02 m throughout the depth of the canopy. The wind was assumed to be steady during a sampling period and the pollen source was assumed to be horizontally uniform. The roughness length and zero-plane displacement height in the model were fixed at $z_0 = 0.15h$ and $d = 0.75h$, respectively, and wind profiles were scaled with u^* and L , where L is the Monin–Obukov length (Stull, 1988). Several properties of the wind are needed to evaluate the accelerations a_u and a_w in Eqs. (1) and (2). These include vertical profiles of the time-average horizontal Eulerian wind velocity, the Eulerian velocity variances and the covariance between u' and w' (where u' and w' are the horizontal and vertical components of the fluctuating wind velocity), the vertical gradients of these quantities, and the Lagrangian timescale T_L . These statistics were obtained in part from the measurements of wind fluctuations made by the sonic and hotwire anemometers and in part from the known

behavior of wind flow in canopies (Raupach et al., 1991; Wilson et al., 1982).

Pollen release rate from a unit area of crop, Q (grains $\text{m}^{-2} \text{s}^{-1}$), cannot be measured directly and is a parameter of the model. It was estimated by comparing the LS-model-calculated pollen concentrations, C_{LS} (grains m^{-3}), with the concentrations measured with the rotorods, C_{meas} . In particular, the model estimate for pollen release rate, Q_{model} (grains $\text{m}^{-2} \text{s}^{-1}$), was found by matching the modeled and measured concentrations (see Aylor and Flesch, 2001; Eq. (17)). In Section 3.3 below, Q_{model} will be compared to the rate of pollen release per plant, $Q_{\text{potential}}$ (grains $\text{plant}^{-1} \text{s}^{-1}$). This requires putting the two release rates on the same basis, which was accomplished by simply dividing Q_{model} by the number of plants per ground area in the crop, N_{P} (plants m^{-2}).

3. Results

3.1. Concentration profiles

Measurements were made during unstable to neutral atmospheric conditions ($L < 0$) over a range of u^* values from about 0.22 to 0.62 m s^{-1} (Table 1). The aerial concentration of pollen decreased rapidly with height above the canopy, with the highest concentrations measured inside the canopy at a height of 2.3 m, where C ranged from 8 to 945 grains m^{-3} .

The measured values of C were standardized by multiplying them by u^* (m s^{-1}) and dividing them by Q_{model} . By scaling C with u^* and Q in this way, concentration profiles measured for various pollen release rates and wind speeds can easily be plotted and compared on the same graph (Fig. 3A).

Table 1

Air temperature (T_{air}), relative humidity (RH), solar irradiance (SR), wind direction (Dir), friction velocity (u^*), Monin–Obukov length (L), and $Q_{\text{model}}/N_{\text{P}}$ at the test site during the pollen measurement periods

Run no.	Date	Time ^a	T_{air} (°C)	RH (%)	SR (W m^{-2})	Dir (°)	u^* (m s^{-1})	L (m)	$Q_{\text{model}}/N_{\text{P}}$ ($\text{plant}^{-1} \text{s}^{-1}$)
1	24 July	14:00	22.5	76.0	198	42	0.24	−46	20.7
2	24 July	15:00	22.9	73.7	209	35	0.26	−97	15.8
3	26 July	08:00	21.6	58.9	568	10	0.34	−43	119.6
4	26 July	09:00	23.1	52.6	711	27	0.32	−34	65.2
5	26 July	10:45	24.5	50.9	800	25	0.31	−30	43.5
6	26 July	11:45	25.6	50.2	894	52	0.31	−21	35.9
7	27 July	08:00	21.1	61.7	392	79	0.24	−20	54.3
8	27 July	09:00	21.3	59.0	302	104	0.27	−40	43.5
9	27 July	10:30	22.0	55.4	403	90	0.29	−37	34.8
10	27 July	11:30	22.3	57.6	357	77	0.31	−53	27.2
11	29 July	08:00	23.1	75.1	553	331	0.41	−83	78.3
12	29 July	09:00	24.5	68.9	695	324	0.33	−40	35.9
13	29 July	10:30	26.3	62.4	725	349	0.27	−34	21.7
14	29 July	11:30	26.9	59.2	548	290	0.22	−112	26.1
15	31 July	08:00	25.4	85.2	235	178	0.48	−221	5.4
16	31 July	09:00	26.7	80.7	407	179	0.48	−165	6.0
17	31 July	10:30	28.1	75.5	599	182	0.58	−181	7.1
18	31 July	11:30	28.3	73.9	546	177	0.62	−263	4.9
19	2 August	08:00	25.3	58.2	512	358	0.33	−72	141.3
20	2 August	09:00	26.3	50.6	617	5	0.34	−79	152.2
21	2 August	11:30	27.9	52.1	570	37	0.25	−39	21.7
22	3 August	08:00	24.0	88.8	183	179	0.24	−26	65.2
23	3 August	09:00	25.2	83.3	292	208	0.22	−16	152.2
24	3 August	10:30	26.7	78.7	547	186	0.37	−40	43.5
25	3 August	11:30	28.0	73.9	695	202	0.36	−30	54.3
26	4 August	08:00	25.4	76.8	502	359	0.48	−143	92.4
27	4 August	09:00	25.8	71.2	614	358	0.44	−77	81.5
28	4 August	10:30	27.5	62.8	810	353	0.40	−51	59.8
29	4 August	11:30	28.3	58.2	827	3	0.41	−66	29.3

^a Local standard time (LST) at the start of each sampling period. Sampling periods were 60 min, except for Run no. 25 which was 75 min.

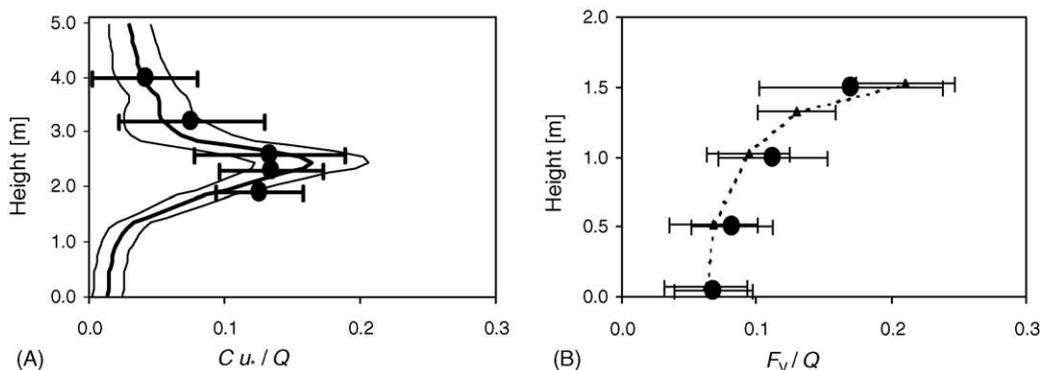


Fig. 3. Vertical profiles of normalized pollen concentrations, $C u^*/Q$ (panel A), and normalized vertical fluxes of pollen in the canopy, F_V/Q (panel B). Solid circles are the means of 29 separate determinations and the error bars are standard deviations from these means. In panel A, the heavy solid line is the average of the 29 individual calculated results for each run using the LS model (with $V_{crit} = 0.45 \text{ m s}^{-1}$), and the lighter lines flanking it indicate the standard deviations of the calculated results. In panel B, the small triangles are average values calculated by the LS model at the measurement heights and the dashed line connecting these points was faired in by eye for visual effect. The calculated and measured values have been displaced slightly in the vertical for clarity of presentation.

For non-depositing particles this grouping is a similarity variable that reduces variation due to wind speed and source strength onto a single curve. The LS model results were fitted to the measured concentrations by dividing them by the modeled pollen release rate, Q_{model} . Having done this, the shapes of the measured normalized concentration profiles ($C u^*/Q$) were described well by the LS model.

3.2. Flux profiles

The average normalized vertical flux of pollen (F_V/Q) measured at silk height was about 0.17 ± 0.07 and

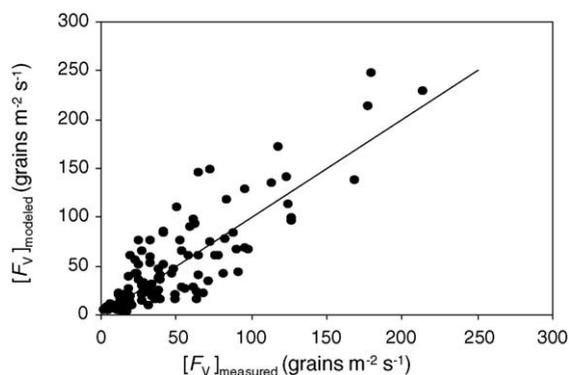


Fig. 4. F_V modeled (grains $\text{m}^{-2} \text{s}^{-1}$) vs. F_V measured (solid circles). The straight line is the 1:1 line. Linear regression fit to the data values gave $y = 1.02x - 0.21$ ($P < 10^{-6}$, d.f. = 113).

decreased steadily with depth in the canopy to about 0.07 ± 0.03 near the ground (Fig. 3B). The agreement between measured and modeled fluxes was within the uncertainty of the experimental and calculated determinations. Although there was considerable scatter, the measured values of F_V/Q were described well by the model ($y = 0.95x$, $P < 10^{-6}$, d.f. = 113) (Fig. 4). The model indicates that F_V/Q tends to increase more or less linearly with increasing u^* at heights low in the canopy (Fig. 5). At silk height, however, there is a large amount of variability and a trend is not so clear.

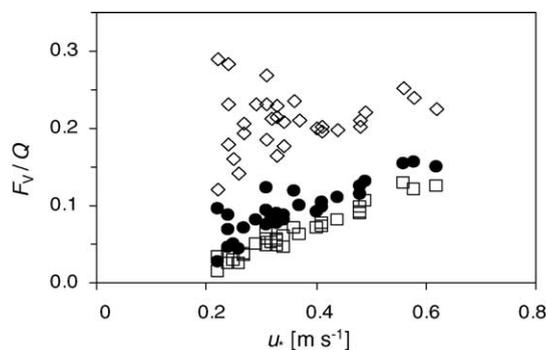


Fig. 5. Values of F_V/Q versus u^* for $V_{crit} = 0.45 \text{ m s}^{-1}$ at three heights: $z = 0.05 \text{ m}$ (open squares), $z = 0.50 \text{ m}$ (solid circles), and $z = 1.5 \text{ m}$ (open diamonds). There is a highly significant correlation between F_V/Q and u^* at $z = 0.05 \text{ m}$ ($y = 0.27x - 0.035$, $r^2 = 0.95$) and at $z = 0.5 \text{ m}$ ($y = 0.25x - 0.005$, $r^2 = 0.75$), but not at $z = 1.5 \text{ m}$ ($y = 0.06x - 0.190$, $r^2 = 0.03$).

Additional model calculations were done to show the sensitivity of the LS model to V_{crit} and to illustrate the importance of rebound and re-entrainment for determining fluxes in the canopy for a range of particle types or canopy wetness or stickiness conditions (Fig. 6). Curves for several hypothetical values of the critical rebound-reentrainment parameter are shown, ranging from $V_{\text{crit}} = 60 \text{ m s}^{-1}$ (where all of the deposited particles stick to the plant) to $V_{\text{crit}} = 0$ (where none of the particles that are calculated to be deposited by impaction remain on the plant). Included in the figure is the curve for $V_{\text{crit}} = 0.45 \text{ m s}^{-1}$, which (with the exception of the other curves in Fig. 6) is the value used for all model calculations in this paper.

3.3. Comparison of Q_{model} with $Q_{\text{potential}}$

For most of the sampling days, we collected pollen from tassels of plants in the field and estimated a potential rate of pollen release per plant per day, $Q_{\text{potential}}$ (grains plant⁻¹ day⁻¹), as described above. $Q_{\text{potential}}$ ranged from about 2×10^5 to 2×10^6 grains plant⁻¹ day⁻¹ (Table 2). Assuming that most of the pollen release occurs during a 6-h period (Aylor, unpublished results; Ogden et al., 1969 (their Fig. 7); Jarosz et al., 2003), this yields an overall average of 35.6 ± 22.2 grains plant⁻¹ s⁻¹. To compare this number with the values calculated using the model, it is first necessary to divide Q_{model} (with units of grains m⁻² s⁻¹) by the plant density in the field, N_{P} (plants m⁻², equal to 12.1 plants m⁻²). After doing this, the model results indicated release rates per plant (i.e., $Q_{\text{model}}/N_{\text{P}}$) ranging from about 4 to 116 grains plant⁻¹ s⁻¹ with an average value of 40.4 ± 32.2 grains plant⁻¹ s⁻¹.

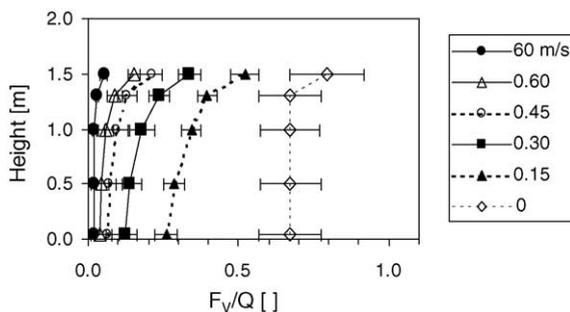


Fig. 6. Vertical profiles of F_v/Q calculated using the LS model for various values of the critical rebound-re-entrainment speed, V_{crit} .

Table 2

Estimated potential daily production of pollen grains, $Q_{\text{potential}}$, in millions of grains per plant per day

Date	$Q_{\text{potential}}$ (grains plant ⁻¹ day ⁻¹ $\times 10^{-6}$)
27 July	1.2 (0.27) ^a
28 July	0.2 (0.13)
30 July	1.1 (0.57)
31 July	0.6 (0.31)
1 August	1.6 (0.28)
2 August	0.2 (0.08)
3 August	0.8 (0.27)
4 August	0.4 (0.19)
5 August	0.8 (0.54)

^a Mean and S.E.M.

4. Discussion and conclusions

The LS model described here offers a means for predicting the number of pollen grains per centimetre square delivered at the height of the silks. The strengths of this approach are that it can be used to examine a wide array of conditions and planting schemes and that the model results are conveniently expressed in terms of the potential pollen production of the “male” parent in the field, allowing ready comparison across inbreds and hybrid varieties. This flexibility should be of particular value to seed producers interested in improving the efficiency and purity of seed production in their fields.

One way the model and present results could be used in designing seed production fields would be to plant only the male parent in a field without detasselling and measure the pollen deposition at silk height at several locations in the field. The advantage of using a non-detasseled field is that the results are less sensitive to the horizontal placement of pollen samplers than they would be in a field where, say, four-fifths of the plants had been detasseled. The measured deposition flux can be used to determine the pollen production potential of the “male”, which in turn can easily be related to that expected in a seed production field using our LS pollen transport model. Calculations using the model indicate that the average pollen flux at silk height in a typical 1:4:1 seed production field (with one-fifth as many males) onto the four female parents is about 23% of the amount expected in a solid male-planted field.

A direct measurement of short-term pollen release rates, Q , is practically impossible for *Z. mays* pollen,

as it is for most pollen and spores. Earlier studies (Aylor and Flesch, 2001; Aylor et al., 2001; Wilson, 2000) have shown that an LS model yields reasonable estimates of Q . As a rough validation of the method in the present case, we obtained average values for release rate based on a generic duration for daily pollen release, which was assumed to occur over a period of ~ 6 h in accordance with our experience with continuous sampling using a Burkard sampler (Aylor, unpublished results) and from earlier studies (Ogden et al., 1969 (their Fig. 7); Jarosz et al., 2003). Although this comparison is admittedly crude, the values of Q obtained from the model (when converted to the same units by dividing by N_p) were within the range expected from the daily release rates and were not significantly different from each other.

An interesting feature of the present study is the apparent lack of dependence on u^* for pollen fluxes at silk height (Fig. 5). Lower in the canopy, on the other hand, pollen fluxes increased steadily with increasing u^* , in concert with the expectation that increasing levels of turbulence will enhance transport of material into a canopy. From a computational perspective, the actual magnitude of the pollen fluxes at any height in the canopy depends on the value of V_{crit} (Fig. 6). The high degree of variability in pollen fluxes at silk height is expected to occur over a range values of V_{crit} (0.3 – 0.6 m s^{-1}) that can be reasonably expected to bracket the potential for re-entrainment of freshly released maize pollen (Aylor et al., 2003).

Canopy architecture can potentially affect pollen fluxes in the canopy. The choice of the canopy structure (i.e., more erect or more horizontal) in the model has a relatively modest effect on flux of maize pollen at silk height. This is true for maize pollen largely because of its inability to stick to surfaces (Aylor et al., 2003) but is not expected to be true for other particles (such as fungus spores) that are retained well on surfaces. The maize canopy studied here had horizontally and vertically projected fractions of leaf area of about 0.7 and 0.5, respectively, for most of the canopy depth (Fig. 2). For a hypothetical canopy for which the values for these two fractions are reversed, the model indicates that the flux at silk height would be increased by only about 3% (to about 24%). If, on the other hand, conditions on the foliage were such that the pollen sticks (e.g., dew on the upper leaves) rather than rebounds, then a relatively small ($\sim 5\%$)

percentage of the pollen released reaches the level of the silks in either case, and there is little difference between these two canopy foliage orientations.

The height of the pollen source can affect the magnitude of pollen fluxes in the canopy. Pollen is shed from the tassel over a period of a few days, with shedding usually starting somewhere near the center of the tassel and proceeding upwards and downwards from there. Theoretically, the higher up on the tassel that pollen is released and the stronger the wind, the greater will be the number of pollen grains that can potentially escape from the canopy and, conversely, the fewer grains that will reach the silks. In the model simulations, pollen grains were released from a range of heights, centered at mid-tassel height and extending for a distance of one-half the tassel length above and below the mid-point, with the starting height of each simulated trajectory selected from a uniform random distribution. In the field, the timing and pattern of tassel development is not identical plant-to-plant. Furthermore, given the natural variation of plant height in the field (the standard deviation of h was approximately one-half the length of the tassel), the present method of taking pollen release to be from a range of heights seems to be a realistic approach.

The present results are applicable mainly to within-field pollen transport since the wind statistics used in the model were treated as horizontally uniform. Other, models (e.g., Jarosz et al., 2004; Boehm and Aylor, *in press*), which consider more complex wind flows, are required to predict the arrival of xenic pollen from distant fields. However, the results of the present study are important for evaluating the genetic impact of xenic pollen already arrived at the field. Detailed understanding of pollen movement in a canopy provided by the present model offers a way to predict pollen transport to the silks, which is needed to evaluate the degree of competition for ovules between locally produced and incoming pollen (Aylor et al., 2003).

The use of a simulation model, such as the one presented here, in conjunction with measured pollen concentrations and wind speeds, offers a good way to quantify pollen release rates and pollen fluxes to the silks. The model requires relatively few inputs, viz., the settling speed of the pollen, the *LAI* of the canopy, the characteristic dimension and orientation of the stems and leaves in the canopy, the friction velocity u^* , and a measure of atmospheric stability. The model

can be used to examine the types of conditions (e.g., dew, honey-dew from aphids, or drought) that could affect pollen retention and enable more or fewer pollen grains to reach the silks. As such, the LS model presented here represents a potentially useful tool in the arsenal for evaluating gene flow either within seed fields or between fields of genetically modified and conventional crops.

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