

Atmospheric pollen dispersion from herbicide-resistant horseweed (*Conyza canadensis* L.)

Junming Wang  · Meilan Qi · Haiyan Huang · Rongjian Ye · Xiangzhen Li · C. Neal Stewart

Received: 12 August 2016 / Accepted: 3 March 2017
© Springer Science+Business Media Dordrecht 2017

Abstract Horseweed (*Conyza canadensis* (L.) Cronq.) with evolved herbicide resistance has become an especially problematic weed in crop production across the USA and on four continents (North America, South America, Asia, and Europe). Spread of herbicide resistance can occur through pollen-mediated gene flow between resistant and susceptible horseweed populations. However, there are little knowledge, preventive guidelines, and mechanism modeling for pollen transport in this system. We need to better understand pollen dispersion and deposition in the context of atmospheric conditions, herbicide-

resistant horseweed patch size, and buffer crop type, height, and field size. A mechanistic model is needed to account for these. A pollen dispersion and deposition model was calibrated and validated using 2013 experimental field data. The validated model was run for various combinations of atmospheric conditions, horseweed characteristics (source strength), and buffer species and size (pollen can be intercepted by crop plants). Large fields with crops with a high leaf area density and tall plants can effectively prevent pollen dispersion. The information will help provide guidelines for preventing herbicide resistance spread from herbicide-resistant weeds and genetically modified plants in general.

Junming Wang, Meilan Qi, Haiyan Huang, and Rongjian Ye have contributed equally to the work.

J. Wang (✉) · H. Huang
Illinois State Water Survey, Prairie Research Institute,
University of Illinois at Urbana-Champaign, 2204 Griffith
Dr., Champaign, IL 61820-7463, USA
e-mail: wangjunming@hotmail.com

M. Qi (✉)
School of Science, Wuhan University of Technology,
Wuhan, Hubei, People's Republic of China
e-mail: qiml@whut.edu.cn

R. Ye · C. Neal Stewart
Department of Plant Sciences, University of Tennessee,
2431 Joe Johnson Dr., Knoxville, TN, USA

X. Li
Chengdu Institute of Biology, Chengdu, Sichuan, People's
Republic of China

Keywords Herbicide resistance · Horseweed · Modeling · Pollen dispersion

1 Introduction

Horseweed (*Conyza canadensis* (L.) Cronq.) with evolved glyphosate resistance (GR) has become an especially problematic weed in crop production across the USA. This plant is considered a significant agricultural weed because it can reduce agricultural yields by 90% at high densities and becomes problematic under low-tillage agriculture (Bruce and Kells 1990; Shields et al. 2006). The spread of GR horseweed has been rapid (through seed dispersion and pollination), with resistant populations covering

millions of hectares in maize, soybean, and cotton fields in the USA (Heap 2014). Horseweed is self-compatible, with 96% of florets being self-pollinated (Smisek 1995; Shields et al. 2006). Major horseweed spread is through seed dispersion. Therefore, horseweed gene flow studies have been largely focused on seed spread (Regehr and Bazzaz 1979; Bruce and Kells 1990; Dauer et al. 2006a, b, 2009; Henry et al. 2008; Shields et al. 2006; Weaver 2001) instead of pollen transport, pollination, and outcrossing. Compared to gene flow from pollen outcrossing, GR horseweed seed dispersion in the air has more GR spread because each horseweed plant can have 200,000 seeds which can be dispersed to far distances. For example, horseweed seeds have been found in the altitude of 68–120 m from horseweed fields (Huang et al. 2015; Dauer et al. 2009). The seeds will potentially be carried for hours before descending (Dauer et al. 2009) and therefore will be transferred long distances.

Gene flow via the transfer of GR via pollen, in addition to long-distance seed movement, is troubling because it could aid in the evolution of multiple resistance (Henry et al. 2008). For example, USA (Delaware, California, Mississippi) and other countries (e.g., Brazil, Canada) found multiple resistance horseweed (resistance to chlorimuron-ethyl, glyphosate, tribenuron-methyl, and/or paraquat) (Heap 2014). Further, a single outcrossed plant can produce more than 200,000 seeds (Smisek 1995; Weaver 2001). Therefore, even with 4% outcrossing (96% self-pollinated), 8000 outcrossed seeds per plant may be produced. Consequently, it is important to study horseweed gene flow through pollen dispersion and outcrossing.

Before outcrossing can occur from GR plants to species-compatible plants, pollen should be dispersed from GR plants to species-compatible plants (to fertilize ovules). Only if there is viable GR pollen dispersed, potential outcrossing may occur. The outcrossing ratio is calculated as the total outcrossed seed number divided by the total seed number of a plant (Wang et al. 2006). Suppose the outcrossed seeds matured; a percentage of matured seeds can be viable and can germinate. Part of the germinated plants will survive and finally mature. Therefore, from pollination to a new outcrossed mature plant involves several steps: pollen dispersion, outcrossing, seed survival, germination, and plant survival. To estimate the final

number of surviving plants, researchers will need the information of the seed number per plant, dispersed and deposited pollen amount, outcrossing ratio, seed survival ratio, germinating ratio, and plant survival ratio. This paper will focus on the research of pollen dispersion and deposition.

Previous gene flow studies have been mainly focused on six major annual crop species. They are oilseed rape (*Brassica napus*), sugar beet (*Beta vulgaris*), potato (*Solanum tuberosum*), maize (*Zea mays*), wheat (*Triticum aestivum*), and barley (*Hordeum vulgare*) (Becker et al. 1992; Lavigne et al. 1998; Kausch et al. 2010). Gene flow studies have also been conducted with transgenic perennial grasses, weeds, trees, and other plants (Loveless and Hamrick 1984; Motten and Antonovics 1992; Wipff and Fricker 2001; Belanger et al. 2003; Austerlitz et al. 2004; Watrud et al. 2004; Reichman et al. 2006; Bae et al. 2008; Huang et al., 2015; Ye et al. 2016).

However, there are little knowledge, preventive guidelines, and mechanism modeling with regard to dynamic pollen dispersion, deposition (especially on flowers), and outcrossing for GR horseweed. In particular, little information is available on the relationship of pollen movement with atmospheric conditions (wind speed, direction, wind variability, and atmospheric stability), buffer plant type, height, size, pollen size, and GR horseweed patch size.

Spatial and temporal extrapolation of pollen movement measurements is most efficient using numerical models (Wang and Yang 2010). The most useful models for pollen movement will be those that can be used to dynamically predict pollen transport from individual locations and ultimately the proportion of the source plant pollen that fertilizes ovules at a given distance, which can then be scaled up to landscapes and regions.

Various empirical models have been used to depict pollen dispersal in horizontal or vertical planes (Wright 1943; Haldane 1948; Levin and Kerster 1974; Fitt et al. 1987; McCartney 1994; Kareiva et al. 2008). Yet these descriptive models do not have the power to analyze the effects of controlling factors, should not be extrapolated outside the observation range, and cannot simulate or predict the dynamics of the dispersal process (Emberlin et al. 1999).

Some mechanic models of atmospheric transport are quite well developed for simulating transport processes in and above vegetation canopies (Aylor

1982; Aylor and Ferrandino 1989; Okubo and Levin 1989; Yang et al. 1991; Raupach 1993; Tufto et al. 1997; Raupach and Briggs 1998; Aylor and Flesch 2001; Klein et al. 2003; Wang and Yang 2010). Transport models can be broadly classified as Lagrangian or Eulerian based on the type of reference frame used for formulation (Shirolkar et al. 1996). The application of Eulerian models for estimating scalar transfer by turbulence within and above plant canopies has been limited by the inability to treat the dispersion of material from nearby sources well. Lagrangian models do not suffer from this deficiency since they can consider the diffusion of materials from both nearby and far away sources explicitly (Van den Hurk and Baldocchi 1990). There were researchers who used Lagrangian models to simulate weed seed dispersion (e.g., Tackenberg 2003). These Lagrangian models provided reasonable simulations. These models simulated better with a seed settling speed > 0.15 m/s than that with a settling speed < 0.15 m/s (settling speed is the downward motion speed of a particle in still air; Aylor 2002). Because the settling speed of horseweed pollen is 0.019 m/s ($\ll 0.15$ m/s) of a $21 \mu\text{m}$ diameter, these models are not good choices for horseweed pollen dispersion. Settling speed was calculated based on Stokes law (De Visscher 2013), pollen density (1218 kg/m^3) (Sosnoskie et al. 2009), and density and viscosity of air (0.0001511 kg/ms and 1.205 kg/m^3). The Lagrangian model in Wang and Yang (2010) simulated corn pollen dispersion with acceptable accuracy. This model can be adapted for horseweed pollen dispersion by changing the corn pollen settling speed to horseweed's and changing other parameters.

After the simulation of the pollen transport, the outcrossing ratio should be calculated based on the transported pollen amount. Researchers (Henry et al. 2008) found that the GR to glyphosate-susceptible (GS) horseweed outcrossing ratio was 4% when paired plants were grown next to one another. Outcrossing ratio is linearly related to a total pollen vertical flux (pollen grains/ m^2) (Wang et al. 2006). Therefore, the relationship of outcrossing ratio to the pollen flux can be deduced if both data sets (outcrossing ratio and flux) are known.

The objectives of our study were to modify, calibrate, and validate a Lagrangian model developed by Wang and Yang (2010) for GR horseweed. The model will be used for GR horseweed pollen transport

simulation and then run the model to determine pollen transport under different atmospheric conditions, buffer plant type, height and size, pollen size, and GR horseweed patch size. This paper is not a genetic study and thus is attempting to provide the pollen dispersal modeling component that could aid in a genetic analysis of gene flow.

2 Materials and methods

Field experiments of horseweed pollen (Huang et al. 2015; Ye et al. 2016) and seed emission and dispersion have been conducted. The Lagrangian model and online tool for pollen dispersion and the model for seed dispersion have been developed.

2.1 Experiments

To calibrate and validate the Lagrangian model, experiments of GR horseweed pollen emission and dispersion were conducted at the University of Tennessee, Knoxville (latitude: $35^\circ 53' 46.57''\text{N}$; longitude: $83^\circ 57' 35.99''\text{W}$; elevation: 250 m). The sampling time period was during horseweed pollination season from August 5, 2013, to September 27, 2013 (Fig. 1a, b). Source plants were GR horseweed in a circular field with a diameter of 6 m. The density was 4 plants/m^2 . The mean plant height was 1.3 m. The atmospheric conditions for model inputs were measured using an anemometer at the height of 2.6 m in the center of the field (CSAT3, Campbell Sci, Utah, USA). The atmospheric conditions were measured at a frequency of 10 Hz and were processed to 15-min intervals following Wang and Yang (2010). During the sampling periods, the average (all the 15-min data) u^* (friction velocity) was 0.15 ± 0.05 m/s (ranged from 0.04 to 0.44 m/s); mean wind direction was $223 \pm 55^\circ$ (ranged from 1° to 346°); and mean L (Monin–Obukhov length) was -0.1 ± 15 m (ranged from -55 to 317 m).

In pollen dispersal experiments, pollen concentration (pollen grains/ m^3) was measured using columns of Rotorod samplers (Model 20, Sampling Technologies, Inc., MN, USA) in the downwind sampling line. One column of Rotorod samplers was located in the center of the source to measure pollen concentration at different heights (Fig. 1a). Combining with wind speed measurements, the horizontal flux (pollen

grains/m²/s) profiles of source production and release can be obtained. There were five Rotorod samplers on the center column. They were at 0.8 m height within the canopy, 1.3 m at the canopy height, and 2.05, 2.8, and 3.55 m above the canopy. Other two columns of Rotorod samplers were set up in the prevailing wind

direction at 1 and 4 m from the source edge. Four Rotorod samplers on each of the two columns were at 0.8, 1.3, 2.05, and 3.05 m heights. A total of 15 Rotorod samplers were used in the experiments.

Microscope slides (2.5 cm × 7.5 cm) covered with silicon grease (Sampling Technologies, Inc., MN,

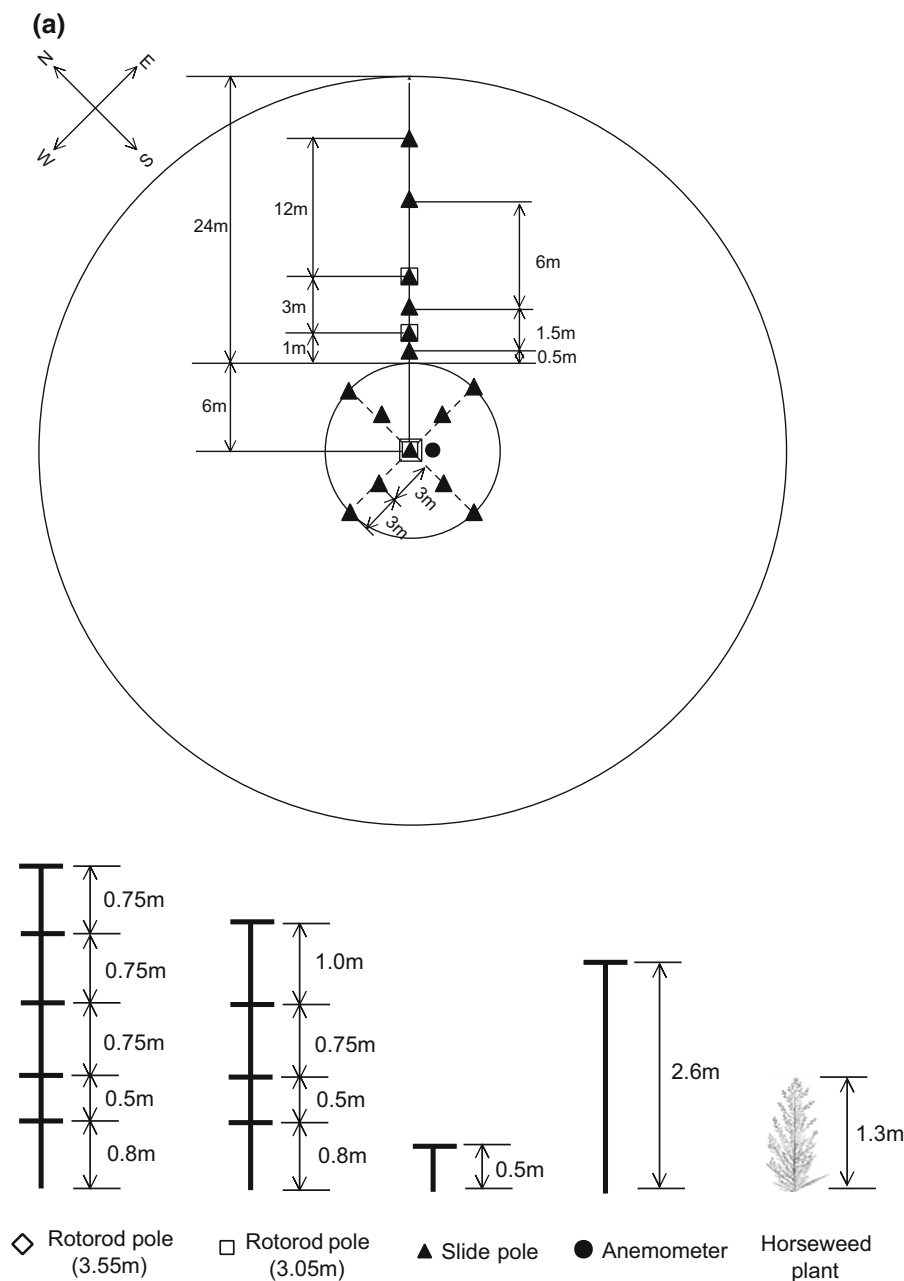
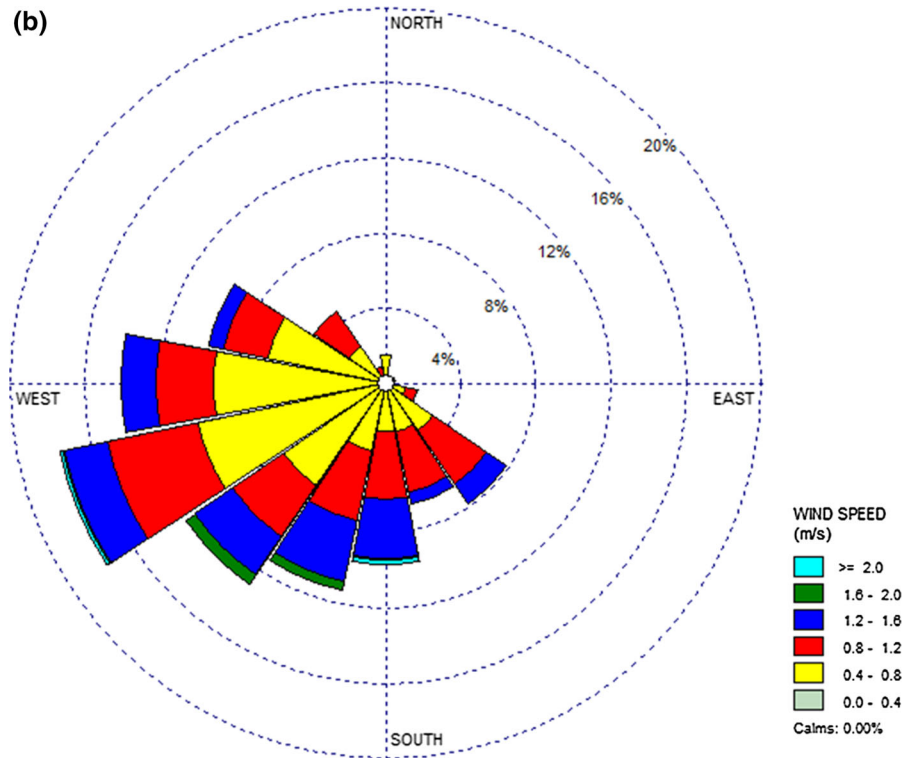


Fig. 1 a Schematic sketch of experimental setup. Locations of the sampling poles in the field (*top*) and vertical positions of the samplers on the poles (*bottom*). b. Windrose during the sampling periods

Fig. 1 continued



USA) were used to measure the deposition flux density (pollen grains/m²/s) at 0.5 m heights along the Rotorod sampling line direction. The details of the experimental setup are provided in Fig. 1a. A total of 15 slide sampling points were used in the experiments.

Pollen concentration and deposition sampling were conducted throughout the pollination season. Each sampling period for the collectors was 2–3-h intervals during each day from 9:00 to 19:30, i.e., each sampling was conducted continuously 2–3 h. Timers on the Rotorod samplers were used to provide different intermittent samplings, as determined by the capacity of the Rotorod samplers to avoid being overloaded. New, fresh sampling rods and slides were placed for each new sampling period.

Pollen concentration, deposition, source strength, and atmospheric parameters during each experimental period were obtained following Wang and Yang (2010).

There were a total of 34 sampling periods with greater than 0 pollen grains/plant/s source strength. The concentration at the 0.8 m height and deposition flux density at the 0.5 m height at the Rotorod pole locations during the first 17 periods were used to

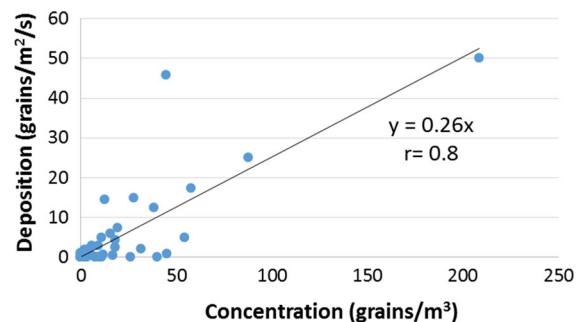


Fig. 2 Deposition velocity calibration (ratio of deposition divided by concentration) using half of the experimental data (first 17 sets of 34 experimental periods). r is the correlation coefficient of the simulated and the measured data ($P < 0.001$)

calibrate the deposition velocity (0.26 m/s, the slope) (Fig. 2). Because there were multiple sampling points during each period, the number of data points in Fig. 2 is more than 17. Deposition velocity is defined as the ratio of deposition flux density at a height to the corresponding concentration. The term is used to calculate deposition flux density if concentration is given (Lin et al. 1994). The remaining data were used to validate the model.

2.2 Lagrangian model

The Lagrangian model in Wang and Yang (2010) was used to simulate horseweed pollen dispersion. The random flight of each pollen particle is simulated in a sequence of short time steps, during each of which the particle moves:

$$dx = [\bar{u} + u]dt, dy = vdt, dz = (w - v_s)dt$$

where $\bar{u}$ is the mean alongwind velocity at the present height of the particle; u , v , and w are the alongwind, crosswind, and vertical turbulent velocities; and v_s is the settling velocity of the pollen grain (0.019 m/s for horseweed pollen of a 21 μm diameter, settling speed was calculated based on Stokes law (De Visscher 2013) and pollen density (Aylor 2002). The velocity fluctuations have been formulated in a Markov chain approach based on inputs of u^* (the friction velocity, m/s), wind direction (degree), and L (the Monin–Obukhov length, m). The pollen release height was evenly distributed from 0.5 to 1.3 m. The simulated instantaneous concentration (pollen grain/ m^3) at a location is calculated as the number of pollen grains in a unit air volume at that location and time. The instantaneous concentration is the concentration at a time, and the time interval is 0.1 s or shorter (when $dt < 0.1$ s). Timing for meteorological and biological simulations was matched during each time step, dt . The average concentration during an averaging time period is the average of all the instantaneous concentrations over that time period.

Pollen grains intercepted by plants (horseweed and coexisting crop plants) were determined by the probability that a pollen grain was intercepted by aerial, vegetative organs of plants (stems and leaves) during a time step based on the canopy horizontal and vertical projection of element area density and pollen grain speed, as described in Wang and Yang (2010). Table 1 lists the plant characteristics used in this paper.

2.3 Outcrossing

Because the outcrossing ratio is linearly related to a total pollen vertical flux (pollen grains/ m^2) (Wang et al. 2006), the outcrossing ratio of source GR horseweed to a GS horseweed was estimated to be the product of 4% (Henry et al. 2008), and the ratio of seasonal total pollen deposition (pollen grains/ m^2) at

Table 1 Canopy characteristics of horseweed, corn, and soybean

Level	Height (cm)	Horseweed			
		LAD (m^3/m^2)	Fx	Fz	Lv (m)
8	114–130	0.000	0.59	0.51	0.003
7	98–114	0.000	0.59	0.51	0.003
6	81–98	0.044	0.59	0.51	0.005
5	65–81	0.044	0.59	0.51	0.005
4	49–65	0.044	0.59	0.51	0.004
3	33–49	0.044	0.00	1.00	0.004
2	16–33	0.032	0.00	1.00	0.002
1	0–16	0.032	0.00	1.00	0.002

Level	Height (cm)	Soybean			
		LAD (m^3/m^2)	Fx	Fz	LAD (m^3/m^2)
8	79–90	0.14	0.91	0.42	0.000
7	68–79	7.11	0.91	0.42	0.000
6	56–68	7.11	0.91	0.42	0.000
5	45–56	7.11	0.71	0.71	0.003
4	34–45	5.9	0.71	0.71	0.003
3	23–34	5.9	0.71	0.71	0.003
2	11–23	5.9	0.50	0.87	0.003
1	0–11	1.13	0.50	0.87	0.003

Level	Height (cm)	Grain corn			
		LAD (m^3/m^2)	Fx	Fz	LAD (m^3/m^2)
8	248–283	0.18	0.14	0.98	0.011
7	212–248	1.15	0.68	0.60	0.038
6	177–212	2.30	0.55	0.69	0.055
5	142–177	2.40	0.75	0.59	0.046
4	106–142	2.74	0.60	0.65	0.054
3	71–106	1.87	0.52	0.76	0.052
2	35–71	1.38	0.58	0.69	0.047
1	0–35	0.30	0.58	0.52	0.037

Level	Height (cm)	Sweet corn			
		LAD (m^3/m^2)	Fx	Fz	LAD (m^3/m^2)
8	150–171	0.10	0.04	0.99	0.038
7	128–150	0.82	0.60	0.75	0.075
6	107–128	1.42	0.68	0.70	0.087
5	86–107	1.47	0.78	0.55	0.065
4	64–86	1.30	0.76	0.56	0.073
3	43–64	1.56	0.71	0.65	0.051
2	21–43	1.20	0.63	0.66	0.046

Table 1 continued

Level	Height (cm)	Sweet corn			
		LAD (m ³ /m ²)	F _x	F _z	LAD (m ³ /m ²)
1	0–21	0.35	0.59	0.69	0.042

Corn data were from Wang and Yang (2010). Horseweed and soybean data were measured in this study by sampling four plants

LAD leaf area density, *F_x* the proportion of leaf area projection on horizontal ground, *F_z* the proportion of leaf area projection in the vertical direction, *L_v* the stem average diameter

the GS horseweed to total pollen production (integrated source strength with time over the whole season, pollen grains/m²: unit converted from pollen grains/plant based on plant density 4 plants/m²). The outcrossed seed number at a location (seed/plant) was estimated to be the product of 200,000 seeds/plant and the corresponding outcrossing ratio.

2.3.1 Model calibration and validation

The model inputs include the atmospheric and plant parameters. The atmospheric parameters are friction velocity, wind direction, and Monin–Obukhov length. Plant data include leaf area index with height. For model calibration and validation, the inputs were measured in the described experiments for each measurement period.

The parameters of pollen settling speed and deposition velocity should be determined. The pollen settling speed was determined as 0.019 m/s from Stokes law (De Visscher 2013) and pollen density (Sosnoskie et al. 2009), as aforementioned. The deposition velocity was calibrated by experimental data (Fig. 2).

2.4 Model application

After validation, the model was applied to predict effects of source strength, horseweed patch size, buffer

plant type and size, and the atmospheric parameters on pollen dispersion and outcrossing from GR horseweeds.

The default parameters are listed in Table 2. Typical noon-time atmospheric parameters (*u*^{*} and *L*) were used for atmospheric inputs. Measured average source strength was used as the default source strength. The default patch size of the horseweed was 1-m-radius circle area that contained 13 horseweed plants (4 plants/m²). The default buffer (surrounding crop field) was uncultivated ground with various herbaceous plants which was periodically mowed.

The model was also used to simulate potential gene flow with various horseweed patch sizes (0.2–100 m), source strengths (0.2–83.3 pollen grains/plant/s), buffer plants, buffer sizes (0–200 m), wind strengths (*u*^{*} from 0.05 to 1.5 m/s), and atmospheric stabilities (*L* from –1000 to 1000 m). When the patch size increased, it affected the wind field. The method in the research (Wang and Yang 2010) was used to account for the interference, i.e., to consider the plant height and the transition change from the source field to other fields.

The domain of the simulations was set by the distance where the deposition flux density was reduced to 0.1% of source strength. The total simulation period for each scenario ranged from 15 to 120 min corresponding to the set domain and aligned pollen survival period in each simulation.

The model outputs 3-D concentration (pollen grains/m³), 2-D deposition flux density (pollen grains/m²/s) at 0.5 m height, and 2-D outcrossing ratio from the source plant. The deposition output was accumulated over time for the whole pollination season. The 1 and 0.1% distances (at which the predicted pollen deposition flux density was 1 and 0.1% of the source strength, respectively) were determined along the prevailing wind direction.

For all simulations except for different source sizes, the total deposition flux (TDF, pollen grains/m²) during the pollen viable period (2 h, van Hout et al. 2008) was estimated at each prediction location by multiplying the deposition flux density by 2 h.

Table 2 Default conditions used for simulations of different source field sizes, source strengths, buffer heights, buffer field sizes, atmospheric conditions, and pollen sizes

<i>u</i> [*] (m/s)	<i>L</i> (m)	Source strength (pollen grains/plant/s)	Horseweed patch size: radius (m)	Buffer	Pollen settling speed (m/s)
0.2	–15	2	1	Grass land	0.019

In simulations for different source sizes, the grand total pollen deposition flux for the whole pollination season was estimated by multiplying the deposition flux density by the daily shedding time of 12.5 h (7:00–19:30) and the pollination season. The daily shedding time was observed in the pollen dispersion experiments.

The 1 and 0.1% distances for total deposition flux in the prevailing wind direction were used as the distance where the deposition flux density was 1 and 0.1% of the source strength. Similarly, the 1 and 0.1% distances in the prevailing wind direction for outcrossing ratio are the distances where the outcrossing ratio was 1 and 0.1%.

3 Results

3.1 Model validation

The model reasonably simulated pollen plumes. Figure 3 shows a sample output from the model with $u^* = 0.1$ m/s and $L = -1$ m. As expected, the pollen

concentration plume height increased with distance, and pollen concentration decreased with height and distance; deposition decreased with downwind and crosswind distances.

Compared with experimental data, the ratio of simulated to the measured pollen concentration was 0.99 and the correlation coefficient was 0.6 (Fig. 4) (the intercept was forced to be 0). If the intercept was not forced to be 0, the intercept was 9.1 grains/m³ representing the model bias and the slope was 0.74 representing the model consistency. The ratio of simulated to the measured deposition flux density was 1.29 and the correlation coefficient was 0.4 (Fig. 5) (if the intercept was not forced to be 0, the intercept was 4.0 grains/m² representing the model bias and the slope was 0.81 representing the model consistency).

3.2 Model application

The model was run to simulate pollen dispersion under different environmental conditions. With increased horseweed patch size, the 1 and 0.1% distances

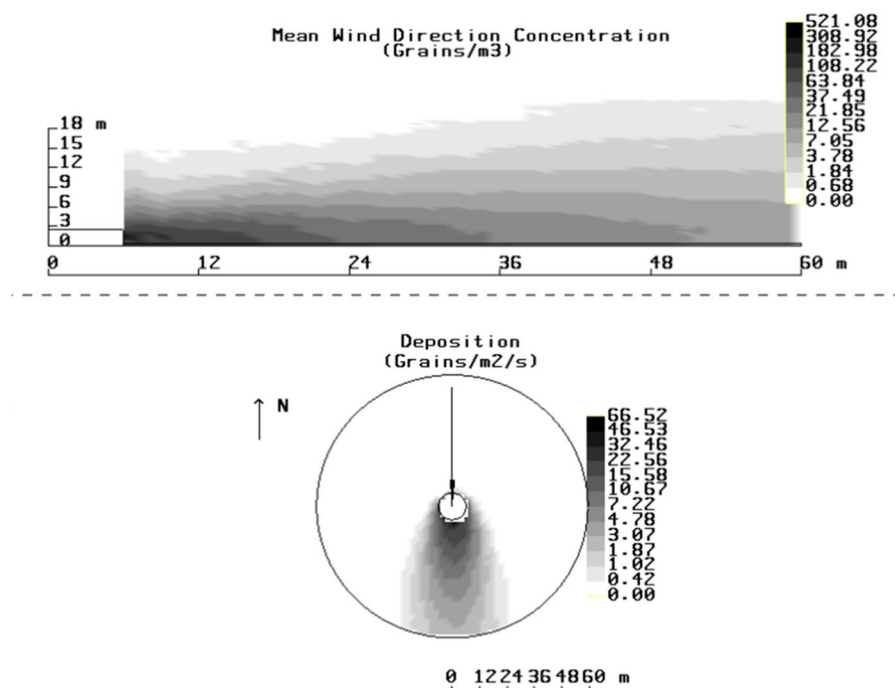


Fig. 3 One sample output from the model during a noon-time 15-min simulation period, when $u^* = 0.1$ m/s, wind direction = 0, $L = -1$ m. The source had a radius of 6 m. The buffer was grass (0.2 m height). The arrow in the deposition graph

shows the wind direction. *Top* concentration with height and downwind distance; *bottom* deposition flux density with distance

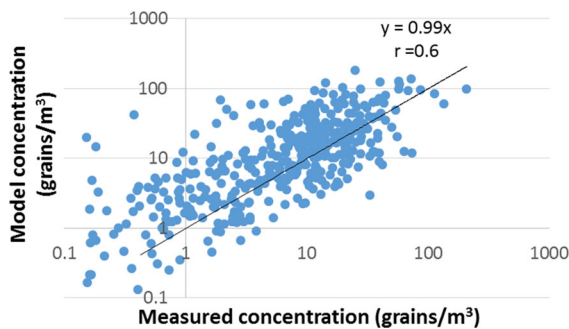


Fig. 4 Simulated versus measured pollen concentration. r is the correlation coefficient of the simulated and the measured data ($P < 0.001$)

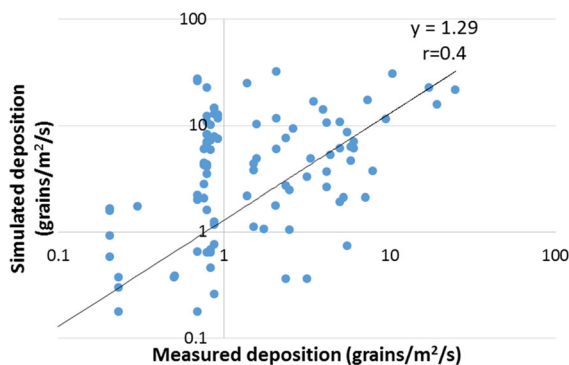


Fig. 5 Simulated versus measured pollen deposition flux. r is the correlation coefficient of the simulated and the measured data ($P < 0.001$)

increased (Table 3). If there is only one GR horseweed plant in a field, it may have 1 and 0.1% deposition distances at 1 m and 7 m, respectively, which can potentially produce 80 seeds/plant at 7 m seasonally if GS horseweed plants there have been outcrossed by the GR pollen ($80 = 4\% \times 0.1\% \times 200,000$ seeds/plant, the calculation method is in Outcrossing section in Materials and Methods). We therefore conclude that one horseweed plant is sufficient to enable GR gene flow. However, because the few GR horseweed plants have a large amount of GR seeds (200,000 seeds/plant) and the seeds can be dispersed to far distances (Dauer et al. 2006b, 2009), the seed dispersal seems to totally swamp the pollen flow in terms of importance to GR spread.

The total deposition flux during any period is linearly related to source strength as shown in Table 4. When the release rate of pollen is the average source strength (two pollen grains/plant/s), the total

deposition flux at the 1 and 0.1% distances can be high (187,200 and 18,720 pollen grains/m²).

With increased wind speed, the average pollen travel distance increased (Table 5), while the 1 and 0.1% distance decreased. This implies that although large wind speed can disperse pollen to further distances, it can dilute pollen concentration and then decrease deposition density. Large wind speed can cause large mechanical turbulence (turbulence is produced by the interference of ground vegetation and ground surface features), and the large mechanical turbulence can dilute the pollen concentration and decrease the deposition also.

The 1 and 0.1% distances of pollen transport reached a maximum under neutral atmospheric stability conditions and generally decreased with distance from neutral, either from neutral to very unstable or from neutral to very stable conditions (Table 6). Under unstable conditions, strong turbulence might dilute the pollen concentration and then the deposition by increasing the spread of pollen. Under stable conditions, the pollen can be transported further with little downward mixing in the more laminar air than under a neutral condition (with vertical mixing air) and therefore pollen concentration and deposition are diluted.

Because there was not much vegetation to intercept the pollen on relatively open ground with native grasses, the 1 and 0.1% distances were highest on this buffer land compared with other buffer plants (soybean, sweet, and grain corn) (Table 7). Although soybean has shorter stature than corn, its leaf area density was much larger than corn (Table 1). Therefore, the 1 and 0.1% distances were smaller in the soybean buffer field than in the corn field. Although grain corn was taller (2.83 m) than sweet corn (1.71 m), the 1 and 0.1% distances were similar in the two buffer fields. The reason may be that although taller plants can intercept more pollen, they can decrease the wind speed more than shorter ones, resulting in less dilution of the pollen concentration and deposition. The vertical wind profile is a function of the distance above the displacement height (displacement height is 65% of the plant height, Wang and Yang 2010), and the higher the distance, the stronger the wind speed. Because the lower corn plant has a lower displacement height, at the same altitude above the ground surface, the distance is longer at the shorter corn field than at the taller corn field. Therefore, the

Table 3 For 1 and 0.1% deposition flux distances simulated from different size source fields (where the grand total deposition fluxes were 200,000 and 20,000 pollen grains/m²,

outcrossing ratios were 0.004 and 0.0004, and outcrossed seed numbers were 800 and 80 seeds/plant, respectively)

Source radius (m)	Plant number	1% distance (m)	0.1% distance (m)
0.28	1	1	7
1	13	13	55
5	314	89	255
10	1256	167	481
20	5024	300	756
56	39,388	627	1609
100	125,600	891	2057

See Table 2 for the default atmospheric and plant conditions

Table 4 Predicted total deposition flux (TDF, pollen grains/m²) during 2-h period at 1 and 0.1% distances from 3.14 m² (1 m radius, 13 plants) herbicide-resistant horseweed plants in different source strengths under normal atmospheric conditions

Source strength (pollen grains/plant/s)	TDF at 1% distance of 13 m (pollen grains/m ²)	TDF at 0.1% distance of 55 m (pollen grains/m ²)
0.2	18,720	1872
2	187,200	18,720
8.3	776,880	77,688
16.7	1,563,120	156,312
33.3	3,116,880	311,688
83.3	7,796,880	779,688

See Table 2 for the default weather and plant conditions

Table 5 Predicted 1 and 0.1% distances and pollen average flight distances during 2-h simulation period from 3.14 m² (1 m radius) herbicide-resistant horseweed plants for different u^*

u^* (m/s)	Wind speed at 1 m above canopy (m/s)	1% distance (TDF = 187,200) (m)	0.1% distance (TDF = 18,720) (m)	Average horizontal flight distance (m)
0.05	0.32	30	90	2687
0.1	0.63	22	75	6628
0.2	1.27	13	57	8264
0.3	1.90	9	49	8821
0.8	5.07	3	27	9467
1.5	9.51	2	16	9638

See Table 2 for the default weather and plant conditions

wind is stronger at the same altitude at the shorter corn field than at the taller corn field.

As expected, if the buffer field size increased, it decreased the 1 and 0.1% distances (Table 8). If the buffer size increased to 50 m (grain corn), all the pollen can be blocked by the buffer and there were no pollen grains deposited after the buffer. To block the

same percentage amount of pollen, the buffer size is longer for blocking horseweed pollen than for blocking corn pollen dispersion (Wang and Yang 2010). In Wang and Yang (2010), the deposition of source pollen from genetically modified corn plants with a 1 m radius (same radius as for the horseweed simulation) with the same default atmospheric conditions

Table 6 Predicted 1 and 0.1% distances with total deposition flux (TDF, pollen grains/m²) during 2-h period from 3.14 m² (1 m radius) herbicide-resistant horseweed plants for different atmospheric stabilities

L (m)	Atmospheric state	1% distance (TDF = 187,200) (m)	0.1% distance (TDF = 18,720) (m)
−5	Very unstable	9	39
−15	Moderate unstable	13	59
−50	Unstable	17	72
−1000	Neutral	24	87
1000	Slightly stable	18	56
50	Stable	17	61

See Table 2 for the default weather and plant conditions

Table 7 Predicted 1 and 0.1% distances with total deposition flux (TDF, pollen grains/m²) during a 2-h simulation period from 3.14 m² (1 m radius) herbicide-resistant plants for different buffer plants under normal atmospheric condition

Buffer height/m	Buffer plant	1% Distance (TDF = 187,200) (m)	0.1% Distance (TDF = 18,720) (m)
0.2	Grass ground	13	59
0.9	Soybean	8	20
1.71	Sweet corn	11	26
2.83	Grain corn	13	23

See Table 2 for the default weather and plant conditions

Table 8 Predicted 1 and 0.1% distances with total deposition flux (TDF, pollen grains/m²) during 2-h simulation period from 3.14 m² herbicide-resistant plants for different buffer sizes (buffer plant characteristics used grain corn data)

Buffer size (m)	1% Distance (TDF = 187,200) (m)	0.1% Distance (TDF = 18,720) (m)	% Deposition at buffer downwind boundary
0	12	54	29
5	2	32	7
10	1	16	2
20	0	1	0.2
30	0	0	0.01
50	0	0	0
100	0	0	0
200	0	0	0

See Table 2 for the default weather and plant conditions

was blocked to <0.1% after 3.5 m from regular grain corn buffer.

4 Discussion

The model performance is comparable to those found in the literature. The model in this study had $r = 0.6$ for a pollen concentration simulation (slope = 0.99) and $r = 0.4$ for the pollen deposition simulation

(slope = 1.29). The model used for corn pollen in Raupach and Briggs (1998) had a similar accuracy ($r = 0.7$, slope = 0.82 for concentration, and $r = 0.7$, slope = 0.85 for deposition). Aylor et al. (2006) used a Lagrangian statistical model to simulate pollen dispersion from near the ground to a 95 m height from a 23-ha corn field, and the predicted concentration was 1.4 times of the measured concentration (40% higher prediction). Therefore, the model accuracy (18% lower concentration prediction) in this study is

comparable to the model in Aylor et al. (2006). In addition, observing the 1:1 plots of predictions versus measurements in Klein et al. (2003) for corn pollen dispersion simulations using a quasi-mechanistic model, the model accuracy in this study is comparable.

The evaluation of the model accuracy was affected by the accuracy of the measured source strength, concentration and deposition data, measured atmospheric data, and the model algorithm. The atmospheric data were point measurements that were assumed spatially horizontally homogenous and extrapolated vertically using an empirical equation. Multiple point measurements of the data may improve the model accuracy. The turbulence simulation in the model assumed that the wind velocity distribution followed a Gaussian distribution. However, the distribution may not be Gaussian and may have different skewness and kurtosis. Therefore, the simulations of the wind velocities may deviate from the actual data and produce errors. All of the above factors affected the evaluation of the model. Future model improvement will determine whether wind velocities follow Gaussian and improve the algorithm accordingly. The improvement will need to have multiple spatial measurements of the atmospheric data.

The horseweed pollen diameter ranged from 16 to 22 μm in Huang et al. (2015). Further, the diameter of the pollen might change during flight because of dehydration (Aylor 2003) which will affect pollen settling velocity (up to 30%) (Chamecki et al. 2011). However, the transport distance does not decrease much with pollen diameter (based on model simulations, the distance change is <4% if horseweed pollen size decreases 30% or <5% if pollen size changes from 16 to 22 μm). Pollen dispersion is affected by wind speed, atmospheric stability, horseweed patch size, source strength, and buffer plant type and size. While the atmospheric factors and horseweed characteristics cannot be controlled, buffer crop type and field size can be chosen to better prevent pollen dispersion. In this study, the buffer plants with a higher leaf area density and larger field size can better prevent pollen dispersion.

5 Conclusion

Compared to the horseweed experimental data, the accuracy of the Lagrangian Stochastic model is

acceptable. Model simulations indicated that while atmospheric conditions cannot be controlled, large fields of crops with high leaf area density and tall plants can effectively prevent pollen dispersion.

Acknowledgements This paper is part of a USDA funded project “Atmospheric Gene Flow in Horseweed” (USDA-NIFA-AFRI-Controlling Weedy and Invasive Plants Grant, 2012-67013-19687). The authors gratefully acknowledge financial support for this research from USDA, and the Illinois State Water Survey at the University of Illinois at Urbana-Champaign. We thank the excellent programming work by Ms. Xiufen Cui. Opinions expressed are those of the authors and not necessarily those of the Illinois State Water Survey, the Prairie Research Institute, the University of Illinois, or the University of Tennessee.

References

- Austerlitz, F., Dick, C. W., Dutech, C. E., Klein, K., Oddou-Muratorio, S., Smouse, P. E., et al. (2004). Using genetic markers to estimate the pollen dispersal curve. *Molecular Ecology*, 13(4), 937–954.
- Aylor, D. E. (1982). Modeling spore dispersal in a barley crop. *Agricultural Meteorology*, 26(3), 215–219. doi:10.1016/0002-1571(82)90032-2.
- Aylor, D. E. (2002). Settling speed of corn (*Zea mays*) pollen. *Journal of Aerosol Science*, 33(11), 1601–1607. doi:10.1016/S0021-8502(02)00105-2.
- Aylor, D. E. (2003). Rate of dehydration of corn (*Zea mays* L.) pollen in the air. *Journal of Experimental Botany*, 54(391), 2307–2312.
- Aylor, D. E., Boehm, M. T., & Shields, E. J. (2006). Quantifying aerial concentrations of maize pollen in the atmospheric surface layer using remote-piloted airplanes and lagrangian stochastic modeling. *Journal of Applied Meteorology and Climatology*, 45(7), 1003–1015. doi:10.1175/JAM2381.1.
- Aylor, D. E., & Ferrandino, F. J. (1989). Dispersion of spores released from an elevated line source within a wheat canopy. *Boundary-Layer Meteorology*, 46(3), 251–273. doi:10.1007/BF00120842.
- Aylor, D. E., & Flesch, T. K. (2001). Estimating spore release rates using a lagrangian stochastic simulation model. *Journal of Applied Meteorology*, 40(7), 1196–1208. doi:10.1175/1520-0450(2001)040<1196:ESRRUA>2.0.CO;2.
- Bae, T. W., Vanjildorj, E., Song, S. Y., Nishiguchi, S., Yang, S. S., Song, I. J., et al. (2008). Environmental risk assessment of genetically engineered herbicide-tolerant zoysia japonica. *Journal of Environmental Quality*, 37, 207–218.
- Becker, H. C., Damgaard, C., & Karlsson, B. (1992). Environmental variation for outcrossing rate in rapeseed (*Brassica napus*). *Theoretical and Applied Genetics*, 84, 303.
- Belanger, F. C., Meagher, T. R., Day, P. R., Plumley, K., & Meyer, W. A. (2003). Interspecific hybridization between *Agrostis stolonifera* and related *Agrostis* species under field conditions. *Crop Science*, 43, 240–246.

- Bruce, J. A., & Kells, J. J. (1990). Horseweed (*Conyza canadensis*) Control in no-tillage soybeans (glycine max) with preplant and preemergence herbicides. *Weed Technology*, 4(3), 642–647. <http://www.jstor.org/stable/3987525>.
- Chamecki, M., Gleicher, S. C., Dufault, N. S., & Isard, S. A. (2011). Diurnal variation in settling velocity of pollen released from maize and consequences for atmospheric dispersion and cross-pollination. *Agricultural and Forest Meteorology*, 151(8), 1055–1065. doi:10.1016/j.agrformet.2011.03.009.
- Dauer, J. T., Mortensen, D. A., & Humston, R. (2006a). Controlled experiments to predict horseweed (*Conyza canadensis*) dispersal distances. *Weed Science*, 54(3), 484–489.
- Dauer, J. T., Mortensen, D. A., Luschei, E. C., Isard, S. A., Shields, E., & Van-Gessel, M. J. (2009). *Conyza canadensis* seed ascent in the lower atmosphere. *Agricultural and Forest Meteorology*, 149(3–4), 526–534. doi:10.1016/j.agrformet.2008.10.005.
- Dauer, J. T., Mortensen, D. A., & Vangessel, M. J. (2006b). Temporal and spatial dynamics of long-distance *Conyza canadensis* seed dispersal. *Journal of Applied Ecology*, 44(1), 105–114. doi:10.1111/j.1365-2664.2006.01256.x.
- De Visscher, A. (2013). *Air dispersion modeling: Foundations and applications*. New York: Wiley.
- Emberlin, J., Beverley, A.-G., & Julie, T. (1999). A report on the dispersal of maize pollen. <http://www.soilassociation.org/>.
- Fitt, B. D. L., Gregory, P. H., Todd, A. D., McCartney, H. A., & Macdonald, O. C. (1987). Spore dispersal and plant disease gradients: a comparison between two empirical models. *Journal of Phytopathology*, 118(3), 227–242. doi:10.1111/j.1439-0434.1987.tb00452.x.
- Haldane, J. B. S. (1948). The theory of a cline. *Journal of Genetics*, 48(3), 277–284. doi:10.1007/BF02986626.
- Heap, I. (2014). *The international survey of herbicide resistant weeds*. www.weedscience.com.
- Henry, R. S., Davis, V. M. D., & Johnson, W. G. (2008). Open-pollinated transfer of glyphosate resistance in horseweed (*Conyza canadensis*) in greenhouse isolation. <http://www.btny.purdue.edu/weedscience/Postslide/Henry08-01.pdf>.
- Huang, H., Ye, R., Qi, M., Li, X., Miller, D. R., Stewart, C. N., et al. (2015). Wind-mediated horseweed (*Conyza canadensis*) gene flow: pollen atmospheric emission, dispersion, and deposition. *Evolution and Ecology*, 5(13): 2646–2658. doi:10.1002/ece3.1540. <http://onlinelibrary.wiley.com/doi/10.1002/ece3.1540/full>.
- Kareiva, P., Morris, W., & Jacobi, C. M. (2008). Studying and managing the risk of cross-fertilization between transgenic crops and wild relatives. *Molecular Ecology*, 3(1), 15–21. doi:10.1111/j.1365-294X.1994.tb00037.x.
- Kausch, A. P., Hague, J., Oliver, M., Watrud, L. S., Mallory-Smith, C., Meier, V., et al. (2010). Gene flow in genetically engineered perennial grasses: Lessons for modification of dedicated bioenergy crops. *Plant Biotechnology for Sustainable Production of Energy and Co-products Biotechnology in Agriculture and Forestry*, 66(3), 285–297. doi:10.1007/978-3-642-13440-1_10.
- Klein, E. K., Lavigne, C., Foueillassar, X., Gouyon, P.-H., & Larédo, C. (2003). Corn pollen dispersal: quasi-mechanistic models and field experiments. *Ecological Monographs*, 73(1), 131–150. doi:10.1890/0012-9615(2003)073[0131:CPDQMM]2.0.CO;2.
- Lavigne, C., Klein, E., Vallée, P., Pierre, J., Godelle, B., & Renard, M. (1998). *Theoretical and Applied Genetics*, 96, 886. doi:10.1007/s001220050816.
- Levin, D. A., & Kerster, H. W. (1974). Gene flow in seed plants. In *Evolutionary biology* (pp. 139–220). Boston, MA: Springer. doi:10.1007/978-1-4615-6944-2_5.
- Lin, J. J., Noll, K. E., & Holsen, T. M. (1994). Dry deposition velocities as a function of particle size in the ambient atmosphere. *Aerosol Science and Technology*, 20(3), 239–252. doi:10.1080/02786829408959680.
- Loveless, M. D., & Hamrick, J. L. (1984). Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics*, 15, 65–95.
- McCartney, H. A. (1994). Dispersal of spores and pollen from crops. *Grana*, 33(2), 76–80. doi:10.1080/00173139409427835.
- Motten, A. F., & Antonovics, J. (1992). Determinants of outcrossing rate in a predominantly self-fertilizing weed, *Datura stramonium* (Solanaceae). *American Journal of Botany*, 79(4), 419–427.
- Okubo, A., & Levin, S. A. (1989). A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, 70(2), 329–338. doi:10.2307/1937537.
- Raupach, M. R. (1993). Dry deposition of gases and particles to vegetation. *Clean Air: Journal of the Clean Air Society of Australia and New Zealand*, 27(4), 200–203.
- Raupach, M. R., & Briggs, P. R. (1998). *Integrative modeling of transport and fate of endosulfan in the riverine environment, summary report*. Canberra, Australia: CSIRO Land and Water.
- Regehr, D. L., & Bazzaz, F. A. (1979). The population dynamics of erigeron *Canadensis*, a successional winter annual. *The Journal of Ecology*, 67(3), 923. doi:10.2307/2259221.
- Reichman, J. R., Watrud, L. S., Lee, E. H., Burdick, C. A., Bollman, M. A., Storm, M. J., et al. (2006). Establishment of transgenic herbicide-resistant creeping bentgrass (*Apostisstolonifera* L.) in nonagricultural habitats. *Molecular Ecology*, 15, 4243–4255.
- Shields, E. J., Dauer, J. T., VanGessel, M. J., & Neumann, G. (2006). Horseweed (*Conyza canadensis*) seed collected in the planetary boundary layer. *Weed Science*, 54(6), 1063–1067. doi:10.1614/WS-06-097R1.1.
- Shirolkar, J. S., Coimbra, C. F. M., & Queiroz McQuay, M. (1996). Fundamental aspects of modeling turbulent particle dispersion in dilute flows. *Progress in Energy and Combustion Science*, 22(4), 363–399. doi:10.1016/S0360-1285(96)00006-8.
- Smisek, A. J. J. (1995). *The evolution of resistance to paraquat in populations of Erigeron canadensis* L. London, Ontario: University of Western Ontario.
- Sosnoskie, L. M., Webster, T. M., Dales, D., Rains, G. C., Grey, T. L., & Culpepper, A. S. (2009). Pollen grain size, density, and settling velocity for *Palmer amaranth* (*Amaranthus palmeri*). *Weed Science*, 57, 404–409.
- Tackenberg, O. (2003). Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, 73(2), 173–189. <http://www.jstor.org/stable/3100012>.
- Tufto, J., Engen, S., & Hindar, K. (1997). Stochastic dispersal processes in plant populations. *Theoretical Population Biology*, 52(1), 16–26. doi:10.1006/tpbi.1997.1306.

- Van den Hurk, B. J. J. M., & Baldocchi, D. D. (1990). *Random-walk models for simulating water vapor exchange within and above a soybean canopy*. Silver Spring, MD: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Research Laboratories, Air Resources Laboratory.
- van Hout, R., Chamecki, M., Brush, G., Katz, J., & Parlange, M. B. (2008). The influence of local meteorological conditions on the circadian rhythm of corn (*Zea mays* L.) pollen emission. *Agricultural and Forest Meteorology*, 148(6–7), 1078–1092. doi:[10.1016/j.agrformet.2008.02.009](https://doi.org/10.1016/j.agrformet.2008.02.009).
- Wang, J., & Yang, X. (2010). Development and validation of atmospheric gene flow model for assessing environmental risks from transgenic corn crops. *International Journal of Agricultural & Biological Engineering*, 3(2), 18–30. doi:[10.3965/j.issn.1934-6344.2010.02.018-030](https://doi.org/10.3965/j.issn.1934-6344.2010.02.018-030).
- Wang, J., Yang, X., Li, Y., & Elliott, P. F. (2006). Pollination competition effects on gene-flow estimation: Using regular vs. male-sterile bait plants. *Agronomy Journal*, 98(4), 1060. doi:[10.2134/agronj2005.0104](https://doi.org/10.2134/agronj2005.0104).
- Watrud, L. S., Lee, E. H., Fairbrother, A., Burdick, C., Reichman, J. R., Bollman, M., et al. (2004). Evidence for landscape-level, pollen-mediated gene flow from genetically modified creeping bentgrass with CP4 EPSPS as a marker. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 14533–14538.
- Weaver, S. E. (2001). The biology of Canadian weeds. 115. *Conyza canadensis*. *Canadian Journal of Plant Science*, 81(4), 867–875. doi:[10.4141/P00-196](https://doi.org/10.4141/P00-196).
- Wipff, J. K., & Fricker, C. (2001). Gene flow from transgenic creeping bentgrass (*Agrostis stolonifera* La.) in the Willamette Valley, Oregon. *International Turfgrass Society Research Journal*, 9, 224–242.
- Wright, S. (1943). Isolation by distance. *Genetics*, 28(2), 114–138.
- Yang, X., Madden, L. V., & Brazee, R. D. (1991). Application of the diffusion equation for modelling splash dispersal of point-source pathogens. *New Phytologist*, 118(2), 295–301. doi:[10.1111/j.1469-8137.1991.tb00980.x](https://doi.org/10.1111/j.1469-8137.1991.tb00980.x).
- Ye, R., Huang, H., Alexander, J., Liu, W., Millwood, R., Wang, J., et al. (2016). Field studies on dynamic pollen production, deposition and dispersion of glyphosate resistant horseweed (*Conyza canadensis*). *Weed Science*, 64(1), 101–111. doi:[10.1614/WS-D-15-00073.1](https://doi.org/10.1614/WS-D-15-00073.1).