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Atmospheric seed emission, dispersion, and deposition from horseweed (Conyza canadensis)

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Abstract:	The wide dispersion of Glyphosate-resistant (GR) horseweed (Conyza canadensis) biotypes has been reported in agricultural fields in many states. GR traits may be transferred though seeds or pollen from fields with existing GR problems to surrounding fields. Understanding seed production and movement is essential when characterizing and predicting the GR horseweed spread. Yet, a literature review indi-cates there is no experimental data on horseweed dynamic (hourly) seed production and horizontal dis-persion and deposition. To fill this knowledge gap, a 43-day field experiment was performed in Cham-paign, Illinois, USA in 2013 to characterize horseweed atmospheric seed emission, dispersion, and depo-sition. Seed concentration and deposition, along with atmospheric data, were measured in a source field (180×46 m) and its surrounding areas up to 1 km downwind horizontally and up to 100 m vertically. The source strength (emission rate) was reported in a range from 0 to 3.9 seeds/m2/s (0-0.41 seeds/plant/s or 0-11,202.2 seeds/ plant/day). The average total seed production was estimated to be 158,876 seeds/plant for the life of the experiment. A regression equation was obtained to determine normalized diurnal source strength based on atmospheric parameters. Horseweed seeds were observed reaching heights of 80 to100 m, making long-distance transport possible. Normalized (by source data) seed dep-osition with distance followed a negative power exponential function. Correlation analysis showed that the seed emission was mainly affected by horizontal wind speed. Horizontal seed transport was mainly affected by horizontal wind speed and horizontal turbulence, while the major atmospheric parameter af-fecting vertical transport was vertical wind velocity. This study investigates how horseweed seeds travel in the atmosphere. The experimental data can also help in developing and

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Atmospheric seed emission, dispersion, and deposition from horse-weed (*Conyza canadensis*)

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Abstract

The wide dispersion of Glyphosate-resistant (GR) horseweed (*Conyza canadensis*) biotypes has been reported in agricultural fields in many states. GR traits may be transferred though seeds or pollen from fields with existing GR problems to surrounding fields. Understanding seed production and movement is essential when characterizing and predicting the GR horseweed spread. Yet, a literature review indicates there is no experimental data on horseweed dynamic (hourly) seed production and horizontal dispersion and deposition. To fill this knowledge gap, a 43-day field experiment was performed in Champaign, Illinois, USA in 2013 to characterize horseweed atmospheric seed emission, dispersion, and deposition. Seed concentration and deposition, along with atmospheric data, were measured in a source field (180×46 m) and its surrounding areas up to 1 km downwind horizontally and up to 100 m vertically.

The source strength (emission rate) was reported in a range from 0 to 3.9 seeds/m^2/s (0-0.41 seeds/plant/s or 0-11,202.2 seeds/ plant/day). The average total seed production was estimated to be 158,876 seeds/plant for the life of the experiment. A regression equation was obtained to determine normalized diurnal source strength based on atmospheric parameters. Horseweed seeds were observed reaching heights of 80 to100 m, making long-distance transport possible. Normalized (by source data) seed deposition with distance followed a negative power exponential function. Correlation analysis showed that the seed emission was mainly affected by horizontal wind speed. Horizontal seed transport was mainly affected by horizontal wind speed and horizontal turbulence, while the major atmospheric parameter affecting vertical transport was vertical wind velocity. This study investigates how horseweed seeds travel in the atmosphere. The experimental data can also help in developing and evaluating seed/particle dispersion models.

KEYWORDS: Atmosphere, dispersion, deposition, emission, horseweed, seeds, source strength

1 Introduction

Horseweed (*Conyza Canadensis)* is a weed commonly found in farmland, orchards, and meadows. It is especially problematic in no-till agriculture due to the resistance to glyphosate (GR) and other herbicides. During the past 14 years, GR horseweed has been documented in 24 states across the United States and in 10 countries worldwide, and has become a major problem across much of North America (Heap 2014). Horseweed plants can reach a height of two meters, and a single plant can produce nearly 200,000 seeds (Bhowmik and Bekech 1993; Regehr and Bazzaz 1979). The seeds are small achenes (1.6-6.4 mm long), with a pappus of tan to white bristles (Loux et al. 2014). Horseweed seeds are lightweight, approximately 1,400,000 seeds per kg or 0.7 mg per seed (Tilley 2012). The seeds have a low gravitational-settlement velocity (0.323 m/s) (Andersen 1993; Dauer et al. 2006).

Strategies to control the spread of horseweed, especially resistant biotypes, across agricultural fields or natural lands require an increased understanding of the seed dispersion process. The dispersal can be influenced by many factors, including seed source strength (release rate), meteorological conditions, and topography. Understanding these factors that influence dispersal distance is essential in policy making. There were experimental studies on seed vertical dispersion in the air (Dauer et al. 2009; Shields et al. 2006). There are no experimental studies on dynamic seed release rate and dispersion and deposition with distance. In particular, little information is available on the relationship of seed release rate and horizontal dispersion and deposition with atmospheric conditions (wind speed, direction, wind variability, and atmospheric stability).

The objectives of the present study were to: 1) measure the atmospheric dynamic (on the order of an hour) and horseweed seed emission, dispersion, and deposition in the vertical direction (up to 100 m) and in the horizontal direction (up to 1000 m); and 2) quantify the correlation between horseweed seed emission, dispersion, and deposition and atmospheric parameters.

2 Materials and methods

The experiment was conducted from 23 Aug to 12 Oct 2013 on the South Research Farm, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA (Latitude: 40° 04' 51.36" N; Longitude: 88° 14' 23.92" W; Elevation: 216 m). This seed dispersion experiment was conducted as part of the pollen dispersion experiment (Huang et al. 2015).

2.1 Experimental site

The experimental design consisted of a 184×46 m field with naturally occurring horseweed, hereafter called the source field (Fig 1). The field was surrounded by various grasses and soybean. Within the source field, the average canopy height of horseweed was 1 m and the average density of the plants was 8 plants/m^2. The estimated total plant number was 35,607. By August 23, the horseweed plants were fully mature and flowering. The prevailing wind direction was from the southwest to the northeast. During rainy days, plants did not release seed, and experiments were not conducted.

2.2 Seed concentration measurement and calculation

Seed concentration was measured by using four columns of Rotorod samplers. One-column Rotorod samplers were placed in the source field to measure the horizontal flux (seeds/m^2/s) profiles of source production and release, with one sampler placed inside the plant canopy at a height of 0.35 m, one at the height of the canopy (1 m), one at 1.65 m, and one at 2.8 m (Fig. 1). On each Rotorod, seeds were collected on a transparent plastic microscope slide (width=25 mm, length=75 mm) that was fixed on a rotating rod (diameter=92.5 mm) (details in Huang et al., 2015). The rod was attached to an electric motor. In order to retain the seeds, silicone grease was applied to the slide prior to sampling. The slide collection efficiency was assumed to be 64% and independent of wind speeds (Ogden & Raynor 1967). The microscope slides were changed to a fresh set every 2 to 3 hours between 08:00 and 19:00. One column of three Rotorod samplers mounted at 1.0, 1.5, and 3.0 m was placed at the edge of the source field to measure downwind concentrations. The concentrations at higher heights (10 m to 100 m) were measured with the Rotorod samplers mounted below two balloons (another two columns of Rotorod samplers). The two balloons were in the downwind direction inside or outside of the field. The downwind distance of the balloons and the sampler heights were adjusted based on whether seed was detectable. Sampler heights ranged from 10 m to 100 m, and the balloon downwind distance ranged from inside the source field to 110 m downwind from the source.

The seed concentration (C, seeds/m^3) was calculated as the total sampled seed number on each slide divided by sampled air volume that was calculated as a function of rotation speed, sampling time, and slide area of the corresponding Rotorod sampler (Huang et al. 2015).

$$C = \frac{N}{\Delta t \times \delta V \times RS} \quad (1)$$

where N was the number of seeds within the slide, RS was the rotation speed of the Rotorod (rps), and δV was the air volume sampled by the sampler during each revolution.

2.3 Seed deposition measurement and calculation

The deposition rate of seed in and outside of the source field in the downwind direction was measured by greased microscope slides placed on the ground (the size of the slides were the same as those used in the Rotorod samplers). The deposition slides in the downwind direction were placed and collected at the same time as the concentration slides. The collection efficiency of the slide traps was assumed to be 100% (Aylor and Ferrandino 1989; Raynor et al. 1972; Wang and Yang 2010). The Rotorod sampler slides and the deposition slides were not overloaded by the sampled seed during each sampling period.

The seed deposition rate (D) (seeds/m^2/s) was determined as total seeds on each slide divided by the sampling area and time:

$$D = \frac{N}{\Delta t \times 25 \times 75 \times 10^{-6}} \qquad (2)$$

where N is the total number of seeds on the slide, and Δt (s) is the duration of each experimental period, $25 \times 75 \times 10^{-6}$ m^2 is the area of the slide.

2.4 Meteorological measurements

The setup and data processing of meteorological parameters were presented in Huang et al. 2015. Three-dimensional wind velocities were measured in the source field with a sonic anemometer placed at 2.3 m above the canopy (CSAT3, Campbell Sci, Utah, IL). The measurements were recorded at 10 Hz using a CR3000 data logger (Campbell Sci). Solar radiation, air temperature, relative humidity, and rainfall were measured by a weather station located about 800 m north of the source field every hour by the Water and Atmospheric Resources Monitoring Program at the Illinois State Water Survey, University of Illinois at Urbana-Champaign.

Parameters denoting atmospheric conditions were calculated from the weather station and the high frequency anemometers for each sampling period after rotating the horizontal wind components into the mean wind direction (Stull 2001). The parameters included friction velocity (u*, m/s), atmospheric stability at anemometer height (3.3 m) (ξ(3.3), unitless), mean vertical wind speed at anemometer height ($\overline{w}$ (3.3), m/s) and its turbulent variability at 3.3 m (σ_w (3.3), m/s, i.e., standard deviation of vertical wind velocity, σ_w (3.3) was used as a term representing turbulence strength), mean wind speed at 3.3 m ($\overline{u}$ (3.3),m/s) and its standard deviation (σ_u (3.3),m/s), and wind direction at 3.3 m (θ (3.3), degree). A joint probability distribution of θ(3.3) and $\overline{u}$ (3.3) graphed as a wind rose (in Fig. 1) was generated for each sampling period from the 3-D sonic data and used to project wind speed on the direction of the sampling lines. The atmospheric parameters of Monin-Obukhov length (L, m) and stability $\xi(3.3)$ were calculated according to Stull (2001).The instruments and heights used to measure the meteorological variables are listed in Table 1, which presents the averages and standard deviations of each meteorological variable during the whole experimental period.

Table 1: Statistics of meteorological variables collected in the experiment.

Parameter	symbol	unit	height (m)	source	mean±standard deviation
Mean wind speed	$\bar{u}(3.3)$	m/s	3.3	sonic anemometer	1.84±0.69
Wind direction	$\Theta(3.3)$	degree	3.3	sonic anemometer	228±71
Mean vertical wind speed	$\bar{w}(3.3)$	m/s	3.3	sonic anemometer	-0.03±0.05
Friction velocity	u*	m/s	3.3	sonic anemometer	0.36±0.12
Stability	$\xi(3.3)$	unitless	z=3.3	sonic anemometer	-2.03 ± 3.75
Air temperature	T	ºC	2.0	weather station	25.42±4.88
Relative humidity	RH	%	2.0	weather station	54.21±14.70
Solar radiation	SR	kw/m^2	2.0	weather station	0.43±0.21
Rainfall	Rainfall	mm/hour	2.0	weather station	0.21±2.00

2.5 Data processing of horizontal flux and source strength

The seed data processing and analysis were the same as described in Huang et al. (2015). The horizontal flux of seed at height z (F(z), seeds/m^2/s) during each sampling period was calculated from seed concentration at height z, C(z) (seeds/m^3), and wind speed at height z ($\bar{u}$(z), m/s), as F(z)=C(z) $\bar{u}$(z) Wind speeds at different heights were calculated from the formulations in Campbell and Norman (1998) and Stull (2001), which are based on the atmospheric similarity theory (inputs were u∗, ξ(z), and height (z). The integrated horizontal flux (IHF) was estimated by integrating F(z) using the trapezoidal method.

The seed source strength is a measure of the amount of seeds produced per unit area or plant per unit time. Source strength Q_0 (seeds/plant/s) was calculated as the summation of IHF and deposition, and then divided by the contribution field distance:

$$Q_0 = (\underbrace{\frac{\int_0^R D\,dx}{R}}_{\mathbf{a}} + \underbrace{\frac{\int_0^\infty C(z)\bar{u}(z)dz}{R}}_{\mathbf{b}})/density_c \qquad (3)$$

where term a was the contribution of deposition, term b was the contribution of IHF, R was the distance between the leading edge of the field to the location of concentration sensors in the wind direction; and $density_c$ was the plant density at the source center (10 plants/m^2). This equation assumes that the source area is of uniform properties. However, as shown in Fig. 1, the plant density of the field varied from about 10 plants/m^2 at the center of the field to less than 2 plants/m^2 at the edge of the source field. In order to take into account the effect of the variation of plant density, we divided the R into several segments ΔR_i at different density areas, and then scaled the ΔR_i to $\Delta R_{scaled,\,i}$ with respect to the corresponding plant density:

$$\Delta \mathrm{Rscaled, i} = \Delta Ri \times \frac{density_i}{density_c} \qquad (4)$$

where $density_c$ is the density at the center of the field (9.5 plants/m^2) as mentioned before and $density_i$ is the density at the location i. The R in equation 3 is the summation of $\Delta R_{scaled,\,i}$.

2.6 Data analysis

Correlation analyses were conducted to examine the effects of atmospheric parameters on seed dispersal parameters. Atmospheric parameters included u∗, ξ(3.3) , $\overline{w}$(3.3), $\sigma_w(3.3), \bar{u}(3.3), and\ \sigma_u$ (3.3) in the sampling directions, air temperature (T) and its standard deviation (σ_T), solar radiation (SR), and relative humidity (RH). Seed dispersal parameters included seed concentration (C) and deposition (D) in the center of the field, IHF and source strength, Q_o (representing source production), the ratio of center concentration at different heights to the canopy height (seed vertical transport), the ratio of concentration at the field edge to that at the field center canopy height (horizontal transport), the ratio of deposition at different distances to source strength (horizontal transport), the ratio of balloon-measured concentration at different heights to the center concentration at canopy height (vertical transport), and the ratio of the balloon-measured concentration at different downwind distances to the center concentration at canopy height (horizontal transport).

3 RESULTS

3.1 Source production

The duration of this experiment was 43 days. During this period 132 samplings were taken and 15,239 seeds in total were collected in the source field in the downwind wind direction. Seed production started on August 29, and the release of seeds was scant at the beginning (Fig. 2). The low release rate continued for about 1 week (August 29 to September 5). Then the seed release gradually increased and reached its peak about 14 days later on September 11. The seed release decreased gradually following that date, and after 12 days, on September 23, the release rate decreased to a very low point. The low release rate continued for about 19 days until October 11. A rainfall event occurred on October 12, after which there were few seeds released because rainfall washed all the seeds to the ground. Most seeds were released from September 6 to September 22.

The diurnal seed release followed an obvious pattern (Fig. 3). In the morning, the seed release rate was low, then gradually increased. The peak occurred during the afternoon around 13:00-15:00. After the peak, the seed release rate decreased gradually and remained low during the late afternoon.

3.2 Concentration with height and distance

Seed concentration decreased with distance and height at both the source and outside of the source (Fig. 4 and 5). The concentration variation with height followed a negative power function. The concentration was maximized at the lowest height and decreased rapidly with height

(Fig. 5). The rapid variation occurred from ground level to 5 m. At 10- to 100-m heights, the concentration decreased slowly and the variation was small.

As shown in Fig. 4 and 5, seeds were found at heights of 80 to 100 m (0-10% of source concentration), which was about 0 to 0.05 seeds/m3. Therefore, seeds can be dispersed to a high altitude and potentially to a far distance.

At 20 to 40 m downwind and at lower heights (<10 m), seed concentration was in the range of 2-90% (0.02 to 0.6 seeds/m^3) of the source concentration (Fig. 4). At a further distance of 40-70 m at low heights (<10 m), 2 to 20% (0.02 to 0.3 seeds/m^3) of seed concentration remained. At 70-150 m in the downwind direction, many concentrations in the air (all heights) were on the order of 0 to 5% of the concentration at the source (about 0 to 0.05 seeds/m^3).

3.3 Deposition with distance

Seed deposition with distance followed a negative-power exponential curve (Fig. 6). The deposition decreased to 43% (0.018 seeds/m^2/s) at 22 m from the source field edge. Then, deposition gradually decreased with distance. At 320 to 480 m, the average deposition was 1.8 to 3.9% (0.0025 to 0.0018 seeds/m^2/s). At 1000 m, seed deposition decreased to 0.

3.4 Influence of meteorological factors

The Pearson correlation coefficient (r), which is applied extensively to test the linear correlation between two variables, was used to estimate the correlation between the seed and meteorological parameters. A two-sided t-test was applied to give the significance (p-value). Usually the significance level threshold (α-value) is chosen to be 0.05 or 0.01; however, we ran multiple tests on the same data, which means an adjustment to α-value was required to avoid Type I errors. In this study we adjusted the α-value by using a Bonferroni correction that is accomplished by dividing the α-value by the number of tests (k) being performed:$\alpha'=\alpha/k$. In this study, we chose $\alpha=0.05$, $k=10$; therefore the new significance level threshold α' becomes 0.005.

3.4.1 Source production

Pearson correlation coefficients (r) of seed parameters in the field and meteorological parameters are presented in Tab 2. Source strength was moderately and positively correlated to horizontal wind speed and u* (|r|>0.45 and <0.7, P<0.005), and weakly correlated to vertical wind speed and solar radiation (|r|≤0.45) or not significantly (P>0.005) correlated to other atmospheric parameters. This means that the release of horseweed seed may be mainly determined by horizontal wind speed (u* is correlated to horizontal wind speed and is an indicator of the strength of horizontal wind speed). This may also explain the fact that the concentration (C_1 to C_4), deposition, and IHF in the source were significantly related to wind speed.

A regression model was obtained to predict diurnal normalized source strength (NSS) based on meteorological parameters. Source strength was normalized with each day's maximum. The regression equation is:

$$NSS = 0.17\bar{u}(3.3) + 0.588SR \quad R^2 = 0.39 \text{ (P<0.005)} \tag{5}$$

3.4.2 Seed vertical transport

Seed vertical transport at a low height (≤3 m) (in the source field) was not significantly related to atmospheric parameters (Table 2). At higher heights, vertical transport was strongly correlated to vertical wind velocity and air temperature at 60-100 m height (|r|>0.7, p<0.005, Table 3). This means that the major atmospheric parameters affecting vertical transport may have been vertical wind velocity (air temperature is correlated to vertical wind speed).

Table 2. Correlation coefficient (r) of meteorological and seed parameters at the source field. Number in the parenthesis is p value. 'C_i' (i=1 to 4) is the concentration in the source plot (seeds/m^3), C_1 is at 2.8 m, C_2 1.7 m, C_3 1.0 m, and C_4 0.35 m; 'CE_i' (i=1to 3) is the concentration at the edge of the source field, CE1 is at 3.0 m, CE_2 1.5 m, and CE_3 1.0 m. Deposition (seeds/m^2/s) is data collected in the center of the field at 0.35 m height. IHF is the integrated horizontal flux (seeds/m^2/s) at the center of the field. u*: friction velocity, m/s; ξ(3.3): atmospheric stability at anemometer height (3.3 m), unitless; $\bar{u}(3.3)$: mean wind speed at anemometer height (3.3 m), m/s; $\bar{w}(3.3)$: mean vertical wind speed at anemometer height (3.3 m), m/s; T: air temperature; RH: relative humidity,%; SR: solar radiation; 'σ ' means standard deviation of the corresponding meteorological parameter.

variable	# of sam-ple	u* (m/s)	$\xi(3.3)$ (unitless)	$\bar{u}(3.3)$ (m/s)	$\sigma_u(3.3)$ (m/s)	$\bar{w}(3.3)$ (m/s)	$\sigma_w(3.3)$ (m/s)	T (ºC)	σ_T(ºC)	RH (%)	SR (W/m^2)
C_1 (m/s)	132	.34*	.08NS	.34*	.08NS	.09NS	-.05NS	.37*	-.11NS	-.2NS	.2NS
C_2(m/s)	132	.42*	.10NS	.42*	.09NS	.17NS	-.07NS	.35*	-.12NS	-.24NS	.25*
C_3(m/s)	132	.42*	.15NS	.43*	.10NS	.16NS	-.06NS	.39*	-.17NS	-.30*	.32*
C_4(m/s)	132	.44*	.16NS	.46*	.12NS	.21NS	-.07NS	.18NS	-.13NS	-.27*	.33*
Deposition (seeds/m^2/s)	132	.50*	.14NS	.50*	.13NS	.13NS	-.06NS	.38*	-.16NS	-.27*	.26*
IHF (seeds/m^2/s)	132	.43*	.11NS	.45*	.16NS	.30*	-.05NS	.18NS	-.13NS	-.21NS	.33*
Source strength (seeds/plant/s)	132	.46*	.12NS	.49*	.15NS	.28*	-.05NS	.21NS	-.14NS	-.22NS	.34*
C_1/C_3 (unitless)	115	.14NS	-.02NS	.13NS	-.07NS	-.02NS	-.02NS	.11NS	.00NS	.02NS	-.01NS
C_2/C_3 (unitless)	115	-.14NS	-.22NS	-.17NS	-.07NS	.19NS	-.07NS	-.10NS	-.02NS	.20NS	-.20NS
C_4/C_3 (unitless)	115	-.23NS	-.14NS	-.19NS	-.08NS	.16NS	-.01NS	-.13NS	.23NS	.01NS	-.17NS
CE_1/C_3 (unitless)	22	.62*	.32NS	.53NS	.48NS	.17NS	-.12NS	.20NS	-36NS	.11NS	.03NS
CE_2/C_3 (unitless)	22	.54NS	.04NS	.52NS	.36NS	.08NS	-.04NS	.49NS	-.21NS	-.34NS	.35NS
CE_3/C_3 (unitless)	22	.15NS	.32NS	.17NS	-.22NS	.39NS	-.44NS	-.13NS	.36NS	.45NS	-.12NS

Table 3: Correlation coefficient (p value) of meteorological parameter and the ratio (concentration at different heights to canopy concentration at field center). Number in the parentheses is the p value. u*: friction velocity, m/s; $\xi(3.3)$: atmospheric stability at anemometer height (3.3 m), unitless; $\bar{u}(3.3)$: mean wind speed at anemometer height (3.3m), m/s; $\bar{w}(3.3)$: mean vertical wind speed at anemometer height (3.3 m), m/s; T: air temperature, ºC; RH: relative humidity,%; SR: solar radiation, W/m^2; 'σ' means standard deviation of the corresponding meteorological parameter.

Vertical Height (m)	**# of sam-ple**	**u*** (m/s)	**$\xi(3.3)$** (unitless)	**$\bar{u}(3.3)$** (m/s)	**$\sigma_u(3.3)$** (m/s)	**$\bar{w}(3.3)$** (m/s)	**$\sigma_w(3.3)$** (m/s)	**T** (ºC)	**σ_T** (ºC)	**RH** (%)	**SR** (W/m^2)
0-20	105	.19NS	.07NS	.19NS	.05NS	-.10NS	.02NS	.10NS	-.03NS	-.04NS	-.01NS

20-40	52	.18NS	.24NS	.06NS	-.03NS	-.24NS	-.24NS	-.17NS	.17NS	-.12NS	-.24NS
40-60	20	-.14NS	-.03NS	-.14NS	-.04NS	.09NS	-.06NS	-.13NS	.07NS	.09NS	-.11NS
60-100	11	-.40NS	.39NS	-.37NS	.10NS	-.94*	.31NS	.87*	.48NS	-.49NS	-.08NS

*: $P<0.005$

NS: not significant

3.4.3 Seed horizontal transport

From the source field to the source edge, the seed horizontal transport (CE_1/C_3) was positively and moderately related to the u∗ (Table 2). As expected, this implies that stronger horizontal wind can bring more source seeds to the field edge.

At further distances (0-50 m), seed concentration was positively related to wind speed and u* and negatively correlated to vertical wind velocity (Table 4). This implies that stronger wind and weaker vertical wind may have transported more seeds to far distances. The horizontal deposition ratio with downwind distance was correlated to wind speed, u*(80-160 m), and variations of wind speed (20-80 m) (Table5).

Table 4: Correlation coefficient of meteorological parameter and the ratio of concentration at different downwind distances to canopy concentration at field center. Number in the parentheses is the p value. u*: friction velocity, m/s; $\xi(3.3)$: atmospheric stability at anemometer height (3.3 m), unitless; $\bar{u}(3.3)$: mean wind speed at anemometer height (3.3 m), m/s; $\bar{w}(3.3)$: mean vertical wind speed at anemometer height (3.3 m), m/s; T: air temperature, ºC; RH: relative humidity,% ;SR:solar radiation, W/m^2; 'σ ' means standard deviation of the corresponding meteorological parameter.

Distance (m)	**# of sample**	**u*** (m/s)	**ξ(3.3)** (unitless)	**$\bar{u}(3.3)$** (m/s)	**$\sigma_u(3.3)$** (m/s)	**$\bar{w}$(3.3)** (m/s)	**σ_w(3.3)** (m/s)	**T** **(ºC)**	**σ_T** **(ºC)**	**RH** **(%)**	**SR** **(**W/m^2**)**
0-50	105	.36*	.03NS	.35*	.02NS	-.21*	-.04NS	.09NS	-.03NS	-.00NS	-.05NS
50-100	52	.20NS	.14NS	.22NS	.28NS	.12NS	-.14NS	.11NS	.18NS	.09NS	-.16NS
100-150	20	-.65NS	.25NS	-.59NS	-.63NS	-.64NS	.19NS	.29NS	.35NS	-.53NS	.13NS

*: $P<0.005$

NS: not significant

Table 5: Correlation coefficient of meteorological parameter and the deposition ratio (deposition at different downwind distances to source strength). Number in the parentheses is the p value. u*: friction velocity, m/s; $\xi(3.3)$: atmospheric stability at anemometer height (3.3 m), unitless; $\bar{u}(3.3)$: mean wind speed at anemometer height (3.3 m), m/s; $\bar{w}(3.3)$: mean vertical wind speed at anemometer height (3.3 m), m/s; T: air temperature, ºC; RH: relative humidity,% ;SR:solar radiation, W/m^2; 'σ ' means standard deviation of the corresponding meteorological parameter.

Distance (m)	**# of sample**	**u*** (m/s)	**$\xi(3.3)$** (unitless)	**$\bar{u}(3.3)$** (m/s)	**$\sigma_u(3.3)$** (m/s)	**$\bar{w}(3.3)$** (m/s)	**$\sigma_w(3.3)$** (m/s)	**T** (ºC)	**σ_T** (ºC)	**RH** (%)	**SR** (W/m^2)
0-20	31	.15NS	.07NS	.19NS	-.42NS	-.06NS	.16NS	.13NS	-.01NS	.00NS	-.08NS
20-40	30	.22NS	.18NS	.18NS	-.54*	.13NS	-.13NS	.04NS	.02NS	-.07NS	.05NS
40-80	27	.41NS	.31NS	.44NS	.63*	-.05NS	-.18NS	.31NS	-.04NS	.10NS	-.12NS
80-160	27	.55*	.31NS	.57*	.35NS	.01NS	.27NS	.03NS	-.38NS	.13NS	.04NS
160-320	16	.27NS	.37NS	.42NS	.12NS	.01NS	-.40NS	.31NS	.03NS	.18NS	-.12NS
320-1000	9	-13NS	-.25NS	-.11NS	-.19NS	.01NS	.27NS	.03NS	-.38NS	.13NS	.04NS

*: P<0.005

NS: not significant

4 Discussion

4.1 Source strength

Two factors are commonly used as determinants of the seed dispersal process: seed weight and production abundancy. As mentioned in the Introduction section, horseweed seed is light-weight, so it can travel with wind easily. On the other hand, horseweed has been documented as a plant with relatively large seed production. For example, Loux et al. (2014) indicates that a single horseweed plant can produce up to 200,000 seeds. In the study carried out by Steckel (2014), the seed production is in a range of 50,000-250,000 seeds/plant. Davis et al. (2009) shows that the seed production is also a function of plant height, and the magnitude of seed production from different biotypes varies from 10,000 to 100,000 per plant. .In this study, the average total number of seeds produced by each plant was 158,876 seeds. The major release days included about 17 days from September 6 to September 22 (Fig. 2). On other days, there was much less release in the range of 0 to 0.0-0.07 seeds/plant/s, which was about 0-17% of the peak day release. There was a rainfall event at the end of the season on October12, and the rainfall washed all the seeds to the ground, with a resulting release of 0. Therefore, a rainfall event is an important parameter that affects seed emission.

The effects of diurnal fluctuation on seed production has been investigated extensively on different species (Selvakumar et al. 2006; Steiner and Opoku-Boateng 1991; Young 2002). Generally the influence of diurnal fluctuation is through the activity of pollinators, cycle of solar radiation, high-low ambient temperature differences and atmospheric stability. The diurnal seed release pattern shown in Fig. 3 was reasonable. The peak release was around 13:00-15:00 when the solar radiation was high, relative humidity was low, and wind speed and turbulence were strong. These atmospheric conditions made seed release and transport easier. The correlation analysis and the regression equation for source strength also showed that strong horizontal wind and solar radiation mainly affected the seed release. This pattern was similar to pollen's in the same experiment in that the peak of pollen release rate was at 11:00 to 13:00 (Huang et al. 2015).

4.2 High altitude and long distance transport

Various studies have been developed to estimate the mechanics of seed dispersal by wind, and to elucidate the relative importance of physical and biological factors that affect seed disposal. It has been long recognized release height is an essential factor in the seed dispersal process (Levin et al. 2003; Nathan et al. 2002; Thomson et al. 2011). The presence of seeds at high altitudes implies that the seeds may be transported to a far distance. Previous studies indicate that to some extent the heights of particles can determine their dispersal range. Shields et al. (2006) reported the horseweed seed concentrations at a height around 80 m were around 0.0001-0.001 seeds/m^3. In this study, the concentration range of 0-0.02 seeds/m^3 at the altitude of 60-100 m was greater than that in their experiments. The differences may be caused by source strength, source field size, atmospheric conditions, and sampling methods. Compared to horseweed pollen dispersion in the experiment, a lower percentage of seeds were dispersed to the same height. For example, pollen concentration of 0-12.5% remained at the height of 60-100 m compared to seed, of which 2.5%

remained at the same height range. This may be caused by the higher settling speed of seed (0.3233 m/s) compared with pollen (0.0165 m/s) (Huang et al. 2015).

According to Fig. 6, most of the seeds fell within 200 m. At a far distance, such as ~480 m, seeds were still detected, but the deposition rate was relatively low (0.01 seeds/m^2/s on a peak release day, or 36 seeds/m^2/hour). At 1000 m, seeds were not found on deposition slides. This was the same as for pollen in the same experiment. That can pose a serious weed spread range from GR horseweeds during a seed dispersion season.

Although the dispersal distance of seed influences many aspects of the biology plants, including spreading of invasive species, metapopulation dynamics, and diversity and dynamics in plant communities (Cain et al. 2000), there are few data sets that characterize the exact dispersal distance due to the limit in detection at far distances or low deposition conditions. There might be some pollen/seeds transferred to 1000 m that the small slides failed to catch. The dispersal distance deserves more explicit explorations using models or wind-tunnel experiments.

4.3 Influence of meteorological factors

4.3.1 Source strength

The information on seed release rate is important for understanding and predicting seed dispersal. Several authors have noted that seed release varies with respect to seed ripening and environmental conditions such as wind speed, turbulence, and air humidity (Skarpaas et al. 2006; Soons & Bullock, 2008). The favorable meteorological conditions which can promote seed release include low humidity, high temperature, unstable atmosphere, strong wind, and little precipitation (Pazos et al. 2013; Savage et al. 2014). The effects of meteorological factors on the release of seed may differ, depending on the local climatic features and topography, as well as the type of plant. As expected, positive correlations were observed between source strength and wind speed, and solar radiation.

This result is quite reasonable because, as suggested by many other studies, high wind speed and turbulence can promote the abscission of seeds from plants (Pazos et al. 2013; Savage et al. 2014; Soons and Bullock 2008). Solar radiation tends to be positively correlated to both concentration and deposition, thus favoring source strength. At the same time, it was also observed that the correlation between relative humidity and concentrations and deposition in the source was negative (Table 1). It has long been recognized that high relative humidity can physically prevent abscission by hindering the opening of the involucres or promoting the closing of the drag-producing fibres, resulting in less seed released (Greene 2005).

In the same experiment, the pollen release was mainly controlled by plant physiology and was not so strongly related to atmospheric parameters as seed (Huang et al. 2015). It also should be noted that in this study the correlation analysis was restrained by tusing the Bonferroni correction to adjust the α-value. The Bonferroni correction helps to avoid false correlation; however, it may be so stringent that it rules out some significant correlations. The seed/pollen release of a plant is a complicated process that can be influenced by many parameters which need further study.

4.3.2 Seed vertical transport and horizontal transport

As expected, the vertical and horizontal transports were correlated to vertical and horizontal wind speed, respectively. Similar results were found for pollen transport in the same experiment (Huang et al. 2015). Similar to our study, the importance of wind in determining the dispersal distance was noted by Raynor et al. (1972) and Jarosz at al. (2005). The seed travel distance increased with higher wind speed. It has long been noted that wind updrafts (vertical wind) provide the key mechanism for long-distance seed transport (Bullock and Clarke 2000; Nathan et al. 2002; Nathan et al. 2003).

Because the seed transport is influenced by different atmospheric parameters (especially horizontal and vertical wind speeds), seed settling speed, canopy structure, and topography, it is not possible to conduct all experiments under all the different parameter conditions. Modeling work is needed to include these parameters and simulate all possible cases.

5 Conclusions

The dynamic source strength (emission rate) of horseweed seed was obtained in this study. The average total seed production was estimated to be 158,876 seeds/plant for the life of the experiment. A regression equation was obtained to determine normalized diurnal source strength based on atmospheric parameters. Horseweed seeds were observed reaching heights of 80 to100 m, making long-distance transport possible. Normalized (by source data) seed deposition with distance followed a negative power exponential function. Normalized seed concentration with height followed a negative power law function. The seed emission was mainly affected by horizontal wind speed. Horizontal seed transport was mainly affected by horizontal wind speed and horizontal turbulence, while the major atmospheric parameter affecting vertical transport was vertical wind velocity.

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the Illinois State Water Survey, the Prairie Research Institute, the University of Illinois, or the University of Tennessee. The authors have no conflict of interest to declare.

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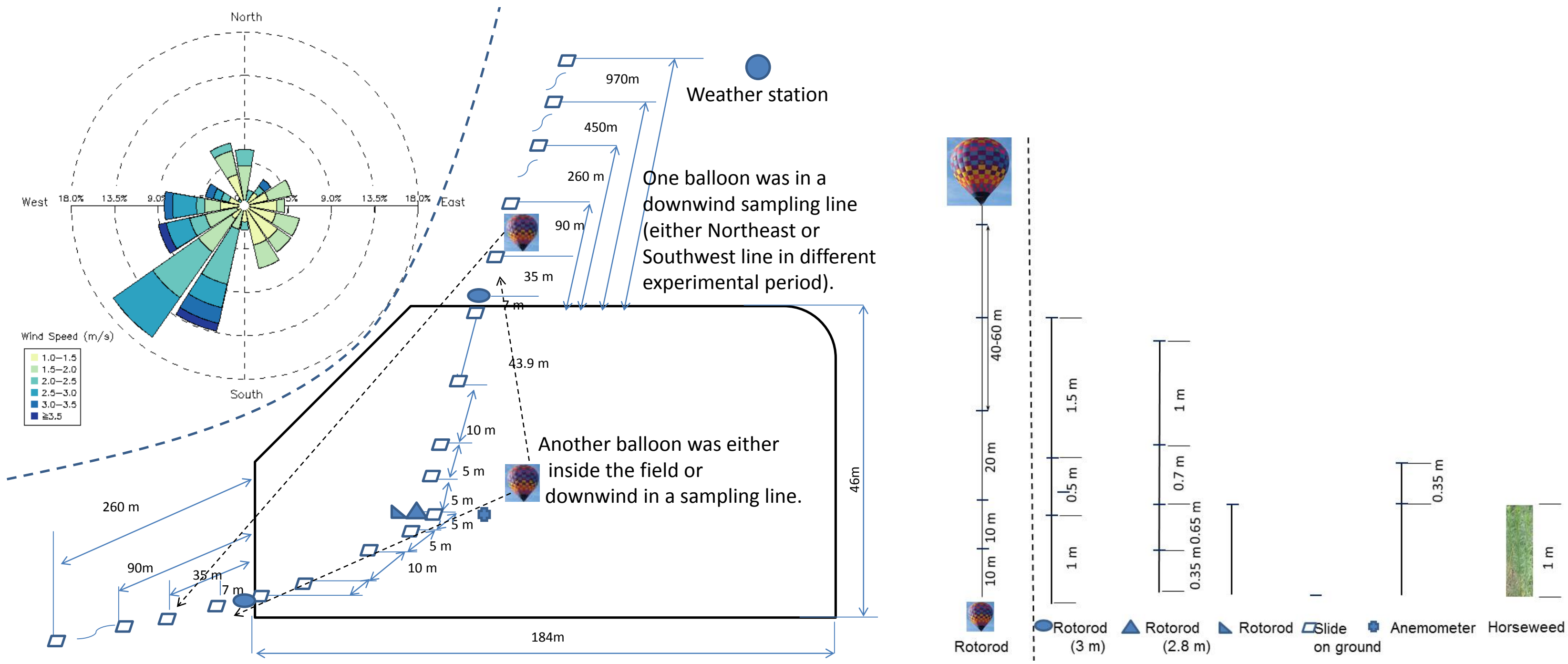

Fig 1: Schematic map and setup of the experiment. The wind rose: left-top, experimental site: left-bottom, sampler heights: right. In each experimental period, only the samplers (slide and Rotorod) along the downwind sampling line (either northeast or southwest direction) were used. Balloon horizontal location and sampler heights on the balloons were adjusted during experiments based on if the seed was detectable at the corresponding sampling heights and location.

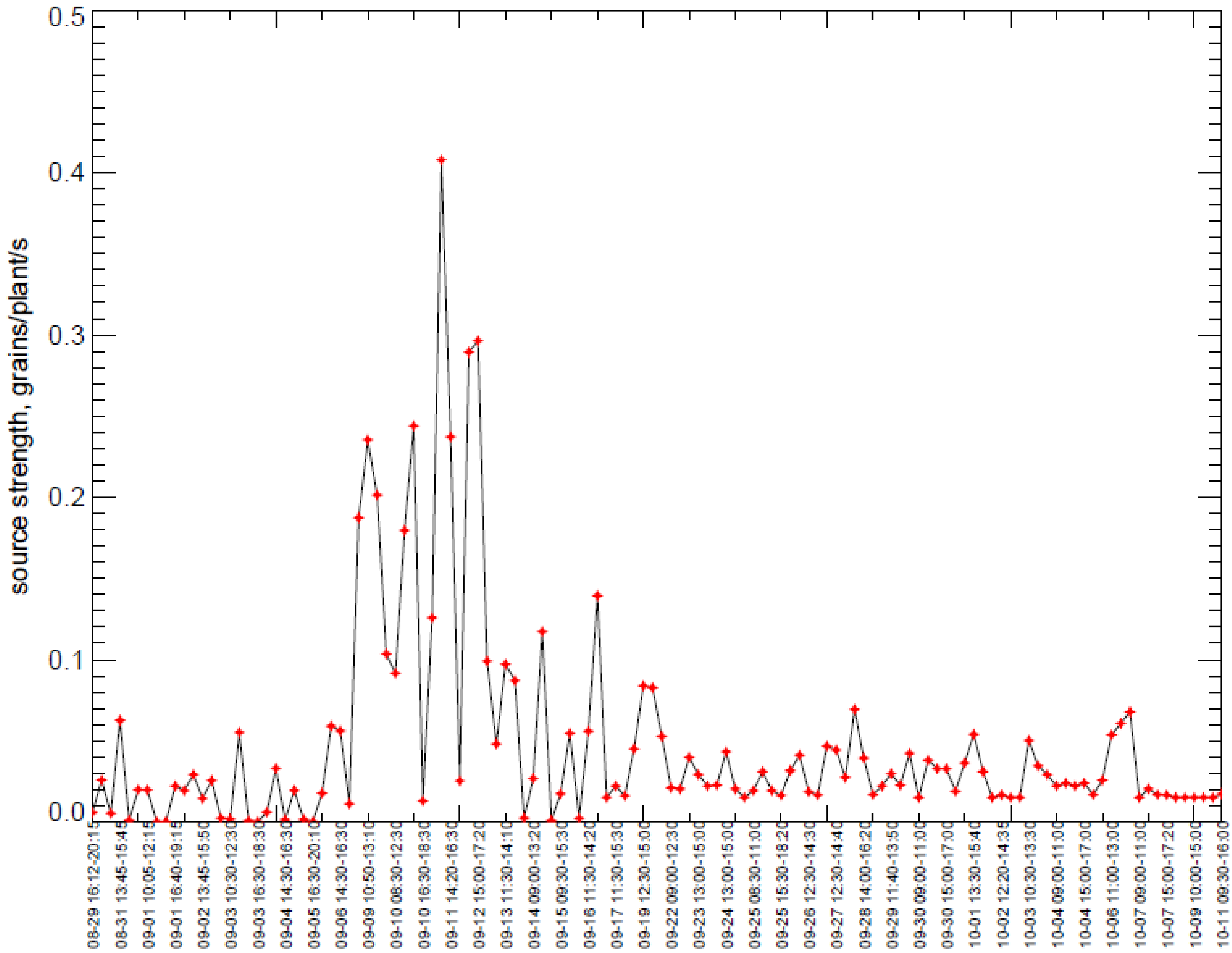

Fig 2. Seed source strength in experiment.

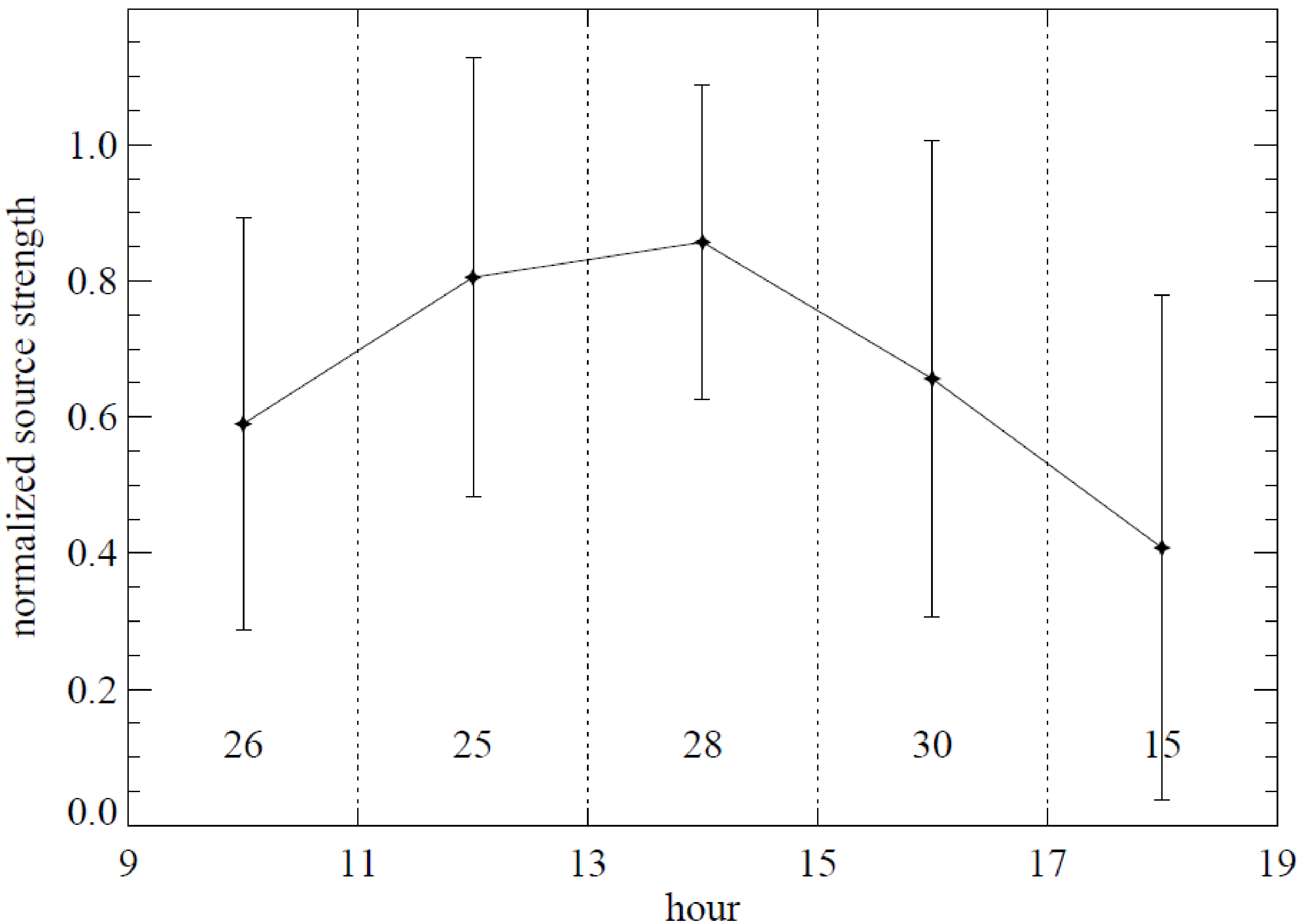

Fig 3. Diurnal variation of normalized seed source strength (normalized by daily maximum; the diamonds are means and bars are standard deviations). Numbers above the X axis are the number of samples used for the corresponding calculations of mean and standard deviation.

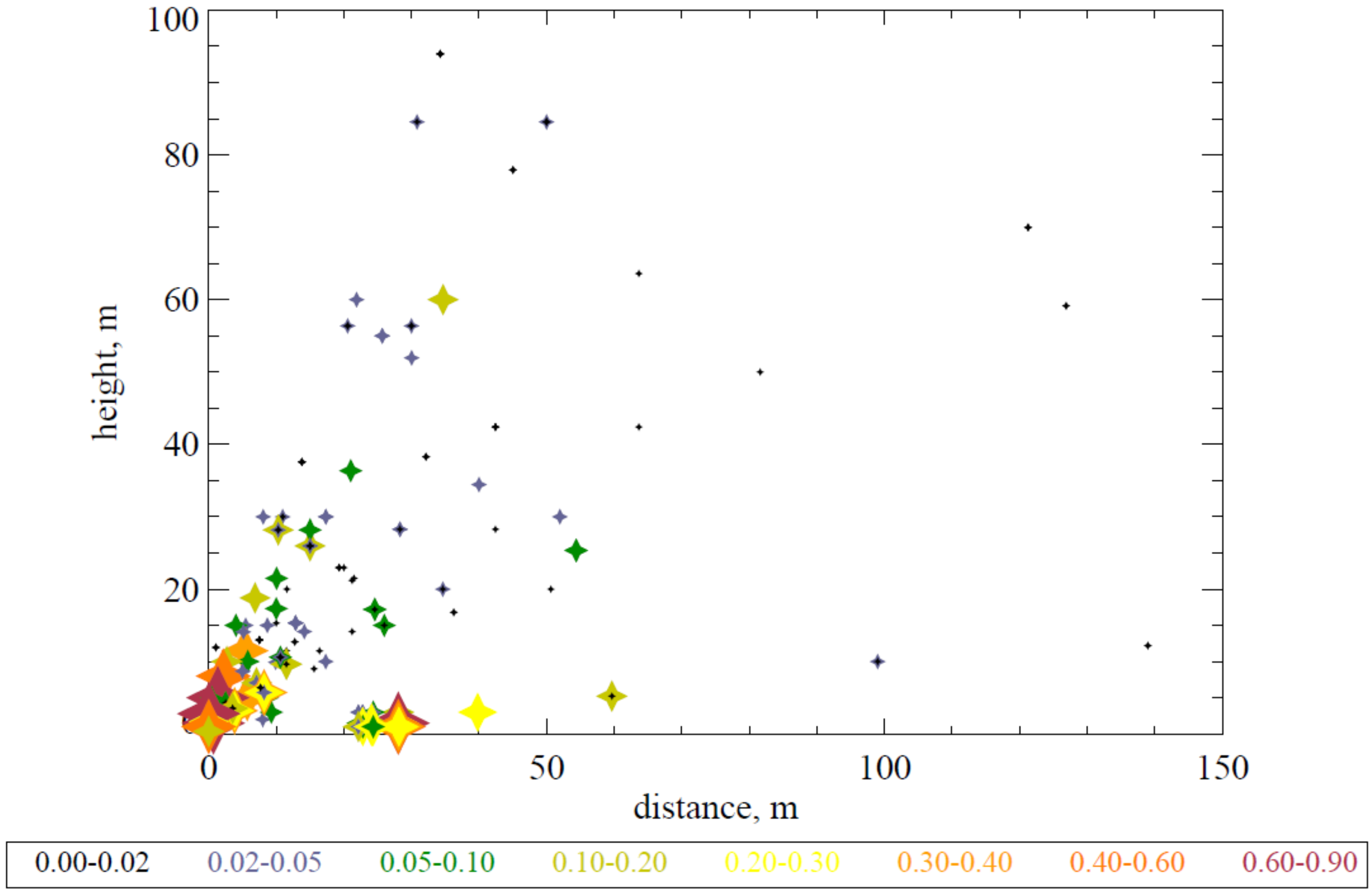

Fig 4. Seed concentration (seeds/m^3) vs. downwind distance and height. The points at distance =0 m at different heights are the averages of the data measured at the corresponding height at distance =0 m during the whole season (showing the averages because the data were too crowded); other data are the data measured during each experimental period.

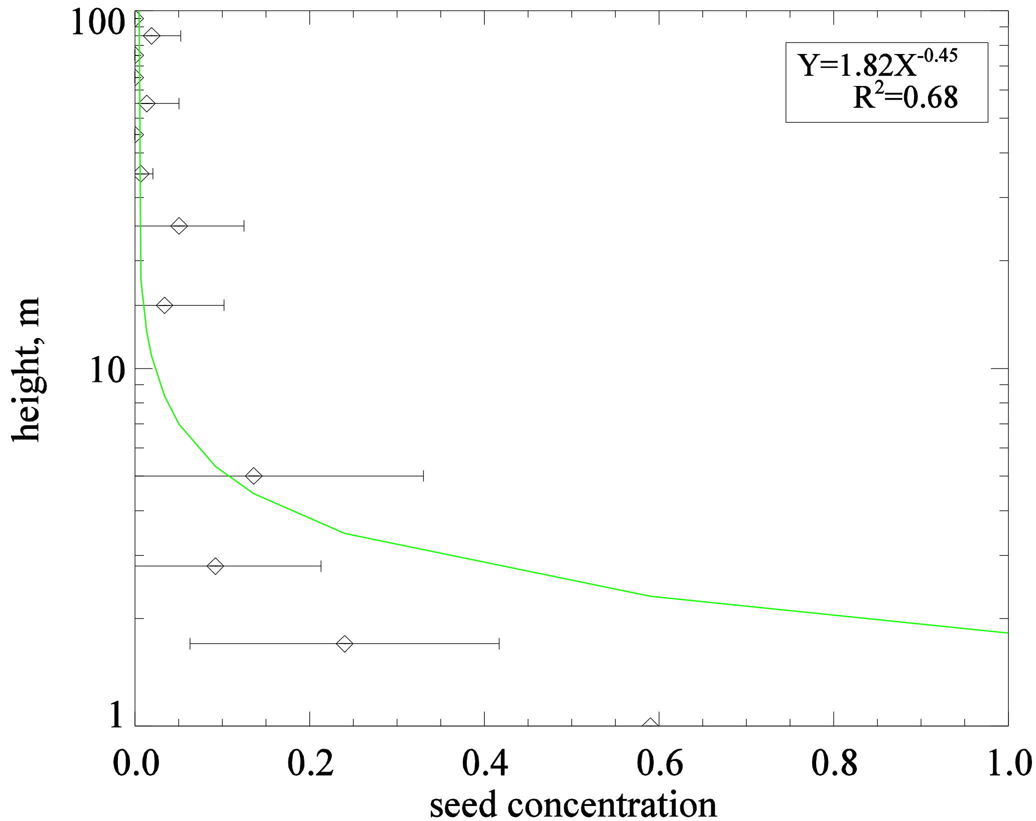

Fig 5. Vertical distribution of normalized seed concentration (normalized by the concentration at 0.35 m height in the source center; the diamonds are means and bars are standard deviations).

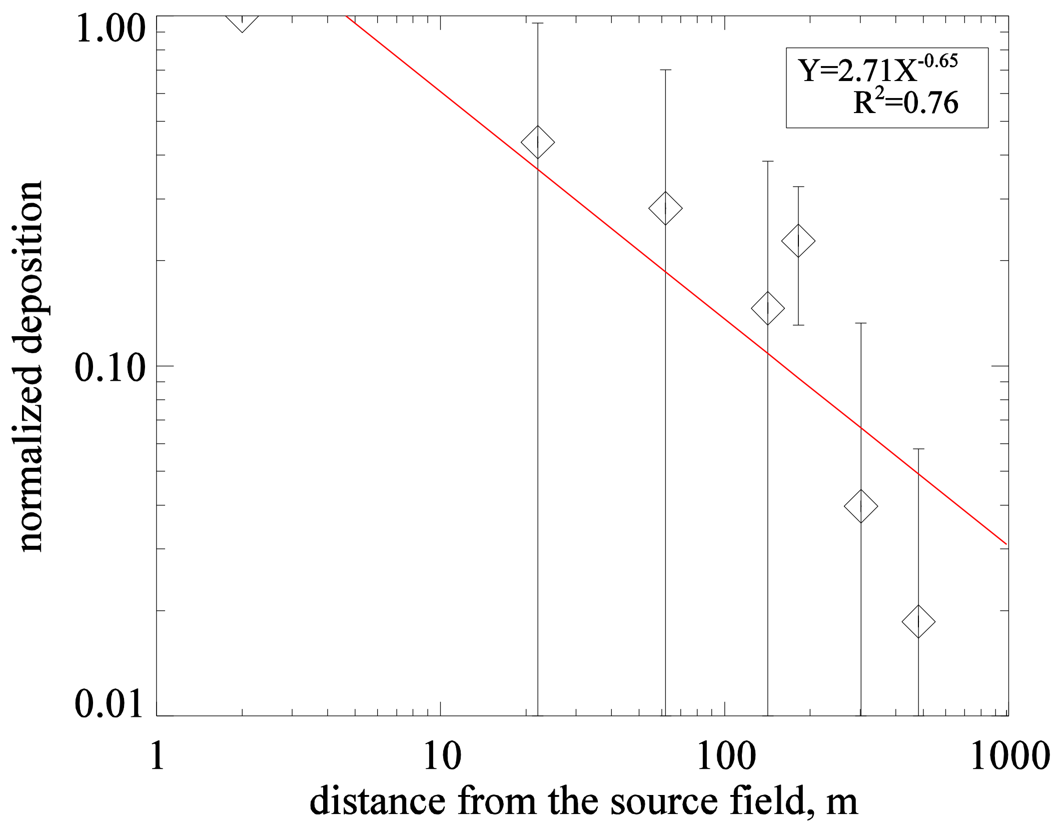

Fig 6. Normalized seed deposition along the downwind direction (seed deposition was normalized by the source strength; the diamonds are means and bars are standard deviations; red line is the fitted trend line).