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

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# **Introduction**

P1: The harms of the Horseweed, and the biological traits caused rapid invasion such as the height of the horseweed plants, powerful productivity of seeds, the shape of seeds, the weight of seeds, and the settling speed of seeds. (no changes on the original paper)

P2: The significance about the horseweed seed emitting and dispersion and the research status about seed emitting and dispersion. The factors influencing seeds dispersion, such as seed source strength, meteorological conditions, and topography. (no changes on the original paper)

P3: The objectives of the present study: 1) measure hourly horseweed seed emission; 2) measure dispersion and deposition in the vertical direction (up to 100m) and in the horizontal direction (up to 1000m); 3) quantify the correlation between emission, dispersion, and deposition and atmospheric parameters;4) comparing the emission, dispersion and deposition between horseweed pollens and seeds in the air. (need be changed)

# **Materials and methods**

## Experimental site and meteorological measurement

P1: The location of source field, and give the explanation that the seed dispersion experiment was part of the pollen dispersion experiment (Huang et al.2015). The briefly description about source field, details shown in Fig.1 and the huang’s previous paper. (need be changed)

P2: The briefly description about meteorological measurements. (delete the original section 2.4 and Table 1).

## Seed concentration and deposition measurement and calculation

P1: The briefly description about the setup of the experiment, details shown in Huang’s previous paper. In summary, pointed out the difference the experiment of pollen and seed(for example, the different outlook traits of pollen and seed , so the different collecting and calculating ways).

## Data processing of horizontal flux and source strength

P1: the formula of Q0, and briefly explanation. The description about the hourly Q0 measurement and data processing.

## Data analysis

Correlation analyses were conducted to examine the effects of atmospheric parameters on seed dispersal parameters. Atmospheric parameters included u\*, *ξ*(3.3) , (3.3), (3.3) in the sampling directions, air temperature (T) and its standard deviation (, 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, *Qo*(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).

# **RESULTS**

## 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.

## 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/m3) 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/m3) 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/m3).

## Deposition with distance

Seed deposition with distance followed a negative-power [exponential](https://www.google.com/search?biw=1517&bih=741&q=logarithmic&spell=1&sa=X&ei=40_FU8flJ8mVyAT5i4H4Aw&ved=0CBoQvwUoAA) curve (Fig. 6). The deposition decreased to 43% (0.018 seeds/m2/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/m2/s). At 1000 m, seed deposition decreased to 0.

## 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:α’=α/k. In this study, we chose α=0.05, k=10; therefore the new significance level threshold α’ becomes 0.005**.**

### 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 (C1 to C4), 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:

 *R*2 = 0*.*39 (P<0.005) (5)

### 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. ‘Ci’ (i=1 to 4) is the concentration in the source plot (seeds/m3), C1 is at 2.8 m, C2 1.7 m, C3 1.0 m, and C4 0.35 m; ‘CEi’ (i=1to 3) is the concentration at the edge of the source field, CE1 is at 3.0 m, CE2 1.5 m, and CE3 1.0 m. Deposition (seeds/m2/s) is data collected in the center of the field at 0.35 m height. IHF is the integrated horizontal flux (seeds/m2/s) at the center of the field. u\*: friction velocity, m/s; *ξ*(3.3): atmospheric stability at anemometer height (3.3 m), unitless; : mean wind speed at anemometer height (3.3 m), m/s;(3.3): mean vertical wind speed at anemometer height (3.3 m), m/s; T: air temperature; RH: relative humidity,%; SR: solar radiation; ‘ ’ means standard deviation of the corresponding meteorological parameter.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **variable** | **# of sample** | **u\***  **(m/s)** | ***ξ*(3.3)**  **(unitless)** | **(m/s)** | **(m/s)** | **(3.3)**  **(m/s)** | **(3.3) (m/s)** | **T (ºC)** | **(ºC)** | **RH (%)** | **SR (W/m2)** |
| **C1 (m/s)** | 132 | .34\* | .08NS | .34\* | .08NS | .09NS | -.05NS | .37\* | -.11NS | -.2NS | .2NS |
| **C2(m/s)** | 132 | .42\* | .10NS | .42\* | .09NS | .17NS | -.07NS | .35\* | -.12NS | -.24NS | .25\* |
| **C3(m/s)** | 132 | .42\* | .15NS | .43\* | .10NS | .16NS | -.06NS | .39\* | -.17NS | -.30\* | .32\* |
| **C4(m/s)** | 132 | .44\* | .16NS | .46\* | .12NS | .21NS | -.07NS | .18NS | -.13NS | -.27\* | .33\* |
| **Deposition (seeds/m2/s)** | 132 | .50\* | .14NS | .50\* | .13NS | .13NS | -.06NS | .38\* | -.16NS | -.27\* | .26\* |
| **IHF (seeds/m2/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\* |
| **C1/C3**  **(unitless)** | 115 | .14NS | -.02NS | .13NS | -.07NS | -.02NS | -.02NS | .11NS | .00NS | .02NS | -.01NS |
| **C2/C3**  **(unitless)** | 115 | -.14NS | -.22NS | -.17NS | -.07NS | .19NS | -.07NS | -.10NS | -.02NS | .20NS | -.20NS |
| **C4/C3**  **(unitless)** | 115 | -.23NS | -.14NS | -.19NS | -.08NS | .16NS | -.01NS | -.13NS | .23NS | .01NS | -.17NS |
| **CE1/C3**  **(unitless)** | 22 | .62\* | .32NS | .53NS | .48NS | .17NS | -.12NS | .20NS | -36NS | .11NS | .03NS |
| **CE2/C3**  **(unitless)** | 22 | .54NS | .04NS | .52NS | .36NS | .08NS | -.04NS | .49NS | -.21NS | -.34NS | .35NS |
| **CE3/C3**  **(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 is the p value, \* means that the p value is less than 0.005, NS means that the p value is not significant. u\*: friction velocity, m/s; *ξ*(3.3): atmospheric stability at anemometer height (3.3 m), unitless; : mean wind speed at anemometer height (3.3m), m/s;(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/m2; ‘ ’ means standard deviation of the corresponding meteorological parameter.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Vertical**  **Height (m)** | **# of sample** | **u\***  (m/s) | ***ξ*(3.3)**  (unitless) | (m/s) | (m/s) | **(3.3)**  (m/s) | **(3.3)**  (m/s) | **T**  **(**ºC**)** | **(**ºC**)** | **RH**  **(%)** | **SR**  **(**W/m2**)** |
| 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

### Seed horizontal transport

From the source field to the source edge, the seed horizontal transport (CE1/C3) 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; *ξ*(3.3): atmospheric stability at anemometer height (3.3 m), unitless; : mean wind speed at anemometer height (3.3 m), m/s;(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/m2; ‘ ’ means standard deviation of the corresponding meteorological parameter.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Distance (m)** | **# of sample** | **u\***  (m/s) | ***ξ*(3.3)**  (unitless) | (m/s) | (m/s) | **(3.3)**  (m/s) | **(3.3)**  (m/s) | **T**  **(**ºC**)** | **(**ºC**)** | **RH**  **(%)** | **SR**  **(**W/m2**)** |
| 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; *ξ*(3.3): atmospheric stability at anemometer height (3.3 m), unitless; : mean wind speed at anemometer height (3.3 m), m/s;(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/m2; ‘ ’ means standard deviation of the corresponding meteorological parameter.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Distance** (m) | **# of sample** | **u\***  (m/s) | ***ξ*(3.3)**  (unitless) | (m/s) | (m/s) | **(3.3)**  (m/s) | **(3.3)**  (m/s) | **T**  **(**ºC**)** | **(**ºC**)** | **RH**  **(%)** | **SR**  **(**W/m2**)** |
| 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

# **Discussion**

## 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).

## 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/m3. In this study, the concentration range of 0-0.02 seeds/m3 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/m2/s on a peak release day, or 36 seeds/m2/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.

## Influence of meteorological factors

### 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.

### 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.

# **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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