FROM EMERGENCE TO IMPACT: *CONYZA CANADENSIS* ADAPTATIONS THAT FACILITATE SEED DISPERAL

A Thesis in
Ecology

by

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ABSTRACT

Adoption of genetically modified glyphosate-resistant crops around the world has increased the selection pressure for weedy species resistant to the commonly applied herbicide glyphosate. Experiments were conducted to examine *C. canadensis* adaptations that facilitate seed dispersal and population spread. Early fall and early spring emerging plants grew taller, set seed earlier, and produced 80,000 – 100,000 more seeds than late spring emerging plants. Management of glyphosate-resistant *C. canadensis* should be effective on early fall and early spring emerging plants since they may be contributing to a greater extent to the spread of the glyphosate resistance gene than late spring emerging plants.

Exploration of seed release and escape from the surface boundary layer (SBL) was conducted by vertical and aerial seed sampling in concert with micrometeorological measurements. Vertical sampling was conducted in 2005 and 2006 in Pennsylvania using a 6 m vertical sampler positioned 14 m downwind of a *C. canadensis* point source. Thermal turbulence were greatest in the afternoon sampling periods which corresponded with the greatest seed collection at 5 and 6 m, the heights above which seed are escaping the SBL. Only 0.04% of seed were predicted to be collected at 5 and 6 m on the vertical sampler, equating to 52 seeds per plant (out of 130,000) predicted to be escaping the SBL. Using the same vertical samplers, remotely piloted airplanes were included in sampling events to quantify the seed concentration profile extending from ground level to 120 m. More seeds (54%) were predicted to escape from the SBL during the afternoon than during the morning (37%), which correlated with maximum mechanical turbulence.
rather than thermal turbulence. Most seed dispersal studies report dispersal distances of tens of meters, but *C. canadensis* seed collected aerially will stay aloft for 5-7 hours and were predicted to travel 20 to 100 km.

A spatially explicit model was developed to assess the changes in glyphosate-resistant (GR) *C. canadensis* spread rate as the agricultural landscape varied with genetically modified GR crop adoption. The model predicted that after 5 years with the current GR adoption in soybean (89%) and corn (21%), 80% of the possible 360 fields would be infested. Adding alfalfa into the current or increased adoption scenarios reduced the number of infested fields after 5 years by 10%. The greatest reduction in spread was accomplished by reducing the amount of glyphosate-resistant crops on the landscape. When encountering a wind dispersed species, like *C. canadensis*, which can easily move among fields, decisions about weed management are not made independent of decisions in neighboring fields, but instead are coupled.
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Prologue

At the 2005 Northeast Weed Science Society annual meeting, a special symposium was held to craft a glyphosate stewardship document to guide producers, extension agents, and land managers on the use of the herbicide glyphosate in glyphosate-resistant crops. Society members discussed the importance of predicting spread rates of glyphosate-resistant weeds and ways of maintaining glyphosate as a viable weed management tool. The resulting herbicide-resistance document warns about common practices that are likely to increase herbicide resistance, e.g. repeated glyphosate applications, but stops short of providing recommendations for producers. Their concern stems from a decade-long change in agriculture that has resulted in an increasing number and spread of glyphosate-resistant weeds.

The rapid adoption of glyphosate-resistant (GR) crops during the last decade has caused U.S. agriculture to become increasingly dependent on the herbicide glyphosate (most common trade name Roundup). After the introduction of GR soybean in 1996, other GR field crops have been released including corn, cotton, canola, and alfalfa although recently GR alfalfa was prohibited from being planted due to concerns about pollen flow to non-GR alfalfa. Adoption of GR soybean has been especially rapid. In just three years after introduction, 40% of soybean area was planted with GR varieties (Carpenter et al. 2002) which increased to 89% of soybean area by 2006 and in some states, rates were near 100%.

1 http://www.nass.usda.gov/Publications/
Increased area planted with GR crops has been coupled with increased glyphosate use. While acre treatments receiving glyphosate have increased in corn and soybean, the number of new herbicide active ingredients introduced has declined since the mid 1980s. Prior to 1996, twelve herbicide active ingredients were sprayed on more than 10% of soybean fields, covering five different modes of action. Ten years later, only glyphosate was sprayed on more than 4% of soybean area².

While glyphosate is environmentally safer than many alternative herbicides, its overuse may result in the loss of this herbicide as an effective weed management tool. As resistant weeds develop, farmers are forced to increase reliance on tillage, increase the use of alternative, more toxic herbicides, or increase herbicide application rates to reduce infestations of uncontrolled weeds. Increased tillage to control weeds can cause soil erosion and sedimentation in waterways (Uri 2000). Alternative herbicides or higher application rates may lead to a greater risk of ground and surface water contamination. Already 97% of water samples drawn from streams near agricultural land (of 83 streams sampled) contain pesticides and Gilliom et al. (2007) found more herbicides in surface water where herbicide use is high.

Plants with resistance to most herbicide modes of action already exist and the strong selection pressure over millions of hectares made glyphosate-resistant weeds a foregone conclusion. Glyphosate-resistance first occurred in grass species in Asia and Australia (Powles et al. 1998; Lee and Ngim 2000) after repeated use in orchards.

² http://www.nass.usda.gov/Statistics_by_Subject/Environmental/
Horseweed (*Conyza canadensis*) was the first broadleaf weed documented resistant to glyphosate (VanGessel 2001). Since 2001, resistant populations have been found in 15 states, Brazil, and China (Heap 2007). A taxonomically related species, *Conyza bonariensis*, has also developed glyphosate-resistance in South Africa, Spain, Brazil, and Colombia. Resistance in *C. canadensis* is not well understood, although researchers have narrowed the mechanism of action to reduced translocation from the leaves to the roots (Feng et al. 2004). Glyphosate-resistant populations are a serious problem for many soybean farmers. At high densities in no-tillage systems, i.e. a heavy infestation, horseweed can reduce soybean yields by 90% (Bruce and Kells 1990) through competition with the crop. Alternative herbicides may solve the immediate problem, but may not be effective in the future because multiple-resistance has been documented for horseweed (Pölös et al. 1988; Smisek et al. 1998; Trainer et al. 2003).

Winter annual weeds, like horseweed (*Conyza canadensis*), have become more abundant with increased no-tillage (Buhler 1992). Horseweed generally germinates in the fall, although spring germination has been documented (Buhler and Owen 1997; Main et al. 2006). Plants bolt in late spring, grow to 2 m or more and flower in July or August (Holm et al. 1997; Weaver 2001). Horseweed outcrosses less than 5% of the time which limits its spread via pollen (Smisek 1995). Therefore, the primary way in which resistant genes are moved main dispersal is seed dispersal. *Conyza* is a prolific seed producer, routinely producing more than 130,000 seeds in August and September (Bhowmik and Bekech 1993; Dauer et al. 2006). The seed are of interest because they are wind dispersed. Seed are small (less than 2 mm), lightweight (less than 0.6 mg), and possess an unbeaked pappus which increases drag and reduces settlement velocity to one
of the lowest in the Asteraceae family (Andersen 1992). Low settlement velocity is critical for long-distance dispersal because the seed can remain airborne longer and be carried farther in the wind.

Seed dispersal is mediated by the seed interaction with the environment. Wind-dispersed organisms pass through a series of transitions described as the aerobiology pathway. Introduced by Benninghoff and Edwards (1972) and later modified by Isard and Gage (2001), the aerobiology pathway describes aerial dispersal as the interaction of ecological and environmental factors with preconditioning, ascent, horizontal movement, descent, and establishment (Figure 1-1). Environmental conditions also affect life-history stages impacting dispersal. Fecundity and plant height determine the seed available for dispersal and the distances seed may travel (Greene and Johnson 1989; Rieger et al. 2002). Time of seed release can be governed by environmental cues like humidity (Maldonado-Ramirez et al. 2005) and synoptic weather patterns (Shields and Testa 1999). Furthermore, turbulent conditions can change dispersal distance from zero to ten or hundreds of kilometers (Isaacs and Byrne 1998; Tackenberg 2003; Soons et al. 2004). Lastly, weed management decisions can directly affect the survival ability and therefore the impact of a weed species. The research contained herein will identify the environmental drivers of dispersal at the preconditioning, release and escape and impact stages of the aerobiology pathway, using glyphosate-resistant horseweed as the motivating force.

Although horseweed is characterized as a winter annual weed, spring emergence may impact the dispersal of the species as outlined in Chapter 2. The role of emergence in shaping beneficial dispersal characteristics is addressed as a part of preconditioning.
Specific attention is paid to plant height, fecundity, and time of seed set which are critical for long-distance dispersal. Plant height determines where in the wind profile the seed will be released which may play a role in long-distance transport. Increased fecundity can play a significant role in lengthening dispersal distance (Dauer et al. 2007). Early seed set provides more opportunity for seed to germinate in the fall and may be tied closely with plant fecundity.

Seed are released within the surface boundary layer (SBL) which extends to 2.5 times the surrounding canopy height (Huschke 1989). Within the SBL, small, frequent turbulent eddies and lower wind speeds increase the likelihood of seed deposition. Therefore, successful seed transport, likely occurs above the SBL, where wind speeds are higher and, during the daytime, large turbulent eddies can maintain seed in the lower atmosphere for hours (Stull 1988; Isard and Gage 2001). Chapters 3 and 4 address the escape of seed from the SBL and transport of seed in the planetary boundary layer (PBL) which extends to 1-2 km above ground level. Firstly, experiments were conducted using a point source and estimating the proportion of seed escaping from a small infestation. The experimental design sampled primarily within the SBL, but also just above the SBL. Seed collected above the SBL were assumed to be transported long distances. Experiments conducted in Chapter 4 extended the height of sampling to include the lower atmosphere. An area source, representing a large glyphosate-resistant population, was utilized to increase the likelihood of seed collection in the atmosphere that sampling was conducted using remotely-piloted airplanes. Chapters 3 and 4 evaluate the role of turbulence in seed movement through the SBL and transport to surrounding fields.
After transport to a new location, impact of the species will depend on recruitment, competitive ability, weather and ability to survive management. The latter is an important aspect with regards to horseweed because populations are resistant to a common weed management tool. In Chapter 5, a spatially explicit model was developed to examine the differences in survival ability between glyphosate and other herbicides and the GR crops. Using a digital aerial photograph of a typical Pennsylvania landscape, fields were assigned crops that may or may not receive glyphosate applications. This model was parameterized for horseweed and predicted the spread of glyphosate-resistant horseweed for five years. Management scenarios represented the current and predicted adoption of GR crops and quantified the scenarios most likely to reduce the spread rate across the landscape.

Collectively, this thesis captures three critical stages in the life history of horseweed. In each stage, the ecological and environmental impacts on the dispersal and spread are quantified and discussed. Glyphosate-resistant horseweed presents a new challenge to resistance management because of its ability to spread long-distances, connecting seemingly independent farmsteads. With the growing dependence on GR crops and glyphosate for weed control, understanding the dispersal ability of glyphosate-resistant weeds among fields will help guide these management decisions.
Figure 1-1: The aerobiology pathway for wind-dispersed organisms taken from Isard and Gage (2001) and modified for plants. The five stages (events) are mediated by environmental and ecological pressures (depicted with arrows).
**Literature Cited**


Chapter 2

Plant Adaptation for Dispersal

Abstract

Management of glyphosate-resistant Conyza canadensis should target life history transitions that contribute to its spread. Recruitment, vegetative growth, and fecundity were monitored in fall and spring germinating Conyza canadensis seedlings to assess differences affecting the fecundity and dispersal ability of the species. Over a two year period, plants at seven sites were monitored along a 400 km transect between central Pennsylvania and southern Delaware in the Eastern US. Year variation affected fecundity but not final plant height although all sites received less precipitation than normal. Emergence was divided into four cohorts; plants emerging before and after October 15th and those emerging before and after May 1st. Early fall emerging and early spring emerging plants achieved similar heights (123 cm) and set seed at a similar time (September 2nd). Plants emerging during these two time periods produced 80,000 – 100,000 more seed than the late spring emerging cohorts. Additionally, plants from the Delaware sites produced 100,000 to 200,000 more seed than Pennsylvania locations which may be why C. canadensis is more problematic in Delaware. The lack of differences between the early fall and early spring germinating plants suggest early spring emerging plants may become a problem because they are not exposed to winter kill, an important source of mortality for fall emerging plants. Management of glyphosate-resistant Conyza canadensis should be effective on both fall and early spring emerging plants.
Early spring management will reduce the spread of the resistant biotype by eliminating the principal source of propagules driving the spread of glyphosate-resistant horseweed.

**Introduction**

Increases in no-tillage agriculture coupled with the adoption of glyphosate-resistant (GR) soybeans (*Glycine max*), cotton (*Gossypium hirsutum*), and corn (*Zea mays*)\(^3\), have resulted in increased winter annual weed abundance (Buhler 1995). In GR soybeans, the glyphosate application is recommended 4 - 6 weeks after planting, but horseweed (*Conyza canadensis*), has been poorly controlled by such late applications (M. VanGessel, personal communication). Over a period of 3-4 years, higher glyphosate application frequencies and larger area treatments led to glyphosate-resistant horseweed populations (VanGessel 2001). Additional glyphosate-resistant horseweed populations have been documented in 15 states in the US, Brazil, and China (Heap 2007). At high densities, horseweed can reduce soybean yield by 90 % (Bruce and Kells 1990) and resistant horseweed will certainly increase the cost of soybean production.

As a winter annual weed, horseweed seed generally germinate in the fall, although spring germination has been documented (Buhler and Owen 1997). Fall emerging plants overwinter as a rosette, then bolt in late spring, before flowering and setting seed through August, September, and early October. Plants can grow to a height of 2 m and a single plant can produce more than 100,000 seeds (Bhowmik and Bekech 1993; Weaver 2001). Seeds are lightweight and wind-dispersed and have been shown to travel long-distances (Regehr and Bazzaz 1979; Shields et al. 2006; Dauer et al. 2007). Recent findings have

\(^{3}\) [http://www.nass.usda.gov/Publications/]
suggested that horseweed seed may germinate in both the fall and spring (Bhowmik and Bekech 1993; Buhler and Owen 1997). The timing of emergence may affect plant survivorship as well as dispersal ability of the species. In Indiana, US, fewer than 20% of late spring emerging plants survived (without management) to produce seed in the fall (W. Johnson, personal communication). The wide window of emergence is beneficial to surviving stochastic environmental conditions and may impact plant fitness.

Marks and Prince (1981) found that fall emerging *Lactuca serriola* (also a winter annual Asteraceae species with wind dispersed seed) produced ten times more seed than spring and summer emerging cohorts. Similar declines in fecundity have been documented for other winter annual species (Mazer 1987; Kelly and Levin 1997), including *Erigeron annuus* (Stratton 1992), a close relative of horseweed. Marks and Prince (1981) suggested *Lactuca* seedlings whose rosette stage lasted 2 - 6 months had the greatest fecundity. Spring emerging cohorts often remain in the rosette stage for a short period of time before bolting (Bhowmik and Bekech 1993). Differences in fecundity will impact the rate of spread of horseweed because dispersal distance is directly proportional to source strength (Rieger et al. 2002; Dauer et al. 2007).

In addition to fecundity, plant height can determine the difference between seed traveling a few meters and tens of meters. Mechanistic models for wind dispersal always include plant height (Greene and Johnson 1989; Okubo and Levin 1989) because height dictates the wind speed encountered by the dispersal propagule. Small changes in height means the seed experience greater wind speed and longer dispersal distances because wind speed increases logarithmically with height above the canopy (Lowry and Lowry 1989). In a wind tunnel experiment, Dauer et al. (2006) found that doubling the wind
speed from 8 kmph to 16 kmph increased the predicted dispersal distance by tens to hundreds of meters. Horseweed growing in corn will disperse seed to 100 m (Regehr and Bazzaz 1979), while horseweed in soybean (seed released above the canopy) will disperse seed to distances of 500 m or farther (Shields et al. 2006; Dauer et al. 2007).

Time of seed release may affect the opportunity to establish. Desert annuals, whose emergence, growth, and reproduction are tied closely to rainfall, have a greater likelihood of completing their life cycle during the wet than during the dry season (Narita 1998). Seed released during the dry season suffered higher mortality at the seedling, vegetative and reproductive stages. In other studies, mortality increased for later emerging cohorts of perennial species, *Viola blanda* (Cook 1980), *Rumex crispus*, and *R. obtusifolius* (Weaver and Cavers 1979), and was connected to seedling size.

Annual weeds may show no selection for emergence timing (Marks and Prince 1981) or even selection against early germinating plants. Baskin and Baskin (1972) found that when *Leavenworthia stylosa*, a winter annual, germinated in July, it encountered the greatest mortality in August or September. In contrast, later emerging cohorts had greater survivorship and viable seed production because they avoided the hot, dry conditions in August. For horseweed, early seed release may increase the opportunities for fall germination since seed can germinate immediately after release (Buhler and Owen 1997), while late released seed may not encounter adequate conditions to germinate.

Managing glyphosate-resistant horseweed will require understanding the effects of emergence periodicity on the dispersal ability of the species. The objective of this research was to quantify how emergence timing affects plant height, seed production, and
time of seed release. Fall germinating plants may produce more seed, have a greater final height, and release seed earlier, resulting in greater area of impact than spring germinating plants. The knowledge gained from this work will help determine the appropriate time to manage for horseweed in order to limit its dispersal ability and reduce the impact to the surrounding farms.

**Materials and Methods**

Experimental plots were established in fall 2004 and 2005 at sites ranging from central Pennsylvania to southern Delaware (470 km transect) in the eastern US. Not all sites were used in both years (Table 2-1). In 2004, one site was located in central Pennsylvania (PA1, Rock Springs, Centre County), one site in southern Delaware (DE1, Georgetown, Sussex County), and a third site in northern Delaware (DE2, Townsend, New Castle County). In 2005, fields adjacent to PA1 and DE1 were used a second year and an additional site was added in Pennsylvania (PA2, Landisville, Lancaster County) located 200 km SW of PA1. Site DE2 was discontinued in 2005 because of problems encountered accessing the site in 2004, and a different location was selected (DE3, Middleford, Sussex County). Locations varied in soil type and annual rainfall (Table 2-1). Experiments were conducted in fields with a history of horseweed presence. In Delaware, fields were previously planted with soybean while the Pennsylvania fields were previously planted with small grains and vegetables. Each field was left fallow the spring prior to initiation of the life history experiment.

Pennsylvania monthly rainfall amounts were compared to 5 year monthly averages and Delaware site data were compared to 50 year monthly averages. Monthly deviations
were tested with a two-sided t-test to determine whether monthly precipitation totals were significantly different than zero at each location.

At each location, locally adapted, naturally emerging plants were classified as early fall (EF, emerged before October 15th), late fall (LF, emerged after October 15th), early spring (ES, emerged after March 15th and before May 1st), and late spring (LS, emerged after May 1st). Emergence cohorts were created by applying a broad spectrum herbicide (glyphosate at 1.8 kg ae/ha in PA and paraquat at 0.53 kg ai/ha in DE) on October 15th, March 15th, and May 1st, using a C02 backpack sprayer applied at 187 L/ha and pressure of 241 kPa. The herbicide application eliminated all emerged plants at the site and horseweed emergence monitoring began two weeks after spraying when ten newly emerged horseweed seedlings were identified and marked with flags in each of four replicates. Plot sizes (10 m x 2 m) were sufficiently large that hundreds of emerged plants were expected. During the growing season, an 18 cm² area surrounding the target plant was maintained weed-free. The LF cohort was not included in the analysis because of poor germination at most locations (Table 2-1).

Emerging horseweed plants were not tested for glyphosate susceptibility. Given the high natural occurrence of glyphosate-resistant horseweed in Delaware it is likely that some of the observed plants were glyphosate-resistant. Emerged horseweed in Pennsylvania were likely glyphosate-susceptible since glyphosate-resistant populations had not been documented within 76 km of the experimental sites. While no studies have compared life history patterns for resistant and susceptible biotypes, we have observed no apparent differences between biotypes (M. VanGessel, personal communication).
Fall germinating and early spring germinating horseweed produce a rosette, but late spring germinating plants rarely produced a rosette (Bhowmik and Bekech 1993). When present, rosette width was measured bimonthly. After plants bolted, plant height was recorded bimonthly until cessation of seed dispersal in September or October. Due to travel time to some sites, recording exact dates of seed set was not possible. Instead, date of seed dispersal initiation was determined to be the first regular sampling date when seed release was observed. Therefore, reported dates of initial seed set were conservative and actual dates may have been 1-13 days prior. Following termination of seed dispersal, final plant height was recorded and plants were harvested. Capitula per plant was measured as a surrogate measure of fecundity and converted to seeds per plant based on previous work that reported 50 seeds per capitula (Dauer et al. 2006).

Analyzing data from individual plants would constitute pseudoreplication, so data were averaged from the number of surviving plants in each plot and provided the response variable for the replicate within the emergence cohorts. This also prevented problems where individual plants within a replicate died during the experiment. To assess the variation between years, data from the two sites replicated in time (PA1 and DE1) were tested for final plant height and seed production (Proc Mixed, SAS 2007).

Year significantly affected seed production \( (P < 0.01) \) but not plant height \( (P > 0.05) \). Data for plant height at DE1 and PA1 were pooled and tested with a linear mixed effects model with state (fixed), cohort (fixed), and replication nested in location (random) (SAS v. 9.1). Data for seed production at DE1 and PA1 were kept separate and tested with a similar linear mixed effects model. Date of seed set was only recorded in PA and was
tested with cohort (fixed) and replication nested in location (random). The effect of final plant height and cohort treatment on fecundity was tested using an analysis of covariance.

**Results**

Most sites received below average precipitation in both years of the study, but only two locations, DE2 and PA1 in 2006, received significantly less precipitation than normal (Table 2-1). Although DE2 received very little rain compared to normal, final plant height and per plant fecundity were not significantly less than plants at other locations.

Emergence time significantly influenced fecundity, plant height, and survival to maturity. Most (86%) early fall germinating plants survived to produce seed, while 78% of early spring and 62% of the late spring emerging plants survived to produce seed. Spring and fall cohorts reached different heights and had different flower initiation dates. DE and PA plants varied significantly ($P < 0.001$) with DE plants attaining greater height (125.8 cm ± 7.00 SE) than PA plants (79.5 cm ± 8.61 SE). Cohorts also significantly affected plant height (Figure 2-1). EF and ES cohorts were not significantly different from each other but were significantly taller than the LS cohort ($P < 0.05$).

There were insufficient DE data to analyze latitudinal differences, but time of emergence was significant ($P = 0.05$) for the date of seed initiation in PA populations (Figure 2-2). EF and ES plants averaged 4 days between seed dispersal initiation (Julian date 244 to 248), but set seed significantly earlier ($P = 0.066$, $P = 0.080$, respectively) than the LS cohort (Julian date 267).

Cohort treatments alone, and interacting with location, did not affect individual plant fecundity, but location was significant ($P < 0.01$, Figure 2-3). Generally, plants grown in DE locations produced 3 – 10 times more seed than PA plants. On average, PA2 plants
produced 30,000 more seed than PA1 grown plants. DE1 plants were not significantly different from either PA site, but plants produced 3-5 times more seed. DE2 plants produced the most (250,000) seeds, but were not significantly different ($P < 0.03$) than DE2 plants, even though DE2 produced 100,000 more seed, on average, than DE1.

Regehr and Bazzaz (1979) found a linear relationship between final plant height and natural log of seed number. Analysis of covariance found cohort treatment alone or interacting with final plant height, did not affect seed production ($P > 0.05$). However, final plant height did significantly ($P < 0.001$) affect fecundity. Stems were analyzed for their affect on capitula production but were non-significant, although this analysis found that treatment by stems interaction did significantly affect seed production ($P < 0.01$). Testing the three-way interaction of treatment by stems by final plant height was not possible because of insufficient data. Following Regehr and Bazzaz, an exponential model found capitula were a function of final plant height (R Development Core Team 2006) and plants produced 11,000 additional seed per 10 cm of increased growth ($P < 0.001$, $r^2 = 0.45$, Figure 2-4).

**Conclusions**

Decisions about managing glyphosate-resistant *Conyza canadensis* should encompass the role of emergence timing on the fecundity, plant height, and time of seed set which all affect spread of the resistant biotype. *C. canadensis* dispersal is dependent on time of seed release, plant height and fecundity. For a winter annual species, early seed release increases the opportunity to germinate in the fall. For a wind-dispersed species, growing to a height that exceeds the surrounding plant community will increase the likelihood of
seed traveling long distances (Greene and Johnson 1989). For all species, maximizing viable seed production increases the likelihood of successfully colonizing new sites.

Study sites were selected to cover a range of growing conditions in the Mid-Atlantic soybean growing region. Surprisingly, the latitudinal gradient only influenced seed production with DE plants producing approximately twice as many seed as PA grown plants. Even though environmental conditions within a location were assumed to be homogeneous (no variation between replicates), variable germination suggested other factors were also important. Poor emergence in some treatments and years, resulted in a few treatment replicates having hundreds of plants while a replicate immediately adjacent had few or no plants. In plots, with high horseweed densities (unmeasured but easily observable), density-dependent restrictions on height and fecundity may have also contributed to the lack of differentiation among cohorts (Bhowmik and Bekech 1993).

Locations also varied in previous crop which can affect residue and impede germination of horseweed (Main et al. 2006). Previous crops can also affect soil moisture and nutrients which can limit cohort establishment and growth (Gross and Smith 1991). Unfortunately, soil moisture was not recorded during this study, but yearly precipitation did not vary from normal at most locations although monthly precipitation patterns may have negatively impacted germination. In 2006, Delaware experienced a fall drought (150+ mm below average at each site), and likely prevented successful establishment of an EF cohort at both locations (Table 2-1). A longer term experiment covering a greater range of climatic conditions would assist in separating the phenotypic effects from the short-term weather impacts.
Plants are involved in a risky game of bet-hedging to allocate resources parsimoniously to maximize fitness. Bet-hedging was defined by Philippi and Seger (1989), following Slatkin (1974), as the tradeoff between the mean and variance of plant fitness. Philippi and Seger suggested that annual plants have diversified bet-hedging phenotypes to increase the phenotypic variation within generations. Evolutionarily, plants exhibiting high fitness in good or bad years will not be as successful as plants that have a lower fitness in the best years, but higher fitness in bad years. In the end, the range of years encountered by a seedbank and seedling population will determine the success of the population. The success of a specific diversification strategy is dependent on the nature of the disturbance regime. When disturbances are occasional rather than consistent, mixtures of phenotypes will be selected. Depending on disturbance frequency and severity (mechanical or chemical), differentiation may occur between pre- and post-disturbance phenotypes (Masuda and Washitani 1992).

Although *C. canadensis* is characterized as a winter annual weed, spring emergence had been previously documented (Buhler 1992; Bhowmik and Bekech 1993; Main et al. 2006). Regehr and Bazzaz (1979) showed fall emerging cohorts produced more seed, but had a lower survival rate. Our results indicate early fall emerging and early spring emerging plants are equally fecund (Figure 2-3). However there was a difference in final plant height and date of seed set (Figures 2-1 and 2-2). EF and ES were not different from each other, but did achieve a greater plant height and earlier seed set than the LS cohort. Since there was no difference in fecundity, ES plants may be at a greater advantage than EF plants because they are less susceptible to low temperature stress.
Winter mortality and weed management may be the disturbances that determine how *C. canadensis* hedges its fitness bet.

With a mild winter, a fall germinating plant would likely out-compete spring emerging plants. In years with a harsh winter, mortality of fall plants will increase, resulting in fewer fall emerging plants contributing to dispersal the following fall. Buhler (1997) and Regehr and Bazzaz (1979) found winter mortality was negatively correlated with rosette size and varied dramatically from 91% to 14%. With high rates of winter mortality, it is likely that spring emerged plants will play an important role in persistence and spread of glyphosate-resistant *Conyza*. When all marked plants in the EF and ES were assessed, mortality for fall plants was 14% (N=136) compared to 38% (N=271) for ES emerging plants. A more comprehensive examination of survivorship could determine whether differences in survivorship exists among resistant and susceptible biotypes. Furthermore, survivorship will be closely tied to winter mortality, necessitating multi-year studies to elucidate such year effects. Masuda and Washitani (1992) reported two ecotypes of *Galium spurium* developed in close proximity to each other based solely on winter burning. The ecotypes were differentiated by yearly disturbance which selected for the ecotype whose dormancy was broken by heat. Masuda and Washitani (1992) postulate that reducing the frequency of the disturbance (burning) may result in a mixture of ecotypes. Instead of disturbance timing, maybe *C. canadensis* ecotypes are developing based on their susceptibility to a management practice? Resistant and susceptible plants may have different emergence and growth patterns that affect the survivorship of the ecotype. A mixture of ecotypes would only have occurred at the Delaware locations because resistant biotypes did not exist at the experimental sites.
However, deciphering glyphosate-resistant versus susceptible biotypes in naturally emerging populations would have been impossible. Segregation of the biotypes will help clarify whether differences exist in germination timing between biotypes.

For effective management, the relative contribution of each cohort to dispersal is crucial for reducing the spread. Early management of *C. canadensis* has always been the most effective strategy for reducing plant growth (Bruce and Kells 1990). Fall management would be critical if fall cohorts produced more seed at a greater height and earlier date than the spring cohorts. The EF cohort was similar to the ES cohort in final plant height, date of seed release and fecundity, so fall management would miss spring emerging plants, plants that are clearly important to spread of this species. However, an early spring management plan would control both EF and ES plants, leaving only the LS emerging cohort. The LS cohort produced fewer capitula (on average about 2000 fewer) at a lower height and later in the season compared to EF and ES cohorts. When winter conditions are increase EF mortality, early spring management will result in control of at least 2/3 of the emerging plants in a given year. Buhler (1997) found that spring emergence can contribute 32% of the total plant density but their reduced fitness will not significantly impact the spread of the resistant biotype. Therefore, it is advantageous, when possible, to manage for *C. canadensis* in the early spring to reduce the dispersal and spread of resistant *C. canadensis*. 

Table 2-1: Descriptions of soil type, average plants per replicate, and precipitation at seven experimental sites in two years in Pennsylvania and Delaware. Each site was setup to contain four replicates containing ten plants and classified into four cohorts: early fall (EF), late fall (LF), early spring (ES), and late spring (LS). Total precipitation at each site was recorded from August in the previous year to October in the labeled year. Stars (*) represent significant deviation ($P < 0.05$) of total precipitation from the total mean precipitation for 5 years (PA) and 50 years (DE).

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Soil Type</th>
<th>EF</th>
<th>LF</th>
<th>ES</th>
<th>LS</th>
<th>Precipitation (mm)</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>Total</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Dev from Norm</td>
</tr>
<tr>
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<td>DE1</td>
<td>Pepperbox loamy sand</td>
<td>9.5</td>
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<td>10.0</td>
<td>1306</td>
<td>-247.4</td>
</tr>
<tr>
<td></td>
<td>DE2</td>
<td>Matapeake silt loam</td>
<td>9.3</td>
<td>9.3</td>
<td>8.3</td>
<td>540</td>
<td>-807.5 *</td>
</tr>
<tr>
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<td>Hagerstown silt loam</td>
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<td>4.8</td>
<td>5.0</td>
<td>593</td>
<td>-261.4</td>
</tr>
<tr>
<td>2006</td>
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<td>9.5</td>
<td>7.5</td>
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<tr>
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<td>-221.2</td>
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<tr>
<td></td>
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<td>6.8</td>
<td>4.0</td>
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<tr>
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<td>8.0</td>
<td>6.7</td>
<td>1521</td>
<td>121.9</td>
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</table>
Figure 2-1: Final plant height pooled across locations for early fall (EF), early spring (ES), and late spring (LS) emerging *Conyza canadensis*. Bars with similar letters were not significantly different ($P < 0.05$).
Figure 2-2: Julian date of initial seed set or early fall (EF), early spring (ES), and late spring (LS) emerging Conyza canadensis at two locations in Pennsylvania (PA1 and PA2). Bars with similar letters were not significantly different ($P < 0.05$).
Figure 2-3: Average seed production per plant pooled across treatments at four locations in Delaware (DE) and Pennsylvania (PA). Bars with similar letters were not significantly different ($P < 0.05$).
Figure 2-4: Seed production per plant pooled across locations and treatments and tested against final plant height using linear least squares. The calculated regression line had a significant relationship ($P < 0.05$) and the form $\text{Ln (Seeds)} = 8.703 + 0.0201 \times \text{plant height}$.
Literature Cited


Chapter 3

Escape of Seed from the Surface Boundary Layer

Abstract

Dispersal experiments were conducted in 2005 and 2006 to quantify the proportion of seed leaving a *Conyza canadensis* infestation and potentially traveling long distances. Using a point source created with transplanted *C. canadensis*, seed production within the source area was estimated at 270 million in 2005 and 90 million in 2006. A vertical sampling device was erected at 14 m in the prevailing wind direction to collect seed as they ascended through the surface boundary layer (SBL) to heights where long-distance transport can take place. Mesh screens were suspended on the device and seed were sampled between 2 and 6 m above ground level (AGL) which positioned 3 screens within the surface boundary layer and 2 screens above the surface boundary layer. Sampling was conducted continuously between 8:00 and 16:00 (divided into 2 hour increments) over nine days in two years during the maximum seed release period each year. Seed concentration (seeds m\(^{-3}\)) always decreased with height. Seed concentrations were lower from 8:00 to 12:00 than from 12:00 to 16:00. More seed were collected at 5 and 6 m AGL from 12:00 to 16:00, suggesting that the proportion of collected seed that successfully ascended through the SBL was greatest later in the afternoon. A greater frequency of thermal than mechanical turbulence was also observed during 12:00 to 16:00, suggesting thermal turbulence may have contributed to vertical seed movement. In 2006, seed collection was estimated at ground level to the base of the vertical sampler and between 2 and 6 m AGL. Most (87\%) of the seed released by the source were
predicted to fall within the first 14 m, while 0.2% were estimated between 2 and 4 m AGL and 0.04% estimated at 5 and 6 m AGL. From a single glyphosate-resistant \textit{C. canadensis} plant that produced 130,000 seed, our results predict at least 52 seeds would ascend through the surface boundary layer and, scaled to the entire patch, 12,000 seed would escape the SBL during the dispersal season, with the potential of traveling long distances.

\textbf{Introduction}

Development of glyphosate-resistant \textit{Conyza canadensis} (VanGessel 2001) has increased attention on the role of weed seed dispersal in transporting the herbicide resistance genes long-distances. Current agricultural practices continue to select for the resistant biotype and development of other glyphosate-resistant (GR) weeds (Heap 2007). Currently, 89% of soybeans and 21% of corn receive glyphosate applications each year, and much of this area is likely planted with glyphosate-resistant varieties.\footnote{http://www.nass.usda.gov/Statistics_by_Subject/Environmental/} If adoption of GR crops continue, distances between safe sites will decrease and dispersal among safe sites (fields only receiving glyphosate for weed management) by GR weeds will increase.

\textit{C. canadensis} is a winter annual weed that has recently increased in abundance in fields where tillage has decreased or been eliminated. Plants can grow to a height of 2 m (Weaver 2001) and at high densities (greater than 100 plants m\textsuperscript{-2}) \textit{C. canadensis} can reduce soybean yield by 90% (Bruce and Kells 1990). Pollen can carry the resistance gene, but \textit{C. canadensis} outcrosses less than 5% of the time (Smisek et al. 1998). The spread of glyphosate resistance genes in this species is overwhelmingly seed mediated.
and a single plant can produce 70,000 to 200,000 seeds equipped with a pappus to aid in wind dispersal (Regehr and Bazzaz 1979; Weaver 2001). Previous work with _C. canadensis_ reported downwind dispersal of 500 m, even though the majority of seed traveled less than 100 m (Dauer et al. 2007). Spores, insects, and pollen have reportedly traveled tens to hundreds of kilometers via wind (Aylor et al. 1982; Shields and Testa 1999; Aylor et al. 2006). Aerial sampling recorded _C. canadensis_ seed at heights of 120 m above the ground level but did not connect these data to atmospheric conditions or determine the proportion of seed reaching these heights (Shields et al. 2006).

During the previous work with this species, a point source was used to accurately quantify dispersal distances and the resulting dispersal kernel (Regehr and Bazzaz 1979; Dauer et al. 2007). Furthermore, a precise estimate of source strength can be calculated and compared to seed collection data to determine the trapping efficiency. With wind dispersed seed traveling 100 m or more, trapping efficiency is low and many of the seed released at the source cannot be accounted for. Dauer et al. (2007) hypothesized that the difference between _C. canadensis_ seed produced at the source and seed predicted to be deposited within the field, were potentially traveling beyond the extent of the sampling design. Transport beyond field borders is considerably more likely if seed are moved vertically where they experience higher wind speeds (Isard and Gage 2001).

Most seed are not transported far from the mother plant. However, some plants are adapted for long-distance wind dispersal and the seed will take advantage of proper atmospheric conditions. One plant adaptation is to grow in a way that seeds are exposed to higher wind speeds. _C. canadensis_ plants generally grow to heights above the soybean canopy and seed released at this height will experience greater wind movement than in or
below the canopy. The surface boundary layer (SBL), which extends to 2.5 times the canopy height (Huschke 1989) during the daytime, is composed of small scale turbulent eddies that can positively or negatively impact an organism’s vertical transport. Once released, seed pass in quick succession between eddies and, disregarding the effects of gravity on airborne seed, are equally likely to descend into the plant canopy (deposition) or escape from the SBL. The SBL is contained within the planetary boundary layer (PBL) which extends from the ground surface to 1-3 km into the atmosphere (Stull 1988). Above the SBL is a region of higher wind speed and long-period turbulent eddies which are conducive to long-distance transport (Lowry and Lowry 1989). Often this layer will remain convectively mixed during daytime, and seed can remain in this layer until the layer breaks down after sunset, at which time the buoyant forces diminish and seed settle to the ground. Research on vertical transport of organisms ascending through the SBL into the PBL above has focused on meteorological conditions conducive to organism transport. Spores may be adapted for nighttime dispersal to avoid harmful UV radiation (Maldonado-Ramirez et al. 2005), and insects may be adapted to disperse when temperatures exceed minimum requirements (Isaacs and Byrne 1998).

Other researchers have studied the meteorological mechanisms that move organisms vertically. Vertical wind movement, in the form of mechanical or thermal turbulence, can carry an organism through the more turbulent SBL and into the PBL above. Thermal turbulence develops from heated air rising from the surface and results in a positive (upward) heat flux. Mechanical turbulence is a result of friction between slow moving air and faster moving air directly above and causes a negative (downward) momentum flux. Seed dispersal researchers have debated whether thermal turbulence or mechanical
turbulence has a greater role in vertical transport (Tackenberg 2003; Soons et al. 2004). Tackenberg argued that calm, sunny days increase thermal turbulence and result in greater vertical seed movement. Soons et al. (2004) contest that windy days lead to greater mechanical turbulence and more vertical seed movement.

Despite the assertion that thermal or mechanical turbulence are more important for vertical seed transport, sampling has not been conducted when seed are actively engaged in the escape process. In this work, we first quantified the total seed production from a point source of *C. canadensis* in order to estimate the proportion of seed ascending through the SBL. Secondly, seed were sampled vertically in the prevailing wind direction with sampling devices located within and above the SBL to quantify the seed concentration decline with height throughout the day. Concurrently, thermal and mechanical turbulence were measured to determine whether maximum, mean or frequency of turbulence correlated with seed collection data. Lastly, all of the measured wind events were used to create a seed concentration profile around the source in order to quantify the proportion of seed predicted to travel long distances. We estimate the proportion of seed that dispersed locally and that traveling beyond the field edges by precisely estimating seed source strength, quantifying vertical seed movement and relating movement to the associated micrometeorological conditions.

**Materials and Methods**

Experiments were conducted in adjacent 3 ha soybean fields in central Pennsylvania during the seed dispersal periods in 2005 and 2006. There were no obstructions within 500 m in any direction to affect wind flow across the field. A 12.6 m² circular source was centrally located in each field (Figure 3-1). In 2005, non-glyphosate-resistant
seedlings were grown in the greenhouse and transplanted into the source at a density of 58.7 plants m\(^{-2}\) on May 12th. For 2006 dispersal measurements, the source was divided into thirds and seedlings were transplanted in the fall, early spring, and late spring at a density of 55.2 plants m\(^{-2}\). Only the fall plants grew to produce seed and the number of plants was approximately 1/3 the number that survived to produce seed in 2005 (232 compared to 740). Plants were covered briefly with a plastic tarp during normal herbicide application in June each year. In 2006, a selective grass herbicide (sethoxydim 0.313 kg ai/ha) was applied to prevent grass competition. Following completion of sampling in 2006, a subset of plants was selected, their height measured and number of stems counted, harvested and all capitula were counted to assess individual plant fecundity.

Seed and micrometeorological measurements were made on four days in 2005 and five days in 2006 during the 6 week *Conyza* dispersal period. Sampling dates were selected when seed movement was expected (days without rain). Weather constraints in 2005 forced sampling to occur over 16 days while sampling took place on five consecutive days in 2006. Each sampling day consisted of four consecutive 2-hour sampling periods: 8:00-10:00, 10:00-12:00, 12:00-14:00, and 14:00-16:00.

Seed capture was conducted using 7.6 m tall towers. Seed deposition density in the surface boundary layer was quantified using a set of towers located 10 m downwind of the edge of the source (14 m from the source center, Figure 3-1). Individual towers consisted of 10 cm PVC pipe buried 1.6 m in the ground, centrally reinforced with wood (3.8 cm x 8.8 cm x 150 cm) and supported by guide wires. Five 15 cm collars separated by 1 m were connected to the towers and raised and lowered via pulley guided ropes.
Two 1 x 0.5 m PVC frames were attached to these collars and 1.5 mm mesh fiberglass screen was attached to the frames. During each sample period, sticky adhesive (Tangle-Trap, exterior formulation; TangleFoot Company, Michigan, USA) was applied to the screens and the screens were raised, positioning them at 2-6 m above ground level (AGL). On the edge of the source in the downwind, upwind, and crosswind directions, four 454 cm² sticky traps were placed on the ground and were used to determine time of seed release.

Turbulence conditions were measured with a 3-dimensional sonic anemometer positioned 2 m from the source at 1.5 m above ground level (approximately 0.5 m above the soybean canopy, Figure 3-1). The sonic anemometer measured horizontal wind speed in the direction of the sensor orientation ($U_x$) and the direction perpendicular to the sensor orientation ($U_y$), vertical wind speed ($U_z$), and temperature ($T$). Data were recorded at 10 hertz and averaged over 1-minute intervals during each trial and recorded on a CR23X datalogger (Campbell Scientific, Logan, UT). Vector analysis of $U_x$ and $U_y$ resulted in the wind speed ($W_{anem}$) and wind direction for each minute interval. An eddy covariance system and fast responding temperature sensors (Campbell Scientific, Logan, UT) were used to calculate the product of instantaneous variation from their respective means in two variables (e.g. vertical wind speed ($U_z$) and temperature ($T$)) and represented the covariance $U_z' T'$ and covariance $U_z' W'$. Covariances were averaged each minute and recorded on the datalogger. Thermal and mechanical turbulence are the processes by which heat and momentum fluxes in the atmosphere and transports seeds vertically. Heat flux and momentum flux were calculated by multiplying the 1-minute average of covariance $U_z' T'$ and covariance $U_z' W'$ by the specific heat capacity of air (at
sea level and 0°C, 1.004 J g\(^{-1}\) K\(^{-1}\)) and the air density (25°C at sea level, 1.168 kg m\(^{-3}\)), respectively. Heat flux and momentum flux are opposite in sign (Table 3-1), but comparable in magnitude. Hereafter heat flux will be referred to as thermal turbulence and momentum flux referred to as thermal turbulence.

Assuming wind speed is zero at the zero-plane displacement \(z_0\), 0.2*canopy height) and increasing logarithmically with height above \(z_0\) (Lowry and Lowry 1989). Wind speed \(W_{anem}\) and anemometer height \(h_{anem}=1.5\) m, wind speed \(W\) at any height \(h\) above the ground was calculated by:

\[
W_h = \frac{W_{anem}}{\ln \left( \frac{h_{anem}}{z_0} \right)} \cdot \ln \left( \frac{h - \delta}{z_0} \right) \quad [1]
\]

where \(\delta\) was the displacement height (0.66*soybean height (1 m), Oke 1992). Wind run (average wind speed * time) was calculated for each minute at each height (2 – 6 m AGL) and multiplied by sampling area (1 m\(^2\)) to determine air volume at each height.

Seed concentration was a function of seed collection and air volume. The wind events used to explain seed movement from the source to the vertical sampler were defined by the downwind direction +/- 18\(^\circ\). During each 2-hour sampling period, seed collection at each height was divided by the volume of air passing through the sampler to yield a seed concentration at each height during each period. Inverse power law models (concentration \(\sim a*Z^{-b}\), with \(z\) as height, \(a\) and \(b\) as shape parameters) have been successfully used to describe the change in spore and pollen concentrations with height (Johnson 1957; Aylor et al. 2006). An inverse power law model was fit to \(C.\ canadensis\) concentration data using non-linear least squares (R Development Core Team 2006).
The 2006 seed collection and micrometeorological data were used to assess the proportion of seed escaping the SBL. Seed traveling downwind were assumed to be deposited on the ground between 0 m and 14 m (distance from the source to the base of the vertical samplers) or collected on the vertical sampling device. Clark et al. (1999) described a 2-dimensional empirical seed deposition model that is a function of radial distance from the source ($r$, meters):

$$f(r) = Q \cdot \frac{p}{\pi \cdot u \cdot \left[1 + \frac{r^2}{u}\right]^{p+1}}$$

[2]

where $Q$ is the source strength (90 million in 2006) and two shape parameters ($p$ and $u$). Previous *C. canadensis* dispersal experiments determined the shape parameters ($p = 0.2667, u = 6.0 \times 10^{-3}$, Dauer et al. 2007). This model assumes seed deposition is isotropic around the source, seed deposition was estimated at 79 million seeds between 0 m and 14 m in 2006. The remaining seed were expected to be moving vertically and would have been collected if vertical samplers had been positioned to sample all possible wind directions.

The 2006 wind speed data in each minute during each 2 hour sampling period on all five days (120 (minutes) x 5 (days) measurements per sampling period) were apportioned into 36° sectors (the width of the towers +/- 5°) based on the 1-minute average wind direction. Each wind event was used to calculate the wind speed at five heights AGL (using Equation 1). Using the 1-minute averages, wind run was multiplied by the area of the sampling device to determine the air volume. Finally, the volumes were summed in each sector.
For example, there were 47 minutes in 2006 among the five sampling days during the 8:00-10:00 sampling period when the wind direction was 0 ± 18º. The wind event from each minute was used to create a wind profile for that minute interval. The wind speeds were multiplied by 60 seconds and 1 m² (area of sampler) to give the volume of air at each of five heights. The sum of the volumes at 2 m was 561 m³ and at 6 m, the total volume was 969 m³ during the 47 minutes. Back-calculating from the concentration curves described earlier, the total seed was estimated in each sector, at five heights AGL during each period. Using the example, the concentration profile for the 8:00-10:00 period predicted a seed concentration of 0.41 and 3.7*10⁻³ seeds m⁻³ at 2 m and 6 m. Multiplying by the volume of air predicted that 233 and 4 seeds would have been collected at 2 m and 6 m AGL, respectively, in the 0º sector during the 8:00-10:00 period.

**Results**

Precise source strength estimates are critical to understand the proportion of seed being transported long-distances. A subset (n = 23) of plants in the source population were harvested and all capitula were counted. Capitula production was affected by height and number of stems and ranged from 2623 to 62,087 capitula per plant. An analysis of covariance found that each additional stem yielded 2547 (SE=763) additional capitula ($P < 0.01$, adj. $r^2 = 0.32$) but height did not significantly affect capitula. There was 23% mortality in source plants resulting in 180 plants of the potential 232 that would have flowered and contributed to seed dispersal. The remaining 157 plants (180 minus the 23 already measured) were assigned the mean stem number (3.46, SE = 0.602) and capitula per plant determined from the regression equation. No plants were harvested in 2005 to determine capitula production and all plants (n = 740) were assigned the mean stem
number (3.46) to calculate capitula production. Total capitula production is directly related to capitula seed production (capitula*50, Dauer et al. 2006), estimated at 270 million in 2005 and 90 million in 2006.

Total seed collected was different among years and among sampling periods. In 2005, 627 seeds were collected on vertical samplers over four sampling days (Table 3-1). Although there were fewer plants the following year, 29,829 seeds were collected on the vertical samplers because the wind direction more frequently paralleled the vector from the source to the vertical sampler. Changes in seed quantity released from the plants during the day was determined by counting the seed found on the sticky traps located at the edge of the source and on the vertical sampler (Figure 3-1). The large variability in seed recovered at the edge of the source showed no significant time of day effect. However, the total seed collected on the sticky traps increased from 1400 total seeds collected during the 8-10 period to 4634 seed during the late afternoon (14:00-16:00 period). The vertical sampler data was dominated by a single day when 10,000 seed were collected during the 12:00-14:00 period in 2006. The next period (14:00-16:00) on the same day, 5000 seed were collected. Over all 9 sampling days, less than 1000 seed were collected on the vertical sampler before 12:00.

Seed collection data were adjusted by air volume, providing an estimate of seed concentration. Seed concentrations were consistently higher after 12:00 than from 8:00 to 12:00 (Figure 3-2). 2005 and 2006 seed concentration profiles were quantified for each sampling period. The exponent (slope) of the power law decay function decreased from 4.21 (SE=4.87) during the 8:00-10:00 period to 2.42 (SE=1.06) during the 14:00-16:00 period because concentration at 5 and 6 m increased during the latter period.
The variation in concentration explained by the variation in height was low ($r^2 < 0.20$) for all concentration profiles.

Thermal and mechanical turbulence also changed during the day. When evaluated over all nine sampling days, wind speed increased significantly ($P < 0.05$) from 8:00 to 16:00, but also varied significantly among days. The magnitude of mean mechanical turbulence increased ($P < 0.01$) during the sampling periods in both years (Table 3-1). Mean thermal turbulence also increased ($P < 0.01$) to a maximum during the 12:00-14:00 period then declined during the 14:00-16:00 period. The maximum thermal turbulence increased significantly ($P < 0.01$) during the sampling period, while the magnitude of the maximum mechanical turbulence showed no relationship with time of day. The frequency of mechanical and thermal turbulence above the 75% percentile (mechanical = -0.105 kg m s$^{-2}$, thermal = 0.147 J m$^{-2}$ s$^{-1}$) were also tested for their relationship with the sampling period. The frequency of mechanical and thermal turbulence above the threshold increased during the sampling periods. However, date of sampling impacted frequency of thermal turbulence but not mechanical turbulence.

In 2006, the volume of air moving in each 36º sector (width of the tower samplers) during each sampling period was determined and the expected seed during each period at each height was calculated from the concentration curves. The predicted seed concentration profiles were nearly isotropic during each 2-hour sampling period, although we predicted a greater number of seed would be collected in the 288º and 324º sectors because of predominant northwesterly wind (Figure 3-3). The concentration profiles (Figure 3-2) were used to predict seed collection in each sector. Later in the day (12:00-14:00 and 14:00-16:00 sampling periods), we predicted more seed would be
collected at 5 and 6 m AGL. Figure 3-3 visualized predicted seed collection over five sampling days, but seed release generally occurs over 40 days (M. VanGessel, personal communication) so total seed was extrapolated by multiplying the predicted seed in each sector by 8 to determine the predicted seed to be collected vertically in each sector over the entire dispersal period. If vertical sampling devices were positioned to sample each sector, the predicted collection at heights 2-4 m AGL would amount to 221,307, while 42,251 seed would be collected at heights 5 m and 6 m AGL. In total we estimated that 0.3% of the seed released would have been collected on the vertical samplers. Taking the difference between seeds recovered on the ground (79 million) and tower samplers (263,557), left 11 million (12.2%) seeds unaccounted for.

Conclusions

Transport of a single *C. canadensis* seed containing the glyphosate-resistance gene can result in a new infestation that potentially affects weed management. The ability to predict these rare events is critical to assessing the sustainability of current and future management strategies. The first step in estimating rare events is quantifying the source strength of the resistant biotype. In contrast to aggregated populations at the whole field scale, it is possible to accurately estimate the source strength of a small patch. The point source in 2006 produced 90 million seed, of which, many fell near the source during periods of low wind, rain, or heavy dew. A smaller number left the plant canopy where turbulent air may have assisted seed escape from the SBL. Quantifying the proportion that travel long distances required data extrapolation to determine seed dispersal around the entire point source.
In Dauer et al. (2007), extrapolation of seed deposition accounted for less than 25% of predicted seed released during the experiments. Their field studies used extensive horizontal sampling to monitor seed densities at canopy height. Vertical sampling near the source would collect those seeds that might otherwise be transported out of the field and would be missed in the Dauer et al. (2007) sampling design. Unfortunately, the size of the vertical sampler limited sampling to one direction. However, extrapolation of seed deposition and vertical movement accounted for 12.2% of released seed, a much higher recovery than 25% recovery reported by Dauer et al. (2007). Multiple vertical samplers, positioned around the source, would have assured greater seed collection but may have affected wind flow at the source. Accounting for all 90 million seeds is nearly impossible, but vertical sampling increased the trapping efficiency without increasing the horizontal seed trapping requirements.

A single stationary sampler efficiently traps seed when the wind blows parallel to the vector extending from the source to the vertical seed sampler. However, wind direction is never constant. For example, during sampling days in 2005, the wind was predominantly from the south, carrying seeds away from the sampler and resulting in few seeds collected (Table 3-1). Alternatively, area sources with a sampler centrally located would prevent missing data during periods of shifting wind. Therefore, a point source may require extra sampling days to accurately assess seed concentration profiles. Area sources provide a consistent source of seed but only mimic the scenario of a very heavy infestation, rather than small patches approximated by point sources. Fewer seeds released from a point source also reduce the likelihood of observing rare events. At 6 m, wind speed in the 14:00-16:00 period averaged 1.71 m s\(^{-1}\), and a cubic meter of air moved
through the sampling device every 0.58 seconds. Seed dilution at 6 m prohibits the use of smaller seed sources to accurately determine seed escape.

Of the 90 million seed released in 2006, 87% landed between the source and the base of the vertical sampler. An additional 0.2% was predicted between 2 and 4 m AGL. Screens at 5 and 6 m AGL were above the SBL, and seed collected here would be expected to be traveling vertically into the convectively mixed PBL where long-distance transport can occur (Isard and Gage 2001). At this position on the sampling device, 0.04% (42,251) was predicted to escape from the source infestation. Seed ascent is dependent on conducive weather conditions. Optimal conditions for wind dispersal vary among species. Spores require humid air and can release at night to prevent desiccation (Maldonado-Ramirez et al. 2005). Insects may only require unstable air (Isaacs and Byrne 1998) or large low pressure systems (Shields and Testa 1999) to initialize transport.

In the case of Conyza canadensis, turbulent air in the afternoon was correlated with increased seed escape from the SBL. Soons et al. (2004) reported that mechanical updrafts were more important for release and escape of seed than thermal turbulence, but the data from these experiments were not as conclusive. Both mean thermal and mechanical turbulence increased from the morning 8:00-10:00 sampling period to the afternoon (12:00-14:00 and 14:00-16:00). However, the maximum mechanical turbulence (during a 2-hour period) did not significantly vary during the sampling periods or among days and the frequency of mechanical turbulence (above a 75% threshold) did not vary much from day to day. In contrast, the maximum thermal turbulence and the frequency (above a threshold) increased during the sampling periods and varied among
sampling days, which may have been a result of the selected sampling days. In an effort to maximize seed collection, sampling days were chosen that did not cover the full range of weather conditions a plant experiences. For example, sampling was never conducted during or immediately following storm fronts. Conditions after the passing of a low pressure system may result in greater mechanical updrafts as observed by Shields and Testa (1999). In order to accomplish the intensive sampling regime, we chose to sample on average days, which were sunny and calm which likely contributed to the strong relationship between thermal turbulence and sampling period. Continued work on seed escape from the SBL will need to address meteorological variation among days and its effect on release and escape of seeds.

The vertical sampling method described herein provided data on the vertical distribution of seed within the SBL. The height of the vertical sampler allowed some sampling above the SBL, based on the estimate that the boundary lies at approximately 2.5 times the soybean canopy height (Huschke 1989). But sampling higher may yield better information about the proportion of seed escaping to the upper bounds of the PBL where wind speeds are faster than near the surface. Such sampling would require a large seed source and the necessary sampling apparatus for sampling at greater heights above the canopy. Area sources produce considerably larger numbers of seed, making seed detection easier at increasing distances from the source but are not conducive to precise source strength calculations. Successful *C. canadensis* trapping was conducted in 2005 (Shields et al. 2006) and coupling aerial sampling with vertical ground-based sampling can comprehensively quantify seed concentration from ground level into the PBL.
While this research focused on estimating the vertical distribution of seed and tying those vertical profiles to micrometeorological conditions, we did limit our sampling to “average days” which had conditions conducive to conducting the sampling protocol. On such days, at least 0.3 percent of seed were moved into the lower PBL and may have traveled long distances. From an average plant producing 130,000 seed, we estimate 52 seeds are moved to the lower PBL, where Shields et al. (2006) estimated seed can travel up to 145 km in a single day. The predicted seed deposition and vertical collection accounted for 87% of seed dispersed in 2006, which is 6 times greater trapping efficiency than horizontal trapping alone (Dauer et al. 2007). Whether these seeds are being deposited locally or being transported long distances needs to be clarified. Regardless, the impact of a few seed containing the glyphosate-resistance gene will be observed in the surrounding farmsteads. This work provides insights into the coupling of morphological adaptations for seed dispersal and suggests micrometeorological conditions likely contribute to long distance dispersal. When the work was initiated, conventional wisdom assumed seed movement was limited to distances of 50-100 m. Through this and related work, we have compelling evidence that small numbers of seed can move distances of 50-150 km in a single day. Given that this species is moving a trait of high agronomic importance, such movement alters our thinking about herbicide resistant management. To limit the recruitment success of these small numbers of seed it is clear that some form of area-wide management will be necessary.
Table 3-1: The total *Conyza canadensis* seed collected between 2 m and 6 m above ground level on four sampling days in 2005 and five sampling days in 2006. Mechanical and thermal turbulence were measured each minute using a 3-D sonic anemometer located near the seed source. The magnitude (absolute value) of mechanical turbulence is presented for comparison with thermal turbulence. The mean value is the 2-hour average of the 1-minute turbulence measurements.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Seed Collected</th>
<th>Mechanical Turbulence</th>
<th>Thermal Turbulence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>kg m s⁻²</td>
<td>J m⁻² s⁻¹</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Maximum</td>
</tr>
<tr>
<td>2005</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8:00-10:00</td>
<td>18</td>
<td>0.023</td>
<td>0.140</td>
</tr>
<tr>
<td>10:00-12:00</td>
<td>94</td>
<td>0.080</td>
<td>0.470</td>
</tr>
<tr>
<td>12:00-14:00</td>
<td>180</td>
<td>0.133</td>
<td>0.599</td>
</tr>
<tr>
<td>14:00-16:00</td>
<td>335</td>
<td>0.142</td>
<td>0.613</td>
</tr>
<tr>
<td>2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8:00-10:00</td>
<td>241</td>
<td>0.028</td>
<td>0.476</td>
</tr>
<tr>
<td>10:00-12:00</td>
<td>691</td>
<td>0.082</td>
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</tr>
<tr>
<td>12:00-14:00</td>
<td>11880</td>
<td>0.098</td>
<td>0.476</td>
</tr>
<tr>
<td>14:00-16:00</td>
<td>17017</td>
<td>0.100</td>
<td>0.572</td>
</tr>
</tbody>
</table>
Figure 3-1: Location of vertical seed sampler in relation to *Conyza canadensis* source population. Sticky traps were located around the source population to assess time of maximum seed release. The 3-D sonic anemometer was positioned in the cross-wind direction and set at 0.5 m above the soybean canopy.
Figure 3-2: Concentration profile of *Conyza canadensis* seed collected in the morning (top frame) and afternoon (bottom frame). Symbols represent seed concentrations during the specified 2-hour sampling period in both 2005 and 2006. Concentration profiles were fit to the combined 2005 and 2006 concentration data using a power law decay model (concentration = $a \times \text{height}^{-b}$). No concentration measurements were taken at 1 m above ground level.
Figure 3-3: Predicted *Coryza canadensis* seed collection at five heights above ground level (AGL) during each 2-hour sampling period (*a* through *d*) in 2006. The volume of air was calculated from the wind speed in each 36° sector. Back-calculating from the concentration gradients in Figure 3-2, seed number were predicted in each sector and height. Predicted seed collections were represented by lines: 2 m AGL (solid), 3 m (dashed), 4 m (dot-dash), 5 m (double dashed) and 6 m (dotted).
Literature Cited


Chapter 4

Release, Escape and Transport of Conyza canadensis seed in the Lower Atmosphere

Abstract

Seed dispersal research often focuses on the near-surface dynamics of abscission, release and deposition, with little attention paid to seed escape and transport beyond the surface boundary layer. This research examined the movement of seed out of the surface boundary layer and into the higher regions of the planetary boundary layer where long-distance dispersal via wind can be maximized. Using a 2.7 ha field infested with Conyza canadensis, the vertical seed concentration profile was measured on five days, three times per day with simultaneous micrometeorological data to connect the mechanisms of release with the process of dispersal. Vertical seed sampling was conducted at 2 - 6 m above ground level with removable screen frames. At heights of 60 m and 120 m above ground level, remotely piloted airplanes were used to quantify seed concentration. Seed collection densities varied among days as well as within the three sampling periods per day, but always decreased with height above the ground level. Seed concentration (seed density per volume of air sampled) was modeled using a power law decay function. Although time periods were not significantly different, the proportion of airborne seed concentration reaching altitudes between 6 m and 200 m was estimated at 37% in the morning compared to 55% and 54% in the early and late afternoon. Thermal and mechanical turbulence varied among days and generally increased throughout the day.
Maximum mechanical turbulence rather than mean or maximum thermal turbulence significantly affected proportion of seed aloft. The predicted dispersal distance for seed collected in the planetary boundary layer ranged from 20 km to 100 km depending on atmospheric conditions. These dispersal distances will dramatically impact surrounding fields that could be invaded rapidly from a single glyphosate-resistant *C. canadensis*.

**Introduction**

To gain insight into conditions that give rise to wind dispersed seed patterns, the temporal scale of seed sampling must match the temporal scale of important weather events (Dauer et al. 2007). Dauer et al. (2007) collected seed deposition data at one week intervals to detect shifts in seed dispersal patterns, but concluded that shorter time intervals, on the order of days or less, would be necessary to link the dispersal mechanisms with the observed patterns. Stull (1988) showed that meteorological monitoring should be on the order or hours or shorter to capture turbulence effects without encountering synoptic weather patterns. Nathan (2002) used 30 minute intervals to simulate turbulence effects on seed dispersal. The importance of long-distance dispersal has been well documented in the last ten years (Nathan 2006), resulting in a Special Feature in Ecology (v. 84 issue 8) and an entire issues of Diversity and Distributions (v. 11 issue 2). In the Ecology Special Feature introduction, Cain, Nathan, and Levin note that long-distance dispersal studies are most limited by data, although modeling dispersal also needs attention. Aylor (2003) described the atmospheric dispersal model for two agricultural pathogens (*Puccinia* and *Peronospora*). This research also studied atmospheric transport but focused on empirical data collection instead of atmospheric modeling. Moreover this research differed from most seed dispersal studies
because the data were sampled vertically instead of horizontally, the temporal scale of
sampling, and the connection between seed collection and the mechanisms that transport
seed through the surface boundary layer. Vectored dispersal, e.g. wind and water, can
transport seeds over long distances and work has largely described the resulting dispersal
pattern (Bullock and Clarke 2000; Dauer et al. 2007). The empirical models fit to these
data can be generalized for weather conditions and argue that day to day variation does
not impact the overall dispersal pattern.

An alternate approach is to study the vector and relate the dynamics of the vector
to seed movement. Recent work has documented seed movement with animals acting as
vectors (Manzano and Malo 2006). Wind can act as an efficient seed vector but visual
tracking of seed movement in the wind is difficult (but see Skarpaas, in press).
Mechanistic models can address variation in meteorological conditions within days, even
within minutes, and project movement based on changes in the conditions encountered by
the organisms. The basic models include settlement velocity of the seed, release height,
wind speed (in 1-dimension) and source strength (Greene and Johnson 1989; Okubo and
Levin 1989). Derivations in the last 15 years have added or modified parameters for
vertical updraft, canopy height, and structure, wind direction, and other factors affecting
meteorological conditions (see Kuparinen 2006 for review). A recent extension of the
mechanistic models has been Lagrangian stochastic (LS) modeling which “tracks” seeds
as they move through the atmosphere, adjusting seed trajectory with wind speed and
direction (Boehm and Aylor 2005). Kuparinen (2006) noted that “LS models are
preferable in modeling dispersal of airborne particles over both short and long distances,”
but parameterization is difficult. Aylor et al. (2006) showed close approximation of a LS
model to corn pollen dispersal. One reason for the high goodness of fit was their ability to overcome the major challenge of research on the mechanisms of long-distance dispersal: the spatial scale for sampling must increase to capture rare long-distance events while the temporal scale must be shortened to more carefully test the correspondence with changing meteorological conditions (Yao et al. 1997; Nathan et al. 2002; Tackenberg 2003). In addition to shorter temporal scales, there has been a push to describe the dispersal distribution at greater distances (Green and Figuerola 2005). When sampling horizontally, there are limitations on distances one can sample and a host of methodological complexities to consider as the distance from the source increases (Skarpaas et al. 2005). For this study, within-day variations of meteorological conditions are considered crucial to determining the dispersal potential of *C. canadensis* seed.

Studies of the vertical seed lift provide insight into seed ascent through the surface boundary layer, a crucial transition underpinning long-distance transport. The planetary boundary layer (PBL) is defined as the region of the atmosphere influenced by earth with the majority (95%) of the influence taking place in the surface boundary layer (SBL) near the ground level (Stull 1988). The PBL to 1 km or more above ground level (AGL) and is characterized by increasing wind speed with height and decreasing turbulence with height. During the daytime, the SBL over a homogeneous canopy extends to 2.5 times the canopy height (Huschke 1989), and contains more short-period turbulence that increase seed deposition. Consequently, many wind-dispersed organisms are adapted to ascend through the (SBL) and be transported long distances by the high wind speed, low turbulent atmospheric conditions higher in the PBL. Insects, pollen, and seeds respond to changes in humidity, pressure, and vertical wind to determine the
optimal dispersal time (Shields and Testa 1999; Rodriguez et al. 2000; Maldonado-Ramirez et al. 2005). These organisms take advantage of the daily and sub-daily fluctuations in atmospheric structure to optimize ascent through the SBL followed by horizontal transport. Seed dispersal research has begun to examine the impact of vertical wind on dispersal distance but not in the context of ascent within the PBL.

_C. canadensis_ seeds exhibit increased release in the early afternoon which corresponded with increased thermal and mechanical turbulence (Chapter 3). Turbulent air is critical to long-distance dispersal (Nathan et al. 2002; Tackenberg 2003; Soons et al. 2004), and may be the result of thermal currents caused by unequal heating of the earth’s surface or mechanical turbulence caused by friction with surface obstructions or slower moving air. Thermal turbulence develops from heated air rising from the surface and results in a positive (upward) heat flux which can transport organisms vertically. Tackenberg (2003) has quantified the impact of thermal turbulence on vertical transport of _Cirsium arvense_ and _Senecio nemorensis_ seed. Meanwhile, mechanical turbulence is a result of friction between slow moving air and faster moving air directly above and causes a negative (downward) momentum flux. Soons et al. (2004) modeled the relative importance of mechanical versus convective updrafts in predicting dispersal of grassland species. They found sustained upward lifting caused by mechanically produced turbulent air movements were more critical than thermal turbulence. They also suggested thermal turbulence would not be a high enough flux to transport seeds aloft and would result in shorter dispersal than higher wind events.

The focus of this study was to quantify the effects of updrafts on the vertical seed concentration profile. _C. canadensis_ is a winter annual broadleaf weed that invades
agricultural fields, roadsides, and waste areas (Holm et al. 1997; Weaver 2001). Quantifying the dispersal distance for this species is critical because populations have developed resistance to the common agricultural herbicide, glyphosate (VanGessel 2001), and have spread to at least 40 thousand hectares of agricultural land in the US (Heap 2007). Over 88% of the soybean area planted in the US received glyphosate applications in 2006 driven in large part by the adoption of glyphosate-resistant soybean (Carpenter et al. 2002). The resistant biotype can become a major problem in soybeans when weed densities surpass 100 plants m\(^{-2}\), reducing yields by 90% (Bruce and Kells 1990). Glyphosate-resistant *C. canadensis*, along with inevitable forthcoming glyphosate-resistant weeds will dramatically alter current practices. Currently, glyphosate-resistant *C. canadensis* densities have become so high, that regions of no-tillage cotton have abandoned the use of conservation tillage practices in order to manage horseweed (W. Johnson, personal communication).

*Conyza canadensis* seed have an unbeaked pappus which reduces settlement velocity to 0.3 m s\(^{-1}\) (Dauer et al. 2006), the lowest settlement velocity of 19 Asteraceae species tested (Andersen 1993). The low settlement velocity increases residency time in the air and extends the dispersal distance. Previous research quantified horizontal seed dispersal patterns to 500 m from a point source and aerial sampling also have detected seed in the PBL at heights of 140 m (Shields et al. 2006; Dauer et al. 2007).

Similar to rare long-distance events in the horizontal plane, quantification of rare vertical movement in the atmosphere is dependent on sufficient source strength. Trapping seeds at these altitudes can be elusive, but successful researchers have collected aphids (Isard et al. 1990), potato leaf hopper (Shields and Testa 1999), and corn pollen
(Aylor et al. 2006). Shields and Testa (1999) reported concentrations of organisms in the PBL between 0.4/1000 m³ for potato leaf hoppers to 30/1000 m³ for Fusarium spores and Shields et al. (2006) recorded C. canadensis concentrations ranging from 0.8 to 7.3 seeds/1000 m³. An area source with varying density was used instead of a point source to generate the requisite seed to improve the likelihood of aerial detection. Furthermore, sampling was conducted multiple times during the day to monitor the change in concentration as observed in spores, pollen, and insects (Yao et al. 1997; Shields and Testa 1999; Jarosz et al. 2003). The ramifications of seed collection in the PBL are significant because even moderate wind speeds at high altitudes in the atmosphere can transport C. canadensis seed kilometers downwind (Shields et al. 2006). Quantifying the concentration in the PBL allowed for extrapolation of dispersal to distances farther than any horizontal collection design can detect.

**Materials and Methods**

Experiments were conducted near Georgetown, Delaware, USA in a 2.73 ha fallow field infested with Conyza canadensis. C. canadensis occurs naturally in Delaware and plant densities within the field ranged from low (0.1 plants m⁻²) to high (70-130 plants m⁻², Figure 4-1). Assuming 130,000 seeds per plant (Dauer et al. 2006), the resulting seed source strength, was estimated to be 125 billion seeds. Seed and meteorological sampling took place over five days in mid-September 2006 during the maximum seed release period (M. VanGessel, personal observation). Extensive daily sampling determined that maximum seed release occurred during early afternoon (Middle, 12:30-14:00, Chapter 3). Two additional sampling periods were chosen: Early (11:00 to 12:30) and Late (14:00-15:30) to provide a thorough quantification of the
change in seed concentration within and among days. Sampling events did not take place at exact time each day but instead the authors evaluated plants each morning and initiated sampling based on sufficient seed drying that seed were easily released when blown. Sampling in the Middle and Late periods was conducted approximately 1 hour after completion of the previous sampling due to equipment constraints. For example, on day 4, sampling was initiated at 11:45, continued at 13:30 and 15:05.

Turbulence conditions were measured with a 3-dimensional sonic anemometer at 1.5 m above ground level (approximately 0.5 m above the soybean canopy, Figure 4-1). The sonic anemometer measured horizontal wind speed in the direction of the sensor orientation \( U_x \) and the direction perpendicular to the sensor orientation \( U_y \), vertical wind speed \( U_z \), and temperature \( T \). Data were recorded at 10 hertz and averaged over 1-minute intervals during each trial and recorded on a CR23X datalogger (Campbell Scientific, Logan, UT). Vector analysis of \( U_x \) and \( U_y \) resulted in the wind speed and wind direction for each minute interval. An eddy covariance system and fast responding temperature sensors (Campbell Scientific, Logan, UT), were used to calculate the product of instantaneous variation from their respective means in two variables (e.g. vertical wind speed \( U_z \) and temperature \( T \)) and represented the covariance \( U_z' T' \) and covariance \( U_z' W' \). Covariances were averaged each minute and recorded on the datalogger. Thermal and mechanical turbulence are the processes by which heat and momentum fluxes in the atmosphere and transports seeds vertically. Heat flux and momentum flux were calculated by multiplying the 1-minute average of covariance \( U_z' T' \) and covariance \( U_z' W' \) by the specific heat capacity of air (at sea level and 0°C, 1.004 J g\(^{-1}\) K\(^{-1}\)) and the air density (25°C at sea level, 1.168 kg m\(^{-3}\)), respectively. Heat flux and momentum flux are
opposite in sign (Table 4-1), but comparable in magnitude. Hereafter heat flux will be referred to as thermal turbulence and momentum flux referred to as thermal turbulence.

Meteorological conditions (wind direction, wind speed, relative humidity, and temperature) were monitored using the University of Delaware weather station located 1 km from the source field (Figure 4-1). The weather station maintains a cup anemometer at 10 m AGL which was combined with the 3-D anemometer data (1.5 m AGL and above the surrounding canopy) to calculate the wind speed gradient. It was assumed that wind speed increased logarithmically with height (Lowry and Lowry 1989). Wind speed directly impacted the volume of air passing through the seed sampling screens on the tower. Wind speed at each height (2 - 6 m) was calculated by fitting an exponential model between the sonic anemometer (1.5 m AGL) and 10 m cup anemometer (Lowry and Lowry 1989). Volume was then calculated as screen area (1 m²) multiplied by wind run (wind speed * time). Sampling frames were realigned before each sampling period and wind direction never varied more than 90° during the sampling period. However, wind direction did vary, which affected the sampling area available for seed collection. The sine of the wind direction relative to the sampling surface was used to scale the wind speed, assuming 100 percent screen trapping efficiency.

Seed deposition density in the surface boundary layer was quantified using a tower located in the center of the 2.73 ha field and could be pivoted to allow sampling in 360 degrees (Figure 4-1). Individual towers consisted of 7.6 m long 10 cm PVC, centrally reinforced with wood (3.8 cm x 8.8 cm x 150 cm) and supported by guide wires. One stationary, pivot tower and four position towers located at 340°, 295°, 250°, and 205° (0° is north), made it possible to connect a position tower with the pivot tower, aligning
the frames close to perpendicular relative to the predicted wind direction for the day. Five 15 cm collars separated by 1 m were connected to the towers and raised and lowered via pulley guided ropes. Two 1 m x 0.5 m PVC frames were attached to these collars and 1.5 mm mesh fiberglass screen was attached to the frames. During each sample period, sticky adhesive (Tangle-Trap, exterior formulation; TangleFoot Company, Michigan, USA) was applied to the screens, the screens were raised, which positioned screens at 2-6 m above ground level (AGL).

Sampling in the planetary boundary layer was conducted by simultaneously flying two large radio controlled monoplanes (Remote Piloted Vehicle, RPV) at 60 m and 120 m AGL (Shields and Testa 1999, Shields et al. 2006). A third plane was flown during the first two days which sampled the atmosphere upwind of the source population ranging from 60 to 120 m. Zero seeds were collected during these days and flying the third plane was discontinued under the assumption that there were no incoming seeds. The RPV was controlled by a ground-based pilot using a hand-held transmitter. Each RPV had a 3 m with two seed sampling devices near each wind tip to minimize any influence of turbulent air streaming off the propeller. RPVs were flown at full throttle setting (96 kmph) because full throttle was easily repeatable and maximized the air volume sampled. Fuel consumption restricted flights to 30 minutes.

The trapping surface within each collector was a removable unit built from a standard 90 mm plastic Petri plate. Each individual trapping surface was constructed from the smaller portion of the Petri plate by removing the bottom of the plate while leaving a 3mm lip around the outside diameter. A 30 micron cloth mesh was glued to the lip. When the collector was closed, the trapping surface was protected from the airflow
and when the collector was opened during the flight, the trapping surface was perpendicular to the airflow. Just prior to a sampling flight, the trapping surfaces were sprayed with a sticky adhesive (Dupont Super X-77™) to retain the seeds striking the trapping surface during flight. Each trapping surface was exposed to approximately 10,000 L of air per min (10 m³/min) when the RPV was traveling 96 km/hr, or a total of 300,000 L of air (300 m³) during the typical 30 min sampling flight.

Each RPV used in this research carried a data logger, GPS antenna, and a telemetry downlink. Additional information about on-board electronics can be found at Shields et al. (2006). Downloaded data allowed the graphic reconstruction of each flight, calculation of average altitude for the flight and calculation of the quantity of air sampled during the flight. The telemetry downlink from the RPV was used to transmit real time data to an “air traffic control trailer” where altitude information was relayed by a technician to the pilot to assist them in maintaining the desired altitude during the duration of the sampling flight. Flight pattern was an approximately 300 m long by 200 m wide oval at a predetermined height at 45 degrees downwind of the seed source. Airplanes actively sampled the atmosphere and the flight pattern negated the effects of wind speed. Volume was calculated as area of the four samplers (254 cm²) multiplied by mean ground speed. Airplane sampling efficiency was not tested but was initially assumed to be 100 percent, suggesting seeds were unaffected by air flow around the sampler and all seeds contacted by the sampler were retained. More appropriately, the sampling efficiency was 20% or lower (Shields and Testa, 1999), because air speed may create a pillow in front of the sampler and prevent contact between the seed and sampling device. In this scenario, seed collected by RPVs would represent 20% or less of the true
seed concentration. Therefore, aerial seed collection was adjusted for the differences in sampling. Seed concentration was multiplied by 5 and 10 to examine how differences in sampling efficiency (20% and 10%, respectively) affect seed concentration profiles.

**Analysis**

The negative exponential model has commonly been used to describe the decline in concentration with height when sampling was conducted only in the SBL (Isaacs and Byrne 1998; Gillies and Berkofsky 2004; Jarosz et al. 2004). However, when sampling included the PBL, the power law decay function \( y = a*x^{-b} \) better described the change in concentration with height (Johnson 1957; Aylor et al. 2003). A power law decay function was fit to seed concentration for each time period in each day using non-linear least squares (R Development Core Team 2006). This represented the concentration profile as a function of height AGL. This profile assumed that the atmospheric conditions remained constant for the 30 minute duration of sampling. Integrating from 6 m AGL to 200 m AGL and dividing by the integral from 0.5 m to 200 m represented the proportion of collected seed that had ascended through the surface boundary layer. The proportions of seed were pooled across days and the mean proportions obtained for each time period.

Extrapolation of the dispersal distances assumed that seed collected at 60 m and 120 m were located in the planetary boundary layer which stayed convectively mixed until sunset (Isard and Gage 2001). Seed were assumed to remain at their altitude until sunset, (4-5 hours after the last sampling event) then settled back to the ground. Therefore, maximum dispersal distance was calculated at the mean wind speed at time of collection multiplied by five hours.
Germination was assessed for a subsample of seed collected on tower screens and all seeds collected on airplane samplers during one trial each day. Seed were place in 9 cm Petri dishes on moistened filter paper in a germination chamber set at 21ºC and photoperiod of 16:8 Light:Dark. Germinated seeds were recorded and removed daily for two weeks. Logistic regression was used to determine whether germination varied with height of collection.

**Results**

Temperature and relative humidity showed expected daily and among day fluctuations. Mean temperature significantly increased from 20.49ºC (SE = 1.6x10⁻³, Early) to 21.18 ºC (SE = 4.8x10⁻³, Late) while the relative humidity significantly dropped from 40.38% (SE = 1.0 x10⁻²) to 36.16% (SE = 3.5 x10⁻⁵) during the same period. Wind direction changed each day from 70º to 115º to 340º to 180º to 205º. Screen locations were changed each morning to align the sampling device close to perpendicular to the wind direction. Wind speed changed significantly during the day and among days ($P < 0.05$), and decreased during the day at both the 1.5 m height (anemometer located at the source) and the 10 m height. The wind speed increased logarithmically with height with a average slope of 2.62 s⁻¹ (SE = 0.198). The slope of the wind speed gradient was not significantly different among days or periods. Maximum wind speed varied significantly among days ($P < 0.05$), with gusts on the first day exceeding 5 m s⁻¹, while gusts on the fourth day did not reach 3 m s⁻¹ (Table 4-1).

Mean vertical wind speed ($U_z$) increased from 11:00 to 15:30 but was significantly different among days (Table 4-1). Mechanical turbulence was highest in mid-afternoon and varied significantly among periods and day ($P < 0.05$). No temporal
pattern was evident in mean thermal turbulence, but as expected, it varied considerably from day to day (Table 4-1).

Seed collection varied significantly with both day and time period \( (P < 0.05, \text{ Table 4-2}) \). More seed were collected in the early period than during the other periods and one day (September 20\textsuperscript{th}) seed collection was three times greater than any other single day. The following day (September 21\textsuperscript{st}), seed collection was \( 1/30 \text{th} \) that of the day before. Regardless of day or time period, seed collection always decreased with height AGL. This temporal pattern held for the RPV collected seed where 2 (out of 10) flights collected seed in the Early time while 3 and 5 flights collected seed in Middle and Late periods, respectively.

During one trial each day, seed from each collection height were tested for viability. Germination did not decrease significantly with height \( (P < 0.05, \text{ Table 4-3}) \), although sample size may have affected our ability to detect differences. For example, seed collected from 2 – 6 m had a 50\% germination, while seed collected with the RPVs was 40\% at 60 m and 20\% at 120 m with only 5 seeds tested at these two heights (Table 4-3).

Seed concentration was a better metric than total seed collected for comparison among days and periods because horizontal wind speed was believed to be the major contributor to seed release and deposition will be a function of concentration and wind speed. As expected, mean seed concentration decreased from \( 9.86 \times 10^{-2} \text{ seed m}^{-3} \) at 2 m AGL to \( 1.56 \times 10^{-3} \text{ seed m}^{-3} \) at 120 m. Concentration values can be modeled as function of height to give a gradient which varied significantly among days and time periods. We
assumed that time periods were different and pooled concentration data across days to generate concentration profiles for each time period (Figure 4-2).

Integrating the area under each curve between set values provided an estimate of total predicted seed concentration between those values. The predicted seed concentration from 6 m to 200 m described the seed concentration that had ascended through the SBL and could travel long distances. Dividing by the total predicted seed concentration (0.5 m to 200 m), proportions ranged from 12.7 to 89.6 percent of total seed concentration. This is the proportion of the seed collected, not the proportion of total seed released. Mean proportion of seed collected was determined by the average of five days and was lowest in the Early period at 37% (SE = 10.7%). By the Middle period mean proportion of seed collected was 55% (SE = 10.7%) then decreased slightly to 54% (SE = 13.6%) during the Late period.

Both the mean and maximum mechanical and thermal turbulence per time period were tested against the proportion of seed collection above the SBL. The mean mechanical and thermal turbulence did not significantly affect the proportion of collected seed that were predicted to have ascended through the SBL ($P > 0.05$). However, the maximum mechanical turbulence during a time period did significantly relate to proportion of collected seed predicted above the SBL ($P < 0.05$), while maximum thermal turbulence had no effect.

**Discussion**

Simultaneously sampling within and above the surface boundary layer was a novel approach to the study of long-distance seed dispersal and requiring techniques that have been used successfully for other organisms but were untested for seeds. Isaacs and
Byrne (1998) used a tower sampler to assess whitefly (*Bemisia tabaci*) abundance in the SBL downwind of a source population. Shields and Testa (1999) successfully implemented remotely-piloted airplane sampling of potato leaf-hopper in the PBL. They recorded potato leaf hopper (*Empoasca fabae*) regularly at 30 m and found increased activity after the front of low pressure systems passed through the area during fall Southern migration. Seed collection at canopy level quantifies seed density in the SBL but at only one level. Seed collection in the PBL has been limited to two studies including a general organism sampling in Australia (White 1970) and more recently, sampling for *C. canadensis* (Shields et al. 2006). This is the first study, to our knowledge, to connect seed abundance within and above the SBL.

While vertically sampling the SBL was not trivial, there were fewer limitations than sampling above the SBL. Collection higher in the PBL was possible because of the use of RPVs, but also limited by their safe operation. Sampling events were limited to days when wind speeds were less than 24 kmph. Additionally, flying RPVs at altitudes lower than 60 m increases the likelihood of crashes, which dictated the floor for sampling heights. Overall, 30 flights were conducted, providing a unique data set from which to more thoroughly quantify daily fluctuations in seed concentration profiles in the PBL.

Daily variations in seed concentration in the PBL were consistent with reports for insects and pollen (Yao et al. 1997; Shields and Testa 1999), suggesting plant adaptation for wind dispersal. Total seed released each day varied from 1127 to 32,750, but the number of seed collected, inferring number of seed released, always decreased from Early to Middle to Late sampling periods (Table 4-2). As the seed quantity decreased, a greater proportion was collected higher on the towers and with the RPVs (Figure 4-2).
Over 50% of seed collected in the late afternoon were predicted to have ascended through the SBL.

Airplane sampling efficiency was not tested during this work. To assess how actual seed collection concentrations differed from estimated seed concentrations when sampling efficiency was reduced to 20% and 10% and concentrations were multiplied by 5 and 10, respectively. Seed concentrations at 60 and 120 m were higher in the Middle and Late periods and seed concentration profiles would be shifted right in comparison to 100% efficiency (reported) data (Figure 4-2). Analysis of the proportion of collected seed above 6 m was conducted and more than 80% of the collected seed were predicted at 20% sampling efficiency to be above 6 m in the Middle and Late periods. At 10% efficiency in the Late period, more than 96% of seed collection was predicted above the SBL. There were fewer seed collected in the afternoon (although this was still in the tens to hundreds), but their potential impact may be greater because they had a greater proportion ascend through the SBL and engage in long-distance dispersal.

The importance of turbulence to long-distance seed dispersal has been shown repeatedly. Tackenberg (2003) argued that convective forces must be driving release of seed while Soons et al. (2004) determined that inertial forces (strong horizontal winds) are causing seed release that may be associated with mechanical turbulence. Skarpaas et al. (2006) quantified increased seed release at lower wind speed and convective turbulent conditions (supporting Tackenberg’s hypothesis) and Greene (2005) determined seed abscission was governed by horizontal wind speed (supporting Soons et al. hypothesis). As a way of testing this, a moderate horizontal wind speed was selected (80th percentile of total horizontal wind, 3.13 m s\(^{-1}\)) and the frequency of recorded wind speeds above this
threshold (gusts) during each time period (Early, Middle and Late) were related to seed densities. Days were significantly different ($P < 0.05$, Table 4-1) but there was no significant sampling period effect although an increase in the frequency of gusts was observed in the afternoon.

Although frequency of horizontal gusts increased in the afternoon, thermal turbulence also increased in the afternoon with temperature increases (Lowry and Lowry 1989). Neither the mean mechanical turbulence nor the thermal turbulence was correlated with proportion of seed collection above 6 m. However, the maximum mechanical turbulence was significantly correlated with the proportion of collected seed above the SBL. This was similar to the Soons et al. (2004) finding that mechanical turbulence was more important than thermal turbulence but different because our findings suggest that short, vertical wind gust, rather than sustained updrafts, may carry more seeds through the SBL. Some work has examined the role of abscission in long-distance movement (Greene 2005; Skarpaas et al. 2006), but these studies need to be intertwined with seed ascent in the PBL.

Collecting viable seeds above the SBL is a large step in determining the potential distances of seed dispersal, but quantifying the realized dispersal distance still remains a challenge. A number of assumptions need to be made to extrapolate vertical seed collection observations to dispersal distance. Primarily, the PBL must stay convectively mixed for five hours (minimum time between seed collected aloft and sunset during September) which would contain long period turbulent eddies to retain seeds aloft (Stull 1988). Secondly, seed viability was assumed to remain unchanged during the period the seed remains aloft. Seeds collected aloft were assumed to be viable, but had likely been
exposed to UV radiation for short periods. Exposure to UV light damages pollen and spores (Aylor 1999) but appears to have little effect on *C. canadensis* survival since seeds can survive on the soil surface to germinate. Lastly, the wind speed at seed collection height was assumed to remain the same for the duration of the flight. The large-scale meteorological forecasting to precisely determine changes in wind speed throughout the PBL during the day is dependent on synoptic weather patterns and beyond the scope of this work. A more precise extrapolation may follow a movement model developed by Isard et al. (2005) that incorporated changes in wind speed, wind direction, and deposition to more accurately predict soybean rust settlement. At least for the period until sunset on the sampling days, the PBL likely remain convectively mixed and wind speeds remained similar to carry *C. canadensis* seed.

With these assumptions, seed collected at 120 m AGL encountered a wind speed of 20 kmph (assuming a logarithmic wind speed increase with slope of 2.6 s\(^{-1}\)). Over 5 hours, the seed would have traveled approximately 100 km. The seed collected aerially during the Early period would remain aloft for 7 or more hours and travel at least 140 kilometers before falling with gravity and being deposited. An alternative scenario assumed the seed fell from 120 m without any additional upward movement, only encountering the slowing wind speed with loss of altitude (in the case where the PBL was not convectively mixed). This scenario may occur if the seed ascended through the SBL late in the day or daily conditions changed. *C. canadensis* seeds move fall with a velocity of 0.3 m s\(^{-1}\), requiring six minutes to reach the ground from 120 m. During the same period of fall, the seed encounters a wind speed decreasing logarithmically, but still moving the seed horizontally. During the six minutes of fall, the seed will have traveled
horizontally at least 1800 meters. Therefore, the long-distance $C. \ canadensis$ seed dispersal events were likely to lie in the range of 2 km to 140 km, considerably farther than previously recorded (Dauer et al. 2007).

The long-distance events for other wind dispersed species will be tied to their ability to ascend through the SBL, but plants with low settlement velocities may have dispersal distances on the order of kilometers rather than meters. Seed collection from near ground level to 120 m AGL advanced our knowledge about this species’ ability to spread, but also raised the question of the proportion of seed engaged in long-distance atmospheric transport.

On a per plant basis, we can conservatively make some assumptions about proportion of seed ascending through the SBL. A single plant produces 130,000 seeds that are released over 6 weeks (M. VanGessel personal observation), resulting in 3,100 seeds released per day. Assuming a uniform release from 10:00 to 17:00 yields 400 seeds released per hour. If the proportion of total seed released ascending through the SBL is greater than 5%, hundreds of seeds are escaping from the field per plant per day.

This research represented a significant change from seed dispersal research because sampling of dispersal tails was done vertically instead of horizontally. Where others have assumed the mechanisms of seed movement in the atmosphere, this research sought to connect the meteorological conditions with vertical movement and imply horizontal movement. The implications for management of this species, and other wind-dispersed species, is profound. Maldonado-Ramirez et al. (2005) noted that movement of $Fusarium$ in the atmosphere impacts the required extent of management to control the species. Controlling individual fields, as is commonly practiced, will have little regional
impact on the *Fusarium* population. The concept can be extended to this system. For example, six glyphosate-resistant *C. canadensis* plants survive in a field and disperse their 1 million seed. If 5000 seed (0.5%) travel even a moderate distance of 2 km, potentially hundreds of surrounding fields could be impacted by a single dispersal event. When infestation of the resistant biotype equates to increased expenditures for management, every neighboring farmer feels the effects of a single resistant patch. When the infestation envelopes multiple farmsteads, increasing the source strength to tens or hundreds of resistant plants, the potential distances increase (Rieger et al. 2002; Dauer et al. 2007).

The impact of wind dispersal in conservation and invasion biology has been recognized (Soons et al. 2005; Trakhtenbrot et al. 2005; Nathan 2006). Much of this work focuses on the connectivity of suitable habitat patches. In current agro-ecosystems, suitable habitat for glyphosate-resistant *C. canadensis* in the US may be defined by fields where glyphosate is the sole method of weed control. Adoption of glyphosate-resistant crops may increase the number of suitable patches for survival of this biotype. While atmospheric transport increases the connectivity of hundreds of farmsteads, when coupled with increases in suitable habitat, spread across the landscape can be very rapid. The development of glyphosate-resistant populations of other weed species, especially those with wind-dispersed pollen or seed, may result in rapid spread throughout suitable habitat in the US.
Table 4-1: *Meteorological Conditions.* Maximum horizontal wind speed (m s\(^{-1}\)), frequency of horizontal wind speed above 3.1 m s\(^{-1}\), mean thermal turbulence (J m\(^{-2}\) s\(^{-1}\)), and magnitude (absolute value) of mean mechanical turbulence (kg m\(^{-1}\) s\(^{-2}\)) for each sampling day. Reported values were significantly different \((P < 0.05)\) among days, but not significantly different among periods within days. The exception was mechanical turbulence which was also significantly different among periods and the magnitudes of the mean values are reported for comparison with thermal turbulence.

<table>
<thead>
<tr>
<th>Date</th>
<th>Maximum Wind Speed (m s(^{-1}))</th>
<th>Frequency of Horizontal Gusts</th>
<th>Thermal Turbulence (J m(^{-2}) s(^{-1}))</th>
<th>Mechanical Turbulence (kg m(^{-1}) s(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>11-Sep</td>
<td>5.722</td>
<td>113</td>
<td>0.1038 (3.0(\times)10(^{-4}))</td>
<td>0.2236 (2.9(\times)10(^{-2}))</td>
</tr>
<tr>
<td>12-Sep</td>
<td>3.923</td>
<td>22</td>
<td>0.1497 (3.7(\times)10(^{-4}))</td>
<td>0.1016 (2.1(\times)10(^{-2}))</td>
</tr>
<tr>
<td>20-Sep</td>
<td>3.672</td>
<td>22</td>
<td>0.1222 (3.1(\times)10(^{-4}))</td>
<td>0.1792 (3.3(\times)10(^{-2}))</td>
</tr>
<tr>
<td>21-Sep</td>
<td>2.944</td>
<td>0</td>
<td>0.1288 (3.4(\times)10(^{-4}))</td>
<td>0.0508 (1.8(\times)10(^{-2}))</td>
</tr>
<tr>
<td>22-Sep</td>
<td>3.169</td>
<td>2</td>
<td>0.1325 (4.3(\times)10(^{-4}))</td>
<td>0.1341 (2.6(\times)10(^{-2}))</td>
</tr>
</tbody>
</table>
Table 4-2: Seed Collection. Total *C. canadensis* seed collected at two heights within the surface boundary layer (SBL) and two heights in the planetary boundary layer (PBL) during five sampling days across three sampling periods (Early, Middle, and Late). Seed collections were significantly different ($P < 0.05$) within and among days. Collection height in the PBL reflected the target sampling height and assumed a 100% sampling efficiency.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Height (m)</th>
<th>11-Sep</th>
<th>12-Sep</th>
<th>20-Sep</th>
<th>21-Sep</th>
<th>22-Sep</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>2</td>
<td>3106</td>
<td>605</td>
<td>4082</td>
<td>152</td>
<td>926</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>650</td>
<td>53</td>
<td>1813</td>
<td>60</td>
<td>159</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle</td>
<td>2</td>
<td>636</td>
<td>980</td>
<td>3132</td>
<td>152</td>
<td>342</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>200</td>
<td>169</td>
<td>2531</td>
<td>56</td>
<td>140</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Late</td>
<td>2</td>
<td>521</td>
<td>82</td>
<td>850</td>
<td>36</td>
<td>241</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>10</td>
<td>26</td>
<td>617</td>
<td>39</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>
Table 4-3: *Seed Concentration and Germination.* *C*on*yz*a *c*anadensis mean (SE) seed collection, air volume, seed concentration (assuming 100% sampling efficiency) and germination at five heights within and two heights above the surface boundary layer. Volumes for tower collections were determined by wind speed at each height while airplane volumes were calculated by ground speed. Ground seed collections were only conducted during the last three sampling days.

<table>
<thead>
<tr>
<th>Height (m)</th>
<th>Seeds/day (SE)</th>
<th>Volume/day (SE)</th>
<th>Concentration (SE)</th>
<th>Germination</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>225.3 (156.28)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>3168.6 (1381.53)</td>
<td>29611 (2055.2)</td>
<td>0.2959 (0.11814)</td>
<td>60% (N=40)</td>
</tr>
<tr>
<td>3</td>
<td>2447.2 (1388.67)</td>
<td>30805 (2139.0)</td>
<td>0.2228 (0.12069)</td>
<td>53% (N=40)</td>
</tr>
<tr>
<td>4</td>
<td>1967.6 (1183.52)</td>
<td>31653 (2198.4)</td>
<td>0.1754 (0.10187)</td>
<td>54% (N=39)</td>
</tr>
<tr>
<td>5</td>
<td>1543.0 (955.89)</td>
<td>32310 (2244.5)</td>
<td>0.1391 (0.08497)</td>
<td>43% (N=40)</td>
</tr>
<tr>
<td>6</td>
<td>1316.0 (919.35)</td>
<td>32847 (2282.2)</td>
<td>0.1163 (0.07986)</td>
<td>51% (N=39)</td>
</tr>
<tr>
<td>68.2 (1.64)</td>
<td>1.2 (0.37)</td>
<td>3396 (95.9)</td>
<td>0.0011 (0.00035)</td>
<td>40% (N=5)</td>
</tr>
<tr>
<td>120.6 (2.62)</td>
<td>2.2 (0.80)</td>
<td>2860 (292.0)</td>
<td>0.0044 (0.00240)</td>
<td>20% (N=5)</td>
</tr>
</tbody>
</table>
Figure 4-1: Schematic view of field and general relationship of tower samplers (A, photo inset) to heaviest concentration of *C. canadensis* (slashed areas, 10 - 130 plants m$^{-2}$). Tower arrangement allowed screen angle to be adjusted so screens were perpendicular to wind direction. Airplane sampling was conducted downwind at a 45 degree angle vertical to the source at approximately 60 m and 120 m above ground level. The 3-dimensional sonic anemometer was located near the tower samplers (B).
Figure 4-2: Concentration gradients of *C. canadensis* seed during three periods pooled across five sampling days. Lines (parameter estimates (SE)) represent log mean concentration during Early (solid, \( h = 2.9(0.27) - 12.8(3.28)c \), \( r^2 = 0.32 \)), Middle (dashed, \( h = 2.6(0.28) - 5.8(2.40)c \), \( r^2 = 0.15 \)) and Late (dotted, \( h = 2.6(0.29) - 23.4(9.05)c \), \( r^2 = 0.17 \)) periods, where \( h \) is the ln height and \( c \) is ln conc + 1. Sampling periods were not significantly different.
Literature Cited


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Chapter 5

Effects of Glyphosate-Resistant Crop Adoption on the Connectivity of a Landscape: An Herbicide-Resistant Weed Perspective

Summary

1. Adoption of genetically modified glyphosate-resistant (GR) crops has increased landscape connectivity and increased the selection pressure for weedy species resistant to glyphosate, a commonly applied herbicide. GR Conyza canadensis weed populations have developed and spread throughout the United States, Brazil, and China, and can affect soybean and cotton yields.

2. An empirically-derived simulation model was developed to quantify GR C. canadensis spread in a 90 km² agricultural landscape with a continuum of weed management strategies. Survival of C. canadensis was dependent on the crop and weed management performed in a given crop. Increasing GR corn adoption increased landscape evenness while adding a perennial crop (alfalfa) with high C. canadensis mortality, increased landscape richness.

3. Under current GR adoption levels, GR C. canadensis was estimated to infest 288 of 360 possible fields after 5 years. Increased GR corn adoption resulted in 35 additional fields being infested. Adding alfalfa acted as a sink because of the zero fecundity for C. canadensis and resulted in fewer fields being infested after 5 years. Under a reduced proportional adoption of GR soybean, approximately half the number of fields were infested and those infestations never exceeded the lowest abundance class.
4. Adding alfalfa to the landscape reduced the likelihood that farms up to 8 km from the source field had a 10% lower chance of infestation compared to corn-soybean rotations. Halving the area plant to GR soybean reduced GR *C. canadensis* to low infestation levels and reduced the probability that distant fields would become infested by the resistant weed biotype to less than 40% after 5 years. Elimination of GR crops resulted in eradication of the resistant biotype.

5. *Synthesis and applications.* Reducing weed management diversity increases connectivity of safe sites for herbicide-resistant weeds. Large-scale reliance on glyphosate for weed management will result in rapid spread of glyphosate-resistant weeds. Landscape scale, or area-wide management that increases crop and weed management diversity will be needed to contain existing resistant weed biotypes and to minimize selection for new resistant weedy biotypes and species.

**Introduction**

A major change in US agroecosystems has occurred in the last 10 years. The diversity of weed management practices has declined precipitously with a resulting increase in connectivity of the landscape for organisms adapted or resistant to the new management. In 1995, 16 different herbicides were applied to more than 1 million soybean hectares of arable cropland in the US. With the introduction of glyphosate-resistant soybeans in 1996 and its rapid adoption, glyphosate has become the dominant soybean herbicide and is currently applied to 89% of the soybean area. Furthermore, glyphosate-resistant varieties of corn, cotton, and alfalfa are now commercially available.

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which will likely result in greater reliance on glyphosate as the sole or primary weed management tactic. As adoption of GR crops has increased, the number of weedy species resistant to glyphosate has also increased from the first reported case in 1996 to 12 species in 2007 (Heap 2007). From a glyphosate-resistant plant perspective, wide-spread adoption of glyphosate-resistant crops increases the suitable habitat when producers rely on glyphosate as the primary form of weed control. The landscape evenness has increased through time as farmers simplify their management (Wiens et al. 1993).

Evenness is a metric in determining landscape connectivity, first defined by Taylor et al. (1993) as “the degree to which the landscape facilitates or impedes movement of organisms within resource patches.” In conservation ecology, losses in connectivity and in resource patches constrain populations. Soons and Ozinga (2005) examined the loss of suitable habitat for four forb species in the Netherlands as the landscape was transformed for agricultural use and drained or developed for human habitation. They estimated suitable habitat (2 best habitat classes) decreased from 3132 ha in 1900 to 24 ha in 1950 and only 4 ha in 2000. At the same time, the distances between suitable habitats increased from 0.14 km to 1.8 km in a hundred years, limiting the ability of populations to disperse among patches. In contrast, increasing connectivity and area of suitable habitat facilitates spread of invasive genotypes and species (Mortensen and Jongejans 2006; Hamilton et al. 2006). Hamilton et al. (2006) found that poor soil quality can reduce dispersal among nearby populations of invasive rabbits in Australia. However, good soil quality may connect two patches that were separated by long-distances, acting as corridors. Corridors between suitable habitats can play an important role in facilitating movement, and increasing landscape connectivity (Levey et
al. 2005), so long as they serve that function (i.e. the organism’s immigration rate increases, Tischendorf and Fahrig 2000).

While quantity of suitable habitat has increased, connectivity of the fields also depends on the ability of the plant species to move among those suitable habitats. *Conyza canadensis* (common names: horseweed, marestail, Canada fleabane) is a winter annual weed that has become an increasing problem in no-tillage agriculture (Tremmel and Peterson 1983), but is also common on roadsides and waste areas (Holm et al. 1997). It outcrosses less than 5% of the time (Smisek et al. 1998) and a single plant has been estimated to produce 70,000 to 200,000 seeds each with an unbeaked pappus which aids in wind dispersal (Regehr and Bazzaz 1979; Bhowmik and Bekech 1993). Glyphosate-resistant populations of *C. canadensis* were first confirmed in 2001 in Delaware and resistant populations have been documented in 15 states in the US, Brazil, and China (VanGessel 2001; Heap 2007). As a wind-dispersed species, seed can travel long distances and have been collected 140 m above the ground surface and to distances of 500 m from a source population (Shields et al. 2006; Dauer et al. 2007).

Through wind-dispersal agricultural fields are interconnected and management dictates the local recruitment success of the species. Monitoring spread on the landscape scale is difficult and simulation modeling offers an opportunity to explore the importance of spatial and/or temporal cropping system diversity on connectivity and spread. Often focusing on gravity-dispersed weed species, modeling has explored dispersal of weed seed among or within fields (Perry and Gonzalez-Andujar 1993; Gonzalez-Andujar and Perry 1995; and Wang et al. 2003). Incorporating farmer decisions into spatial weed spread, Gonzalez-Andujar et al. (2001) found controlling weeds when they reach a
“threshold” only spread weeds among surrounding fields instead of reducing abundance. Wadsworth et al. (2000) compared management techniques (directed vs. random) and found management must be sustained and highly effective to eradicate invasive riparian weeds in the UK.

We report on the results of a model assessing the impact of crop management decisions at the landscape scale on the invasion rate of a herbicide resistant weed. Our model differs from previous studies because *C. canadensis* dispersal distances are greater than many intra-field distances, thereby connecting many surrounding fields and does not utilize the commonly used cellular automata grid to describe the landscape. Because grids do not properly represent the landscape where fields are an oddly shaped jigsaw, we chose to calculate interfield distances for real landscapes in our study system. The benefit of representing the system as a jigsaw rather than a grid resides in the spatial scale of the correlation between events in the lifecycle. An agricultural field is a natural unit within which life-history transitions are correlated by weed management strategies, followed by dispersal, which decorrelates the fate of individuals. While polygons are easy to create, using them to model population spread can be highly complex. Principally, distance between polygons is not simply the distance between centroids, the minimum distance between edges, or the maximum distance between edges, rather some combination of all of these. Without knowledge of the location of plants in a polygon, plants can be uniformly assigned to a polygon, and the distances to other polygons integrated over the distribution of distances. By including the variation in distance among polygons, shape and size of the polygons are incorporated into the transmission
rate. Seed movement can then be reduced to the probability of moving between two fields which is dependent on their arrangement in the landscape.

Cellular automata (CA) models have been utilized to explore myriad complex spatial questions. For a CA model, the landscape is divided into cells, usually of equal size. Cells can be assigned a habitat type which influences organismal survival (unsuitable habitat, corridors, etc.) There are two common approaches to defining dispersal in CA models – nearest neighbor and buffer distance. Nearest neighbor assigns probability of dispersal to a predetermined number of surrounding cells (Silvertown et al. 1992; Wang et al. 2003). Using a square grid, dispersal from a source is determined for the 4, 8, or 12 nearest cells. Buffer distance CA overlays an empirically derived dispersal curve that “deposits” a proportion of the total seed as a function of distance from the source to other cells (Bianchi and van der Werf 2004). The dispersal distance is defined by the distance between centroids (but see Lurz et al. 2001). Both approaches have a set number of cells that are influenced by a single source. Moilanen and Nieminem (2002) challenged the nearest neighbor and buffer distance approaches and noted that measures of connectivity should include “focal size [source strength] and size and distance to all potential source populations.” Including all potential sources considers the potential for long-distance dispersers to contribute to the radially expanding population in a stratified dispersal (Shigesada and Kawasaki 1997). Moreover, source strength can impact dispersal distance of wind-dispersed organisms (Rieger et al. 2002; Dauer et al. 2007).

CA models have been used to describe dispersal between habitats (Humston et al. 2004) where individual habitats have certain characteristics. In our research, habitats were considered homogeneous within a polygon. Instead of treating the agricultural
landscape as a grid, we propose to view it as a jigsaw of polygons where borders are determined by age old pressures: forests, water, agreements, and roads. The only difference between polygonar and cellular automata is the definition of a cell but similar questions can be asked in an agricultural context.

From the perspective of a producer, spread may be defined as the likelihood their farmstead receives the resistant biotype. In our model, spread was defined as the likelihood that a field separated from the initial infestation contained resistant biotype plants after a given number of years. This likelihood was a conservative estimate because the defined dispersal capability does not include the rare long-distance events that are known to occur with this species (Shields et al. 2006). Instead, the likelihood will be the result of local (500 m) dispersal quantified in earlier work (Dauer et al. 2007).

Our spatially explicit model was used to explore the following important questions regarding the spread of herbicide resistance in the face of landscape-level management choices. How has widespread adoption of glyphosate-resistant soybean influenced the spread of glyphosate-resistant \textit{Conyza canadensis}? How fast does the resistant biotype spread if the landscape evenness is increased through increased glyphosate-resistant crop adoption? Can survivorship be altered through crop diversification (increased landscape richness) to slow the spread of the resistant biotype?

**Methods**

**Model Description**

Let the subscripts ‘R’ and ‘S’ refer to glyphosate resistant and susceptible biotypes of horseweed. Resistant plants occur in any given field either through independent mutation or emigration where it is assumed that outcrossing rates are
negligibly small (Smisek 1995, Feng). As the relative fitness $R:S$ may be much larger than unity within the GR cropping system, we speculated that the spread rate of the species would depend on the degree to which the dispersing seed had access to the suitable patches.

The agricultural fields comprising the possible diffusive pathways for the R-type tend to be managed as a single unit with weeds often at sufficiently low density that precise spatial information is impractically costly. Rather than use grid-based models which require rectangular spatial units, or continuous-space models that might have a great deal of uncertainty in the description of the state (e.g. positions of R-type plants), we choose to use a spatially realistic (Hanski and Gilpin 1997) polygonal representation of a typical Pennsylvania agricultural area.

A 10 km by 9 km aerial photograph (DOQ, 1 m ground resolution, North American Datum 1983, N40.1029, W76.43027) near Lancaster, Pennsylvania, USA (Columbia East Quadrangle)\textsuperscript{6} was used as a basis for dispersal simulations (Figure 5-1).

The perimeters of farm fields were traced manually in ESRI ArcGIS 9.1 resulting in 360 field polygons. The average polygon was 11 ha (SE = 0.47) and polygons comprised 41.7% of the total area, with the remaining area in forest, residential, and riparian corridors which were deemed unsuitable for \textit{C. canadensis} growth.

Our spatial demographic model then, contained a set of polygons having connectivity that could be computed numerically given any sort two-dimensional vector function describing seed dispersal. The seed dispersal kernel estimated in a prior

\textsuperscript{6} http://www.pasda.psu.edu
manuscript (Dauer et al. 2007) was used to calculate the probability mass or “flux” that represented the redistribution of seeds amongst fields. The expression for the flux between one source and target polygon is:

\[ \vartheta_{A,B} = \frac{1}{k} \int_{\Omega_A} \int_{\Omega_B} f(r_{A} - r_{B}) \cdot p(r_{A} - r_{B}) d\Omega_A d\Omega_B \]  

(5.1)

Where \( r_A \) and \( r_B \) are vectors from an arbitrary origin to a point in polygons A and B respectively as shown in Figure (5-2). The source-specific normalization constant \( k \) was chosen such that the flux \( \vartheta \) would integrate to unity over all space.

\[ k \equiv \int_{\Omega} f(r) \cdot p(r) d\Omega \]  

(5.2)

Equation 1.1 was computed using Monte-Carlo integration, randomly drawing points in source and target polygons (Beyer 2004), then computing the size of the dispersal kernel at the corresponding distance. We explored the number of samples required to converge and found a sample size of twenty points per polygon was accurate to within 4%. This level of accuracy was more than sufficient given the other approximations in our spatial population model.

The dispersal kernel (seeds m\(^{-2}\)) was defined as a function of distance from the source \( r \) (meters) and source strength \( Q \) (seeds). Clark et al. (1999) explored the use of one such dispersal function (the radially isotropic “2Dt” type):

\[ f(r) = Q \cdot p \cdot \left( \pi u \left( 1 + \frac{r^2}{u} \right) \right)^{\gamma - p} \]  

(5.3)

Which has two shape parameters, \( p \) and \( u \), that we estimated \( (p = 0.27, u = 6.0 \times 10^{-3}) \) in a prior manuscript (Dauer et al. 2007). The full spatial model can be compactly written:
\[
N_{t+1} = \Lambda \Phi \tilde{N}_t \tag{5.4}
\]

\(N\) is a vector, with each position corresponding to a specific polygon. \(\Lambda\) is an \(n\)-dimensional square matrix with the system-specific population growth rates, \(\lambda\) on the diagonal. This local, field-specific growth rate was assumed to depend only on the choice of cropping system. The \(\Phi\) matrix is an \(n\)-dimensional matrix with the quantity given by Equation 5-1 for the row-column associated with polygons A and B respectively. In essence, Equation 5-4 decomposes the dynamics into two parts, a spatial reshuffling (\(\Phi\)) and a system-specific mosaic of habitat quality/fitness (\(\Lambda\)) determined by the large scale land-use choices of land managers.

The latter process is governed by survivorship and fecundity over the annual cycle. As the seedbank was considered ephemeral, all sources of seed loss (e.g. overwinter decay, fatal germination, seedling death, etc.) can be included within survivorship. In general, studies have shown the transition of seed to plant is mediated abiotically by environmental conditions (Regehr and Bazzaz 1979; Main et al. 2006) and biotically by weed management practices.

Habitat quality (\(\Lambda\)) is a compilation of system independent and system-dependent vital rates (Table 5-1). Regehr and Bazzaz (1979) characterized life-history transitions for \textit{C. canadensis} independent of weed management strategies. They recorded 6.8% fall germination, although we observed, and used in our model, germination rates of 1%. Fall germinating \textit{C. canadensis} plants form rosettes which usually survive (99%) to winter. Of the surviving fall rosettes, 14% survive to spring (in the case of high winter mortality) and 94% of these survive to late spring when weed management generally takes place.
Summer mortality from competition with crops and other weedy species reduced viable plants by 14% (unpublished study, Chapter 2). Combining all mortality sources, 0.11% of seeds released in fall survive to produce seed the following fall (assuming no dormancy or spring germination). The seedbank was also assumed to be so ephemeral that it could be ignored for the purposes of estimating habitat-dependent rates of spread.

Mortality due to chemical or mechanical control reduces this percent further. In non-GR crops, herbicide efficacy (mortality) was assumed to be 99%. Mortality was lower in GR crops, but still eliminated the majority of *C. canadensis* plants. Mortality in GR soybeans was assumed to be 75% while the use of other herbicides in conjunction with glyphosate in corn increased mortality to 90%. These percentages include mortality of *C. canadensis* and reduction in fecundity which has been observed in resistant populations (M. VanGessel, personal communication). Mortality in alfalfa was assumed to be 100% because of repeated intraseason harvest. *C. canadensis* fecundity in corn was quantified as 74,700 seeds (Regehr and Bazzaz 1979) while fecundity in soybeans was higher at 133,000 (Dauer et al. 2006) and zero seeds were assumed to be produced in alfalfa. Multiplying chemical mortality by average yearly mortality and crop-specific morality resulted in an estimate of the number of plants expected per seed produced.

**Scenario Selection**

Scenarios were developed to explore the impact of spatial GR crop adoption patterns on spread rates of GR *C. canadensis*, focusing on landscape connectivity and the role of evenness and richness. For this model, landscape richness was defined by the number of different crops and landscape evenness was defined by the proportion of the crops planted with GR varieties. The current (CUR) management scenario divided the
landscape into 50% corn and 50% soybeans and represented a baseline scenario. Using 2006 GR crop planting records averaged across the US\textsuperscript{7}, 21% of the corn polygons were designated GR corn, and 89% of the soybean polygons were designated GR soybeans (Table 5-2). Adding alfalfa to the system (CUR+ALF) increased landscape richness and changed the proportion of polygons in the landscape in each field type. Corn and soybean were reduced to 40% of all polygons, and alfalfa was assigned to 20% of polygons, with the percentage of GR crops (landscape evenness) unchanged. The CURALF scenario was compared to the CUR scenario to determine the effect of increased landscape richness on spread of GR \textit{C. canadensis}.

To assess the effect of increased GR adoption (increased evenness), the percent of corn polygons using GR technology was doubled from 21% to 42% (HIGR), with percent of GR soybeans unchanged from the CUR scenario. The landscape evenness was unchanged from the CUR scenario. A fourth scenario simulated increased GR corn adoption but also added alfalfa into the system (HIGR+ALF), changing the corn and soybean to 40% of polygons and remaining polygons assigned alfalfa. Both landscape evenness and landscape richness were increased and examined the possible antagonism between increased crop diversity and decreased herbicide diversity. Two scenarios were included to simulate a lower percent of GR corn and soybean compared to the CUR scenario. The PRE96 scenario represented the landscape in 1995, prior to introduction of GR crops (0% GR), but containing 50% of polygons in corn and soybean (Decreased landscape evenness). With no safe sites, GR \textit{C. canadensis} was expected disappear

\textsuperscript{7} http://www.nass.usda.gov/Publications/
rapidly from the landscape. The LOWGR scenario reduced the percent of GR soybean by half from 89% to 45%, while GR corn percent remained as the CUR scenario. The LOWGR scenario represented a reduction in GR soybeans that may arise from mandated reductions in planting GR soybeans, planting the same percent of GR soybeans as CUR, but using additional herbicides to reduce the area only receiving glyphosate, or area-wide cooperation to try and reduce the spread of a GR weed.

*Simulating Spread*

The model was used to simulate a two year corn-soybean rotation and when alfalfa was added to the simulation, the landscape was divided into 40% corn and soybean and 20% alfalfa. In these simulations (CUR+ALF and HIGR+ALF), corn and soybean were rotated annually, while fields assigned alfalfa, a perennial crop would remain for 3 years, and then rotated to corn for 2 years. This is a typical corn-alfalfa rotation for the Northeastern US. The initial alfalfa fields were randomly assigned as 1st, 2nd, or 3rd year alfalfa. An infestation of five resistant plants was randomly assigned to a central soybean field and simulations began with the fall dispersal of seed from the infestation.

The Monte-Carlo simulation of spatial dynamics occurred in time steps of 1 year and simulated spread was continued to the end of the 5th year and repeated 100 times per scenario. The likelihood of polygons becoming infested by glyphosate resistant *C. canadensis* after each year was a useful metric for assessing cropping systems effects since growers annually choose what to plant and how to manage weed infestations. In years 3 and 5 (out of 5 years) infested fields were assigned a value of 1 and uninfested fields assigned a value of 0. A logistic equation \( y = \frac{\exp(a+b*x)}{1+\exp(a+b*x)} \)
determined the infestation probability ($y$) as a function of distance from the source ($x$) and two shape parameters $a$ and $b$ (MacDonald and Rushton 2003). An additional spread metric was calculated to examine the level of infestation in the landscape. Polygons were classed by the number of plants per field and divided into zero plants, low infestation (1 – 30 plants), medium infestation (30 – 60 plants) and high infestation (60+ plants). With an average size of 11 ha, the high infestation averaged approximately 6 plants per hectare, a level that farmers would likely recognize as problematic.

**Results**

The scenarios evaluated with the model strongly influenced the spread of the glyphosate-resistant biotype. Under the CUR scenario more than 44% of polygons were infested after 3 years which increased to 337 polygons (94%) infested after 5 years (Table 5-2). Diversifying cultural practices through increased alfalfa planting (CUR+ALF) reduced the number of polygons infested by 11% in 3 years and 21% after 5 years. Increased adoption of GR corn (HIGR) increased the number of fields infested from the CUR scenario. Three years after the infestation began, 20% more fields were infested in HIGR compared to CUR, representing a greater rate of spread. This percentage dropped over the next two years and only 4% more fields were infested five years after the beginning of the infestation. Adding alfalfa to the high GR adoption (HIGR+ALF) reduced the rate of spread more than adding alfalfa to the CUR scenario, but only in the short run (3 years). The HIGR+ALF scenario reduced the number of polygons infested by 50 after 3 years (14% compared to CUR+ALF reduction of 11%). After five years the pattern switched and CUR+ALF reduced the number of polygons infested more than HIGR+ALF (20% compared to 15%).
As expected, the PRE96 scenario where glyphosate-resistant crops were not planted provided no safe sites for the glyphosate-resistant plants and zero polygons were infested after 5 years. The LOWGR scenario reduced landscape evenness and therefore provided fewer safe sites (GR polygons) than the CUR scenario, thereby reducing spread, but not eliminating the resistant biotype. After 5 years, the fewest number of polygons (153) were infested in the LOWGR scenario, compared to all scenarios except the PRE96.

Logistic regression can be used to determine the probability a field at a given distance will be infested after a given time. Under the CUR scenario a field at 4 km from the original source had a 20% chance of developing resistant plant infestation in 3 years, but this increased to 80% by year 5 (Figure 5-2). Increasing landscape richness (CUR+ALF) decreased that probability to 60% no matter the distance of the field from the original source.

Increased adoption of GR crops consistently increased the probability of becoming infested with resistant biotypes to a greater distance from the source population (Figure 5-2). HIGR+ALF insured that a field would become infested (100% likelihood of infestation) if fields were located within 4 km of the original infestation. Again, adding alfalfa (HIGR+ALF) reduced the likelihood of infestation by 5% to 20%, depending on the distance from the initial source. In CUR+ALF and HIGR+ALF, the alfalfa had a mediating effect and 5 years after the initial infestation, the likelihood was almost the same no matter the distance from the source polygon. When landscape evenness was reduced, the percent of GR soybean (LOWGR) and corn and soybean (PRE96) was reduced, the likelihood of infestation dropped considerably. With the
PRE96 scenario, the likelihood after 3 years was essentially zero and dropped to zero after five years. The LOWGR scenario approached zero likelihood at greater distance from the source after 3 years but polygons less than 1 km from the original source still had greater than 40% chance of having resistant plants after 3 years. After 5 years, the likelihood in LOWGR was steady near 50%, irrespective of distance from the original polygon.

After 5 years, spread resulted in much of the landscape being infested in the CUR and HIGR+ALF scenarios (Figure 5-4). The addition of alfalfa to the landscape reduced the number of infested polygons and the abundance in each polygon (HIGR+ALF and CUR+ALF). Except for the PRE96 scenario in which GR *C. canadensis* went extinct, LOWGR represented the slowest rate of spread with only 30 of the 360 polygons having a low infestation (fewer than 30 plants per polygon) and no polygons heavily infested after 5 years.

**Conclusions**

The rate of spread for an invasive species or genotype may be described as the transport and successful colonization of sites. Transport of *C. canadensis* seed is primarily accomplished via wind which connects hundreds of surrounding fields. Once a plant sets seed, preventing aerial transport is impossible. Therefore, the rate of spread for *C. canadensis* will be constrained by the colonization and survival of seeds within fields. As more weeds develop resistance to glyphosate, the connectivity of the landscape, mediated by landscape evenness and richness and species’ dispersal ability, will determine the rate of spread for each species. Increasing landscape evenness had the greatest positive impact on the rate of spread. Even though the model excludes long-
distance dispersal events, GR *C. canadensis* was estimated to occur in greater than 96% of fields in a 90 km² area at densities greater than the CUR scenario (Figure 5-4).

The cultural solution of adding alfalfa to the landscape diversified the landscape composition, increased *C. canadensis* mortality, and reduced the rate of spread. Unfortunately the benefit was not uniform for all polygons. Polygons located near the initial infestation were 20% less likely to receive the resistant biotype while fields farther from the source have less than 5% better chance of not receiving the resistant biotype compared to scenarios without alfalfa (Figure 5-4). For producers, high crop diversity may provide opportunities for reducing the rate of spread because these crops can act as sinks for resistant seed, diluting the amount of available seed that may otherwise infest corn and soybean fields in the surrounding landscape.

From a glyphosate-resistance standpoint, alfalfa was unsuitable habitat which increased the landscape richness and reduced the landscape connectivity. With a large amount of suitable habitat in close proximity, spread of an invasive will be dictated by its dispersal ability and unconstrained by fragmentation (With 2004). Potentially, the positioning of alfalfa in the landscape could influence how rapidly GR weeds will spread among the fields. Therefore, alfalfa in the landscape may not be sufficient if the unsuitable habitat (alfalfa) is clumped rather than spread out.

Carriere et al. (2006) modeled the effects of landscape composition on movement of a cotton pest, western tarnished plant bug (*Lygus hesperus*) and found the arrangement of alfalfa fields (sources of the pest) to the cotton fields directly affected the abundance of insects in the cotton fields. The size, structure, and arrangement of crops have been a major component of maintaining the viability of *Bacillus thuringiensis (Bt)* crops. In
1999, the US Environmental Protection Agency mandated refugia be included in all Bt corn plantings to provide an area where potentially resistant insects would breed with susceptible insects. Within a field, refugia planted randomly increased the likelihood of resistant alleles remaining in the population while blocks of non-Bt crop refugia reduced the likelihood (Cerda and Wright 2004). On a larger spatial scale, Peck et al. (1999) found time to resistance development was longer when the fields were repeatedly planted as refugia instead of randomizing the refuge fields each year. Currently our model assigns crops randomly to polygons, but future work will determine how the arrangement of trap crops (like alfalfa) may slow the rate of spread of GR C. canadensis.

One might suggest the solution to GR C. canadensis is simply adding different herbicides to the glyphosate application. This “solution” masks a number of potential problems. In particular, the trends in glyphosate use do not support the concept that farmers would be willing to implement this practice. The soybean acreage receiving glyphosate has steadily increased while the acreage receiving other herbicides continues to decline. Secondly, adding additional herbicides changes the selection pressure, but C. canadensis populations have developed multiple-resistance to a number of commonly used herbicide active ingredients (Gressel et al. 1982; Pölös et al. 1988; Smisek et al. 1998; Trainer et al. 2005). Lastly, just managing the landscape for GR C. canadensis ignores the impending development of glyphosate-resistance in other species.

Since GR C. canadensis populations have been documented, nine additional weed species have developed resistance to glyphosate, bringing the total to 12 species (Heap

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8 http://www.nass.usda.gov/Statistics_by_Subject/Environmental/
2007). Other herbicide modes of action have shown similar trends of resistance (Heap 2007), suggesting that the number of glyphosate-resistant species will only increase. To understand how these species will spread, a thorough quantification of their dispersal dynamics is needed. Species similar to *C. canadensis* with wind-dispersed life stages (pollen or seed) that carry the resistance gene, will likely be spread beyond the boundaries of a single field, connecting a plethora of fields on a landscape. Restricting spread of wind-dispersed organisms depends almost exclusively on the crop management. In contrast, resistant species whose dispersal is vectored by animals (including humans) may appear to have limited ability to increase their distribution and local abundance. In fact, recent studies have documented the role of human mediated dispersal of invasive species by boats (Leung et al. 2006) and automobiles (Van der Lippe and Kowarik 2007). There is considerable evidence supporting the role that movement of invasive plants via contaminated crop seed and hay (Magda and Gonnet 2001). In fact, vectors like crop seed, equipment (combines), movement of silage feed and manure applications almost certainly will play an increasingly important role in movement of invasive herbicide resistant biotypes as there is little indication that the simplicity in crop and weed management choice will change any time soon.

Clearly, the continued adoption of GR crops further accelerate the spread of GR weeds, leading to a landscape with high crop evenness and high level of connectivity. Add to the GR crop the ability of GR *C. canadensis* to disperse long-distances and the rate of spread has been very rapid. Increased adoption of GR corn will further increase the number of safe sites for GR *C. canadensis* and increase the rate of spread. Our model indicates the factors that will most profoundly slow the spread of herbicide resistance are
diversity of mortality sources thereby reducing the selection pressure for resistance.

While it is unlikely that use of GR soybean and corn will be discontinued, it is possible to limit the use of such crops to minimize the buildup of herbicide resistant populations. The LOWGR scenario represents one in which GR crops would be grown every other year. Such a strategy was seriously considered in the recent debate of a voluntary glyphosate stewardship plan by the Northeast Weed Science Society and is currently in effect in Australia. Models like that reported herein provide an enormously valuable resource for assessing the impact of cropping practices and their stewardship and should play a more important role in assessing future GR crop regulatory decisions and cropping systems recommendations.
Table 5-1: Mortality sources, natural and human-mediated, affecting the survivorship of *Conyza canadensis* from seed in year, $t$ to plants in year, $t+1$.

<table>
<thead>
<tr>
<th>Transition</th>
<th>Mortality</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Natural Growth</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall Germination</td>
<td>99%</td>
<td>Personal Observation</td>
</tr>
<tr>
<td>Fall to Early Winter</td>
<td>1%</td>
<td>Regehr and Bazzaz 1979</td>
</tr>
<tr>
<td>Winter</td>
<td>86%</td>
<td>Regehr and Bazzaz 1979</td>
</tr>
<tr>
<td>Spring</td>
<td>6%</td>
<td>Regehr and Bazzaz 1979</td>
</tr>
<tr>
<td>Late Spring to Seed Set</td>
<td>14%</td>
<td>Unpublished, Chapter 1</td>
</tr>
<tr>
<td><strong>Management</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-Glyphosate-Resistant Crops</td>
<td>99%</td>
<td></td>
</tr>
<tr>
<td>Glyphosate-Resistant Soybean</td>
<td>75%</td>
<td></td>
</tr>
<tr>
<td>Glyphosate-Resistant Corn</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>Alfalfa</td>
<td>100%</td>
<td></td>
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</tbody>
</table>
Table 5-2: The proportion of 360 polygons within the extent of the aerial photo (Figure 5-1) assigned to corn, soybean and alfalfa for six scenarios. Polygons were further partitioned into glyphosate-resistant (GR) varieties in parentheses and non-GR varieties. Polygons assigned to alfalfa were not partitioned into GR and non-GR varieties because GR Conyza canadensis growth rates will be zero in both alfalfa varieties.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Corn (GR Corn)</th>
<th>Soybean (GR Soybean)</th>
<th>Alfalfa</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRE96</td>
<td>50% (0%)</td>
<td>50% (0%)</td>
<td>-</td>
</tr>
<tr>
<td>CUR</td>
<td>50% (21%)</td>
<td>50% (89%)</td>
<td>-</td>
</tr>
<tr>
<td>CUR+ALF</td>
<td>40% (21%)</td>
<td>40% (89%)</td>
<td>20%</td>
</tr>
<tr>
<td>HIGR</td>
<td>50% (42%)</td>
<td>50% (89%)</td>
<td>-</td>
</tr>
<tr>
<td>HIGR+ALF</td>
<td>40% (42%)</td>
<td>40% (89%)</td>
<td>20%</td>
</tr>
<tr>
<td>LOWGR</td>
<td>50% (21%)</td>
<td>50% (45%)</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 5-3: Comparison of scenario effects on mean polygons infested (SE) by GR *Conyza canadensis* after 3 and 5 years following 100 iterations for each scenario. Shape parameters ($a$ and $b$) for logistic regression equation for polygons infested after 3 and 5 years.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Number of Polygons Infested after 3 Years</th>
<th>Number of Polygons Infested after 5 Years</th>
<th>Year 3</th>
<th>Year 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td><strong>PRE96</strong></td>
<td>0.3 (0.06)</td>
<td>0.0 (0.01)</td>
<td>-5.49</td>
<td>-6.40E-04</td>
</tr>
<tr>
<td>CUR</td>
<td>160.3 (2.87)</td>
<td>337.5 (6.61)</td>
<td>0.67</td>
<td>-2.80E-04</td>
</tr>
<tr>
<td>CUR+ALF</td>
<td>120.6 (2.58)</td>
<td>263.9 (4.90)</td>
<td>-0.16</td>
<td>-2.90E-04</td>
</tr>
<tr>
<td>HIGR</td>
<td>199.8 (4.00)</td>
<td>349.3 (5.38)</td>
<td>1.10</td>
<td>-2.86E-04</td>
</tr>
<tr>
<td>HIGR+ALF</td>
<td>149.6 (2.29)</td>
<td>294.7 (2.72)</td>
<td>0.56</td>
<td>-3.05E-04</td>
</tr>
<tr>
<td>LOWGR</td>
<td>74.2 (1.99)</td>
<td>185.3 (4.23)</td>
<td>-0.43</td>
<td>-3.28E-04</td>
</tr>
</tbody>
</table>
Figure 5-1: Aerial photograph (Columbia East DOQ, NAD 1983) near Lancaster, Pennsylvania, USA. Polygons were hand drawn using ESRI ArcGIS 9.1.
Figure 5-2: The distance between a source polygon (A) and a target polygon (B) used to calculate the flux between polygons according to Equation 5-1.
Figure 5-3: Likelihood of *Conyza canadensis* infestation as a function of distance from original source population. In Current and Increased GR adoption frames, CUR and HIGR, respectively, are denoted by solid lines and CUR+ALF and HIGR+ALF, respectively, are denoted with dashed lines. In the decreased GR adoption frame, PRE96 is dotted and only present in year 3. LOWGR is denoted with dash-dot lines.
Figure 5-4: Visualization of *Conyza canadensis* spread in a landscape under various scenarios covering a spectrum of adoption of glyphosate-resistant crops (see text for further scenario definitions). The initial population was established centrally and was the same for each scenario to allow for visual comparison. Each scenario represents one possible outcome 5 years after the initial infestation.
Literature Cited


Epilogue

Research on seed dispersal continues to be split between small scale meteorological data and large scale patterns. We began by examining the role of emergence timing on fecundity, plant height, and time of seed set, which all affect long-distance seed dispersal. Then we conducted a series of experiments that coupled seed and release with meteorological conditions in the field to assess how small temporal scale turbulence can increase escape and transport of seed in the planetary boundary layer. Then, with a spatially explicit model, we explored factors influencing the change in distribution and abundance of glyphosate-resistant *Conyza*. Factors included frequency of cropping practices and the intensity of glyphosate use. In total, I have tried to connect the small scale environmental effects with the dispersal ability of the species.

One overarching goal was to compare the relative importance of mechanical and thermal turbulence in seed escape. Instead of finding one critical factor, it appears to be a synergy of the two forces that play the greatest role. Mechanical turbulence likely has a greater role in abscission of seed, but thermal turbulence can transport seeds upwards to atmospheric levels where long-distance transport is common. Both thermal and mechanical turbulence are also affected by day-to-day variation and synoptic weather patterns. Large-scale meteorological events are likely moving seed very long-distances, but predicting these events requires knowledge about weather forecasting. There is reason to believe, at least in the Mid-Atlantic States, that other seed transport mechanisms besides the prevailing wind is contributing to the spread of glyphosate-resistant *Conyza*. Westerly winds would have blown seed from Delaware (where
resistance was first documented) into the ocean, but, instead, genetically related resistant populations have been found in Maryland, Pennsylvania, and New Jersey (R.D. Sammons, personal communication). Time of seed dispersal does coincide with hurricane season, although the rain associated with hurricanes would suggest seed dispersal is limited. It is also possible that seed move via inter-field and inter-farm movement of farm equipment as G. Snyder, a custom herbicide applicator in Lehigh county, Pennsylvania would speculate. Instead of resistant populations speckled around a field as expected from wind-dispersed seed, there seems to be patches, often near the edges. Whether these patches are all resistant plants, herbicide application skips, or combine deposition sites needs to be explored.

Predicting where seed are traveling in a heterogeneous landscape is challenging and models usually use oversimplified assumptions. The dispersal model described in this thesis is purposefully simplified to look at specific questions relating to crop adoption. In particular, only local dispersal is considered in the model, while we know that seed can easily travel tens of kilometers. Incorporating long-distance dispersal of *C. canadensis* would have to be done within the framework of a weather driven deposition model. The trade-off for large scale movement is that the majority of seed remain near the source and therefore the plant dynamics on this level will drive local management. Ideally, the models could run jointly so that producers, policy makers, and researchers can better understand how local management affects larger community plant dynamics.

Agricultural stewardship considers the larger impact of local agricultural practices on living organisms “downstream” of a farming operation. For many years, this has not always been the case as farmers squeezed every possible bushel out of the land to make
ends meet, sometimes at the expense of environment. The hypoxic zone of the Gulf of Mexico, the severe contamination of the Chesapeake Bay and other disaster stories around the world showcase the impacts of agricultural use on downstream organisms. For many of these farmers, glyphosate-resistant crops are a solution to the problem; the same yield with cheaper, more environmentally-friendly herbicides and less work means greater profit. And it is hard to blame them when the corporations selling the crops and herbicides are touting its ‘silver bullet’ qualities. The Monsanto-directed website weedresistancemanagement.com has a 5-point plan to combat herbicide resistance and provide good land stewardship. Second on the list, behind start with a clean field, is to use Roundup-Ready (glyphosate-resistant) crops as the basis for the weed management program, followed by adding herbicide or mechanical control that coincides with the Roundup-Ready cropping system.

Ultimately it was clear that the selection pressure of glyphosate applied to millions of hectares would lead to glyphosate resistance. Initial resistant cases were spread apart and occurred in Australia and Asia in 1996 and 1997. However, development of glyphosate-resistance in horseweed in 2001 opened the floodgate. Not only was horseweed a broadleaf weed that could disperse seeds over long distances, but it could decrease soybean yield, providing an impetus to determine the mechanism of resistance, the rate of spread, and alternative management. Since 1996, the cumulative number of glyphosate-resistant species has continued to grow with 12 species currently reported glyphosate-resistant. An exponential curve fit the data very well ($y = 2 \times 10^{210} \times \exp(0.242 \times \text{year})$, $r^2 = 0.9556$) and predicted that more than 35 species will have acquired resistance to glyphosate by 2010. While high densities of glyphosate-resistant horseweed
are required to reduce yield, some of the weeds that may soon have documented resistance are more problematic. Populations of common lambsquarter (*Chenopodium album*), ragweed (*Ambrosia artemisiifolia*), giant ragweed (*Ambrosia trifida*), and Palmer amaranth (*Amaranthus palmerii*) have been shown to be resistant to glyphosate in the Eastern United States.

What is not well understood, and should be researched more fully, is the role of continued GR crop adoption, concomitant with increasing glyphosate use, on connecting farmsteads and assisting in the spread of glyphosate-resistant weeds. Adjacent farmsteads planted with the same crop and managed the same way are intimately connected by organisms that can move between them. Adopting the ‘silver bullet’ management scenario only acts to connect the entire landscape into a homogeneous area. The glyphosate-resistant weeds that will develop and spread in the homogeneous landscape will be controlled by different techniques, but ultimately the farmer pays doubly for the technology: first for the privilege of its use, then for the additional practices needed to address its shortcomings.

Instead, herbicide-resistant crops should be viewed as a tool in the weed management toolbox and should be employed with consideration of potential herbicide-resistance weed populations. Area-wide management faces challenges related to logistical complications in organizing farmers around a central idea. Implementing such an approach must be well supported by extension agents and regional leaders comfortable with alternative management scenarios to reduce spread. Practitioners must take the problem seriously in order to consider alternative management practices. Some do not see the agronomic challenges posed by glyphosate-resistant horseweed serious enough to
alter management. However, more problematic species almost certainly will alter this short-sighted view.

Integrated pest management can be challenging for farmers to accept, especially if farmers are told that weed diversity in their farmland is not only acceptable, but desired. As Steven Radosevich wrote in his novel, “Good Wood”, farmers fear “…too much diversity of plants and animals causes complications, complexity, and competition (p. 95).” But much of this fear may stem from a lack of understanding of the beneficial food webs that are supported in agro-ecological niches. Instead of constantly battling the weeds, maybe we can learn to accept weeds as an integral part of a functioning plant community.
Appendix A

Spatially Explicit Model Code

This appendix contains the code for the spatially explicit model used in Chapter 5 to explore the movement of GR C. canadensis seed across a landscape. The model was written for simulation using R, a statistical software package available for free download at http://www.r-project.org/. It is best to copy this code into a companion package TINN-R, also available for free download at http://www.sciviews.org/Tinn-R/. Note – line wrapping necessary to present the code herein may need to be corrected before implementing the code. The model is annotated to help decipher the processes. Annotations always begin with # which R interprets as a comment and not code.

The data files are available by contacting Dr. David Mortensen, The Pennsylvania State University at dmortensen@psu.edu.

The files are located in the weed ecology archive under the folder

personnel\dauer\thesis\appendices\appendixA\Density01.txt
personnel\dauer\thesis\appendices\appendixA\area.csv

#Read the data of points in each polygon
lanc=read.table("C:\Z-work\PhDwork\SimulationModel\Density01.txt",sep="",header=T)
#represents 1 point per 100 m2
#the area of each polygon
areatab=read.table("C:\Z-work\PhDwork\SimulationModel\area.csv",sep="",header=T)
#number of polygons in the landscape
polnum=360

# Dispersal function that yields seeds m\(^{-2}\) at any distance (x, meters) from source
TwoDT=function(x){  # only independent variable is distance, x, in meters
  p=0.2667; u=6.0e-3
  out=  p/(u*(1+x/u)^p+1)  # pi removed since this is 2-dimensional
  return(out)
}

# Matrix of the target polygon weighted probability of transport from any polygon (j) to
# any other polygon (i)
# number of connections between polygons
ptnum=20
phat=matrix(0,nrow=polnum,ncol=polnum)

# Calculating the phat matrix takes a very long time (hours)
count=1
for(i in 1:polnum){
  for(j in 1:polnum){
    first=subset(lanc, OBJECTID==j, select=c(OBJECTID,xcoord, ycoord))
    first$ID=seq(1:dim(first)[1])
    second=subset(lanc, OBJECTID==i, select=c(OBJECTID,xcoord, ycoord))
    second$ID=seq(1:dim(second)[1])
    secarea=areatab$Area[i]
    gset1=sample(first$ID,ptnum,replace=F)
    if (i==j) gset2=sample(second[-gset1,$ID],ptnum,replace=F) else
      gset2=sample(second$ID,ptnum,replace=F)
    tmp=rep(NA,ptnum)
    for(m in 1:ptnum){
      tmp[m]=(sqrt(outer(first$xcoord[gset1[m]], second$xcoord[gset2[m]],"-"))^2+outer(first$ycoord[gset1[m]], second$ycoord[gset2[m]],"-"^2)))
    phat[j,i]=mean(TwoDT(tmp)*secarea/ptnum/8.13466)
  # prob of transport*area of target/allocation of area to points/ integral of entire area
}
#(ratio or target area to total possible area)
count=count+1}}

#Assign crops and percent GR to each field
#requires percent of total fields in corn (co) and soybeans (so), and percent in GR
cropper=function(percentcorn,percentsoy,perGRcorn,perGRsoy,years){
crop=matrix(NA,nrow=polnum,ncol=years)
polys=seq(1:polnum)
percorn=percentcorn #percent of fields with corn
persoy=percentsoy  #percent of fields with soybeans
peralf=100-percorn-persoy
resample <- function(x, size) {  #need to account for times when no crop is present
  if(length(x) <= 1) { if(!missing(size) && size == 0) x[FALSE] else x
  } else sample(x, size, replace=FALSE)}
#randomly assign crops to fields
if (percorn==0) noircorn=0 else noircorn=resample(polys,round(percorn/100*polnum))
if (sum(noircorn)==0) soysub=polys else soysub=polys[-(noircorn)]
if (persoy==0) noirsoy=0 else noirsoy=resample(soysub,round(persoy/100*polnum))
if (sum(noirsoy)==0) noiralf=soysub else noiralf=polys[-c(noircorn,noirsoy)]
crop[noiralf,1]=3 #turns these to alfalfa
crop[noirsoy,1]=2 #set random fields to soybeans
crop[noircorn,1]=1 #corn goes in last
crop[noircorn,c(3,5)]=2; crop[noircorn,c(2,4)]=1
crop[noirsoy,c(3,5)]=1; crop[noirsoy,c(2,4)]=2
#change some fields to glyphosate-resistant corn (4) and soybean (5)
GRcorn=resample(noircorn,round(perGRcorn/100*length(noircorn)))
GRsoy=resample(noirsoy,round(perGRsoy/100*length(noirsoy)))
crop[GRcorn,1]=4; crop[GRsoy,1]=5
for (j in 2:5){
  GRcorn35=resample(noircorn,round(perGRcorn/100*length(noircorn)))
}
GRsoy35 = resample(noirsoy, round(perGRsoy/100*length(noirsoy)))
GRsoy24 = resample(noircorn, round(perGRsoy/100*length(noircorn)))
GRcorn24 = resample(noirsoy, round(perGRcorn/100*length(noirsoy)))

# changes a few fields to Glyph-Resistant
if (j==2) {
crop[GRsoy24,j] = 5; crop[GRcorn24,j] = 4
}
if (j==3) {
crop[GRcorn35,j] = 4; crop[GRsoy35,j] = 5
}
if (j==4) {
crop[GRsoy24,j] = 5; crop[GRcorn24,j] = 4
}
if (j==5) {
crop[GRcorn35,j] = 4; crop[GRsoy35,j] = 5
}

# changing to get an alfalfa-corn system
secalf = resample(noiralf, round(1/3*length(noiralf)))  # sample 1/3 from all the alfalfa fields
subsecalf = polys[-c(noirsoy, noircorn, secalf)]
thirdalf = resample(subsecalf, round(1/3*length(noiralf)))  # sample 1/3 of remaining fields
crop[noiralf,c(2,3)] = 3  # these fields start in first year alfalfa so go AAACC
crop[noiralf,c(4,5)] = 1

crop[secalf,c(2,5)] = 3  # these fields start in 2nd year alfalfa so go AACCA

crop[secalf,c(3,4)] = 1

crop[thirdalf,c(4,5)] = 3  # these fields start in 3rd year alfalfa so go ACCAA

crop[thirdalf,c(2,3)] = 1

return(crop)}  # ends the cropper function

########################################################################
# this function orders the fields according to the cropper function
# assigns fields survivorship and fecundity given values
# then keeps track of the number of plants in each field for the specified iterations

synthesizer = function(years, iterations, percentcorn, percentsoy, perGRcorn, perGRsoy, lamcorn, lamGRco, lamsoy, lamGRsoy) {
  year1 = year2 = year3 = year4 = year5 = matrix(0, nrow=360, ncol=iterations)
  year1bin = year2bin = year3bin = year4bin = year5bin = matrix(0, nrow=360, ncol=iterations)
  polyholder = matrix(NA, nrow=360, ncol=iterations)
  maxdist = rep(NA, iterations)
  year3total = rep(NA, iterations)
year5total=rep(NA,iterations)
meanyr1=meanyr2=meanyr3=meanyr4=meanyr5=rep(NA,360)
initialfield=rep(NA,iterations) #hold the initial field for each iteration
for (k in 1:iterations){
  #call the cropper function to determine the arrangement of crops for the iteration
crop=do.call(cropper,list(percentcorn=percentcorn,percentsoy=percentsoy,perGRcorn=perGRcorn,perGRsoy=perGRsoy,years=years))
cfec=74700 #from Regehr and Bazzaz J. Ecol 1979
sfec=130000 #soybean fecundity from Dauer et al. Weed Science 2006
alfec=0 # corroborated by Marvin Hall (Forage Specialist at PSU)
csurv=lamcorn/cfec
cGRsurv=lamGRco/cfec
ssurv=lamsoy/sfec
sGRsurv=lamGRsoy/sfec
asurv=0 #al/alfec zero unless we change the fecundity in alfalfa
cropfec=cropsurv=crop #making copies, but will change the cropfec and cropsurv
cropfec[cropfec[,]==1]=cfec #replace corn with corn fecundity
cropfec[cropfec[,]==4]=cfec #corn fecundity is same in GR corn
cropfec[cropfec[,]==2]=sfec #replace soybean with soybean fecundity
cropfec[cropfec[,]==5]=sfec #soybean fecundity is same in GR soy
cropfec[cropfec[,]==3]=0 #set to zero since fecundity in alfalfa is 0
cropsurv[cropsurv[,]==1]=csurv #replace corn with corn survivorship
cropsurv[cropsurv[,]==4]=cGRsurv #GR corn survivorship is different
cropsurv[cropsurv[,]==2]=ssurv #replace soy with soy survivorship
cropsurv[cropsurv[,]==5]=sGRsurv #GR soy survivorship is different
cropsurv[cropsurv[,]==3]=asurv #alfalfa survivorship (zero)
#the matrix mutliplier - this is where the meat hits the grinder
potentfields=c(seq(40,46),seq(52,69),seq(75,83),96,seq(133,138))
#limiting initial field to central fields
#guarantees that initial field is GR soybean unless no GR soy, then selects soybean field
if (perGRsoy==0) subpotent=subset(potentfields, crop[potentfields,1]==2) else
subpotent=subset(potentfields,crop[potentfields,1]==5)
if (length(subpotent)==0)initfield=sample(potentfields,1) else
initfield=sample(subpotent,1)
gmac=matrix(0,nrow=polnum,ncol=years)
gmac[initfield,1]=5  #number of plants to begin infestation
year1[,k]=gmac[,1] #dumps this into the year1 matrix
year1bin[initfield,k]=1 #starts binom matrix
polyholder[,k]= meandist[initfield,] #distance from initial field to all fields (meters)
tmp2=rep(0,polnum) #number of seed being dumped into each receiver field
tmp3=rep(0,polnum) #holds whether field infested or not
initialfield[k]=initfield #record the initial field

for(j in 2:years){
  seed=diag(cropfec[,,(j-1)])%*%gmac[,,(j-1)] #call the fecundity matrix
  distrib=phat%*%seed #keeping the decimal of seeds
  tempsurv= diag(cropsurv[,j])%*%distrib #call surv matrix to determine number surviving
  for(i in 1:polnum){
    if (runif(1,0,1)<(tempsurv[i]-trunc(tempsurv[i]))) tmp2[i]=ceiling(tempsurv[i]) else
    tmp2[i]=floor(tempsurv[i])  #demographic stochasticity effects
    if (tmp2[i]>0) tmp3[i]=1 else tmp3[i]=0   }
  gmac[,j]= tmp2#plants that survive
  #dumps the infestation (1 or 0) into year2bin and dumps plant number into year2
  if (j==2) {year2[,k]=tmp2; year2bin[,k]=tmp3}
  if (j==3) {year3[,k]=tmp2; year3bin[,k]=tmp3}
  if (j==4) {year4[,k]=tmp2; year4bin[,k]=tmp3}
  if (j==5) {year5[,k]=tmp2; year5bin[,k]=tmp3}}  #ends the years index
if (sum(tmp2)==0) maxdist[k]= 0 else maxdist[k]=max(polyholder[(tmp3==1),k])
year3total[k]=sum(year3bin[,k]) #number of polygons infested in year 3
year5total[k]=sum(year5bin[,k]) #number of polygons infested in year 5
#ends the iteration

tmplist=list(poly=polyholder,maxdist=maxdist,year3tot=year3total,year5tot=year5total,one=year1,two=year2,three=year3,four=year4,five=year5,lone=year1bin,ltwo=year2bin,lthree=year3bin,lfour=year4bin,lfive=year5bin)
return(tmplist)} #ends the function

########################################################################
#Simulation starts here

#change the percent corn, soybeans and percent that is GR according to scenarios
years=5;iterations=100
lamcorn=0.418;lamGRco=8.2;lamsoy=0.728;lamGRsoy=36.4 #call the lambda values
percentcorn=40;percentsoy=40 #call the percent of corn and soybean in the environment
perGRcorn=42;perGRsoy=89 #percent of the corn and soybean fields planted with GR
yeehaw=synthesizer(years,iterations,percentcorn,percentsoy,perGRcorn,perGRsoy,lamcorn,lamGRco,lamsoy,lamGRsoy)

########################################################################
#how does proportion of fields change in time

#yr1per=as.vector(yeehaw$lone)
#yr2per=as.vector(yeehaw$ltwo)
#yr3per=as.vector(yeehaw$lthree)
#yr4per=as.vector(yeehaw$lfour)
#yr5per=as.vector(yeehaw$lfive)
#connect years (1-5) with whether field was infested, only 1 of these
distances=as.vector(yeehaw$poly[,])
#connect the distances with whether that field was infested, for each year
#perinfest=cbind(rep(c(1,2,3,4,5),each=length(yr1per)),c(yr1per,yr2per,yr3per,yr4per,yr5per))

########################################################################
#Assess the likelihood function for time and distance
# percentinfest = glm(perinfest[,2] ~ perinfest[,1], family = binomial())

distanceinfest5 = glm(distinfest5[,2] ~ distinfest5[,1], family = binomial())

# depending on the scenario you select above, select (delete the #) the correct line

# Pre96per = percentinfest$coef; Pre96d3 = distanceinfest3$coef;
# Pre96d5 = distanceinfest5$coef
# CURper = percentinfest$coef; CURd3 = distanceinfest3$coef;
# CURd5 = distanceinfest5$coef
# CURALFper = percentinfest$coef; CURALFd3 = distanceinfest3$coef;
# CURALFd5 = distanceinfest5$coef
# HIGRper = percentinfest$coef; HIGRd3 = distanceinfest3$coef;
# HIGRd5 = distanceinfest5$coef
# GRALFper = percentinfest$coef; GRALFd3 = distanceinfest3$coef;
# GRALFd5 = distanceinfest5$coef
# LOWGRper = percentinfest$coef; LOWGRd3 = distanceinfest3$coef;
# LOWGRd5 = distanceinfest5$coef
Appendix B

Biweekly Plant Height Data

In addition to measuring the final plant height, fecundity and time of seed set reported in Chapter 2, rosette width (when present) and plant height were recorded every two weeks. The sites were those described in Chapter 2. Early fall, late fall and early spring emerging plants generally formed a rosette before bolting. Width was measured from tip of a leaf, directly across the center to the tip of a leaf directly opposite. Plant height was measured from ground level to the topmost leaf tip.

In the data set, **plant heights** were placed in bold font to delineate those measurements from rosette widths. Zero values represent no plant present or plant death. For instance, early spring emerging plants did not exist during all measurement dates preceding May 1\textsuperscript{st} and zero was recorded for their width. If plant widths or heights were recorded and then the plant died, a zero was recorded for all dates after death. Missing data were denoted with Not Available (NA).

The data file is available by contacting Dr. David Mortensen, The Pennsylvania State University at dmortensen@psu.edu.

The file is located in the weed ecology archive under the folder personnel\dauer\thesis\appendices\appendixB\compiled.xls.

**Column Headings**

State – de=Delaware, pa=Pennsylvania  
loc – field name, abbreviated  
ID – combination of field name and location (loc). See chapter 2 for explanation
Lat – Latitude in hours, minutes seconds (HHMMSS)
trt – treatment number, 1=Early Fall, 2=Late Fall, 3=Early Spring, 4=Late Spring
rep – replication number, 1 – 4
plant – 1 – 10, although some treatment/replicates had fewer than 10 plants. In Chapter
   2, averages were taken for the response variables over the number of plants in the
   replicate.
N15 – 01 – sampling month and day. For example, November 15th, December 1st, values
   are the rosette width or plant height (cm) with plant height in bold.
FirstFlower – nearest sampling date (julian) of first seed set (not date of first flower).
   Julian dates are cover two years
Stems – Upon destructive harvest for fecundity estimation, the number of stalks
   containing flowers
capitula – number of capitula (flower heads) produced by the plant
Appendix C

Seed Collection at 3 points Downwind of a C. canadensis Point Source

The data described herein describes an unrepeated experiment to determine the vertical flight path of horseweed seeds as they move downwind from a point source. This work was conducted in connection with experiments described in Chapter 3. In addition to the vertical sampling device described in Chapter 3, two additional vertical sampling devices were located at 50 m and 100 m from the edge of the source population at 12º ENE from the source population (the presumed downwind direction during September). Vertical sampling towers were identical to those described in Chapter 3 – 7.6 m reinforced PVC towers which supported up to four 0.5 m² sampling screens at 2 – 6 m above the ground level.

Because of the low number of expected seeds at 100 m from the source, sampling was conducted for 24 hours instead of 2 hour intervals described in Chapter 3. Screens were raised at 8:00 and remained for 24 hours. Also to counter the dilution of seeds, a different number of screens (sampling area) were used at each distance from the source. On the farthest tower (100 m from the source), 4 screens (2 m²) were placed at the 5 heights and stretched the full width of the towers. Two screens were used on the 50 m towers and were positioned in the center of the orifice. A single screen was used at the 10 m distance and was positioned on the sides of the orifice, alternating sides. The thinking was that we would remove as few seeds as possible at the first two distances (10 m and 50 m) but still have enough data to interpret the pattern.
Weather data were available from two sources. The first two sampling dates (September 20 and 25th), data were taken from the weather station data collected at the Russel E Larson Agricultural farm. September 26th, lightning struck the meteorological tower and damaged the equipment and no data is available for this day. The 3-D weather station described in chapters 3 and 4 was available for the last two sampling dates (October 3rd and 6th). Units for weather conditions varied and are recorded in column headings within the weather data files. The weather file has four separate tabs, one for each day.

The data files are available by contacting Dr. David Mortensen, The Pennsylvania State University at dmortensen@psu.edu.

The files are located in the weed ecology archive under the folder personnel\dauer\thesis\appendices\appendixC\3_ddata.xls and personnel\dauer\thesis\appendices\appendixC\weather.xls

**Column Headings (Seed data)**

Day – date of sampling. Sampling started at 8:00 on the day recorded and continued to 8:00 on the next day

Tower – numbering the towers from closest to farthest (1 – 3)

Distance – distance (m) from downwind edge of the source

Height – height (m) above the ground level for the middle of the screen

Screens – the number of screens (dependent on distance)

sc1-sc4 – seeds per screen (number of columns used is dependent on screens)

totseeds – sum of sc1-sc4

seeds/m2 – totseeds divided by product of screens and 0.5 m²
Column Headings (weather data)

September 20th and 25th

Time – Eastern standard time, data were monitored every minute

Temp – Air temperature (Fahrenheit)

Dew Pt – Dew Point (Fahrenheit)

Rel Hum – Relative humidity (percent)

Wind Spd – Wind speed (miles per hour)

Wind Direction – Direction from which the wind was coming (0 = North)

In Hg – Pressure (Inches mercury)

Accum Rainfall – total accumulated rainfall from 00:01 to 23:59 (millimeters)

October 3rd and 6th

Time – Eastern Standard time, data monitored every 5 minutes

Bar.Pressure – Pressure (bar)

Temperature – Air Temperature (Celsius)

RH – relative humidity (percent)

Wind Dir – Direction from which the wind was coming (0 = North)

Wind Gust – highest recorded gust during previous 5 minutes

Wind Speed – wind speed (kilometers per hour)

Rainfall – rainfall in previous five minutes (millimeters)
VITA

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