

Do Common Waterhemp (*Amaranthus rudis*) Seedling Emergence Patterns Meet Criteria for Herbicide Resistance Simulation Modeling?

Brian J. Schutte and Adam S. Davis*

A study was conducted to quantify the magnitude and sources of variation in common waterhemp temporal patterns of emergence over 1 yr. In 2008 and 2010, emergence patterns in the absence of soil disturbance were determined for replicated samples of maternal families (progeny from one individual) separately harvested during the previous year from four plants within each of four agricultural fields (16 maternal families yr^{-1}) at a university research farm near Urbana, IL. Combining data across years, variance partitioning indicated that seed sample within maternal family explained 48% of total variation in the percentage of viable, buried seeds that produced seedlings. Differences within, rather than among, maternal families also accounted for large fractions (60 to 99%) of total variation in cumulative percentage emergence at specific points during the growing season. Within years, seed samples characterized by delayed or accelerated emergence patterns did not originate from specific maternal plants. These results indicate that common waterhemp seed populations are without strong maternal plant effects that limit emergence to narrow intervals within the overall emergence period. Thus, results of this study support the use of contemporary approaches for modeling herbicide resistance evolution in common waterhemp, which assume seedling cohorts contain offspring from all individuals occurring within the maternal population.

Nomenclature: Common waterhemp, *Amaranthus rudis* Sauer AMATA.

Key words: Emergence modeling, maternal effects, seed germination, seedbank persistence, variance partitioning.

Se realizó un estudio para cuantificar la magnitud y las fuentes de variación en los patrones temporales de emergencia de *Amaranthus rudis* durante un año. En 2008 y 2010, se determinaron los patrones de emergencia en ausencia de perturbación del suelo de muestras replicadas de familias maternas (progenie de un individuo) cosechadas separadamente durante el año previo a partir de cuatro plantas por campo, provenientes de cuatro campos agrícolas (16 familias maternas por año), en una finca experimental universitaria cerca de Urbana, Illinois. Combinando los años, la partición de la varianza indicó que la muestra de semilla dentro de la familia materna explicó el 48% del total de la variación del porcentaje de semilla viable que produjo plántulas. Diferencias dentro y no entre familias maternas también fue responsable de gran parte (60 a 99%) del total de la variación en el porcentaje de emergencia acumulado en momentos específicos durante la temporada de crecimiento. Dentro de los años, muestras de semillas caracterizadas por mostrar patrones de emergencia retrasados o acelerados no se originaron a partir de plantas maternas específicas. Estos resultados indican que las poblaciones de semillas de *A. rudis* no tienen fuertes efectos maternos que limiten la emergencia a intervalos cortos dentro del periodo de emergencia general. De esta forma, los resultados de este estudio apoyan el uso de métodos contemporáneos para el modelaje de la evolución de resistencia a herbicidas en *A. rudis*, los cuales asumen que los cohortes de plántulas contienen progenie proveniente de todos los individuos que están presentes dentro de la población materna.

Conventional chemical weed control strategies for corn and soybean production in the midwestern United States are threatened by the continuing evolution of herbicide resistance in common water-

hemp. Common waterhemp is a dioecious, summer annual weed capable of rapid growth (Horak and Loughin 2000), high seed production (Bensch et al. 2003) and prolonged periods of seedling emergence that compel multiple management interventions during a single growing season (Refsell and Hartzler 2009). To date, common waterhemp populations in the midwestern United States have evolved resistance to acetolactate synthase (ALS) inhibitors (Horak and Peterson 1995), photosystem II inhibitors (Anderson et al. 1996), protoporphyrinogen oxidase (PPO) inhibitors (Shoup et al. 2003),

DOI: 10.1614/WT-D-13-00139.1

* First and second authors: Postdoctoral Research Ecologist, and Research Ecologist, United States Department of Agriculture-Agricultural Research Service, Global Change and Photosynthesis Research Unit, 1102 S. Goodwin Avenue, Urbana, IL 61801. Current address of first author: Department of Entomology, Plant Pathology and Weed Science; New Mexico State University, Las Cruces, NM 88003. Corresponding author's E-mail: bschutte@nmsu.edu

glycines (Legleiter and Bradley 2008), 4-hydroxyphenylpyruvate dioxygenase (HPPD)-inhibitors (Hausman et al. 2011; McMullan and Green 2011) and synthetic auxins (Bernards et al. 2012). Of particular concern are common waterhemp populations resistant to multiple herbicides with different sites of action (Bell et al. 2013; Tranel et al. 2011). These populations undermine resistance management recommendations that call for novel sites of action to replace or supplement the ineffective herbicide. In broader terms, common waterhemp populations resistant to multiple herbicides expose the limitations of chemical-only approaches to weed management, exemplify the abilities of weed populations to evolve in response to selection pressures from anthropogenic forces, and hasten the need for multi-tactic, evolution-enlightened weed management strategies.

Evolutionary responses of weed populations to management interventions are understood through field trials (Collavo et al. 2013; Legleiter and Bradley 2009) and simulation studies (Maxwell et al. 1990; Neve 2008) that measure and project, respectively, demographic and genetic changes in weed populations over time. Compared to field trials that can be prolonged and prohibitively expensive, simulation studies provide rapid, low-cost assessments of evolution in weed populations exposed to various management scenarios, including management strategies designed to mitigate and prevent resistance evolution (Neve et al. 2003, 2011). In addition, simulation studies facilitate clarification of the biological, ecological, and management factors that increase propensity for resistance evolution (Jasieniuk et al. 1996; Manalil et al. 2012; Maxwell et al. 1990). Although simulation studies can improve management and understanding of herbicide resistance in weed populations, simulation studies focused on resistance evolution have yet to be conducted for common waterhemp.

Simulations of resistance evolution require quantified knowledge of demographic rates and life-stage transitions of weed populations within specific cropping systems. Critical prerequisites for simulation studies include information on temporal patterns of emergence represented by changes in cumulative percentage emergence over time. These data are used to establish weed cohorts differentiated by emergence timings (Neve 2008; Thornby

and Walker 2009). Generally, each cohort is assumed to contain offspring from all plants occurring within the population of maternal plants. Such an assumption results in the occurrence of herbicide-resistant plants in each simulated emergence cohort (Bagavathiannan et al. 2013; Neve 2008; Thornby and Walker 2009) and is consistent with theoretical models that indicate selection in unpredictable environments favors phenotypes that diversify offspring emergence timing, an emergence strategy suggestive of bet-hedging (Childs et al. 2010; Simons 2011). Few studies have examined emergence periods of progeny collected from individual weeds, but, for exceptions see Mercer et al. (2011) and Schutte et al. (2008).

Plant populations in early successional environments can consist of phenotypes that differ in offspring emergence period (Mercer et al. 2011; Schutte et al. 2008). If progeny from specific individuals (i.e., maternal families) emerge in narrow intervals within the overall emergence period, a key assumption that underpins simulations of herbicide resistance evolution may be violated. To test for strong maternal effects in common waterhemp emergence period, we conducted a study to quantify the magnitude and sources of variation in common waterhemp temporal patterns of emergence represented by changes in cumulative percentage emergence over time. With respect to this objective, we hypothesized that (1) differences among seed samples from individual plants explain a greater percentage of variance in temporal patterns of emergence than differences among maternal plants and maternal fields, and (2) diversified emergence within, rather than among, maternal families is responsible for extreme emergence behaviors indicated by exceptionally high or low values in cumulative percentage emergence at specific points in time. Confirmation of these hypotheses will support use of contemporary modeling approaches for simulation of herbicide resistance evolution in common waterhemp.

Materials and Methods

Temporal patterns of seedling emergence over 1 yr (November 3, 2007 to October 12, 2008 and November 1, 2009 to October 14, 2010) were studied at the University of Illinois, Crop Sciences Research and Education Center (CSREC; 40.05°N,

88.23°W), which is a 400-ha research farm that produces corn and soybean using weed control and soil management practices typical for the region (Nafziger 2009). Common waterhemp plants that escaped control in corn and soybean fields at CSREC provided the seed populations that were used to quantify sources of variation in parameters pertaining to emergence timing. Seeds were separately harvested from four plants within each of four fields, producing a total of 16 maternal families year⁻¹. Fields from which seeds were collected were randomly selected from the annual population of CSREC corn and soybean fields that contained common waterhemp plants visible from field edges at latter reproductive stages of crop development. Seed collection fields were spaced at least 0.7 km, but not more than 3.5 km apart. Within fields, one plant bearing mature seeds was selected from each of the four corner regions. Previous research determined that common waterhemp pollen deposition declines rapidly and exponentially within 50 m of pollen sources (Liu et al. 2012), and thus, pollen transfer was likely minimal between seed collection fields. However, close genetic associations among the collected maternal families may be expected because fields were likely managed with the same equipment, which can assist in the spread of weed seeds across fields.

Inflorescences from selected plants were harvested by hand and were brought to the laboratory for drying in the absence of direct sunlight for 14 to 20 d. Dried inflorescences were hand-threshed and sequential combinations of sieving and forced-air separation were used to separate seeds from chaff. Standardized seed cleaning procedures were optimized for the removal of seeds that did not contain mature embryos, thereby increasing likelihood of emergence in the subsequent growing season. Collected seeds were those that: (1) were retained on a 425- μ m sieve cloth meeting ASTM E-11 standard specifications, and (2) descended to the lowest chamber of an air-column separator (757 South Dakota Seed Blower, Seedburro Equipment Company, 2293 S. Mt. Prospect Rd., Des Plaines, IL 60018) following two, 3-min aspiration sessions. After forced-air separation, 100-seed weight averaged $0.028 \pm \text{SE } 0.002$ g across seed samples and was not influenced by maternal plant within field within year ($F_{24,96} = 1.59$, $P = 0.06$). Seeds were stored for no longer than one month in plastic,

airtight containers at 5 C. Just prior to burial, initial viability for each maternal family was determined by tetrazolium staining assay with 1.0% (v/v) aqueous solution of 2,3,5-triphenyl-tetrazolium chloride (Peters 2000). Seed viability before burial was determined to be high ($> 97\%$) in all maternal families.

Experimental units were maternal family seed samples (100 seeds sample⁻¹) buried 1 cm, a depth that was previously determined to be within the range conducive to common waterhemp seedling emergence (Refsell and Hartzler 2009). Seed samples were buried in baskets (5-cm width, 5-cm length, 3-cm depth) fabricated from aluminum mesh (0.5 mm square opening) and incorporated into the soil at CSREC so that basket tops formed a lip 1 cm above the soil surface. Baskets were filled with soil (Flanagan silt loam [fine, smectitic, mesic, Aquic Argiudoll]) collected from a sward that was not cultivated for at least 15 yr. Mechanical elutriation (Wiles et al. 1996) of soil used to fill baskets indicated that the soil did not contain a background population of common waterhemp seeds. The study was designed as a randomized complete block with four replicates set in a row. Adjacent replicates were spaced 1 m apart. Individual replicates comprised 16 baskets contiguously arranged in a four-by-four grid. Soil surfaces between replicates were covered with wood chip mulch; however, the layer of wood chip mulch did not contact experimental units. Throughout the study, the study area was protected from surface-foraging seed predators by a mesh fence (6.4 mm square openings) and was kept free of unwanted vegetation with combinations of hand weeding and herbicide applications (glyphosate at 0.9 kg ai ha⁻¹).

At weekly intervals beginning March 1, emerged seedlings were counted and removed without soil disturbance by uprooting entire seedlings with forceps. Approximately one year after burial, baskets were excavated and ungerminated seeds were recovered with mechanical elutriation. Recovered seeds were tested for viability with tetrazolium staining assays described above.

Data Analyses. Seed recovery data were used to calculate the following fates for seed populations: emergence (percentage of viable seeds added at the start of the experiment that produced a seedling), persistence (percentage of viable seeds added at the start of the experiment that were recovered after 1

yr), mortality (percentage of viable seeds added at the start of the experiment that did not emerge or persist). Emergence periods were evaluated by determining the days of first and final emergence in both day-of-year (DOY) and growing degree day (GDD), which is described below. Measurements of emergence period also included duration of emergence, which was determined by calculating the GDD difference between first and final day of emergence. To evaluate temporal patterns of emergence, seedling emergence data were converted to cumulative percentage emergence and plotted as a function of GDD. Cumulative percentages emergence at specific GDD (100, 300, 600, 900, 1,200 GDD) were determined with linear least-squares regression models fitted to data for GDDs immediately before and after the specific GDD of interest.

GDD was calculated using daily mean soil temperatures at the 1-cm depth, which were simulated by the Soil Temperature and Moisture Model (Spokas and Forcella 2009) using air temperature data obtained from the CSREC weather station that was 4.1 km from the study site. The base temperature for GDD calculations was 10 C, which was previously identified as the minimum temperature for germination for common waterhemp (Leon et al. 2004). For analyses on emergence periods, GDD accumulated from March 1. Typically, common waterhemp emergence begins late April to early May in the study region. For analyses on temporal patterns of emergence, GDD accumulated from the day of first emergence for a given year. Different initiation points for GDD accumulation between emergence period variables and emergence pattern variables allowed for clarification of thermal influences on inter-annual variability in both day of first emergence and emergence progressions.

Variances in individual response variables related to seedbank fate, emergence period, and emergence pattern were partitioned into components of year, maternal field within year, maternal plant within field, and seed sample within maternal plant using the *nlme* library of the statistical software program R (v.3.0.1, The R Foundation for Statistical Computing, <http://www.r-project.org>). Specifically, *nlme* was used to produce restricted maximum likelihood, linear mixed-effects models for responses of variables to the hierarchical structures of seed sampling,

year(field(plant)), which were specified as random effects. Fixed effects were terms for model intercepts. Following methods of Crawley (2007), estimates for random effects were used to determine the percentages of total variation explained by the components specified above.

Within years, maternal influences on emergence patterns were determined by examining maternal family diversity in the population of experimental units characterized by extreme values in cumulative percentage emergence at 100, 300, 600, 900, and 1,200 GDD after first emergence. Extreme values in cumulative percentage emergence were those that were less than the 10th percentile, or greater than the 90th percentile of the data for a specific GDD. Cumulative percentage emergence values greater than the 90th percentile were considered indicative of accelerated emergence, whereas values for cumulative percentage emergence less than the 10th percentile were considered indicative of delayed emergence. For experimental units that were repeatedly detected as extreme, only data for the first GDD in which they were observed were included in the analysis. For each emergence extreme type (delayed and accelerated), the number of experimental units (hereafter referred to as “ ε_{eu} ”) and the number of maternal families (hereafter referred to as “ ε_{mf} ”) were compared using a paired *t* test for the one-tailed hypothesis $\varepsilon_{eu} - \varepsilon_{mf} > 0$. Rejection of the null hypothesis ($\alpha = 0.05$) indicated that the populations of experimental units with extreme values for cumulative percentage emergence comprised fewer maternal families than would have been expected based on random distributions of maternal families across the range of values for cumulative percentage emergence.

Results and Discussion

Annual rates of seedling emergence averaged 23.5 \pm SD 16.6% (Table 1) and ranged from 0 to 65% across experimental units. Variability in seedling emergence among experimental units largely reflected differences among seed samples within maternal plants, which comprised approximately 48% of the total variation in seedling emergence (Table 2). Approximately 14% of total variation in seedling emergence was explained by differences among maternal families. The variance component “year”, which included annual differences in both

Table 1. Summary statistics for measurements of seedbank fate, emergence period, and temporal patterns of emergence over 1 yr for 128 common waterhemp seedbanks near Urbana, IL during 2008 and 2010. The population of seedbanks comprised replicated samples of maternal families that matured in different fields in 2007 and 2009.

	Units ^a	Mean	SD	Percentile				
				10 th	25 th	50 th	75 th	90 th
Seedbank fate								
Persistence	%	44.0	24.3	11.4	23.0	43.1	65.0	76.3
Emergence	%	23.5	16.6	4.1	8.2	21.0	36.1	46.0
Mortality	%	32.5	21.5	4.4	16.0	30.1	45.4	65.0
Emergence period								
First emergence	DOY	136	26	106	106	137	164	164
First emergence	GDD ^b	363.3	216.5	174.8	174.8	338.7	559.6	559.6
Last emergence	DOY	179	16	164	172	177	189	205
Last emergence	GDD	926.9	278.5	559.6	676.1	1011.5	1186.9	1209.3
Duration	GDD	562.7	379.2	12.8	221.9	631.6	837.7	1035.5
Emergence pattern ^c								
Emergence at 100 GDD ^d	%	10.9	17.0	0	0	3.1	15.0	31.4
Emergence at 300 GDD	%	18.5	23.6	0	0	9.5	30.0	48.7
Emergence at 600 GDD	%	73.7	28.9	29.1	49.0	85.7	100.0	100.0
Emergence at 900 GDD	%	96.6	13.4	95.1	100.0	100.0	100.0	100.0
Emergence at 1,200 GDD	%	98.8	9.1	100.0	100.0	100.0	100.0	100.0

^a Abbreviations: DOY, day of year; GDD, growing degree day calculated using base temperature of 10 C.

^b GDD for measurements of emergence period accumulated from DOY 61 (March 1).

^c Measurements of emergence pattern were cumulative percentage emergence at specific GDD.

^d GDD for measurements of emergence pattern accumulated from the day of first emergence for a given year.

burial environment and seed populations, accounted for nearly 33% of total variation in seedling emergence. Rates of seedling emergence were inversely related to rates of seedbank persistence (-0.49 , $P < 0.001$), which averaged $44.0 \pm$ SD 24.3% and ranged from 0 to 89% across experimental units. Variability among experimental units in seedbank persistence was mostly caused by differences among maternal plants within fields, which accounted for 56% of the total variation in seedbank persistence. Annual rates of mortality, which included losses by seed death and fatal germination, averaged $32.5 \pm$ SD 21.5% and ranged from 0 to 92%. Variability in mortality among experimental units primarily reflected differences among seed samples within maternal plants. Seed sample effects on mortality and emergence, coupled with strong maternal plant effects on seedbank persistence suggest that germination was largely influenced by maternal plant but the probability of emergence following germination was mostly determined by burial microenvironments of seed samples.

The overall mean for seedling emergence percentage was three to four times greater than seedling emergence percentages previously reported for common waterhemp populations after one year of burial (Buhler and Hartzler 2001; Refsell and Hartzler 2009). Differences in seedling emergence rates between this and previous studies reflected, at least in part, dissimilarities in procedures for seed burial. Burial procedures in previous studies included soil mixing to at least the 5-cm depth (Buhler and Hartzler 2001), which was likely to have placed some seeds at depths not conducive to emergence (Refsell and Hartzler 2009). By placing seeds at a specific depth favorable for emergence, our burial procedure promoted seedling emergence compared to burial procedures of previous studies. Thus, emergence data reported in this study are representative of seedling emergence potential in agricultural systems characterized by shallow tillage and minimum amounts of crop residue on soil surfaces. Despite the conditions that favored seedling emergence, mortality was prominent in this study (Table 1).

Table 2. Partitioning of variance according to spatial-temporal structure of maturation and burial environment factors hypothesized to influence seedbank and emergence dynamics of common waterhemp.

Response variable	Variance component			
	Year	Maternal field within year	Maternal plant within field	Seed sample within maternal plant
	% of total variance explained			
Seedbank fate				
Persistence	< 0.1	12.1	56.1	31.8
Emergence	32.8	6.0	13.5	47.7
Mortality	6.2	2.3	33.9	57.7
Emergence period				
First emergence (DOY) ^a	67.8	6.8	2.6	22.8
First emergence (GDD)	22.9	16.0	1.3	59.8
Final emergence (DOY)	< 0.1	< 0.1	5.1	94.9
Final emergence (GDD)	36.5	< 0.1	3.6	59.9
Emergence duration (GDD)	49.7	6.2	4.5	39.6
Emergence pattern ^b				
Emergence at 100 GDD	26.0	< 0.1	13.7	60.3
Emergence at 300 GDD	12.4	2.8	9.9	74.9
Emergence at 600 GDD	59.2	3.6	< 0.1	37.2
Emergence at 900 GDD	2.2	< 0.1	8.9	88.9
Emergence at 1,200 GDD	0.9	< 0.1	< 0.1	99.1

^a Abbreviations: DOY, day of year; GDD, growing degree day calculated using base temperature of 10 C.

^b Measurements of emergence pattern were cumulative percentage emergence at specific GDD.

Similar to common waterhemp seedling emergence periods reported in previous studies conducted in the midwestern United States (Hartzler et al. 1999; Refsell and Hartzler 2009), common waterhemp seedling emergence initiated in spring and continued to mid-summer (Table 1). In 2009, seedling emergence across all experimental units began on May 9 (DOY 130) and concluded on August 7 (DOY 220). In 2011, seedling emergence began on April 15 (DOY 106) and concluded on July 27 (DOY 209). Inter-annual differences in DOY of first emergence were partly explained by variability in early season accumulation of GDD, as indicated by the percentage of total variation explained by year for GDD of first emergence (Table 2). Year explained substantial percentages (> 36%) of total variation in both duration of emergence and GDD of final emergence; however, year explained less than 1% of total variation in DOY of final emergence. Together, these results indicate that annual emergence periods were influenced by both accumulation of GDD and temperature-independent controls on seedling emergence (e.g., soil moisture) that were irregular

with respect to GDD, but consistent with respect to DOY, between years.

Nearly forty percent of total variation in duration of emergence was explained by seed samples within maternal plant. Seed samples within maternal plant also accounted for a majority of the total variation in cumulative percentage emergence at specific GDD, with the exception of cumulative percentage of emergence at 600 GDD. At 100, 300, 900, and 1,200 GDD after first emergence, seed samples in maternal plants explained 60% to 97% of the total variation in cumulative percentage emergence. At 600 GDD after first emergence, variation in cumulative percentage emergence was primarily because of differences between years (Table 2). Across all specified GDD's, maternal field and maternal plant explained less than 14% of the total variation in cumulative percentage emergence. These results are consistent with previous research indicating that common waterhemp exhibits greater amounts of genetic variation within populations than between populations (Thinglum et al. 2011).

Increasing GDD from first emergence corresponded with a greater number of experimental units reaching 100% cumulative emergence (Table

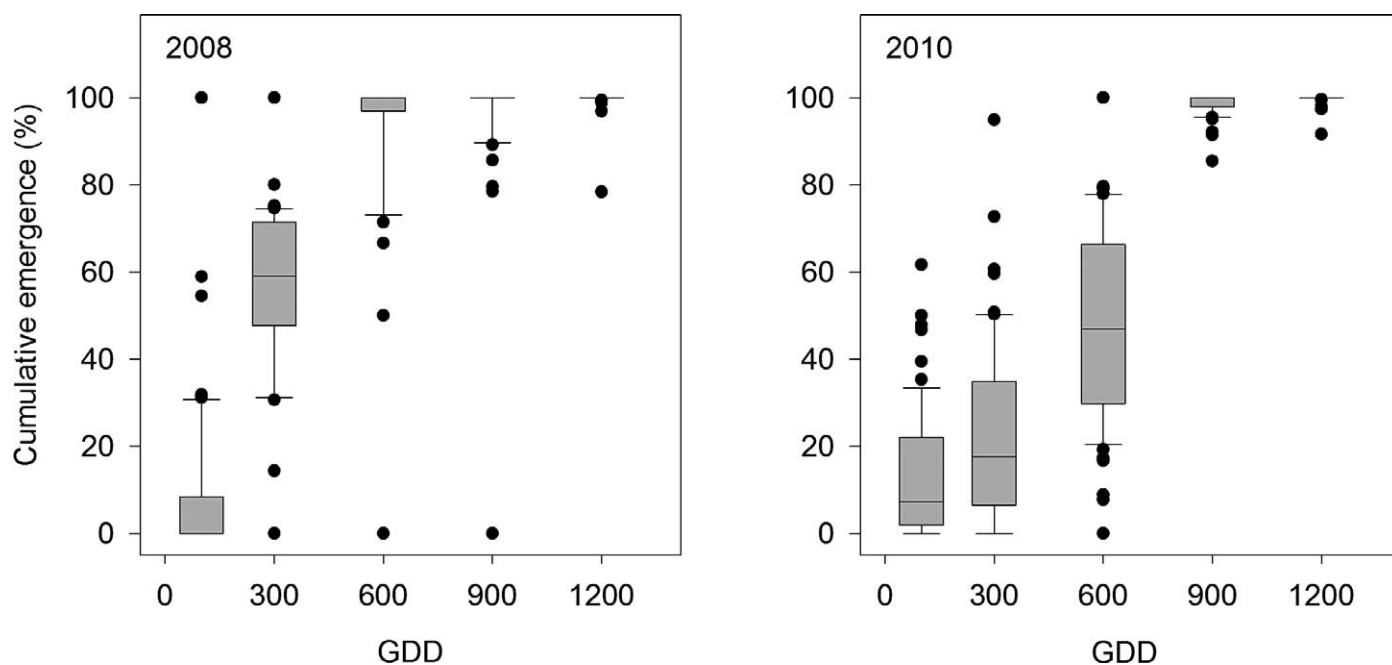


Figure 1. Box plots for the relationships between cumulative percentage emergence over 1 yr and growing degree day (GDD) after first emergence for 128 common waterhemp seedbanks near Urbana, IL during 2008 and 2010. Ends of boxes are 25th and 75th percentile, box midlines are median values and ends of bars are the 10th and 90th percentiles. Filled dots represent observations greater than the 90th percentile and less than the 10th percentile of the data.

1). However, as late as 1,200 GDD from first emergence during both 2008 and 2010, several experimental units had yet to complete emergence (Figure 1). Cumulative percentage emergence less than 100% at 1,200 GDD was indicative of delayed emergence. The population of experimental units exhibiting delayed emergence was characterized by levels of maternal diversity expected for random sampling of maternal families. Specifically, within the population of experimental units with delayed emergence, ε_{eu} (the number of experimental units) was not greater than ε_{mf} (the number of maternal families), $t(5) = 2.91$, $P = 0.98$. Similarly, within the population of experimental units with accelerated emergence, ε_{eu} was not greater than ε_{mf} , $t(4) = 2.67$, $P = 0.97$.

Experimental units represented in the accelerated emergence cohort did not differ from the overall population with respect to persistence and emergence, but experimental units in the delayed emergence cohort featured less emergence and increased persistence compared to the overall population (Figure 2). This suggests that the determinants for late-season emergence also influenced persistence in the soil seedbank. Increased knowledge on factors that contribute to the spread

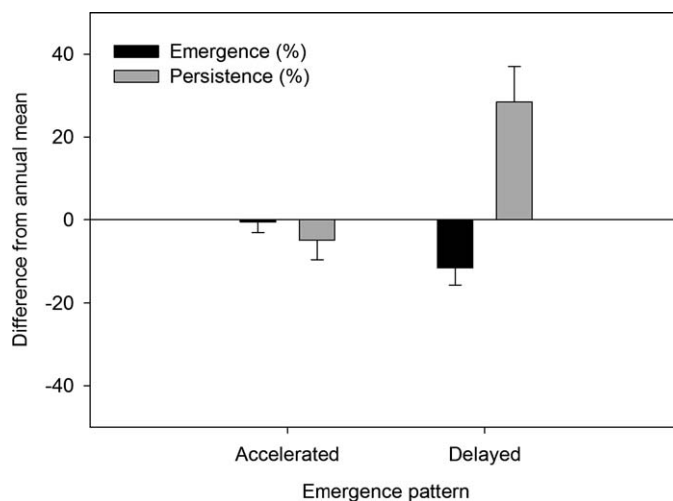


Figure 2. Differences from annual means in the percentages of viable seeds that produced a seedling (emergence) and percentages of viable seeds that were recovered after 1 yr (persistence) for common waterhemp seedbanks exhibiting accelerated and delayed temporal patterns of emergence. Bars represent means + SE, with $n = 19$ for accelerated emergence types and $n = 17$ for delayed emergence types. Accelerated emergence was indicated by cumulative percentage emergence values greater than the 90th percentile of the data at specific times after first emergence. Delayed emergence was indicated by cumulative percentage emergence values less than the 10th percentile of the data at specific times after first emergence.

of emergence both within and among years may be especially important for understanding herbicide resistance evolution in common waterhemp because previous studies determined that herbicide resistance can influence germination and dormancy loss under controlled conditions (Goulart et al. 2012; Owen et al. 2011). However, Sosnoskie et al. (2013) determined that herbicide resistance does not influence Palmer amaranth (*Amaranthus palmeri* S. Wats) seed longevity under field conditions, and Délye et al. (2013) determined that the pleiotropic effects of herbicide resistance on germination timing were contingent on the allele conferring herbicide resistance. Thus, putative associations between herbicide resistance and seed longevity are likely influenced by the genetic background of the weed population and the conditions under which seeds are studied.

In principle, prolonged periods of seedling emergence can arise from variation in emergence timing within maternal families, from variation in emergence timing among maternal families, or from combinations of intra- and interfamily variation in emergence timing (Andersson and Milberg 1998). Differences in common waterhemp emergence timing within 1 yr of burial were primarily consequences of dissimilarities within, rather than among, maternal families. This finding is consistent with evolutionary theory that predicts (1) diversified emergence strategies are advantageous in unpredictable environments, and (2) diversification in emergence timing occurs at the individual-level (Childs et al. 2010). Diverse emergence timing among progeny from one individual is considered initial evidence for bet-hedging (Childs et al. 2010), with more conclusive evidence for bet-hedging involving demonstration of fitness advantages conferred by variable emergence timing (Simons 2011). The degree to which diversified bet-hedging is the cause of asynchronous emergence in common waterhemp was, until now, poorly understood. Possible mechanisms for bet-hedging include seed-to-seed differences in germination requirements caused by variable conditions during maturation of the indeterminate inflorescences, architectural constraints within individual plants (Guterman 2000), and extreme sensitivity to changes in soil microenvironments of individual seeds (Simons and Johnston 2006).

In addition to spreading emergence within years, bet-hedging can spread emergence among years. The percentage of seeds that persisted in the seedbank after 1 yr was influenced more by maternal plant within field than by seed batch within maternal plant. This suggests the presence of phenotypic variation necessary for evolutionary responses to selection pressures from anthropogenic forces that accelerate seedbank losses. However, it must be noted that this study neither determined phenotypic variation in response to specific seedbank depletion tactics (e.g., stale seedbeds, biocontrol with seed pathogens and predators [Gallandt 2006]) nor demonstrated heritability in seedbank persistence. Thus, conclusions regarding adaptability of common waterhemp to seedbank depletion tactics are currently tenuous. Nonetheless, strong maternal effects on seedbank persistence, as evidenced by the relatively high percentage of total variation in seedbank persistence explained by maternal plant, suggest that a majority of long-lived seeds within common waterhemp seed populations (i.e., seeds that remain viable after 4 yr of burial [Buhler and Hartzler 2001]) may originate from specific plants within the population of maternal plants.

Current approaches to modeling herbicide resistance evolution first assume inherited resistance is omnipresent across all emergence cohorts. Then models project demographic performances of herbicide-resistant individuals based on their time-dependent interactions with management and the environment. Projections of herbicide resistance evolution simulations are potentially incorrect if prolonged periods of emergence observed at population levels are a consequence of differences in emergence periods among maternal families because such variation may limit occurrences of specific traits to subsets of emergence cohorts. Variation in common waterhemp emergence timing over 1 yr was primarily, but not exclusively, caused by differences within maternal families. Differences among maternal families did contribute to the total variation in emergence, which may be important in herbicide resistance modeling if genes for resistance are linked with genes for emergence. But, without current evidence of genetic linkages between emergence and herbicide resistance in common waterhemp, and considering the low percentage of total variation in emergence explained by differences

among maternal families compared to differences within maternal families, our results support the application of contemporary modeling approaches to herbicide resistance evolution in common waterhemp in central Illinois.

Acknowledgments

This work was supported by the USDA Agricultural Research Service. Mention of trade names or commercial products in this article is solely for the purpose of providing scientific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Literature Cited

- Anderson DD, Roeth FW, Martin AR (1996) Occurrence and control of triazine-resistant common waterhemp (*Amaranthus rudis*) in field corn (*Zea mays*). *Weed Technol* 10:570–575
- Andersson L, Milberg P (1998) Variation in seed dormancy among mother plants, populations and years of seed collection. *Seed Sci Res* 8:29–38
- Bagavathiannan M, Norsworthy JK, Smith KL, Neve P (2013) Modeling the evolution of glyphosate resistance in barnyardgrass (*Echinochloa crus-galli*) in cotton-based production systems of the midsouthern United States. *Weed Technol* 27:475–487
- Bell MS, Hager AG, Tranel PJ (2013) Multiple resistance to herbicides from four site-of-action groups in waterhemp (*Amaranthus tuberculatus*). *Weed Sci* 61:460–468
- Bensch CN, Horak MJ, Peterson D (2003) Interference of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*) in soybean. *Weed Sci* 51:37–43
- Bernards ML, Crespo RJ, Kruger GR, Gaussoin R, Tranel PJ (2012) A Waterhemp (*Amaranthus tuberculatus*) population resistant to 2,4-D. *Weed Sci* 60:379–384
- Buhler DD, Hartzler RG (2001) Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. *Weed Sci* 49:230–235
- Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *P Roy Soc B-Biol Sci* 277:3055–3064
- Collavo A, Streck H, Beffa R, Sattin M (2013) Management of an ACCase-inhibitor-resistant *Lolium rigidum* population based on the use of ALS inhibitors: weed population evolution observed over a 7 year field-scale investigation. *Pest Manag Sci* 69:200–208
- Crawley MJ (2007) *The R Book* Hoboken, NJ: John Wiley & Sons, Ltd
- Delye C, Menchari Y, Michel S, Cadet E, Le Corre V (2013) A new insight into arable weed adaptive evolution: mutations endowing herbicide resistance also affect germination dynamics and seedling emergence. *Ann Bot-London* 111:681–691
- Gallandt ER (2006) How can we target the weed seedbank? *Weed Sci* 54:588–596
- Goulart ICGR, Matzenbacher FO, Merotto A (2012) Differential germination pattern of rice cultivars resistant to imidazolinone herbicides carrying different acetolactate synthase gene mutations. *Weed Res* 52:224–232
- Guterman Y (2000) Maternal effects on seeds during development. Pages 59–84 in Fenner M, ed. *Seeds: The Ecology of Regeneration in Plant Communities* New York: CAB International
- Hartzler RG, Buhler DD, Stoltenberg DE (1999) Emergence characteristics of four annual weed species. *Weed Sci* 47:578–584
- Hausman NE, Singh S, Tranel PJ, Riechers DE, Kaundun SS, Polge ND, Thomas DA, Hager AG (2011) Resistance to HPPD-inhibiting herbicides in a population of waterhemp (*Amaranthus tuberculatus*) from Illinois, United States. *Pest Manag Sci* 67:258–261
- Horak MJ, Loughin TM (2000) Growth analysis of four *Amaranthus* species. *Weed Sci* 48:347–355
- Horak MJ, Peterson DE (1995) Biotypes of Palmer amaranth (*Amaranthus palmeri*) and common waterhemp (*Amaranthus rudis*) are resistant to imazethapyr and thifensulfuron. *Weed Technol* 9:192–195
- Jasieniuk M, BruleBabel AL, Morrison IN (1996) The evolution and genetics of herbicide resistance in weeds. *Weed Sci* 44:176–193
- Legleiter TR, Bradley KW (2008) Glyphosate and multiple herbicide resistance in common waterhemp (*Amaranthus rudis*) populations from Missouri. *Weed Sci* 56:582–587
- Legleiter TR, Bradley KW (2009) Evaluation of herbicide programs for the management of glyphosate-resistant waterhemp (*Amaranthus rudis*) in Maize. *Crop Prot* 28:917–922
- Leon RG, Knapp AD, Owen MDK (2004) Effect of temperature on the germination of common waterhemp (*Amaranthus tuberculatus*), giant foxtail (*Setaria faberi*), and velvetleaf (*Abutilon theophrasti*). *Weed Sci* 52:67–73
- Liu JY, Davis AS, Tranel PJ (2012) Pollen biology and dispersal dynamics in waterhemp (*Amaranthus tuberculatus*). *Weed Sci* 60:416–422
- Manalil S, Renton M, Diggle A, Busi R, Powles SB (2012) Simulation modelling identifies polygenic basis of herbicide resistance in a weed population and predicts rapid evolution of herbicide resistance at low herbicide rates. *Crop Prot* 40:114–120
- Maxwell BD, Roush ML, Radosevich SR (1990) Predicting the evolution and dynamics of herbicide resistance in weed populations. *Weed Technol* 4:2–13
- McMullan PM, Green JM (2011) Identification of a tall waterhemp (*Amaranthus tuberculatus*) biotype resistant to HPPD-Inhibiting herbicides, atrazine, and thifensulfuron in Iowa. *Weed Technol* 25:514–518
- Mercer KL, Alexander HM, Snow AA (2011) Selection on seedling emergence timing and size in an annual plant, *Helianthus annuus* (common sunflower, Asteraceae). *Am J Bot* 98:975–985
- Nafziger E, ed. 2009. *Illinois Agronomy Handbook*. 24 ed. Urbana, IL: University of Illinois Extension. Pp. 224

- Neve P (2008) Simulation modelling to understand the evolution and management of glyphosate resistant in weeds. *Pest Manag Sci* 64:392–401
- Neve P, Diggle AJ, Smith FP, Powles SB (2003) Simulating evolution of glyphosate resistance in *Lolium rigidum* II: past, present and future glyphosate use in Australian cropping. *Weed Res* 43:418–427
- Neve P, Norsworthy JK, Smith KL, Zelaya IA (2011) Modeling glyphosate resistance management strategies for Palmer amaranth (*Amaranthus palmeri*) in Cotton. *Weed Technol* 25:335–343
- Owen MJ, Michael PJ, Renton M, Steadman KJ, Powles SB (2011) Towards large-scale prediction of *Lolium rigidum* emergence. II. Correlation between dormancy and herbicide resistance levels suggests an impact of cropping systems. *Weed Res* 51:133–141
- Peters J, ed. 2000. Tetrazolium testing handbook. Contrib. No. 29 to the handbook on seed testing. Lincoln, NE: Association of Official Seed Analysts
- Refsell DE, Hartzler RG (2009) Effect of tillage on common waterhemp (*Amaranthus rudis*) emergence and vertical distribution of seed in the soil. *Weed Technol* 23:129–133
- Schutte BJ, Regnier EE, Harrison SK (2008) The association between seed size and seed longevity among maternal families in *Ambrosia trifida* L. populations. *Seed Sci Res* 18:201–211
- Shoup DE, Al-Khatib K, Peterson DE (2003) Common waterhemp (*Amaranthus rudis*) resistance to protoporphyrinogen oxidase-inhibiting herbicides. *Weed Sci* 51:145–150
- Simons AM (2011) Modes of response to environmental change and the elusive empirical evidence for bet hedging. *P Roy Soc B-Biol Sci* 278:1601–1609
- Simons AM, Johnston MO (2006) Environmental and genetic sources of diversification in the timing of seed germination: Implications for the evolution of bet hedging. *Evolution* 60:2280–2292
- Sosnoskie LM, Webster TM, Culpepper AS (2013) Glyphosate resistance does not affect Palmer amaranth (*Amaranthus palmeri*) seedbank longevity. *Weed Sci* 61:283–288
- Spokas K, Forcella F (2009) Software Tools for Weed Seed Germination Modeling. *Weed Sci* 57:216–227
- Thinglum KA, Riggins CW, Davis AS, Bradley KW, Al-Khatib K, Tranel PJ (2011) Wide distribution of the waterhemp (*Amaranthus tuberculatus*) delta G210 PPX2 mutation, which confers resistance to PPO-inhibiting herbicides. *Weed Sci* 59:22–27
- Thornby DF, Walker SR (2009) Simulating the evolution of glyphosate resistance in grains farming in northern Australia. *Ann Bot-London* 104:747–756
- Tranel PJ, Riggins CW, Bell MS, Hager AG (2011) Herbicide resistances in *Amaranthus tuberculatus*: A call for new options. *J Agr Food Chem* 59:5808–5812
- Wiles LJ, Barlin DH, Schweizer EE, Duke HR, Whitt DE (1996) A new soil sampler and elutriator for collecting and extracting weed seeds from soil. *Weed Technol* 10:35–41

Received September 13, 2013, and approved December 6, 2013.