Effects of crop rotation on common waterhemp population dynamics: prospective analysis and simulation of seed production and plant surivial rate

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# Introduction

In arable land, a low-density weed seedbank is highly desired. A weed species' seedbank persistence is influenced by multiple factors, including burial depth, tillage regime, and crop environment (Steckel et al., 2007). Common waterhemp (*Amaranthus tuberculatus* (Moq.) J.D. Sauer) is an agronomically challenging weed species (Johnson et al., 2009; Prince et al., 2012) whose high fecundity, high relative growth rate (Heneghan and Johnson, 2017), rapid herbicide resistance development (Tranel, 2021), and extended emergence pattern (Buhler and Hartzler, 2001) can help maintain an abundant seedbank (Davis, 2008; Korres et al., 2018).

To increase labor use efficiency in waterhemp management and to better regulate a weed's population dynamics, it is helpful to know possible choke points throughout the weed's life cycle, where intervention can substantially reduce the population growth rate. Following the population in complete life cycles in different crop environments can help identify the choke points where management could be focused (Caswell, 2001). Combining demographic parameters from multiple sources and organizing them in different scenarios can facilitate the evaluation of population responses without extensive field measurement (Caswell, 2001; Davis, 2002; Ullrich, 2000). In addition, retrospective perturbation analysis can be used to examine how a population would change if changes occurred at different points throughout the species' life cycle (Caswell, 2001; Davis, 2002; Ullrich, 2000).

Interseeding red clover (*Trifolium pratense* L.) with wheat (*Triticum aestivum* L.) followed by spring tillage can delay and reduce giant foxtail (*Setaria faberi* Herrm.) seedling emergence as compared with three other interseeding and tillage timing combinations (Davis and Liebman, 2003). Cool-season crops, such as oat (*Avena sativa* L.), red clover, and alfalfa (*Medicago sativa* L.), can be planted in early spring or the fall to limit waterhemp's exposure to sunlight at the time of its emergence because, by the time of waterhemp emergence, oat, red clover, and alfalfa have developed fairly dense canopy (personal observation). Our search of the scientific literature did not return any information on waterhemp's population dynamics in other cool-season crops, so we measured the following characteristics of waterhemp in cool-season crop environments: plant fecundity (Nguyen and Liebman, 2022a), soil seedbank density, the timing of seedling emergence and resultant densities, and plant survival (from seedling to maturity).

Extending a conventional 2-year rotation of corn and soybean to contain oat, red clover, and alfalfa effectively maintained a weed community at an abundance level that did not coincide with a reduction in crop yields (Nguyen and Liebman, 2022b). Even though waterhemp's reproductive potentials could be reduced without heavy reliance on herbicides (Nguyen and Liebman, 2022a), the effects of cropping system diversification on waterhemp abundance throughout its life cycle were not clearly defined (Nguyen and Liebman, 2022b). A heuristic model for waterhemp population dynamics in corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.) (two warm-season annual crops) with or without a rye (*Secale cereale* L.) cover crop (a cool-season species) in between the corn and soybean phases indicated that the cover crop would provide minimal suppression of waterhemp population densities. To explore other options for regulating waterhemp population dynamics, we conducted a prospective analysis using a population matrix approach (Caswell, 2001; Davis, 2002; Ullrich, 2000). We also applied retrospective perturbation analysis to determine elasticities and to examine how population dynamics would be altered if changes occurred throughout the species’ life cycle (Caswell, 2001; Davis, 2002; Ullrich, 2000). Finally, we simulated how a waterhemp population could be kept from increasing () by manipulating seed production (seeds m-2) or mature plant density (plants m-2) to establish two sets of thresholds. These thresholds provide reference points for the control efficacy necessary to stabilize the waterhemp seedbank.

We employed a periodic matrix model that described the product of sub-annual processes (Caswell, 2001; Cousens and Mortimer, 1995), to examine how various crop management activities that occur throughout the life cycle of waterhemp affect population change rates, . We used the general equation of (Caswell, 2001) to study from one period to another. The waterhemp populations in our study were depth-structured for the soil seedbank and cohort-structured for plant emergence timing and were subject to two levels of control efficacy: high (resulting in low reproductive potentials) and low (resulting in high reproductive potentials). The structuring of the population helped accommodate different seed survival rates (Buhler and Hartzler, 2001; Yenish et al., 1992) and seedling emergence rates (Werle et al., 2014) from different depths, plant survival rates, plant size, and fecundity of different cohorts (Hartzler et al., 2004; Nordby and Hartzler, 2004).

The modeling approach used in this study combined demographic parameters from the literature and empirical data from our fieldwork. We hypothesized that extending a conventional 2-year rotation of corn and soybean with the cool-season crops oat, red clover, and alfalfa could accelerate the depletion of waterhemp seedbanks in the soil.

# Materials and methods

### Experiment design

To study how common waterhemp's demography differed in three cropping systems suitable for the Midwestern USA, we used data from a field experiment employing a factorial design with nine crop identities crossed with two weed management regimes. Crop identity was assigned to main plots and comprised the combination of crop species and rotation system. The different weed management regimes were assigned to split plots and comprised conventional versus low herbicide regimes applied to the corn phase of each of the three rotation systems. The rotation systems used in this study comprised a 2-year corn-soybean rotation, a 3-year corn - soybean - oat (*Avena sativa* L.) intercropped with red clover (*Trifolium pratense* L.) rotation, and a 4-year corn - soybean - oat intercropped with alfalfa (*Medicago sativa* L.) - alfalfa rotation. There were four replications of each crop identity x herbicide regime combination. Field plots were located at the Iowa State University Agricultural Engineering and Agronomy Research Farm in Boone County, Iowa, USA.

A description of the general experiment design was provided by Nguyen and Liebman (2022a), but a more specific description, including tillage regimes used for each treatment, is shown in Figure 1. Contrasting herbicide regimes were used for corn at the experiment site from 2008 through 2020; soybean plots in the contrasting weed management regimes were treated with different herbicides during the 2008-2016 period but with the same herbicide regime during 2017-2020. During the present study, data were collected in each experimental unit (eu) to accommodate the different weed management programs used in the corn phase of all crop rotations.

### Data collection and analysis

The demographic information presented here is only for female waterhemp seeds and plants because 1) waterhemp is a dioecious species with a roughly 1 : 1 sex ratio (Costea et al., 2005; Montgomery et al., 2021; Montgomery et al., 2019); 2) only female individuals bear seeds (Costea et al., 2005); and 3) pollen grains are abundantly available during reproduction (Liu et al., 2012). All plant characteristics were reported for each seedling emergence cohort, and seedbank densities were reported for two soil strata: 0 - 2 cm and 2 - 20 cm.

#### Seed densities and seed fates in the soil seedbank

Nine groups of four 20-cm deep soil cores arranged in a 3 x 3 grid were collected in the fall of 2019 from each experimental unit (eu). Each soil core was cut into two sections, the top 0 - 2 cm and the bottom 2 - 20 cm. No deeper sampling was conducted because the tillage regimes applied affected the top 0 - 20 cm of the soil. All the 0 – 2 cm sections in each eu were packed separately from all the 2 – 20 cm sections, so each eu yielded two data points, one for each of the two soil strata. Seeds were separated from the soil materials and plant residues using elutriation and flotation (Forcella et al., 2003). Clean seeds were placed on germination paper imbibed with distilled water in Petri dishes and incubated in 28/18 degree Celsius light/dark - 18/8 hour night/day conditions for five days. Proportions of dormant, readily germinable, and dead seeds were classified as follows: germinated as readily germinable; firm and unyielding to forceps pressure as dormant; and yielding to forceps pressure as dead (Borza et al., 2007). Readily germinable and dormant seeds were grouped as viable and used to calculate the emergence proportion (details on how the 2019 fall soil seedbank sample was used with data for 2020 seedling emergence to determine the emergence proportion are provided in Appendix B – Matrix assembly).

#### Seedling emergence pattern and timing

In the 2019 field season, non-destructive emergence surveys were conducted once every two to three weeks (weather permitting) in eight quadrats per eu. Seedlings were marked with color-coded toothpicks for cohort identification. Within an eu, seedlings in the same cohort were marked with the same toothpick color. Six cohorts of plants were followed from seedling to senescence.

In the 2020 field season, destructive emergence surveys were conducted in eight quadrats per eu. Seedlings were clipped at the base of the plant without disturbing the soil. With the intention of evaluating the proportion of seeds germinated from the top 2 cm layer of the soil, eight to ten cohorts (depending on the crop environments) were recorded. However, only the first six cohorts were used in population trajectories and simulation for consistency. Since the first six waterhemp cohorts of the 2020 field season contributed at least 97% of the total emerged seedlings (Table A4), we felt that using these six cohorts would suffice for modeling purposes.

The number of seedlings in each cohort was converted to population density (seedlings m). In examining the data, the empirically estimated emergence rates () were noted to differ strongly from the results of Schutte and Davis (2014) and Buhler and Hartzler (2001). Because we had only a single year’s data, we chose to use estimates to reflect higher emergence rates (Appendix B – Matrix assembly). We used a 20% germination rate following Schutte and Davis (2014)'s results because their investigation comprised 129 waterhemp populations. The emergence rates were then adjusted according to the relative potency of the weed control program to which the seedbanks were exposed (Table A5). For our data, the date of first emergence detection in a crop identity was noted as the date that cohort 1 emerged in that crop identity.

#### Statistical analysis of the measured parameters

All the response variables were analyzed with factorial mixed-effect models, in which crop identity (crop species in each rotation) was the main-plot effect, corn weed management was the split-plot effect, and cohort identity was the covariance. The response variables were transformed as needed to correct heteroscedasticity.  
For the emergence timing evaluation, a factorial model with crop species, instead of crop identity, was used as the main-plot factor, and corn weed management was used as the split-plot factor. The model was fitted on Julian's dates of the first emergence because of small sample sizes in cohorts 2 and beyond. We feel that a slight modification of the statistical model was acceptable because we were interested in the difference in waterhemp emergence in different crop environments.

### Model assumptions

The assumptions used in the modeling exercise in this manuscript are listed in Table 1.

### Matrix form

Each rotation transition matrix () is the product of two, three, or four annual projection matrices, (r = 2, 3, or 4, corresponding to the number of crop phases in each rotation, and w = conventional (conv) or low, corresponding to the weed management regime applied in the corn phase). Each set of annual projection matrices, corresponding to a crop environment, , is the product of six sub-annual matrices, , with . The six sub-annual matrices, in chronological order from spring to winter, are pre-planting tillage-induced seed vertical movement (), emergence (), summer seed and seedling survival (), fecundity (), post-harvest tillage induced vertical seed movement (), and overwinter seed survival ().

Any transition matrix (periodic sub-annual (), annual (), or rotational ()), is of eight rows by eight columns (8 x 8) and consists of four blocks using the format of matrix 4.8 in Chapter 4 of Caswell (2001).

where,  
, 2 x 2, is the transition within the seedbank population (tillage-induced seed movement and summer and overwinter seed survival),  
, 6 x 6, is the transition within the plant population (seedling survival to maturity),  
, 6 x 2, is the transition from the seedbank to the plant population (emergence), and  
, 2 x 6, is the transition from the plant to the seedbank population (distribution of newly produced seeds to the soil seedbank).

The compilation of each matrix, from the published literature, empirical measurement, or both sources of parameters is detailed in the *Parameterization* section. In total, eighteen sets of six sub-annual periodic matrices were used. Each set of sub-annual matrices was constructed for every crop identity crossed with a corn weed management combination. Population transition matrices were calculated using Wood's quadratic programming method (Section 6.2, Caswell, 2001).

### Parameterization

Waterhemp plant size is highly variable; consequently, individual plant fecundity is highly variable. For example, the biomass of the smallest recorded waterhemp in our experiment was < 0.001 g, whereas the dried weight of the largest plant was about 1 kg (data not shown). The control efficacy of the weed management programs on waterhemp is, therefore, more informatively reflected by fecundity (seeds/plant) or seed production (seeds m) than plant density.

To accommodate the elasticity of plant size and to examine the impact of different levels of control efficacy on population dynamics, two scenarios of control efficacy levels reflected by seed production are presented in this chapter. The fecundity values for the two scenarios were assessed with different approaches (see *Plant fecundity* for details). In scenario 1, plant cohorts were recorded. In Scenario 2, plant cohorts were assigned by size, assuming that plant size decreases as emergence is delayed (Table 1). All the population parameters were calculated for a female-only population because only female plants bear seeds. Consequently, the modeled population size reflected about half of the population size in reality. How a whole population (with both sexes present) affects crop production can be examined using crop performance in different weed pressure levels. The seedbank densities of the whole population (male and female) from 2014 through 2019 are shown in Figure A2.

The lower-level demographic parameters are demographic parameters at each sub-annual period () filling elements at positions that describe seed and plant dynamics. From left to right, the eight columns of a matrix are named as s\_t, s\_b, pt\_co\_1, …, p\_co\_6. The columns s\_t and s\_b represent two strata of the soil seedbank: the top 0 – 2 cm and the bottom 2-20 cm. The columns p\_co\_1 through p\_co\_6 represent the plant cohorts 1 through 6. The same order is applied down eight rows of .

The examined lower-level demographic parameters can be grouped based on their impacts on preserving and producing new seeds, hereafter referred to as seed production, seed preservation, and neutral parameters. The seed preserving parameters are the probability of seeds not emerging (). The seed-producing parameters are the emergence probabilities (), the survival rates of seeds () and seedlings () during summer, the fecundity rate (), and the survival rate over winter (). Even though emergence reduces the seedbank, the number of seeds produced from an emerged seedling that succeeds until seed production is substantial, so emergence is considered positively impacting new seed production (Davis, 2008). The neutral parameters for both seed preservation and seed production are tillage-induced seed movement across soil strata at the pre-planting () and post-harvest ) periods. The tillage-induced seed vertical movement rates are considered neutral parameters because the seeds that are kept at or moved to the 0-2 cm soil layer can be exposed to emergence stimulants or granivores, while the seeds that are kept at or moved to the 2-20 cm soil layer can germinate without reaching the soil surface (fatal germination), are exposed to decaying stimuli; or preserved at optimal conditions (Burnside et al., 1996; Davis et al., 2005; Davis and Renner, 2007).

Details of how each matrix was formed are in the Appendix, but a summary of each parameter's range is provided below.

### Modeling

Within a year, the waterhemp population projection from the sub-annual period to was reflected by the changes in the number of seeds and plants and calculated as follows (Chapters 2, 3, and 4, Caswell, 2001).

where,  
 is the square transition matrix from time to time , and  
 is the population vector (in column matrix form) of eight rows and one column.  
Waterhemp population transition in one crop phase, from pre-planting tillage to winter seed dormancy, is calculated with

where,  
 is the index for the crop phase in a particular rotation,  
 is the Leslie population matrix (Leslie, 1945) in the crop phase corn weed management , and  
 is the population transition matrix during summer

The main factors contributing to the success of the control practices used for waterhemp are tillage regime, herbicides, cultivation practice, and crop competitiveness. Waterhemp emergence proportion, mature plant size, and fecundity collectively reflect crop competitiveness and management practices efficacy. The mature plant size was not included in this study, but it was used as an intermediate value to calculate fecundity.

Matrix calculation in this study was performed in R version 4.2.0 (R Development Core Team, 2022).

#### Population growth rate

We projected population growth rates under two scenarios of high and low control efficacy reflected via seed production. The high-efficacy scenario (Scenario 1) and the low-efficacy scenario (Scenarios 2) used different fecundity values in the seed production sub-annual period but the same vital rates in all other sub-annual periods. The eigen.analysis function in the popbio package version 2.7 (Stubben et al., 2020) was applied on the matrices , , and to obtain the population growth rate () in each crop phase crossed with the corn weed management regime during the full crop cycle.

The rotation-wise population growth rates (, ) were extracted from the $lambda element in the comprehensive output of eigen.analysis for each of , , and . The annualized population growth rates for each rotation crossed with corn weed management regime (, , and ) were obtained by taking the square root, cubic root, and fourth root of , , and .

#### Simulations

Since plant fecundity was the most influential parameter on population growth (as shown in the elasticity analysis) and waterhemp was more prolific in the warm-season crop environments than the cool-season crop environments (Nguyen and Liebman, 2022a), we followed up with a simulation of seed production and mature plant density thresholds in corn and soybean. We used a theoretical plot of 1 m2 with 10000 seeds in the top 0 - 2 cm soil stratum and 0 seeds in the 2 - 20 cm soil stratum. We followed that theoretical plot in three rotations (2-year, 3-year, and 4-year) crossed with two corn weed management regimes (conventional and low herbicide), as we did with empirical data collection at our research site. We were interested in the following question: ***How much weed control efficacy, in terms of seed production threshold or mature plant density threshold, is necessary to stabilize a waterhemp population ()?***

Waterhemp control efficacy in this study is indicated by seed production (seeds m) instead of seedling density (plants m) because waterhemp individual plant size is highly variable.

In each seed production threshold simulation iteration, a randomized number of seeds was generated for cohorts 1 through 3 using function rlnorm(1, m, s), in which m is the mean fecundity on the natural logarithm scale and s is the standard deviation on the natural logarithm scale. m and s were obtained from the general relationship of ln(individual fecundity +1) against ln(individual aboveground mass + 0.005) (Nguyen and Liebman 2022a) that pooled all the 389 data points from the whole experiment. Twenty-four pairs of m and s were estimated (details are in Table A5 in Appendix C). Different pairs of m and s were tried in the simulation until the rotation of interest's annualized (m = m\*). Six values of m\* were identified for each corn and soybean phase of the three rotations. All the population characteristics, except for plant fecundity of cohorts 1 through 3, were kept as in the prospective modeling exercise. We estimated the necessary control efficacy in the corn and soybean crop environments by simulating the seed production threshold for plant cohorts 1 through 3. We only manipulated the fecundity of cohorts 1 through 3 because 1) the first three cohorts are more likely exposed to herbicides or cultivation than the later cohorts; 2) the first three cohorts, especially cohorts 1 and 2, have higher survival rates than the later cohorts; and 3) in general, the earlier cohorts of higher reproductive potential than the later cohorts.

In each simulation iteration for the mature plant density threshold, the input survival rates of cohorts 1 through 3 in the summer survival sub-annual matrix () were reduced until annualized in each treatment. If improving the control efficacy for mature plants above 99.999% (equivalent to reducing survival rates of cohorts 1 through 3 below 0.001) would not stabilize the population size, the later cohorts' survival rates were manipulated. If 99.999% control efficacy of all six cohorts in corn and soybean would not stabilize the population size, intervention in soybean's subsequent crops (oat and alfalfa) was applied. All the other five sub-annual matrices were kept the same as in the population projection exercise. The final manipulated survival rates were used with the unmanipulated survival rates to calculate the cohort-based mature plant density and population-wise plant density.

# Results and discussion

All the multi-year variables failed Levene's test for equal variance, so those data were analyzed by year.

## Waterhemp sub-annual demographic parameters from empirical measurement

### Seedling emergence pattern and timing

Within the same calendar year, cumulative whole-season and cohort-based seedling densities were lower in the warm-season crops (corn and soybean) than in the cool-season crops (oat, red clover, and alfalfa) (Figure 2). Seedling emergence was delayed in the cool-season crops compared to warm-season crops (Tables 3 and 4). Waterhemp emergence was delayed by two weeks to a month in the alfalfa crop environment compared to the corn and soybean environments. Waterhemp emergence was nine to sixteen days earlier in oat than in alfalfa.

### 2019 soil seedbank and emergence proportion

In 2019, the waterhemp soil seedbank densities measured in the cool-season crop environments (O3, O4, and A4) in the fall after crop harvests were substantially higher than those of the warm-season crops. The waterhemp soil seedbank densities in the soybean environments were the lowest among all the crop environments (Table 5).

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## Waterhemp population growth rates

All the data sets for the empirically estimated sub-annual parameters were measured once. In 2019, individual plant size at maturity was measured for six cohorts in each quadrat of each eu, and two strata of soil seedbank were estimated between crop harvest and post-harvest tillage. In 2018, a different number of cohorts was followed in different crop environments because of limited labor availability and adverse weather conditions. The 2019 data were used for Scenario 1 because 2019 was the only year the soil seedbank samples were stratified (0 – 2 cm top stratum and 2 – 20 cm bottom stratum). Within the same rotation, a consistent top : bottom partitioning of seed densities pattern was observed between two corn weed management regimes. The seedbanks’ top : bottom partitioning patterns were consistent in the same crop phase within the same rotation in both control efficacy levels. The top and bottom soil strata were evenly populated after the corn and soybean phases in all rotations crossed with corn weed management treatments. The top soil stratum was less populated than the bottom soil stratum after oat intercropped with red clover (O3) but more populated than the bottom after oat intercropped with alfalfa (O4). After alfalfa (A4), larger proportions of the soil seedbanks were found in the bottom stratum.

### Scenario 1 – High control efficacy for seed production

In the high control efficacy, as reflected by the 2019 fecundity rates that were estimated from individual plant sizes using eighteen equations from Nguyen and Liebman (2022a), waterhemp population densities were projected to decrease or slightly increase (Figure 3). Waterhemp seedbank densities were projected to decrease in the 3-year rotation regardless of the corn weed management program ( and and in the 2-year and 4-year rotations where conventional weed management was applied on the corn phase ( and (Table 6). Waterhemp seedbank densities were projected to increase in the 2-year and 4-year rotations where low herbicide weed management was applied in corn ( and ) (Table 6).

### Scenario 2 – Low control efficacy for seed production

In the low control efficacy level, as reflected by the 2018 reproduction potentials, waterhemp population densities were projected to increase rapidly in all rotations, but most quickly in the 2-year rotation ( and ) and slowest in the 4-year rotation ( and ) (Figure 4 and Table 7).

The alfalfa phase of the 4-year rotation (A4) offered opportunities for decreasing , which was not possible in any other crop phases in the three examined rotations. However, the declines in phase-wise in A4 ( and ) were not strong enough to deplete seed replenishment occurring in the corn phase (, and ), soybean phase (, and ), and oat phase (, and ).

population growth rates are followed by their variances in brackets. The model years are labeled with the main crop species names’ abbreviations: C - corn, S - soybean, O - oat, and A - alfalfa.

## Simulation

The simulations here concern possible changes applied to the waterhemp populations under low control efficacy levels.

### Seed production threshold

Keeping all the input matrices as in the population projection exercise except the seed production matrix (Bf), the seed production thresholds presented here were converted from seeds plant-1 to seeds m-2.

The phase-wise seed production threshold in the 2-year rotation’s corn and soybean phases was higher than in the 3-year and 4-year rotations, but the rotation-wise seed production threshold of the 3-year and 4-year rotations were higher than that of the 2-year rotation (Figure 5). The seed production thresholds presented below are rounded up to the closest integers. An initial population density of 10000 seeds m in the top 0 – 2 cm soil stratum would remain stable if seed production by the first three waterhemp cohorts in C2 was capped at 3320 seeds mand 11843 seeds min conventional and low herbicide management, respectively; and if seed production by the first three waterhemp cohorts in S2 was capped at 1568 seeds mand 1115 seeds m in conventional and low herbicide management, respectively. The same initial population of seeds would remain stable in the 3-year rotation if the first three waterhemp cohorts’ seed production were capped at 652 seeds m-2 in C3 under conventional herbicide, 270 seeds m-2 in S3 that followed C3 under conventional herbicide; 13783 seeds m-2 in C3 under low herbicide weed management, 807 seeds m-2 in S3 that followed C3 under low herbicide weed management. The seed production threshold in the 4-year rotation’s corn and soybean phases were slightly lower than those in the 3-year rotation. The same initial population of seeds would remain stable in the 4-year rotation if the first three waterhemp cohorts’ seed production were capped at 647 seeds m-2 in C4 under conventional herbicide, 235 seeds m-2 in S4 that followed C4 under conventional herbicide; 12238 seeds m-2 in C4 under low herbicide weed management, 476 seeds m-2 in S4 that followed C3 under low herbicide weed management.

While it was not necessary to expose the waterhemp cohorts 4 and beyond to control measures in the corn and soybean phases of the 2-year rotation, it would be necessary to expand weed control measures after the first three waterhemp cohorts in the soybean phase in the 3-year and 4-year rotations (S3 and S4) that followed under conventional corn weed management to control the plants that emerged later but were of high reproductive potentials, 271 seeds m-2 and 235 seeds m-2, respectively. The waterhemp cohorts 4 and beyond in the corn phase under conventional herbicide in the 3-year and 4-year rotations were of low fecundity (under 300 seeds plant-1 and under 750 seeds plant-1, respectively), so we did not simulate additional control efficacy on them, as it would be impractical. As no herbicide was applied in the cool-season crops, weed control efficacy in those crop environments would be largely dependent on the crop’s competitiveness, such as canopy closure, allelochemical exudation and retention, and on physical weed control, such as post-harvest stubble clipping in O3 and hay cut in A4, and on granivore activity enhancement in O3, O4, and A4.

### Mature plant density threshold

Keeping all the input matrices as in the population projection exercise except the seed production matrix (Bs), the mature plant densities presented here are plant m-2 immediately before seed production.

The patterns shown for mature plant density thresholds are similar to seed production thresholds (Figure 6). Regardless of the corn weed management program, the 4-year rotation could tolerate higher mature waterhemp densities in the corn phase than the 3-year and 2-year rotations.

Among all the cool-season crops, no additional control efficacy was needed, except in the oat phase of the 3-year rotation that followed conventional herbicide corn weed management. More aggressive stubble clipping after oat harvest would be necessary in this case, as 99.999% control efficacy in the corn and soybean phases was insufficient to stabilize the population size. Even though the simulation showed that additional control efficacy might not be necessary in the oat and alfalfa phases of the 4-year rotation, it might be required in reality because achieving 0.00052 plants m-2 to 0.002 plants m-2 (equivalent to above 99.999% efficacy with respect to density) might be impossible. Similarly, the mature waterhemp plant density in O3 that followed conventional corn weed management would need to be reduced to lower than 0.59 plants m-2.

# Conclusion

Delayed but steady emergence (Tables 3 and 4, Figure 2) of waterhemp in the cool-season crop environments decreased population fecundity in the oat and alfalfa phases and thus, accelerated seedbank size reduction in Scenario 1 and slowed seedbank size increases in Scenario 2.

The cohort-based female survival rates at the experiment site were not realistically estimated due to the small sample size in a high-efficacy weed management program (Table A1). Future experiments should focus on assessing cohort-based female survival rates in cool-season crop environments.

The hypothesis that “extending a conventional 2-year rotation of corn and soybean with cool-season crops can accelerate soil seedbank depletion” was supported by Scenario 1 in the projection exercise and the follow-up simulation. Unlike giant foxtail, whose bottleneck point in the life cycle was the overwinter seed survival rates (Davis, 2002), waterhemp’s bottleneck point in its life cycle was seedling emergence rate and seedling to maturity survival success rate. An elasticity analysis suggested that fecundity overrode all the population dynamics and dictated the population growth. Even though the elasticity analysis was not informative, it was consistent with waterhemp’s competitiveness, that is, even with an extremely low survival rate, if the early emerged plants were unaffected by weed control programs and completed their life cycle, either through herbicide resistance or escape from cultivation, a small number of large, prolific female plants would sufficiently replenish the soil seedbank.

A reduction in the mass of applied herbicide active ingredients (Nguyen and Liebman, 2022b) was not coincident with the population decline in Scenario 1 () but did coincide with population increases in Scenario 2 (). Even though population sizes were projected to increase in Scenario 2, the increase rates were lower in the extended rotations. Considering Scenario 2, it would be useful to examine how many years of continuous overwinter crops would be necessary and which cool-season crop species would be most efficient in decreasing waterhemp after steady seedbank replenishment. Such an investigation is needed because even if the increased abundance of waterhemp and other weed species has not been observed at the experiment site (Nguyen and Liebman, 2022b), an abundant seedbank of a highly competitive weed species harbors risks of weed outbreaks.

The weed control pressure for the corn and soybean phases could be lessened with more extended rotations as waterhemp plants of higher reproductive potentials in cohorts 1 through 3 could be tolerated in the 3-year and 4-year rotations than in the 2-year rotation. This higher tolerance can be attributed to the weed control effects achieved by extending a cropping system of corn and soybean with cool-season crops. The more stable moisture provided by the alfalfa crop environment (compared with other crop environments) might be responsible for the steady and higher relative abundant emergence rates in A4. Empirical measurement in alfalfa is needed to test the relatively high emergence rates (approximately 45% of the top 0 – 2 cm soil seedbank) reported in this study.

Waterhemp seed production and mature plant density thresholds complement each other well in simulating required control efficacy. Using plant density alone would cause erroneous estimations for a species with highly variable individual sizes. In addition, waterhemp’s high relative growth rate and opportunistic germination patterns can allow a few plants to escape control measures and establish high reproductive potential. As waterhemp fecundity was manipulated mostly for cohorts 1 through 3 in corn and soybean environments only, it is implied that: 1) if efforts were made to severely suppress waterhemp in corn and soybean phases, no additional weed management might be needed in the oat and alfalfa phases, and thus, even large waterhemp plants in oat and alfalfa phases might not require attention; and 2) conversely if efforts in suppressing waterhemp cohorts 1 through 3 failed in the warm-season crop phases, either intervention on the waterhemp cohorts 4 and beyond in the warm-season crop phases or higher control efficacy in the cool-season crop phases would be necessary.

Similarly, as waterhemp mature plant densities were manipulated for when weed control measures would be feasible in our experiment design (a few weeks after corn and soybean sowing, after oat harvest, or alfalfa readiness and weather-permitting hay cut), it is implied that effective and efficient weed management was crucial to keep the population of concern from increasing. In our experiment, the oat, red clover, and alfalfa in the 3-year and 4-year rotations allowed for more frequent physical weed control at stages that waterhemp could be most vulnerable to severe reproductive potential loss. A more comprehensive simulation combining the seed production and mature plant density thresholds could address a suite of more diverse population compositions in the field.

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