Population dynamics of common waterhemp (*Amaranthus tuberculatus*) in simple and more diversified cropping systems: a prospective analysis

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## Introduction

The ultimate goal of any weed control program is to prevent the target population from growing. One approach to doing so is to deplete the soil seedbank. Seedbank depletion can be promoted by inducing seed fatal germination so that seeds germinate, but the seedlings fail to reach the soil surface and thus die (**davisInfluenceSeedDepth2007?**), and by fostering granivore activities so that viable, dormant seeds are consumed or damaged (**bagavathiannanPostdispersalLossImportant2013?**; **kurstjensPreciseTillageSystems2007?**). Seedbank depletion can also be promoted by targeting attacking the weed population at multiple other life-history stages which eventually limits the total number of seeds entering the soil seedbank (**liebmanManyLittleHammers1997?**). Waterhemp can replenish its soil seedbank after just one year of prolific seed production so multiple tactics are required to effectively limit the number of seeds entering the soil seedbank (**davisWeedSeedPools2008?**). For waterhemp management, literature has stressed the importance of seed shattering reduction, removal of seeds on the soil surface, and customization of tillage systems because the persistence of waterhemp seedbank is highly dependent on the local crop management techniques (**bagavathiannanPostdispersalLossImportant2013?**; **korresSeedbankPersistencePalmer2018?**; **menalledEffectsCompostedSwine2005?**).

Prospective analysis using a population matrix approach can be used to examine how a population would change over a period given the input parameters, but without extensive field trials (**caswellMatrixPopulationModels2001?**; **davisCroppingSystemEffects2002?**; **ullrichWeedPopulationDynamics2000?**). In this case, the input parameters for waterhemp population dynamics are seedbank density, emergence rate, seed and plant survival rates, fecundity, and seed viability loss. I will use a periodic matrix model (**caswellMatrixPopulationModels2001?**; **cousensDynamicsWeedPopulations1995?**) to study waterhemp population dynamics because periodic matrices accommodate the examination of the effect of various events, i.e., crop management activities, that occur throughout the life cycle of waterhemp on the population change rate. The periodic matrices are sub-divisions of an annual projection matrix: each is constructed based on critical points in a weed species’ life cycle, which will provide a means to track when and where major changes in population dynamics happen. Details on periodic matrices construction and justification are provided in the next section.

## Materials and methods

### Experiment design

The general experiment design is provided in **Article 1**, but a summary of crop sequences in the experiment is provided below.  
2-year: Corn (C2) - Soybean (S2)  
3-year: Corn (C3) - Soybean (S3) - Oat/red clover (O3) (“/” means intercropped)  
4-year: Corn (C4) - Soybean (S4) - Oat/alfalfa (O4) - Alfalfa (A4) (Oat and alfalfa are interseeded in year 3 of the 4-year rotation. Alfalfa is allowed to grow for another year after oat harvest.)

As mentioned in the previous section, contrasting herbicide regimes have been used for corn and soybean at the experiment site from 2008. Soybean plots were managed by conventional herbicide starting in 2017 but the data files are organized to distinguish historical herbicide information for soybean plots because the herbicide change was recent while the legacy effect of weed control program on each subplot may last for a few years (**rasmussenLegacyPesticidePollution2015?**; **gibsonBenchmarkStudyGlyphosateresistant2016?**).  
Population transition matrices were calculated using Wood’s quadratic programming method (Section 6.2, **caswellMatrixPopulationModels2001?**). The waterhemp population is considered size-structured with overlapping cohorts. Cohorts in this experiment reflected the time stamps when the waterhemp sub-populations were surveyed. Two consecutive surveys were approximately two-week apart.

### Matrix construction

Overall, transition matrices were partitioned into four blocks using the format of matrix 4.8 in Matrix Population Models Construction, Analysis and Interpretation (Chapter 4, **caswellMatrixPopulationModels2001?**). Each transition matrix, is developed for one rotation and is the product of five population matrices, , corresponding to the number of crop phase in each rotation. The general form of is presented below.

where  
 is the transition within the aboveground population,  
 is the transition within the seedbank population,  
 is the transition from the seedbank to the aboveground population (germination), and  
 is the transition from the aboveground to the seedbank population (distribution of newly produced seeds to the soil seedbank)

As of now, the available field-measured demographic rates, i.e., soil seedbank densities, plant densities, plant fecundity, and biomass, are treatment-average. Plant biomass was used as an intermediate parameter to estimate plant fecundity (Article 2).

Transition matrices in this exercise are fixed at 8x8 in dimensions, with two strata of seeds in the soil and six cohorts of germination. The number of germination cohorts, which were the number of germination surveys conducted in 2019, are used as placeholders only. The model, in its improved format, is expected to accommodate flexibility in the number of cohorts, dried biomass at maturity and fecundity that are under varying *field conditions,* such as temperature, moisture, and granivore activities. *These issues will be addressed in Article 5.*

Waterhemp population projection from time to is size-based and calculated as follow (Chapters 2, 3 and 4, **caswellMatrixPopulationModels2001?**).

where,  
 is the square transition matrix from time to time . Time interval can be year (as in the rotation-wise matrices) or month (as in phase-wise matrices).  
 is the population vector (in column matrix form) whose dimension equals the number of groups of seeds (2 strata) plus the number of plant cohorts (6). Waterhemp population transition in one crop phase, from spring (crop/weed germination) to fall (crop harvest/weed seed shed) is presented below

where,  
 is the index for the crop phase in a particular rotation,  
 is the Leslie’s population matrix in crop phase (**leslieUseMatricesCertain1945?**)  
 is the population transition matrix during summer

The main factors that contribute to the success of the control practices are tillage regime, chemical herbicide, cultivation practice and crops’ competitiveness. Among those four factors, crop competitiveness will not be factorized because this factor is dependent on other factors.  
I will use matrices dominant eigen values s when studying waterhemp population transition from crop to .  
The following parameters were collected and plugged into a general population model to examine when and where large changes in population dynamics might occur. The list of parameters and the corresponding formula is presented in Table 4.1 below.

Table 4.1 - Model parameters

| Parameter | Formula | Notation | Definition | Reference |
| --- | --- | --- | --- | --- |
| Common indexes |  |  | Cohort number, 1 to 6 |  |
|  |  |  | Top (1) and bottom (2) soil strata |  |
|  |  |  | The time between two consecutive measurements |  |
|  |  |  | Crop: corn, soybean, oat, alfalfa |  |
|  |  |  | Rotation: 2-,3-,4-year |  |
|  |  |  | Herbicide: low or conventional |  |
|  |  |  | Seedbank density at stratum |  |
|  |  |  | Cohort plant density |  |
| ——— | ————————- | ——————- | —————————– | ————– |
| Seedling establishment |  |  | The proportion of the seedbank’s top stratum to germinate to cohort |  |
| Surface seedbank density |  |  | in Crop , rotation , herbicide |  |
| Seedling density |  |  | in Crop , rotation , herbicide |  |
| ——— | ————————- | ——————- | —————————– | ————– |
| Plant survival |  |  | The proportion seedling in each cohort that survives until the end of the crop season |  |
| Mature plant density |  |  | in Crop , rotation , herbicide |  |
| ——— | ————————- | ——————- | —————————– | ————– |
| Initial chemical resistance ratio |  |  |  | Equation 3.16, (**caswellMatrixPopulationModels2001?**); Table 8.1, (**mortimerEvolutionHerbicideResistance1995?**) |
|  |  |  | probability of survival (1) or death (0) when exposed to an herbicide mechanism of action |  |
|  |  |  | vector of coefficient, transposed |  |
|  |  |  | vector of the threshold at which a population is considered resistant to a particular herbicide mechanism of action |  |
| Resistance to individual herbicide mechanism of action |  |  |  | (Table 8.1, **mortimerEvolutionHerbicideResistance1995?**) |
|  |  |  | The fraction of resistant plant after n repetitions of exposure |  |
|  |  |  | average seed survival years in the soil |  |
|  |  |  | resistant:susceptible ratio |  |
|  |  |  | fecundity of a surviving plant (presumably resistant) relative to a susceptible one |  |
| Resistance to multiple herbicide mechanisms of action |  |  |  |  |
| Mechanisms of action |  |  | from 1 to M (M to be determined) |  |
| ——— | ————————- | ——————- | —————————– | ————– |
| Tolerance to physical control |  | This parameter is not directly measured but will be used to roughly estimate after it is screened by the Jha group |  |  |

### Model assumptions

Table 4.2 - Female-only population dynamics model assumptions for common waterhemp (*Amaranthus tuberculatus*)

| **Stage** | **Assumption** | **References** |
| --- | --- | --- |
| *All* | Sex is stable throughout the life cycle. | (**schaffnerObservationsExperimentsSex1935?**); (**murrayGeneticsSexDetermination1940?**) |
|  | Individuals (seeds and plants) are evenly distributed spatially. | Seeds and plant densities are grid-sampled, 6x2 clusters of 3 soil cores and 4x2 quadrats, along field length x width, for seeds and plants, respectively. |
|  | Equal growth rate across individuals of the same size and shape under the same treatments (crop x rotation x herbicide) | Chapter 8, (**caswellMatrixPopulationModels2001?**) |
| *Seed* | Equal germination probability across sexes |  |
|  | The sex ratio is 1:1. | (**costeaBiologyInvasiveAlien2005?**) |
|  | Seeds only germinate from the 0-2cm soil layer | Deduced collectively from the recommended sowing depth of 1-3 times the seed diameter (Chapter 3, **foodandagricultureorganizationoftheunitednationsAridZoneForestry1989?**) and AMATA seed size of 1 mm or less in diameter (**costeaBiologyInvasiveAlien2005?**). |
|  | Equal decay rate in the soil across sexes |  |
|  | Equal decay rate across all burial depths | (**buhlerEmergencePersistenceSeed2001a?**), (**steckelTillageCroppingSystem2007?**) |
|  | Equal palatability to granivores across sexes |  |
|  | Granivore activities are an important threat. | (**vanderlaatPostdispersalWeedSeed2015?**) |
| *Young plant* | Female plants are more likely to survive under stressful conditions than male plants. | Deduced collectively from the general 1:1 sex ratio (**costeaBiologyInvasiveAlien2005?**) and differentiated sex ratio at maturity across weed management systems at the experiment site in 2018. |
|  | Crops are the main competitors for resources. | Deduced from weeds being effectively suppressed under contrasting cropping systems at the experiment site (**huntReducingFreshwaterToxicity2017?**). |
|  | Competition with other weeds and intraspecific competition is neglected. |  |
|  | The weed control program is the main cause of mortality. | (**huntReducingFreshwaterToxicity2017?**) |
| *Mature plant* | Pollen source is unlimited due to (i) the longevity and mobility of pollen grains and (ii) average plant density at the experiment site. | (**liuPollenBiologyDispersal2012?**) and personal observation |
|  | 50% of the seeds produced by each female plant are female. | (**costeaBiologyInvasiveAlien2005?**) |
|  | Male : female ratio can deviate from 1:1 ratio under different conditions: (i) more males than females observed at the experiment site when composted swine manure was applied (ii) 5 to 10 females per 1 male in a low-density population in Ohio. | (**menalledImpactCompostedSwine2004?**); (**prattAmaranthusRudisTuberculatus2001?**) |
|  | Genetic material exchange is more likely to occur within 0 to 50 meters around the pollen source. | (**sarangiPollenmediatedGeneFlow2017?**); (**liuPollenBiologyDispersal2012?**) |
|  | Fitness cost is negligible in populations with resistance to atrazine, protoporphyrinogen oxidase inhibitors, 4‐hydroxyphenylpryuvate dioxygenase inhibitors or glyphosate. | (**wuLimitedFitnessCosts2018?**) |

### Population vector

The population vector includes numbers of female individuals in different stage-position classes.

Collective seedbank density and age-specific seedbank density at the soil surface and buried are currently unavailable, so I have to assign seedbank vertical distribution based on the historical tillage regime.

I assume that seeds distribute evenly within each stratum. At the moment, the initial vertical distribution of seeds in the soil is established under the following grounds, based on (**yenishEffectsTillageVertical1992?**) findings:  
(i) seeds distribute evenly from 0 to 20 cm soil depths under moldboard tillage;  
(ii) 30% of seeds are at the top stratum and the rest at the bottom stratum under chisel tillage (**yenishEffectsTillageVertical1992?**); and  
(iii) 60% of seeds are at the top stratum and the rest at the bottom stratum under notill management (**yenishEffectsTillageVertical1992?**).

Those numbers were used to estimate the 2019 surface seed density from the total seed density, that was averaged from 2014 to 2017 soil seedbank surveys and then used to calculate the seedling emergence rate ( in Table 4.1). On a side note, seedbank density from 0 to 20 cm depth was unavailable for the 2018 field season due to adverse fall weather conditions.  
The formula for seedling emergence is

where,

is viable seed density at the top stratum,  
 are plant densities at cohort , .  
This formula assumes that the probability that a viable seed emerges is the same regardless of its age. *More details are presented in the Overwintering section.*

One difficulty in calculating the initial seedbank vertical distribution vector is the low precision of soil seedbank density estimate. Seedbank density estimation requires studying a large number of soil cores. Four hundred soil cores are expected to be studied to achieve estimates of seedbank densities whose the standard error to mean ratio is 0.1, (Equation 5, Dessaint et al. 1996) while only 36 cores were studied at our experiment site. Even though 36 cores were acceptable for whole-community seedbank estimation, more cores are needed for single species seedbank density. Consequently, > 1, which means the number of emerged seedlings is greater than the number of seeds that is present, was obtained frequently by using our current seedbank densities with the tillage-induced seedbank vertical redistribution matrices (**spokasSeedChaserVerticalSoil2007?**) and the overwintering survival rate (**yenishEffectsTillageVertical1992?**; **buhlerEmergencePersistenceSeed2001a?**; **steckelTillageCroppingSystem2007?**).  
A quick fix, for the model to function mechanically, was to calculate the average seedbank density by experiment unit and add the upper bounds of standard deviations to the means to use as the maximum seedbank densities. This > 1 error will be further addressed once the 2019 soil seedbank density at the top (0-2cm) and bottom (2-20cm) strata is available.

### Transition matrices

Each set of transition matrices is treatment-specific and is female only. There are nine sets of transition matrices for 18 crop x rotation x herbicide treatments. Each set contains five transition matrices, namely seedling establishment , survival of seedling to maturity and survival of non-germinated seed in the seedbank , fecundity , tillage , and overwinter survival .  
Each transition matrix shown below is in its general form. Detailed conditions are listed in Table 3.  
The aggregate population change, from germination to seed production, in each crop phase is the product of the five periodical transition matrices listed above,

where,

denotes the phase number (corresponding to the order that a crop phase appear in each system),  
 denotes the total number of crop phases, , and  
 denotes the herbicide regime in a specific treatment, .  
For , corn is phase 1, soybean 2, oat 3, and alfalfa 4.

The whole-system net change per each rotation x herbicide treatment is the product of all the matrices within that treatment.  
For example, is the rotation-wise transition matrix for the 2 year rotation under conventional herbicide and for the 3-year rotation under low herbicide.

The key output of the prospective analysis here is the population change rate, (). is the dominant eigen vector of the annual projection matrix. means a population is decreasing but, means the population is growing. Prospective analysis consists of the sensitivity and elasticity of in response to varying input parameters. These analyses will be done by the default algorithm in the popbio package (**stubbenPopbioConstructionAnalysis2018?**). Let and denote the elements of each and matrices. The sensitivity of is then the total derivative of with regard to each of the vital rates in matrices (Equation 9.63, **caswellMatrixPopulationModels2001?**). Using the same notation, the elasticity of is the proportional sensitivities (Equation 9.70, **caswellMatrixPopulationModels2001?**).

#### Seedling establishment matrix

The seedling establishment matrix describes the emergence probability from the 0-2 cm stratum to each of the six cohorts.

#### Survival matrix from spring to fall

The diagonal of the top left section of matrix describes the survival probability of seeds at the top (0-2cm) and bottom (2-20cm) strata. The diagonal of the bottom right section of matrix describes the cohort-specific survival probabilities of the emerged female seedlings to maturity.

is the mortality rate at strata for top or bottom stratum.  
 is the survival rate of cohort ()

In this matrix, we used and with months, from Figures 1 and 2 in (**sosnoskieGlyphosateResistanceDoes2013?**), respectively.

Multiple scenarios of population densities at maturity will be reported. However, as the seedbank density may not be accurately assessed with the current sampling scheme, empirical numbers from the experiment site may not be used to calculate the number of seed germinated to the number of seed produced.

###### Survival against chemical versus physical weed control

I assume that the two causes of plant mortality in our experiment are physical and chemical controls. That is to assume the interspecific competition among the weed community is negligible. I do not distinguish the causes of death by physical weeders and from the competition with crops. In reality, the weed management programs differed by crop species and the weed control efficacy varied by multiple factors, such as the resistance profile of the exposed weed population, application timing, weather, and machine function, etc., different levels of survival rates will be used in the final model. The survival rate from the empirical measurement at the experiment site will be used as a baseline value.

The general formula for cohort survival rate, (more details are provided in the general introduction), is . is the cohort-specific total mortality rate. , where  
 is the mortality rate by physical injury and  
 is the mortality rate by chemical injury.  
Of the total waterhemp plants killed per each weed control event, the proportions of susceptible and herbicide-resistant plants are unknown. Per each individual herbicide mechanism of action, I will use the following formula to partition the proportion of susceptible and resistant plants.

is the resistance rate against a particular herbicide mechanism of action (Table 4.1).

#### Fecundity

The diagonal of the top left section of the fecundity matrix are 1’s. The diagonal of the bottom right section of the female plant fecundity matrix are cohort-specific fecundity. Those numbers were obtained using the regression of plant biomass and fecundity. Biomass data is provided in the **Supplementary Data** section

Female plant size at maturity was evaluated on an individual basis in 2019 only, using the same plants in the cohort survival survey. At the end of the season, each plant were sexed and dried separately. The sex ratio, female plant size and fecundity were reported in another manuscript. The eighteen established equations for fecundity calculation from aboveground mass will be used in matrix with the assumption that the reproductive potential in different cohorts are driven by plant size only. For example, to within the 2-year corn under conventional weed management (C2 conv) will be calculated from one equation that is associated to “C2 conv.”

#### Vertical redistribution of newly produced seeds to the soil seedbank

Fall tillage, if applied, is implemented after the completion of crop harvest, weed biomass, and soil seedbank density surveys. The current soil seedbank distribution by the depth and by seed age in the experiment site are unknown. In fall 2019, we collected soil cores for seedbank densities estimation at two soil strata, 0-2cm as the top (1), and 2-20 cm depth as the bottom (2).

The redistribution of female seeds that were produced at the end of the crop season is calculated per each crop phase under each rotation using the transition matrices corresponding to each tillage regime by Spokas et al. (**spokasSeedChaserVerticalSoil2007?**). No-till is represented by an identical matrix after Cousens and Mortimer (**cousensModelEffectsCultivation1990?**).

where,  
 is the probability of a seed moving across strata for and stay in the same stratum for .

#### Overwinter survival rate

The diagonal of the top left section of each matrix describes the overwinter survival probability of seeds at the top (0-2cm) and bottom (2-20cm) strata.

In this matrix, I used and with months from Figures 1 and 3 in (**sosnoskieGlyphosateResistanceDoes2013?**), respectively. The crop-specific overwinter survival rate was extrapolated from the third data point in each figure. The maximum values was used for crop phases that were followed by notill, means for ones followed by chisel, and minimum for ones followed by moldboard. That extrapolation was based on the assumption that the more aggressive the tillage regime is, the less granivory activities are disturbed.  
Seed granivory results are highly dependent on specific field conditions (**vanderlaatPostdispersalWeedSeed2015?**; **forcellaDebitingSeedbankPriorities2003?**) so seed granivory will be used as a varying parameter in the model.

Two main sources of seed mortality, which are seed decay rate and seed predation rate, are very challenging to quantify exactly. Therefore, these rates will be incorporated in the model in ranges that are appropriate for waterhemp. For example, different scenarios of post-harvest seed consumption by gravivores can be 10% to 90% of the freshly produced seeds.

Dessaint, F., G. Barralis, M. L. Caixinhas, J.-P. Mayor, J. Recasens, and G. Zanin. 1996. “Precision of Soil Seedbank Sampling: How Many Soil Cores?” *Weed Research* 36 (2): 143–51. <https://doi.org/dtkg8b>.