

Depletion of an Artificial Seed Bank of Palmer Amaranth (*Amaranthus palmeri*) over Four Years of Burial*

Prashant Jha¹, Jason K. Norsworthy², Josefina Garcia¹

¹Southern Agricultural Research Center, Montana State University, Huntley, USA

²Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville, USA

Email: pjha@montana.edu

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Abstract

An artificial seed bank study was conducted at Pendleton, SC, USA, to investigate the persistence of Palmer amaranth seeds buried uniformly across a 10-cm depth in soil inside polyvinyl chloride (PVC) cylindrical pipes over 4 years. The experiment was conducted using a split-plot design, with year as the main plot factor and with or without soil disturbance (shallow tillage to a depth of 10 cm) as the subplot factor. Annual soil disturbance through tillage in the spring stimulated emergence during the first and second year after burial. A total of 0.5% to 0.8% of the seed bank emerged during the 4-yr burial period, and 99% or more of the 4-yr total emergence occurred during the first two years of burial. Seeds retrieved from 0 to 5 cm and 5 to 10 cm depths did not differ in viability. Soil disturbance influenced the decline of the artificial seed bank at least in the first year, with fewer viable seeds remaining in annually-disturbed plots. Regardless of soil disturbance, a small fraction of seeds (0.01% to 0.03% of original seed bank) remained viable in the soil after four years of burial. In conclusion, Palmer amaranth seeds buried across a 10 cm soil depth in the artificial seed bank had low persistence, which implies that burial may aid management of the weed seed bank.

Keywords

Burial, Dormancy, Persistence, Soil Seed Bank, Seedling Emergence, Tillage

1. Introduction

Seed bank persistence is one of the major factors influencing weed infestations in agricultural production systems

*Palmer amaranth seed bank persistence.

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[1]. Weed species that form persistent seed banks are a concern for future weed management [2]. In the absence of viable seed production, there is a decline in weed seed banks because of seed mortality through physiological age, herbivory, and microbial decay [3]-[5]. Additionally, seed banks decline as seeds germinate and emerge under favorable environmental conditions or germinate and fail to emerge (fatal germination) [6].

Physical and physiological dormancies are important mechanisms of weed seed persistence in the soil seed bank [7]. Weed seeds in the soil undergo changes in dormancy, which are often regulated by environmental factors such as temperature, light, moisture, nutrients, and gaseous environment [6]. Agronomic practices such as presence or absence of crop, crop rotation, and tillage influence the environmental factors present at the micro-site [8] [9], which implies that crop production practices influence weed seed dormancy and persistence.

Tillage brings buried seeds to or near the soil surface (favoring emergence and seed bank depletion) or buries freshly shed seeds deeper into the soil (favoring seed dormancy and persistence) [10]. However, the effect of tillage on weed seed persistence is affected by vertical distribution of seeds in the soil profile [10]. At soil depths of 0 to 6 cm, seed bank persistence of small-seeded *Amaranthus* species was lower in no-till than in tilled soil due to greater seedling emergence; however, at soil depths >6 cm, seed persistence was not affected by soil disturbance [10] [11]. In a 5-yr study on persistence of hemp sesbania (*Sesbania herbacea* (Raf.) Rydb. Ex A. W. Hill), morningglory spp. (*Ipomoea* spp.), prickly sida (*Sida spinosa* L.), and spurred anoda [*Anoda cristata* (L.) Schlecht.], the annual decline of the weed seed bank through emergence was not affected by spring tillage (up to a depth of 15 cm) [5].

Seed bank persistence of a few *Amaranthus* species has been previously studied [3] [5] [10]; however, literature on seed persistence of Palmer amaranth (*Amaranthus palmeri* S. Watson) is lacking. Palmer amaranth is a prolific seed producer, with a single female plant producing up to 600,000 seeds [12]. It exhibits seasonal seed dormancy and an extended emergence period [9], causing season-long interference and severe yield reductions in soybean [*Glycine max* (L.) Merr.], cotton (*Gossypium hirsutum* L.), and corn (*Zea mays* L.) in USA [13]-[15]. Palmer amaranth has developed resistance to multiple herbicide chemistries including ALS-inhibitors, dinitroaniline, triazine, HPPD-inhibitors, and also to glyphosate [16]. Owing to the high seed bank replenishment potential of Palmer amaranth, knowledge of its seed bank persistence over time would aid in developing long-term weed management strategies and anticipating the impact of weed control technologies on seed bank depletion. The objective of this research was to quantify the effect of soil disturbance through tillage and burial depth on persistence of Palmer amaranth seeds buried uniformly across a 10-cm depth in soil over 4 years.

2. Materials and Methods

2.1. Seed Source

Palmer amaranth seeds used for the experiment were collected in late September of 2004 from an agricultural site near Pendleton, SC, USA. Seeds were cleaned and air-dried at room temperature until burial in the field. Percent viability of seeds just prior to burial was determined by placing four replicate samples of fifty seeds in a 9-cm-diam petri dish (Fisher Scientific, 3970 Johns Creek Court, Suwanee, GA 30024, USA) between two layers of filter paper (Whatman's No. 1, Fisher Scientific, 3970 Johns Creek Court, Suwanee, GA 30024, USA) moistened with a 5 ml of 1% (v/v) fungicide (Captan 4-L fungicide, Drexel Chemical Company, P.O. Box 13327, Memphis, TN 38113-0327, USA) solution in deionized water. Preliminary experiments showed no adverse effect of 1% (v/v) fungicide on seed germination of Palmer amaranth. Petri dishes were wrapped with a transparent film (Fisher Scientific, 3970 Johns Creek Court, Suwanee, GA 30024, USA) to minimize moisture loss and were incubated for 14 days in the dark at 30°C, which is an optimum temperature for germination of Palmer amaranth [17]. Seeds with radicle protrusion of at least 1 mm were considered germinated. Viability of the non-germinated seeds was determined using a crush test as described previously [18]. Germination and viability tests revealed that 98% of seeds used for the burial experiment were viable, with >90% being non-dormant (data not shown).

2.2. Field Experiment

An artificial seed bank study was initiated in a field in 2004 at the Simpson Research Station near Pendleton, SC, USA (34.6506°N, 82.7808°W), to evaluate the persistence of Palmer amaranth in soil over 4 yrs (2005 to 2008), approximately 1 month after collecting mature seeds. The experimental site was maintained with tall fescue

(*Festuca arundinacea* L.) turf for at least 15 yr prior to initiation of the experiment, ensuring no recent establishment and direct seed rain of Palmer amaranth in the experimental area. The soil was a Cecil sandy-loam (fine, kaolinitic, thermic Typic kanhapludults). In August 2004, the experimental site was sprayed with glyphosate at $870 \text{ g}\cdot\text{ae}\cdot\text{ha}^{-1}$ to kill the existing vegetation, disked with two passes and then roto-tilled once to an approximate depth of 15 cm.

Artificial seed banks were established in late October 2004 using polyvinyl chloride (PVC) cylindrical pipes of 15 cm height and 50 cm diam with openings at both ends and were placed vertically to a depth of 10 cm into the soil by excavating the soil. The remaining 5 cm length of the pipe remained above the soil surface to prevent off-site movement of seeds. The excavated soil from a 0 to 10 cm depth was placed in a bucket. Twenty thousand viable seeds $\cdot\text{m}^{-2}$ were thoroughly mixed with soil in the bucket and the soil/seed mixture was returned to the pipe. Fine polypropylene microfilament mesh screens similar to those used by previous researchers [2] [19] were placed at the bottom of the pipe to prevent any downward movement of Palmer amaranth seeds beneath the 10 cm depth, without restricting drainage and water or gas permeability. The experiment was conducted as a split-plot design with year being the main plot factor and with or without soil disturbance being the subplot factor, with eight replications. The subplot treatments were randomly assigned in the first year of the experiment and were permanent throughout the period of the study. To simulate soil disturbance during a shallow spring tillage, soil inside the pipe was uniformly stirred with a hand-tiller to a depth of 10 cm once annually in March prior to weed emergence, which corresponds with the timing of spring seedbed preparation in the region. Palmer amaranth seedling emergence was monitored twice monthly from March through November each year. All the emerged seedlings were counted and removed subsequently by hand. The experimental site was kept free from other weeds throughout the study using glyphosate or by hand weeding. Soil temperature at a 10 cm soil depth was recorded hourly throughout the study period using data loggers (WatchDog Data Logger, Spectrum Technologies, Inc., 23939 West Andrew Road, Plantfield, IL 60644, USA) in two to three PVC pipes per treatment. Soil temperature data were used to estimate mean monthly soil temperatures at the 10 cm depth during the 4-yr study period (Table 1). Daily rainfall data were collected from a weather station located approximately 1.5 km from the experimental site, and were used to estimate monthly rainfall during the 4-yr study period (Table 1).

2.3. Greenhouse Experiment

Each November, soil from depths of 0 to 5 and 5 to 10 cm was excavated separately from each pipe, with a total of 32 soil samples from 16 plots [2 treatments (with and without soil disturbance) by 8 replications]. The excavated soil was stored at 4°C until placed in flat trays in the greenhouse at $30^\circ\text{C}/24^\circ\text{C}$ (day/night) and 16 h photoperiod.

Table 1. Mean monthly soil temperatures at 10 cm soil depth and rainfall during the seed burial experiment at Pendleton, SC, USA.

| Month | Soil temperature ($^\circ\text{C}$) | | | | Rainfall (cm) | | | |
|-----------|---------------------------------------|------|------|------|---------------|------|------|------|
| | 2005 | 2006 | 2007 | 2008 | 2005 | 2006 | 2007 | 2008 |
| January | 9 | 9 | 10 | 7 | 5.5 | 10.9 | 14.6 | 6.2 |
| February | 9 | 8 | 7 | 8 | 6.6 | 5.0 | 10.0 | 12.2 |
| March | 10 | 12 | 12 | 11 | 7.1 | 4.7 | 9.2 | 11.8 |
| April | 16 | 17 | 16 | 16 | 8.7 | 10.3 | 2.8 | 9.2 |
| May | 21 | 21 | 22 | 21 | 10.5 | 2.8 | 3.8 | 5.8 |
| June | 23 | 26 | 27 | 27 | 24.6 | 21.0 | 8.5 | 1.5 |
| July | 28 | 28 | 27 | 28 | 23.0 | 5.5 | 7.7 | 3.6 |
| August | 29 | 28 | 29 | 28 | 9.8 | 6.6 | 4.3 | 17.0 |
| September | 27 | 25 | 27 | 26 | 1.7 | 13.0 | 5.7 | 1.2 |
| October | 22 | 20 | 22 | 20 | 7.2 | 11.4 | 4.1 | 6.7 |
| November | 15 | 14 | 14 | 12 | 9.5 | 7.4 | 3.2 | 4.9 |
| December | 7 | 11 | 11 | 10 | 13.8 | 11.2 | 14.6 | 11.7 |

Multiple trays were used to accommodate the entire soil volume that was excavated for each burial depth. The soil was uniformly spread on the tray to a depth of 2.5 cm, which was chosen since *Amaranthus* species including Palmer amaranth can emerge only from shallow depths up to 2.5 cm [9]. The trays were watered to field capacity daily and emerged seedlings were identified, counted, and removed. The soil in each tray was occasionally air-dried and then stirred to bring the non-germinated seeds near the soil surface. With no further emergence after 12 wk, the trays were placed at 4°C constant and the soil was kept moist (moist stratification) to alleviate dormancy of viable seeds. Following 6 wk of stratification, soil samples were placed back in the greenhouse under similar conditions for monitoring germination for an additional 4- to 6-wk period as described previously. At the end of the greenhouse assay (conducted for 6 mo) each year, soil samples for each plot were pooled, mixed thoroughly, and divided into multiple batches of 500 g sub-samples that were used for extraction of any remaining viable seeds using a floatation/centrifugation procedure as described by [20]. Viability of those seeds were further determined using the crush test as mentioned above.

2.4. Statistical Analyses

All weed emergence and viability data were expressed as number per m² and as a percentage of the original seed bank. Also, emergence each year as a percentage of the 4-yr total was calculated. Data were tested for homogeneity of variance and normality assumptions using Levene's and Shapiro-Wilk's tests, respectively. Data met both assumptions; hence, analyses were performed on non-transformed data. All data were subjected to ANOVA using PROC MIXED in SAS. Year, soil disturbance (with and without), and the interaction of year and soil disturbance were fixed effects, and replication and replication by year were random effects in the model used for determining the field emergence. Viability data were analyzed as a split-split plot design with year being the main plot, soil disturbance (with or without) being the subplot, and burial depths (0 to 5 and 5 to 10 cm) being the sub-subplot factor. Year, soil disturbance, and burial depth and their relevant interactions were fixed effects in the model, and replication, replication by year, and replication by year by soil disturbance were random effects. Means for the significant main effects and interactions were separated using Fisher's Protected LSD test at $P < 0.05$.

3. Results and Discussion

3.1. Field Emergence of Palmer Amaranth from the Artificial Seed Bank

The interaction of year by soil disturbance was significant for Palmer amaranth emergence from the seed bank (P -value = 0.0002). The effect of tillage-mediated annual soil disturbance on emergence was observed during the first two years following seed burial, with greater differences between the soil disturbance treatments in 2006 relative to 2005.

In 2006, 0.28% (56 seedlings·m⁻²) of initial seed bank (20,000 seeds·m⁻²) emerged in plots with annual soil disturbance compared with 0.07% (14 seedlings·m⁻²) of initial seed bank that emerged in plots disturbed once only during burial, a four-fold difference (Table 2). Weed emergence in 2007 and 2008 did not differ between annually disturbed and undisturbed plots. A total of 0.5% to 0.8% of the Palmer amaranth seed bank emerged in the field over the 4-yr burial period. Most emergence occurred in the first year following burial. A faster decline in emergence as a percent of 4-yr total emergence was evident in plots without annual soil disturbance compared to plots tilled annually (Table 2).

The stimulatory effect of annual soil disturbance through a shallow spring tillage on Palmer amaranth emergence observed during the first two years (2005 and 2006) after burial might be due to improved soil aeration, soil-seed contact, and light exposure that enhanced germination of buried Palmer amaranth seeds from the seed bank. Also reported in other small seeded weed species, shallow spring tillage (to a depth of 10 cm) stimulated seedling emergence due to increased exposure of seeds to a favorable microclimate for germination [9]. A secondary soil disturbance through hoeing to a depth of 8 to 10 cm in the spring increased redroot pigweed (*Amaranthus retroflexus* L.) emergence and contributed to 3-fold greater seed bank depletion compared to undisturbed soil [21]. Conversely in other research, redroot pigweed, and common waterhemp (*Amaranthus rudis* L.) emergence was reduced by tillage-induced soil disturbance compared to nondisturbed soil [10] [22]. The differences might be because in those studies seeds were lying on the soil surface prior to any soil disturbance, implying greater number of seeds left on or near the soil surface in nontilled compared to tilled conditions.

Table 2. Effect of annual soil disturbance (with and without) on Palmer amaranth field emergence from the artificial seed bank in Pendleton, SC, USA, over 4 years.

| Year ^b | Field emergence ^a | | | | | | | |
|-------------------|-------------------------------|-----|---------------------|-----|----------------------|-----|---------------------|-----|
| | With disturbance ^c | | Without disturbance | | With disturbance | | Without disturbance | |
| | % of initial seed bank | | | | % of total emergence | | | |
| 2005 | 0.51 | a A | 0.44 | b A | 64 | b A | 86 | a A |
| 2006 | 0.28 | a B | 0.07 | b B | 35 | a B | 14 | b B |
| 2007 | 0.01 | a C | 0.00 | a B | 1 | a C | 0 | a C |
| 2008 | 0.00 | a C | 0.00 | a B | 0 | a C | 0 | a C |
| S.E. ± | | | 0.021 | | | | 1.311 | |

^aThe initial seed bank was comprised of 20,000 seeds·m⁻² buried in the top 10 cm of the soil in October 2004. Palmer amaranth emergence was monitored in the field every other week from the date of first observed seedling emergence until emergence ceased each year in September. ^bMeans within a year (row) followed by the same lowercase letter are not significantly different based on Fisher's protected LSD test at $P < 0.05$. ^cMeans within a soil disturbance treatment (column) followed by the same uppercase letter are not significantly different based on Fisher's protected LSD test at $P < 0.05$.

However, in the present study, the initial seed bank contained seeds uniformly distributed in the top 10 cm of soil and subsequently disturbed once a year or kept undisturbed for the remaining 4-yr burial period, methodology similar to that used in other natural or artificial weed seed bank studies [3]. Moreover, a shallow spring tillage (to a depth of 10 cm) had no significant effect on Palmer amaranth emergence even with a natural seed bank comprising seeds senesced the previous fall and lying on the soil surface [9].

Consistent with our results on Palmer amaranth, the effect of mechanical soil disturbance (to a depth of 10 cm) on redroot pigweed emergence was evident only in the first year during a 5-yr burial study [5]. Also reported in other weeds including common waterhemp, velvetleaf (*Abutilon theophrasti* Medic.) and spurred anoda, soil disturbance had a minimal effect on weed seed bank emergence after the first 1 to 2 yr of burial [5] [10]. Furthermore, the trend for decline of Palmer amaranth emergence over time in the absence of reseeding resembled those exhibited by other *Amaranthus* species [3] [10]. Out of a total of 0.6% to 2.3% of the redroot pigweed seed bank (comprising 2000 seeds added to the soil) that emerged over a 5-yr period, 0.4% to 2% of the seed bank emerged in the first year after burial [5]. In a seed bank study on common waterhemp, approximately 97% of the 4-yr total emergence occurred during the first 2 yr after seed burial [10].

3.2. Viable Seeds Remaining in the Artificial Seed Bank

Data shown in Table 3 represent the fate of the remaining seeds (those that fail to germinate in the field) in the soil seed bank, which were tested for germination in the greenhouse with a follow-up viability test to determine whether the seed bank was indeed depleted, or whether there was a substantial portion of the seed bank that was dormant and required a much longer stratification period. Burial depth did not influence viability of Palmer amaranth seeds in soil collected each year from 0 to 5 cm and 5 to 10 cm depths with or without annual soil disturbance (data not shown). The interaction of year by soil disturbance was significant for Palmer amaranth viable seeds remaining in the soil seed bank ($P = 0.036$). The effect of soil disturbance was evident only in the first year after burial.

In 2005, averaged over burial depths, 1.06% (212 viable seeds·m⁻²) of initial seed bank remained in the absence of annual soil disturbance compared with 0.63% (126 viable seeds·m⁻²) of initial seed bank that remained in annually disturbed tilled plots, a 1.7-fold reduction (Table 3). The lower percentage of seed bank remaining in annually disturbed compared with once only disturbed soil was consistent with the greater field emergence observed in those plots in 2005 (Table 2). Irrespective of soil disturbance, there was a significant decline in viable seeds remaining in the artificial seed bank after the first year (Table 3). Out of the total seeds that were recovered from 0 to 10 cm depth of soil after 4 years of burial, only 0.01% to 0.03% (2 to 6 seeds·m⁻²) of the initial seed bank remained viable.

Similar to our findings on Palmer amaranth, previous researchers [2] reported lack of burial depth effect on the persistence of redroot pigweed. Differences in seed persistence of Palmer amaranth may have been more

Table 3. Effect of annual soil disturbance on remaining viable seeds of Palmer amaranth in soil samples collected from the artificial seed bank in each of the 4 years, averaged across burial depths in Pendleton, SC, USA.

| Year ^b | Remaining viable seeds ^a | | | |
|-------------------|-------------------------------------|-----|---------------------|-----|
| | With disturbance ^c | | Without disturbance | |
| | % of initial seed bank | | | |
| 2005 | 0.63 | b A | 1.06 | a A |
| 2006 | 0.04 | a B | 0.09 | a B |
| 2007 | 0.03 | a B | 0.06 | a B |
| 2008 | 0.01 | a B | 0.03 | a B |
| S.E. ± | | | 0.065 | |

^aThe initial seed bank was comprised of 20,000 seeds·m⁻² buried in the top 10 cm of the soil in October 2004. Viability of seeds in soil samples collected from the field plots in November each year was assessed by monitoring the emergence in the greenhouse at 30/24 C (day/night) and 16 h photoperiod for 6 months, and any remaining seeds were recovered through flotation/centrifugation technique and tested for viability. Data shown in the table represent the total viable seeds that germinated or emerged in the greenhouse plus those that were tested positive for viability. ^bMeans within a year (row) followed by the same lowercase letter are not significantly different based on Fisher's protected LSD test at P < 0.05. ^cMeans within a soil disturbance treatment (column) followed by the same uppercase letter are not significantly different based on Fisher's protected LSD test at P < 0.05.

likely to occur between burial depths of 0 to 2 cm and below 2 cm as evident in common waterhemp, with seeds in the top 0 to 2 cm of soil, the zone of germination, being less persistent compared with seeds buried below 2 cm; however, difference in seed persistence was not evident between 2 to 6 and 6 to 12 cm of the soil profile [10]. Furthermore, depth-mediated dormancy of buried Palmer amaranth seeds was likely responsible for the greater percentage of the artificial seed bank that survived during the first year after burial in plots that were only disturbed during burial in our study. Tillage enhanced the weed seed demise in soil; however, the effect on seed bank dissipation was limited to the first year after burial, also reported in several other weed species including common waterhemp, redroot pigweed, velvetleaf (*Abutilon theophrasti* Medik.), prickly sida, and morningglory species [5] [10].

In the present study on Palmer amaranth, accounting for total viable seeds in the 0 to 10 cm of the soil that included nondormant seeds that emerged in the field or germinated in the greenhouse bioassay plus dormant seeds recovered from the soil and were tested viable, approximately 98% of the artificial seed bank was lost during the 4-yr burial period. This confirms the previous findings that *Amaranthus* species have low persistence in soil seed banks [5] [10]. Similarly, there was a dramatic decline in the redroot pigweed seed bank within two years of burial, with no viable seeds remaining in the upper 0 to 15 cm depth of soil after the third year [5]. Irrespective of tillage, only 0.004% of the common waterhemp seed bank remained at the end of a 4-yr burial period [10].

The rapid decline of *Amaranthus* seed bank within a year of burial might be due to physiological death of seeds, fatal germination, seed herbivory, or microbial seed degradation in the soil, as reported in other natural or artificial seed bank studies [3] [4] [23] [24]. Pigweed seeds are a preferred food source for field mice (*Peromyscus* spp.) and insects including field cricket (*Gryllus pennsylvanicus* DeGeer) and ground-dwelling carabid beetles (*Harpalus pennsylvanicus*) [25] [26]. Although burial containers may limit the seed predation by larger insects, the possibility of seed bank decline in those containers through insect predation cannot be completely eliminated, also evidenced by [27].

Due to variability in methodology used by different researchers for seed burial, results from these experiments should be interpreted with caution. Weed seed survival in artificial seed banks may not mimic those in natural seed banks [19]. Soil temperature, moisture, and soil physical characteristics inside burial containers used in our and other artificial seed bank studies [3] [27] can differ from those in a natural seed bank [28], resulting in differences in weed seed response to those environment. Furthermore, higher seed densities in an artificial seed bank may increase seed mortality by fungal pathogens compared to a natural seed bank [29]. However, accurate determination of weed seed number, depth, and species composition is the major limitation of natural seed banks [28]. Long-term artificial seed bank studies are still capable of determining outer limits of seed survival in the soil and providing information for economic threshold modeling [19], which can be utilized by researchers and land managers to design time-sensitive weed management programs.

4. Conclusion

Deep burial of Palmer amaranth seeds would be a promising strategy for depleting the soil seed bank. Soil disturbance through shallow spring tillage reduced the Palmer amaranth seed bank through emergence losses, at least in the first year after seed burial. However, it should be recognized that Palmer amaranth is a prolific seed producer with a single plant producing almost 600,000 seeds [12], and 0.01% to 0.03% of the initial seed bank that remained viable after 4 years of burial would be sufficient to produce enough plants to repopulate the soil seed bank, if conditions were conducive for emergence. Hence, strategies aimed at depleting the Palmer amaranth soil seed bank must extend beyond four years of no seed production. Future research is needed to investigate the persistence of Palmer amaranth seeds under different soil and environmental conditions for extrapolation of these findings to a larger agricultural setting.

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